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Drosophila as models to understand the adaptive process during invasion

Patricia Gibert · Matthew Hill · Marta Pascual · Christophe Plantamp · John S. Terblanche · Amir Yassin · Carla M. Sgrò

Abstract The last few decades have seen a growing number of species invasions globally, including many insect species. In *drosophilids*, there are several examples of successful invasions, i.e. *Zaprionus indianus* and *Drosophila subobscura* some decades ago, but the most recent and prominent example is the invasion of Europe and North America by the pest species, *Drosophila suzukii*. During the invasive process, species often encounter diverse environmental conditions that they must respond to, either through rapid genetic adaptive shifts or phenotypic plasticity, or by some combination of both. Consequently, invasive species constitute powerful models for investigating various questions related to the adaptive processes that underpin successful invasions. In this paper, we highlight how *Drosophila* have been and remain a valuable model group for understanding these underlying adaptive processes, and how they enable insight into key questions in invasion biology, including how quickly adaptive responses can occur when species are faced with new environmental conditions.

Keywords Local adaptation · Phenotypic plasticity · *Drosophila subobscura* · *Drosophila suzukii* · *Zaprionus indianus*

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P. Gibert (✉) · C. Plantamp
CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, Université Lyon 1, 69622 Villeurbanne, France
e-mail: patricia.gibert@univ-lyon1.fr

M. Hill · J. S. Terblanche
Centre for Invasion Biology, Department of Conservation Ecology and Entomology, Faculty of AgriSciences, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

M. Pascual
Departament de Genètica – IRBio, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain

A. Yassin
Laboratory of Genetics, University of Wisconsin, 425-G Henry Mall, Madison, WI 53706, USA

C. M. Sgrò
School of Biological Sciences, Monash University, Wellington Rd Clayton, Melbourne 3800, Australia

Introduction

The majority of agriculturally-important invasive species are insects (Ziska et al. 2010). Many of these species are flies (Diptera) (e.g. Tephritidae Hill et al. this special issue) and include the so-called "fruit flies" (Diptera: Drosophilidae). For instance, the well known cosmopolitan species *Drosophila melanogaster* has an Afrotropical origin, colonizing Europe circa 16,000 ya (Li and Stephan 2006), and subsequently the rest of the world most likely assisted by human migration (David and Capy 1988; Laurent et al.

2011). *Zaprionus indianus* and *Drosophila subobscura* also represent examples of more recent colonizations on the American continents (Brncic et al. 1981; Vilela 1999). But the most recent, and high profile, example is probably the successful invasion of Europe and North America by the pest species, *Drosophila suzukii* (Calabria et al. 2012; Cini et al. 2012; Asplen et al. 2015).

During the invasion process, species often encounter diverse environmental conditions that they must respond to either by rapid evolutionary shifts, phenotypic plasticity or more probably, by a combination of these two mechanisms. Indeed, many invasive species display evidence of rapid adaptive evolution (Simberloff and Rejmánek 2011; Urbanski et al. 2012; Hill et al. 2013 see also Prentis et al. 2008 for review in plants). Consequently, they represent powerful models for investigating various questions related to the adaptive processes that can occur during invasions: how quickly and by what mechanisms do invaders evolve adaptations? What are the most common mechanisms involved? Is plasticity more important than genetic adaptation or is some combination of both the norm for invasive species in the newly invaded range? Invasive species enable these questions to be addressed using either a synchronic approach, i.e. by comparing populations in the native range and in the newly colonized area, or a diachronic approach, i.e. by monitoring population's genetic (or phenotypic) variation over time (Hendry and Kinnison 1999).

In this perspective, we outline why *Drosophila* species are highly valuable model organisms to investigate biological invasions. Due to the wealth of research conducted on these species, there are a number of established protocols and techniques that promote using *Drosophila* species for such studies. First, in many cases *Drosophila* species are easy to rear in the laboratory, and their short generation time (e.g. about 14 days at 25 °C in *D. melanogaster*) allows for a diverse array of laboratory experiments, in particular common garden experiments, quantitative genetic and experimental evolution studies. The experiments can most easily be achieved through the method of isofemale lines (established by isolating females collected in nature in separate culture vials to initiate half-sib families) (see Hoffmann and Parsons 1988; David et al. 2005 for a discussion about the pros and cons of this method). Second, because of their short generation time and the fact that they can have several generations during a year, *Drosophila* species are able to undergo rapid evolutionary shifts as shown either by experimental evolution in the laboratory (e.g. Hoffmann et al. 2003 on *D. melanogaster* and Santos et al. 2012 on *D. subobscura*) or by following populations of an invasive species through time (Balanyà et al. 2009, on *D. subobscura*). Third, the number of *Drosophila* species, in addition to *D. melanogaster,* that have molecular tools and genomic data available (over 12 sequenced *Drosophila* genomes, Clark et al. 2007), is expanding rapidly, enabling in-depth studies of the genetic mechanism(s) that underpin the invasion process. Finally, many *Drosophila* species have broad geographic ranges (David and Tsacas 1981) that span environmental gradients. This further promotes the use of *Drosophila* in studies dissecting the genetic basis of adaptation to new environments at the phenotypic and molecular level. For example, *D. melanogaster* has a cosmopolitan distribution, with latitudinal clines observed in different continents for many morphological (pigmentation: David et al. 1985; Munjal et al. 1997; Telonis-Scott et al. 2011; Bastide et al. 2014—body size: Coyne and Beecham 1987; Capy et al. 1993; Imasheva et al. 1994; James et al. 1995; Van't Land et al. 1995) and physiological traits (alcohol and acetic tolerance: David and Bocquet 1975; Parsons 1983; desiccation and starvation resistance: Karan et al. 1998; Hoffmann et al. 2001; high and low temperature resistance: Hoffmann et al. 2001; Sgrò et al. 2010; circadian rhythm modulation: Sawyer 1997; Kyriacou et al. 2008). Such latitudinal clines, which exist for several other widespread species of *Drosophila* are generally interpreted as being a consequence of adaptation to local climatic conditions, with temperature generally considered as the major environmental factor.

In this paper we highlight how *Drosophila* are a powerful system with which to empirically understand the adaptive processes that mediate the invasion of new environments.

The invasion process needs a rapid adaptive response to new environmental conditions

Understanding the importance of genetic variation during the invasion process

In the case that an invasive species encounters novel environmental conditions and thus new selection

pressures, a rapid evolutionary change is often required for population persistence (Sakai et al. 2001; Lee 2002). Such rapid adaptive responses require adequate genetic variation in the trait(s) under selection. However, the invasion process may start with a small number of initial propagules. Such bottlenecks can result in strong genetic drift and a subsequent reduction of genetic variation in newly established population(s) (Nei et al. 1975), thereby limiting their capacity to evolve. However, it has also been demonstrated that under certain conditions, bottlenecks can lead to the purge of deleterious alleles that lead to inbreeding depression (e.g. Swindell and Bouzat 2006 in *D. melanogaster*). Such effects could have positive consequences on the fitness of the invader and help facilitate invasion (Facon et al. 2011). Evaluating the extent of change in genetic diversity during and after the colonization of novel environments may help understand the invasion process, which can be achieved by addressing key questions: What is the source population for the invasion? How much genetic variation is lost during the first step of the invasion (size of the propagule, multiple introductions)? What is the temporal and spatial pattern of invasion?

In *Drosophila*, the genetic variance and adaptive capacity of populations can be investigated using quantitative genetic breeding designs (e.g. van Heerwaarden and Sgrò 2013; Blackburn et al. 2014) and selection experiments (e.g. Kristensen et al. 2015). Alternatively, comparison of isofemale lines (each line established by a single field-inseminated female) can be used to estimate the genetic variability of a population by calculating the coefficient of intraclass correlation, *t* (Hoffmann and Parsons 1988; Falconer 1989). While genetic variability estimated using this method is likely to include dominance and epistatic effects in addition to the additive genetic variance of the traits in question, it nonetheless provides some insight into the adaptive capacity of populations (David et al. 2005). Further, maintaining isofemale lines at a large census population size and assessing them within several generations of being initiated will minimize any potential effects of inbreeding (Hoffmann and Parsons 1988). For example, Arthur et al. (2008) compared isofemale lines of *Drosophila simulans* collected from along the east coast of Australia to understand the link between genetic variance, climatic selection and phenotypic evolution. Their

study revealed complex patterns of adaptive divergence in response to climatic selection; while body size and starvation resistance showed linear clines, a non-linear pattern was evident for female, but not male, cold resistance, while no clines were evident for development time and desiccation resistance.

The importance of phenotypic plasticity

Phenotypic plasticity, the ability of an individual to express different phenotypes in response to environmental conditions (Bradshaw 1965; Pigliucci 2001; West-Eberhard 2003; DeWitt and Scheiner 2004), allows populations to respond to changing environments within very short time scales (intra-generation) and can play an important role in the survival of invasive species (Richards et al. 2006; Chown et al. 2007). Invasive species are thought to have a greater plasticity in ecologically important traits than non-invasive species, and populations of invasive species are expected to evolve greater phenotypic plasticity in their new invasive range compared to populations within the native range (but see Richards et al. 2006 for a discussion in plants and Lande 2015 for recent theoretical work). The hypothesis that greater phenotypic plasticity contributes to the success of an invasion has been supported by some studies (e.g. Trussell and Smith 2000; Sexton et al. 2002; Daehler 2003; Nyamukondiwa et al. 2010), but not others (e.g. Chown et al. 2007). According to Lande (2015), this discrepancy can be explained by several parameters including the optimal phenotype, the environment in the new colonized range (mean variance and predictability), the cost of plasticity and the type of plasticity (reversible vs irreversible plasticity). It has also been argued that phenotypic plasticity, by allowing populations to persist under new conditions, may allow for novel genetic variation that is better suited to the new conditions to arise (Pigliucci 2005). Specifically, it has been suggested that a rapid transient increase in plasticity will be followed by slow genetic assimilation and decreased plasticity (Pigliucci et al. 2006; Lande 2015). Such a mechanism could occur during the common lag-time between initial colonization and the rapid population growth that is characteristic of many invasions.

The study of phenotypic plasticity requires measurements on many genetically identical individuals, however clones are easily available in plants but not in

most animals. For natural populations of *Drosophila*, isofemale lines are a practical substitute for clonal populations: individuals of the same line are genetically more similar than individuals from different lines, and the descendants of a given line may be subjected to an environmental gradient where phenotypes of interest are assessed, thus producing a reaction norm (David et al. 2004, 2005). Different lines sourced from the same population will have slightly different reaction norms (significant genotype × environment interaction) demonstrating the presence of genetic variation for phenotypic plasticity (e.g. David et al. 1997; Gibert et al. 2000, 2004). Comparison of the reaction norm shape, and therefore levels of plasticity, between populations can then be easily undertaken. In most studies of phenotypic plasticity in *Drosophila*, the environmental factor most often considered is developmental temperature (e.g. Delpuech et al. 1995; David et al. 1997; Klepsatel et al. 2013), but there are also some studies testing the effect of nutrient quality (Chippindale et al. 1993) or photoperiod (Bauerfeind et al. 2014).

Figure 1 shows an example of phenotypic plasticity in response to developmental temperature measured in 5 isofemale lines of two populations (Paris, France and Barcelona, Spain) of the invasive *D. suzukii* (unpub. results). Climatic conditions in these two locations are very different, with a typically hotter and dryer climate in Barcelona than in Paris that could result in local adaptation of the populations. Measured traits included recovery time from chill coma (16 h at 0 °C), a trait related to cold tolerance in *Drosophila* (Gibert et al. 2001) and wing size. Values of recovery time (ranging between 7 and 15 min after development at 20 °C) suggest that *D. suzukii* is a temperate species (Gibert et al. 2001). As expected, phenotypic plasticity was highly significant for both traits. No significant differences were observed between the two populations collected at the same time in 2012, a few years after the first observation of *D. suzukii* in both countries. It is possible that these results may be experimental artefacts, i.e. caused by low statistical power or convergent evolution to laboratory conditions. However, it is also plausible that the lack of significant differences in the thermal reaction norms between the two populations is due to the fact that too little time has passed since the two populations diverged, due to the very high expansion rate of this species (see Fig. 2A). It will be important to compare

these two populations in few years' time, to determine whether divergence in traits that underpin climatic adaptation have evolved to match local environmental conditions. Determining whether there are significant and critical tradeoffs between plasticity and basal trait expression will also provide further insight into the processes that sustain a population across these environments. On the other hand, immigration may be significant owing to repeated introductions into these locations (i.e. high propagule pressure), which in turn may limit adaptive differentiation. This can be readily tracked using population genomics techniques (Chown et al. 2015).

When populations have diverged over a longer time period, significant differences are often found not only for the mean trait values but also for phenotypic plasticity itself. For instance, comparisons of thermal reaction norms between tropical (Congo) and temperate (France) populations of *D. melanogaster* for body size (Haerty et al. 2003) and ovariole number (a trait related to fecundity in *Drosophila*, Delpuech et al. 1995) have been performed. Both traits exhibit concave reaction norms, with a maximum phenotypic value at an intermediate developmental temperature. However this temperature is significantly lower in the temperate than in the tropical population (confirming the general latitudinal trend known for these traits, see Gibert et al. 2004). The most interesting result to emerge from these comparisons was that, for body size, the temperature of the maximum phenotype was significantly higher for the tropical compared to the temperate population, suggesting a lateral adaptive shift in the reaction norms across populations (Morin et al. 1999).

Investigating the invasion process in *Drosophila*: case studies

A number of *Drosophila* species are known to be invasive, including the most obvious example of the domestic African species *Drosophila melanogaster*. *D melanogaster* first colonized the Eurasian continent about 10,000–15,000 years ago (Capy and Gibert 2004; Lachaise and Silvain 2004) and spread more recently to the American and Australian continents around 100 years ago (see Hoffmann and Weeks 2007 for a review). Other invasions have been described more recently, and we have chosen to focus on two examples; *D. subobscura* on the American continent
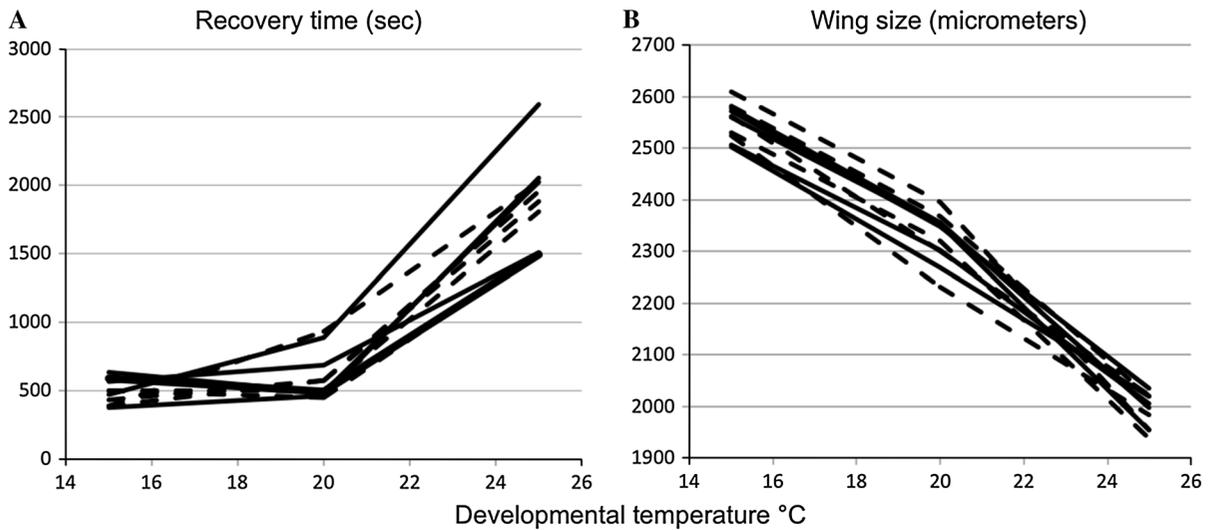
Fig. 1 Phenotypic plasticity of chill coma recovery time (**A**) and wing size (**B**) in females of different isofemale lines from two populations (Barcelona, Spain *plain lines* and Paris, France *dotted lines*) of *D. suzukii* collected in 2012. Lines had been kept in laboratory conditions on standard *Drosophila* medium at 21 °C LD12:12 for 6 months prior to the experiments. For each line, after a day of oviposition at room temperature (about 20–22 °C), groups of 50 eggs were placed into 3 different vials and placed at one of the three developmental temperatures (15, 20 and 25 °C) to complete development. On emergence, adults were transferred to fresh food and examined a few days later. Chill coma recovery was recorded after 16 h at 0 °C for about 10 individuals for each line and developmental temperature. Wing size was measured in 5 individuals for each line and developmental temperature. Data were analysed by using a generalized linear model with a gamma family and inverse link for the chill coma recovery and a Gaussian family and an identity link for the wing size. A highly significant temperature effect was found for both traits ($p < 0.001$) but no significant differences were found between the two populations for either recovery time ($p = 0.58$) and wing size ($p = 0.14$)

(Beckenbach and Prevosti 1986; Pascual et al. 2007) and *Zaprionus indianus* in Asia and America (Vilela 1999; David et al. 2006), to illustrate how *Drosophilids* can be used to provide insight into the adaptive processes that underpin successful invasions.

When the invasion is recent and the history of the invasion is relatively well known, the process of adaptation can be investigated either by comparing divergence between the populations in the introduced and ancestral ranges or by following populations during the process of invasion in real time. This is increasingly undertaken to elucidate pathways of invasion in other insects, including e.g. the Asian ladybird *Harmonia axyridis* (Lombaert et al. 2010), Mediterranean fruit fly *Ceratitis capitata* (Karsten et al. 2015), and Western Corn Rootworm, *Diabrotica virgifera virgifera* (Ciosi et al. 2008).

*Zaprionus indianus* Gupta (1970) (Fig. 2B)

The genus *Drosophila* is paraphyletic, i.e. it comprises different groups of species that are classified under different genus names (Yassin 2013). Of these, species belonging to the genus *Zaprionus* form a distinct group, that is closely related to species of the subgenus *Drosophila* of *Drosophila* (Yassin et al. 2010; Yassin 2013). Among its 70 Afrotropical and Oriental species, only one, *Z. indianus*, has recently become invasive. Despite its name, *Z. indianus*, is an African species from the sub-Sahara (Tsacas 1985; van der Linde et al. 2006; Commar et al. 2012) and now commonly known as the "African fig fly". From Africa, *Z. indianus* is thought to have first expanded east into Asia (India) (David et al. 2006; Yassin et al. 2008), where it was collected for the first time in 1966 (Gupta 1970) and then, from another African propagule, to America (Yassin et al. 2008). The Indian invasion has then expanded westward into Pakistan (Okada and Carson 1983), Saudi Arabia (Chassagnard and Kraaijeveld 1991), Israel (Harry et al. 1999), Egypt (Yassin and Abou-Youssef 2004; Yassin et al. 2009a) and Spain (Carles-Tolrá 2009). In the Americas, the species was recorded for the first time in Brazil in 1999 (Vilela 1999) and rapidly spread
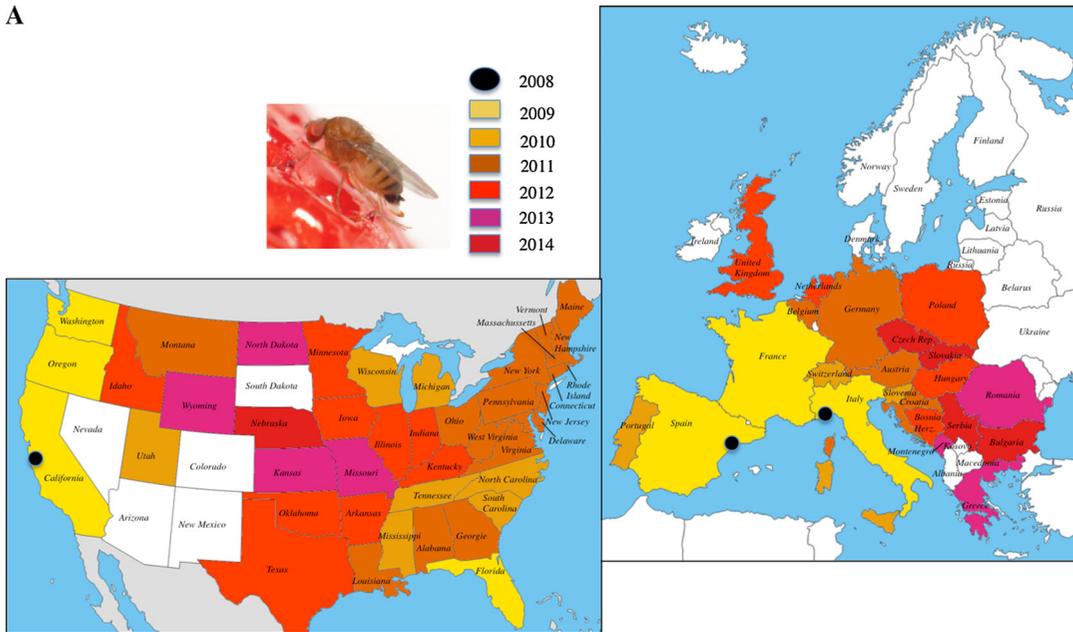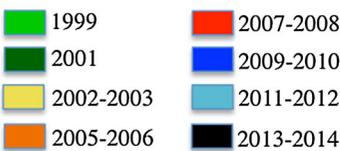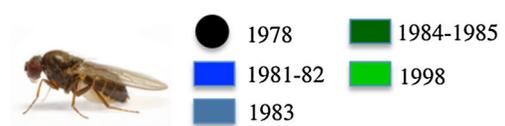
Fig. 2 A Rate of range expansion of *D. suzukii* in Europe and USA *Source* Asplen et al. 2015; CABI 2014. **B** Rate of range expansion of *Z. indianus* in the Americas. **C** Rate of range expansion of *D. subobscura* in the Americas

throughout Brazil and South America (van der Linde et al. 2006) where it became a major pest of fig production. It has since been reported in southern Mexico in 2002 (Castrezena 2007; Markow et al. 2014) and then rapidly spread throughout the USA (Florida in 2005; van der Linde et al. 2006; California and Arizona in 2006; Castrezena 2007; Wisconsin in 2012; JE Pool; pers. comm.; Pennsylvania in 2014; Joshi et al. 2014; Michigan in 2014; van Timmeren and Isaacs 2014) and Canada (Ontario and Quebec, Renkema et al. 2013). The Canadian records most likely represent recurrent introductions from the south during the warmer summer season rather than well-established populations, given the extreme cold that occurs in Ontario and Quebec during winter.

The rate of genetic differentiation between populations of *Z. indianus* has been investigated by comparing populations from the three continents (Africa, Asia and South America). Several studies focusing on a range of traits/characteristics, including genome size (Nardon et al. 2005), chromosomal inversions (Ananina et al. 2007; Yassin et al. 2009a), quantitative traits (size and sternopleural bristles number, David et al. 2006; Yassin et al. 2009b), and mitochondrial DNA (CO-I and CO-II, Yassin et al. 2008, 2009a) concluded that old world populations (Africa and Asia) were always more similar to each other compared to the American populations. For mitochondrial DNA, however, the level of genetic variation was highest in Africa, consistent with the colonization history (Bouiges et al. 2013).

Within continents, significant genetic differences between populations have been described in India (Karan et al. 1998, 2000) and Brazil (Loh and Bitner-Mathé 2005). For instance, in India, latitudinal clines indicative of rapid adaptive shifts between populations were observed for size traits (body weights, wing length and thorax length), reproductive traits (ovarioles number) (Karan et al. 2000) and physiological traits (desiccation and starvation tolerance of adults) (Karan et al. 1998). Results from ecological niche modeling of *Z. indianus* also suggest that the species has undergone shifts in species-environment

relationships allowing for expansion into novel climatic conditions (da Mata et al. 2010). These shifts and range expansions may or may not be associated with adaptive shifts in traits between populations.

Since the South American continent was the most recently invaded, it provided the opportunity to investigate the rate of the geographical genetic differentiation after invasion. In Brazil, significant differences in wing size and shape between three populations from three different habitats in Rio de Janeiro state were observed within only 2 years of the first record of *Z. indianus* (Loh and Bitner-Mathé 2005). Once again these results highlight the fact that rapid adaptive shifts can occur during the invasion process when species harbor the required genetic diversity for selection to act upon. In contrast to the results of Loh and Bitner-Mathé (2005) and David et al. (2006) compared body size (wing and thorax size) of populations collected in South America (n = 5) with African (n = 11 populations) and Indian populations (n = 11 populations). While they did find genetically-based differences in size among the Brazilian populations, these differences did not vary with latitude. In contrast, a significant increase with latitude was observed within the Indian and, to a lesser degree, the African populations. These results further confirm the fact that divergence in these traits can arise relatively quickly in response to climatic selection. The absence of latitudinal differentiation in body size of the American populations may be a consequence of insufficient evolutionary time.

Another interesting result of the David et al. (2006) study was that the American and African populations displayed similar levels of genetic variability (measured as the intraclass correlation between isofemales lines and genetic coefficients of variation) suggesting that the American colonizing propagule was of a sufficient size to carry all the genetic diversity of the origin population. Mattos Machado et al. (2005) found similar results for the introduced Brazilian populations. Using allozyme electrophoresis, they compared the level of polymorphism of Brazilian, African and Asian populations. They found that genetic distances and Fst indices among Brazilian populations were small and generally non-significant, suggesting colonization from a single propagule followed by a rapid demographic expansion.

Only one experimental study has examined how plasticity might contribute to the invasive success of *Z.*

indianus. By comparing the reaction norms for wing size and shape across five different growth temperatures, Loh et al. (2008) demonstrated that the Brazilian population (from the colder climate) was significantly larger than the African one. More interestingly, they also found that the shape of the thermal response curve was different; the temperature at which size was maximum was about 3 °C higher in the warmer African population compared to the Brazilian population. These results are consistent with those obtained in *D. melanogaster* (Morin et al. 1999, cited earlier) and suggest that genetically based differences in plasticity may contribute to divergence during an invasion.

Thus, the recent invasion of *Zaprionus indianus* in America constitutes a highly informative system for investigating the evolutionary processes that underpin the invasive process. The rapid evolution of latitudinal clines in key traits in India highlights the importance of local selective forces in driving adaptive divergence, and studies conducted in Brazil confirm that evolutionary processes can occur over very short timeframes. Continuing this kind of study, and in particular following the rate of local adaptation in Brazil, will be a very exciting area of research. It would be also very interesting to investigate the extent to which phenotypic plasticity is contributing to the successful invasion of this species by considering more traits, types of environments and populations.

Drosophila subobscura Collin in Gordon (1936) (Fig. 2C)

Drosophila subobscura belongs to the *obscura* species group of the subgenus *Sophophora* of *Drosophila*. Until 1978, *D. subobscura* was a Paleartic species with a geographic distribution extending from northern Africa to southern Scandinavia (Prevosti et al. 1988). At that time, *D. subobscura* was found for the first time in Puerto Montt, Chile (Brncic and Budnik 1980) where it then quickly spread all over Chile (Brncic et al. 1981) and up the Atlantic coast of Argentina (López 1985). In North America, it was observed for the first time in 1982 in Port Townsend (WA) in the northwest US (Beckenbach and Prevosti 1986) and then quickly spread to the south (Davis, California in 1983) and east (Provo, Utah 1998) (Beckenbach and Prevosti 1986; Noor 1998). The colonization of the Americas by *D. subobscura* was considered 'a grand

experiment in evolution' (Ayala et al. 1989), and was analyzed from its earliest stages (Brncic et al. 1981; Beckenbach and Prevosti 1986). It provided an excellent opportunity to investigate both evolutionary mechanisms operating in nature and the species ecology in the invaded region (Pascual et al. 1993; Noor 1998; Huey and Pascual 2009; Gibert et al. 2010). The colonization of this vast area was sequential with only a few effective founders first introduced to South America with a subsequent larger set reaching North America without noticeable secondary founder events (Pascual et al. 2007). This resulted in particularly low genetic diversity, however secondary bottlenecks were detected in their subsequent expansion to harsher environments within each new colonized area (Noor et al. 2000; Fernández Iriarte et al. 2009). Despite their low diversity, the species has proved able to adapt to highly diverse environmental conditions and respond rapidly to global warming (Balanyà et al. 2006). Rapid latitudinal changes in chromosomal inversion frequencies were observed after a few years of its introduction, on both continents and in the same direction as in the native Old World, providing strong experimental support for their adaptive value (Prevosti et al. 1988). Initial continuous surveys in the colonized area suggested that these clines were still evolving and converging towards the Old World baseline (Prevosti et al. 1990). Thus the evolution of inversion frequency clines seemed predictable and remarkably rapid. However, posterior surveys showed that inversion clines did not consistently increase in steepness over time nor continue to converge (Balanyà et al. 2003) but rather weakened and even changed sign, suggesting that active behavioral thermoregulation might buffer environmental variation (Castañeda et al. 2013; Huey and Pascual 2009). However other processes could be responsible for this lack of continued convergence. The strong bottleneck due to the founder event (Pascual et al. 2007), the strong linkage disequilibrium between inversions and several genetic markers (Mestres et al. 1995; Gómez-Baldó et al. 2008) and the recombination reduction mediated by inversions observed in *D. subobscura* (Pegueroles et al. 2010) could cause an impoverishment of genetic variation, with an overall reduction of haplotypes in introduced flies relative to ancestral ones, therefore reducing the capacity to evolve steeper clines. Similarly the persistence of lethal genes in the colonizing

populations, completely or partially associated with chromosomal inversions, suggests that those arrangements, despite carrying a lethal gene, could have a heterotic effect on the heterokaryotypes, reducing their fitness over time (Mestres et al. 2001), and also constraining ongoing clinal evolution. If this is the case, little additional evolution would be expected in the invading populations unless new coadapted gene complexes arise as indicated by Balanyà et al. (2003).

Other traits have also been investigated, with several studies on wing size in *D. subobscura* revealing a pronounced latitudinal cline in wing size among ancestral European populations (Pegueroles et al. 1995). One decade after the introduction, no significant latitudinal clines in wing size had evolved in either North or South America (Pegueroles et al. 1995). However only two decades after the introduction, clines in wing size had evolved in the two invaded hemispheres (Huey et al. 2000; Gilchrist et al. 2004), largely converging on the ancestral cline. Even more interesting, these authors observed that while overall clinal patterns of wing size were similar, the region of the wing that generated the size cline for females differed among all three continents; the European cline was obtained through changing the proximal portion of the wing, the North American cline was the result of changes in the distal portion of the wing, whereas in South America both parts of the wing contributed to the cline (Gilchrist et al. 2004). The results for the South American populations may in part reflect the fact that different associations between wing shape and chromosomal inversions are observed in native and colonizing (South American) populations, which have been related to the founder event (Fragata et al. 2010).

The *D. subobscura* invasion enabled both diachronic and synchronic rates of evolution to be quantified for both American continents. Although estimation of allochronic rates requires an actual time series, whereas synchronic rates of evolution are computed from divergent populations sampled at a single time (Hendry and Kinnison 1999), both were similar in magnitude (Gilchrist et al. 2004). On both continents, the highest allochronic rates of evolution were generally at the highest latitude populations in accordance with the Mediterranean region of Europe being the most likely source of the New World founders (Pascual et al. 2007). A meta-analysis of microevolution on contemporary time scales in nature revealed a

tendency towards increasing evolutionary diversification with time and a decrease of evolutionary rates (Kinnison and Hendry 2001). Experimental evolution studies also enable investigation of the colonization processes and can be readily applied in *Drosophila*. For instance the impact of founder effects on evolutionary dynamics during laboratory adaptation in *D. subobscura* have shown significantly higher rate of decline in genetic variability during the first few generations in the laboratory along with a higher rate of change at several life history traits (Simões et al. 2008; Santos et al. 2012) supporting the hypothesis that evolution slows when populations approach new optima or as genetic variation is depleted (Kinnison and Hendry 2001). Unfortunately the evolution of fitness related traits in *D. subobscura* have only been analyzed using native populations. It would be very interesting to study the evolutionary dynamics of colonized populations under similar laboratory conditions to further examine how evolutionary trajectories change over time.

Unfortunately, the role of phenotypic plasticity in the successful invasion of *D. subobscura* has not been investigated.

Conclusions and perspectives

In conclusion, *Drosophila* species, which are typically used as animal models in many biological disciplines, are also powerful models for studying the evolutionary mechanisms that underpin adaptation to new environments (Balanyà et al. 2006; Santos et al. 2012), including biological invasions. While much work has already been carried out on two invasive species, *D. subobscura* and *Z. indianus,* there is still great potential to use these species, and other *Drosophila*, to further understand biological invasion processes.

The two examples detailed in this paper clearly demonstrate that rapid adaption to environmental change is possible. However, in many invasive insects, the genetic basis of this adaptation (and the role that phenotypic plasticity undertakes) is not well known. The role of genetic variation in the success of invaders can be investigated by focusing on divergence in quantitative traits known to affect performance in different environments, and divergence in genetic markers (Simões et al. 2012). Recent advances in genomic (RAD-Seq, GBS) and transcriptomic (RNA-

Seq) approaches have been developed providing more powerful tools to better understand the genetic basis of invasion (review in Chown et al. 2015). While some of these new technologies can be used on non-model organisms that lack a reference genome assembly, the existence of reference genomes will nonetheless greatly facilitate insight into the genomic basis of invasion.

The importance of phenotypic plasticity in the invasion process remains poorly documented. Studying phenotypic plasticity should ideally involve assessments of phenotypic responses over several environmental conditions (Murren et al. 2014), such as over the complete thermal range of a particular species (which may be best considered through the use of latitudinal clines). While such studies are perhaps considered labour intensive (e.g. several lines/genotypes assessed at several temperatures), they will be necessary to understand the importance of plasticity in successful invasions. Moreover, important questions that must be resolved when investigating phenotypic plasticity such as which environmental factors to use (e.g. temperature, humidity, photoperiod) and which traits to focus on, must also be considered. Further, many studies on *Drosophila* have focused on developmental (irreversible) plasticity of morphometrical traits (e.g. David et al. 2004) but reversible plasticity of behavioral or physiological traits may also have an important role to play during invasions (i.e. Rego et al. 2010). Finally, the ecological relevance of the laboratory and assay conditions will also be important to determine, to ensure that the results can be extrapolated to field situations (e.g. Terblanche et al. 2011). This requires some insight into the ecology of the investigated species, which traditionally has been largely lacking in *Drosophila* studies. Indeed, it is interesting to note that in contrast to the level of detail provided with respect to their molecular and developmental biology, the ecology of most *Drosophila* species is typically neglected and not reported.

Understanding the rate of change in levels of phenotypic plasticity during invasion is also particularly important. It has been argued that phenotypic plasticity, by allowing introduced populations to survive under new environmental conditions, can provide the necessary time for new, adaptively important genetic variants to arise (Pigliucci 2005; Lande 2015). If the new selection pressures persist in the new environment, we may expect to observe a decrease in the plasticity and a 'genetic assimilation' of the trait(s).

Such mechanisms that could be common during the well-known 'lag phase' of biological invasions, have to our knowledge not yet been documented. The very recent invasion of Europe and North America by *D. suzukii*, although apparently not related (Adrion et al. 2014), would constitute a perfect empirical system with which to address this question.

Finally, invasions enable the predictability of evolution to be empirically assessed by comparing the rate of adaptive shifts in the native and invaded range. Such comparisons have been performed to some degree in *D. subobscura*. However, once again, the simultaneous invasion of North America and Europe by the Asian species *D. suzukii* provides the opportunity to compare the mechanisms of this successful invasion in two different regions at the same time. Moreover, *D. suzukii* is a pest of small and stone fruits with huge economic impacts in both America and Europe, and in that respect is the target of on-going important monitoring that should allow the collection of accurate information on its ecology. For all these reasons, we think that *D. suzukii* constitutes the perfect biological model with which to comprehensively examine the evolutionary and ecological processes that underpin successful invasions, especially for insects but also for the field as a whole.

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