

Adaptability of endemic and widespread species to environmental change: a case study in *Drosophila*

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Introduction

We are living in a changing world, and conservation is facing an ever increasing number of challenges, mostly due to the consequences of direct and indirect anthropogenic disturbance. Human activities have been for long a source of environmental disturbance with effects as diverse as habitat destruction and fragmentation, introduction of alien species or global warming (Millennium Ecosystem Assessment, 2005; IUCN, 2006). To make matters worse, in some cases their effects are not independent, that is they can act synergistically. For instance, global warming may lead to habitat loss and also facilitate the invasion by alien species (Samways, 2005). In the last century the pressure of anthropogenic activity on natural habitats has increased and the rate of change has posed increasing hardships on the environment and biological diversity (e.g. Sodhi *et al.*, 2009), making biodiversity conservation one of the greatest challenges for the 21st century (e.g. Leadley *et al.*, 2010).

Oceanic islands are natural laboratories whose importance in biology has been for long recognized. They provide essential information when addressing areas as diverse as adaptation, speciation, impact of invasive species and community assembly among others. Islands are also reservoirs of biodiversity, their isolation and lack of initial competition during colonization have given rise to spectacular radiations in many groups of organisms (e.g. Whittaker & Fernández-Palacios, 2007). However, the same characteristics that have made islands particularly prone to speciation events have also made them vulnerable to extinction. This is corroborated by the fact that the majority of documented extinctions occurred on islands usually as a direct or indirect consequence of anthropogenic activities (Reid & Miller, 1989; Cronk, 1997; Sadler, 1999), with island endemics being more prone to extinction (see

Frankham, 1998 and references therein; Fontaine *et al.*, 2007; Fordham & Brook, 2010). The Macaronesian archipelagos, in particular Madeira and the Canary Islands, are extremely rich in endemic species (Borges *et al.*, 2008; Arechavaleta *et al.*, 2010) and as such are part of the biodiversity hotspots important for conservation at a global scale (Myers *et al.*, 2000). Nevertheless, a considerable number of species went extinct in these islands during the last centuries as a consequence of anthropogenic activities (e.g. Goodfriend *et al.*, 1994; Fontaine *et al.*, 2007).

In recent years the awareness of the possible impact of human induced climate change has been growing. Consequently, several efforts have been made to predict its effects in an attempt to delineate conservation strategies aiming to reduce its consequences on global biodiversity. However, climate change includes more than the increase in mean temperatures, it also involves changes in precipitation patterns and in the frequency and intensity of extreme events, like heat and cold waves, tornadoes, floods etc, which might prove a greater challenge than the actual rise in mean temperature.

Conserving biodiversity - the role of captive populations

When faced with environmental change in their habitats species can adjust in two basic ways: adapt to the new conditions or shift their distributions moving to more suitable habitats. So, when planning more effective conservation measures, it is important to consider whether species have the ability to adapt to current and future environmental changes in their natural habitats. For instance, the evolutionary potential of threatened species should be taken in consideration when deciding where to place protected areas and their boundaries, as it is important to understand if it will be sufficient to establish and maintain protected areas in their current distribution or allow measures to increase protection in additional areas, accounting for possible range shifts due to global warming (Hole *et al.*, 2009). However, in many cases suitable habitats are not readily available and this has led to the implementation of *ex situ* conservation programs for many endangered species using captive breeding. Unfortunately, it is estimated that, in the future, many more will need this type of intervention to prevent extinction (Soulé *et al.*, 1986; Seal, 1991; Tudge, 1995; Lacy, 2006; Frankham *et al.*, 2010). Further, nowadays several animal and plant species only exist in captivity, being presumed extinct in the wild (e.g. Frankham, 2008).

Captive breeding involves maintaining and managing captive populations of endangered species usually outside their natural habitat with the ultimate goal of reintroducing them in the wild once suitable conditions are available (Frankham *et al.*, 2010). However, to use captive breeding as a more effective conservation tool it is necessary to understand the consequences of keeping individuals in captivity, in many cases in what we perceive as “optimum” conditions with ample supplies of food, reduced competition, absence of predators and parasites. All these conditions can translate in relaxed selective pressures leading to individuals that could have reduced fitness under natural conditions (e.g. Woodworth *et al.*, 2002; Frankham, 2008). Several factors can lead to detrimental effects of captive breeding on populations. Captive populations are in most cases small due to space limitations, size of many endangered species and the space necessary to maintain them. This may lead to reduced fitness due to inbreeding, loss of genetic diversity and/or accumulation of new mildly deleterious mutations. Another factor to take in consideration is that adaptation to captivity may lead to genetic changes that make captive breed individuals less fit in their natural habitat (Frankham *et al.*, 2010).

Adaptation to captivity has been documented in many organisms and, in general, characteristics selected under captive conditions are extremely disadvantageous in the wild (see Frankham, 2008 for a review). For instance, the success of biological control programs is negatively related to time in captivity (Myers & Sabath, 1980) and reintroduction programs using translocated wild individuals have been more successful than the ones using captive breed populations (e.g. Griffith *et al.*, 1989; Fischer & Lindenmayer, 2000). Further the problems created by the impact of adaptation to captivity will likely increase in the future, as in some cases it will be necessary to maintain captive populations for longer periods of time, until suitable habitats are available for reintroduction in the wild (Soulé, 1986).

The primary targets of the genetic management of captive populations of threatened species are maintaining genetic diversity and minimizing inbreeding (see Frankham, 2010). However, the most important challenge today is to introduce measures to minimize genetic adaptation in captive populations to reduce its deleterious impacts on reintroductions. Some suggestions have been made like minimizing generations in captivity and or using population fragmentation (see Margan *et al.*, 1998; Frankham, 2008). However, we still lack important information on how to optimize procedures in order to apply them in practical management (Frankham, 2010). Also, one important question that must be addressed is the fact that when studying the problems associated with adaptation to captivity, most research has focused on model organisms like *Drosophila melanogaster*, a generalist species with a wide distribution

(e.g. Woodworth *et al.*, 2002; Gilligan & Frankham, 2003), due to the unfeasibility of using the threatened species themselves. This leads to a potential problem: how general are these findings? Can we extrapolate to specialist species, particularly ones with restricted distributions? This issue is particularly important since many endangered species are specialists with localized distributions.

Adaptation and conservation - adaptive potential

An important question when predicting the consequences of environmental change and conservation planning, that has received little attention, is whether species, particularly endangered ones, have the ability to adapt to changes in their environment. Many species are now facing new conditions due to habitat fragmentation and climate change, leading to rapid changes in species distributions as well as changes in phenology, quantitative traits and genetic markers (e.g. Hughes, 2000; Bradshaw & Holzapfel, 2001; Warren *et al.*, 2001; Rezende *et al.*, 2010).

In order to have more effective conservation measures, it is important to understand if different species have the ability to adapt to environmental change. Evolutionary potential is most directly measured by estimating the quantitative genetic variation for reproductive fitness. Unfortunately, this quantitative genetic variation is the most difficult to measure and is the aspect of genetic diversity for which we have least information for threatened species. Nevertheless, it is generally assumed that populations have high genetic variation in quantitative traits for adaptation (Lewontin, 1974). This is mostly due to the fact that selection experiments have demonstrated genetic variance for quantitative traits, which has led to the general assumption that all traits have relatively high levels of genetic variance and evolutionary potential. However, these studies have focused on generalist widespread species and on traits that are usually unrelated with the distribution and abundance of species (Roff, 1997).

The ecological limits of species have been for some time an important issue in evolutionary biology and many explanations have been proposed for their interpretation. However, few empirical studies have been able to determine why species may be limited and an obvious explanation that has been generally overlooked is low genetic variance (Blows & Hoffmann, 2005). Many estimates of molecular genetic diversity have been obtained in threatened and non-threatened species (see Spielman *et al.*, 2004; Evans & Sheldon, 2008).

However, correlations between molecular and quantitative measures of genetic diversity are often low, as the ability of species to evolve is determined primarily by quantitative genetic variation rather than molecular variation for neutral and weakly selected loci (e.g. Reed & Frankham, 2001; Kellermann *et al.*, 2006). Further, the particular quantitative traits considered are relevant as well as the species range (wide vs. restricted distributions). For instance, several traits potentially related with adaptation to climate change, like desiccation resistance, have revealed high heritability and quantitative variation in populations of widespread *Drosophila* species, reflecting high adaptive potential to this kind of stress (e.g. Hoffmann & Parsons, 1989; Blows & Hoffmann, 1993; Gibbs, *et al.*, 1997; Schiffer *et al.*, 2004). On the other hand, Kellermann and colleagues (2006) found little quantitative variation for this trait and high variation in two morphological traits in two *Drosophila* species with restricted distributions, contradicting the general assumption that all quantitative traits have high genetic variance (Roff, 1997). This raises the question of how credible are generalizations from generalist widespread species to small ranged specialists in what concerns their responses to environmental change.

Experimental evolution, which involves the study of populations across several generations under defined and reproducible conditions (see Rose & Garland, 2009 and references therein), is another useful tool we can use to estimate species' adaptive potential to different conditions. In the last decades it has been used to tackle different questions in evolutionary biology such as adaptation to particular conditions, selection, speciation and domestication among others (reviewed in Garland & Rose, 2009). This approach has also been used in conservation genetics to assess the implications of inbreeding and captive breeding on managed populations. Laboratorial adaptation (or adaptation to captivity) can be seen as a proxy to study adaptation considering the lab as just another type of habitat with its own evolutionary mechanisms (Matos *et al.*, 2000a).

Adaptive potential in endemic and widespread species – the case of *Drosophila madeirensis* and *D. subobscura*

The model system: *Drosophila madeirensis* – *D. subobscura*

Drosophila madeirensis is an endemic species from Madeira Island and is strictly associated with Laurisilva (Monclús, 1984). This habitat once covered the circum-Mediterranean area but nowadays is restricted to the Macaronesian archipelagos (Azores,

Madeira and the Canaries). On the other hand, *D. subobscura* (the closest relative of *D. madeirensis*) is a native Palearctic species with a distribution ranging from Northern Africa to Scandinavia, being also present in the Azores, Madeira and the Canary archipelagos. However, in the last decades its range changed dramatically: in its native continent its distribution expanded 700km northwards probably in response to climate change (Krimbas, 1992) and its current northern limits are unknown. Further, in the last 30 years this species successfully colonized, first the South (Brncic & Budnik, 1980) and then the North American continents (Beckenbach & Prevosti, 1986). *Drosophila subobscura* is a generalist species able to explore a wide range of resources and its breeding sites include decaying fruits, fermenting sap, as well as decaying vegetation and fungi (Krimbas, 1993). Unfortunately, little is known about the ecology of the endemic *D. madeirensis*.

The two species are morphologically rather similar and very closely related, having diverged less than 1 million years ago (Ramos & Onsins *et al.*, 1998). Genetic data from chromosomal inversions and the *rp49* gene sequence indicate that the most probable scenario for their divergence involves two independent colonization events from continental ancestral *D. subobscura* populations, the first adapting to the native forest originating *D. madeirensis* and the second remaining as *D. subobscura* (Khadem *et al.*, 1998). The speciation event between *D. madeirensis* and *D. subobscura* is rather recent and it is possible to obtain hybrids between these species, especially if the former is the mother species (Khadem & Krimbas, 1991, 1993; Papaceit *et al.*, 1991; Rego *et al.*, 2006, 2007a). An interesting point about the hybridization between these species is that, contrary to what it was reported initially, it is possible to obtain in laboratory viable and fertile hybrids from both cross directions, but with varying success rates (Rego *et al.*, 2006, 2007a).

Differentiation between *Drosophila madeirensis* and *D. subobscura*

The analysis of the differentiation in polytene chromosomes indicates a high homology between the two species (Krimbas & Loukas, 1984; Papaceit *et al.*, 1991), the X-chromosome being the only one that underwent structural variation during the speciation process (Papaceit & Prevosti, 1989; Papaceit *et al.*, 1991), which is in accordance with the expectation that the sexual chromosome is the one showing more rearrangements when comparing closely related species. *Drosophila subobscura* presents one of the richest chromosomal inversion polymorphisms in this genus, with more than 80 arrangements (Balanyà *et al.*, 2009). In the

last decades changes in inversion polymorphism have been linked with response to global warming (e.g. Balanyà *et al.*, 2006) and it has been suggested that they could be good genetic markers to track the impact of climate change on natural populations (reviewed in Balanyà *et al.*, 2009; Rezende *et al.*, 2010). However, the inversion polymorphism of *D. madeirensis* and *D. subobscura* in Madeira is extremely poor, with *D. madeirensis* carrying the ancestral form of several of them (Khadem *et al.*, 1998). The scarcity of inversions in Madeiran populations of *D. subobscura*, when compared with European ones, might suggest that the insular populations of both species have low genetic variability. However, evidence from the number of insertion points of transposable elements revealed high genetic variability in both species and showed that *D. madeirensis* and *D. subobscura* present little genetic structuring in Madeira Island suggesting that both species are represented by one single large population, in spite of the topographical extremes of this island, with deep valleys surrounded by high mountains (Lepetit *et al.*, 2002).

Rego and co-workers, using replicated laboratorial populations of *D. madeirensis* and *D. subobscura* derived from recent collections from the wild, compared the two species in terms of several morphological, behavioral, stress related and life-history traits (Rego *et al.*, 2006, 2007a, 2010). They also followed the adaptation of both species to a new common environment (the laboratory) for several generations and compared their evolutionary trajectories in terms of fecundity related traits (Rego *et al.*, 2007b). Their results show that the two species are clearly differentiated in terms of morphometry, *D. madeirensis* being bigger (Rego *et al.*, 2006); life history traits, with *D. subobscura* being more fecund and having a lower age of first reproduction, i.e. females from this species start to lay eggs at a younger age (Rego *et al.*, 2007a,b). Both species are also clearly differentiated in terms of starvation resistance, *D. madeirensis* being less resistant to this kind of stress than its widespread congener despite its bigger size (Rego *et al.*, 2007b).

Evolutionary trajectories of fecundity related traits

Rego and colleagues (2007b) analyzed the evolutionary trajectories of the fecundity related traits age of first reproduction (the number of days elapsed until the female laid the first egg), early fecundity (the number of eggs laid in the first week) and peak fecundity (the number of eggs laid in the second week of life). Their results indicate that both species showed signs of evolutionary change for some of the traits, however, their evolutionary trajectories differed.

During the adaptation to the new environment *D. subobscura* improved in age of first reproduction, females maturing faster starting to lay eggs earlier, while *D. madeirensis* showed no such tendency (Fig. 1a). The interspecific comparison of the evolutionary trajectories for this trait revealed that they were significantly different ($t = -0.024$, $p < 0.01$, tested by differences in average slope between species, see Rego *et al.* 2007b).

In the case of early fecundity both species showed significant tendencies to increase the number of eggs laid in the first week of life (Fig. 1b), but *D. subobscura* had a better performance as shown by the steeper slope of the evolutionary trajectory for this species. Also in this case the average slope of both species was significantly different ($t = 0.684$, $p < 0.05$). The results for peak fecundity were somewhat surprising as neither species showed signs of improvement. On the contrary, *D. madeirensis* showed a significant tendency to reduce the number of eggs laid with time as shown by the negative slope of the evolutionary trajectory (Fig. 1c). However, a comparison of the average slope for both species revealed no significant differences ($t = 0.783$, n.s). Overall, the results of this study indicate a tendency for improvement in fecundity related traits specially the ones related with early reproduction. The two species tended to improve in age of first reproduction and early fecundity during adaptation to the new conditions, the rate being higher in *D. subobscura*. This is in accordance with previous works on laboratory adaptation that indicated an improvement in early reproduction, however most of these studies analyzed only one species and in general a widespread one (*D. melanogaster*: Sgrò & Partridge, 2000; *D. subobscura*: Matos *et al.*, 2000b, 2002; but see Hercus & Hoffmann, 1999 for a study on *D. birchii*, *D. serrata* and their hybrids).

The lack of evolutionary trend in peak fecundity for *D. subobscura* was unexpected given previous experiments on this species (e.g. Matos *et al.*, 2002). Possible explanations for this might be related with differences in genetic background or founder events as the *D. subobscura* populations used in both studies were from different geographical origins and the number of founders of the laboratorial populations was also different, but further work is needed to clarify this issue. The differences found in the evolutionary potential of these species have to be interpreted with some caution, as the study dealt with two species with different ecological requirements: *D. subobscura* being a generalist species with a wide distribution and *D. madeirensis* being an endemic species specialized in a particular habitat. Species with greater geographical ranges are expected to be generalists and consequently to have a higher ability to adapt to environmental change (Parsons, 1982).

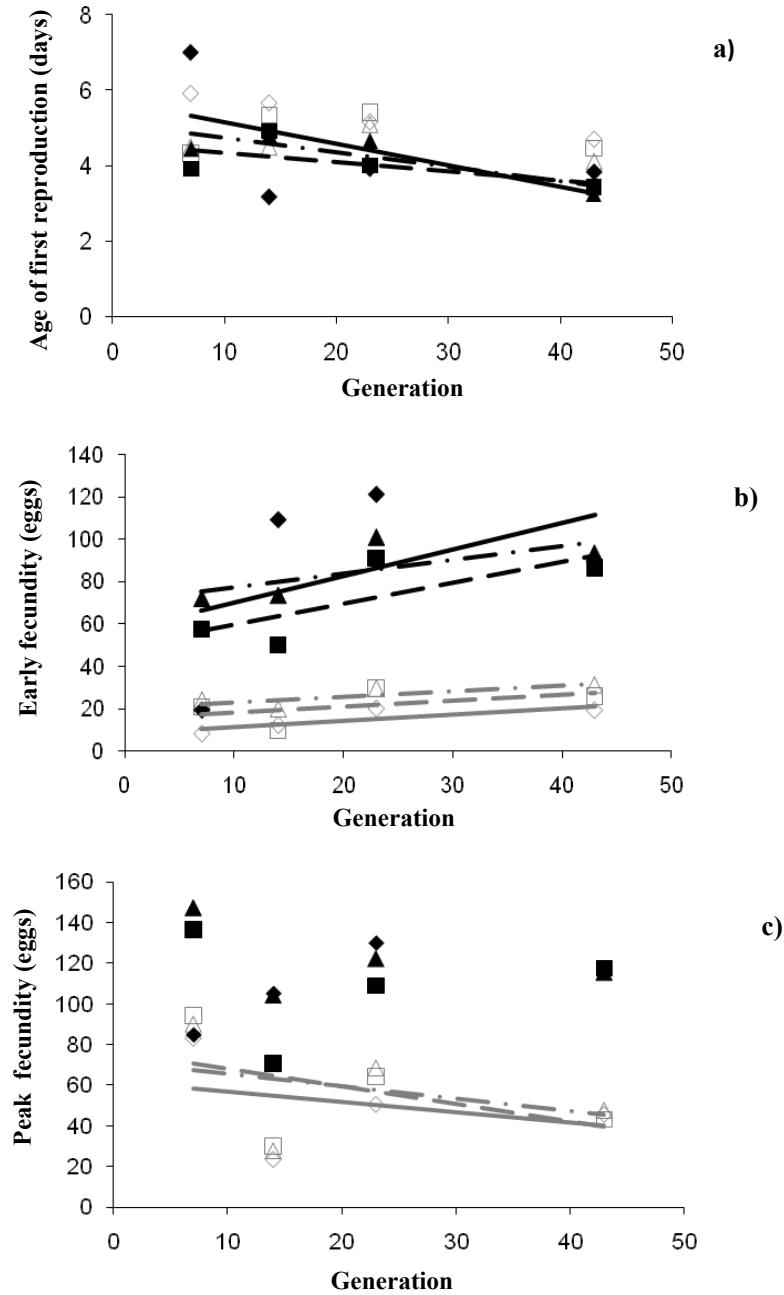


Figure 1. Evolutionary trajectories for age of first reproduction a), early fecundity b) and peak fecundity c). Plots of means of each trait as a function of generation number for *Drosophila madeirensis* (grey) and *Drosophila subobscura* (black). Data points show the mean values of replicate populations of each species. Significant linear trends were obtained only for *D. subobscura* for age of first reproduction ($P < 0.05$), for both species for early fecundity (*D. madeirensis*, $P < 0.001$; *D. subobscura*, $P < 0.05$) and only for *D. madeirensis* in the case of peak fecundity. Full line, diamonds - replicate 1; dashed line, squares - replicate 2; dotted dashed line, triangles - replicate 3.

Adaptive potential generally depends on quantitative genetic variation (e.g. Frankham, 1995, 2005), which in turn is expected to be lower in populations with more restricted distributions (Lienert *et al.*, 2002). *Drosophila madeirensis* occurs only in Laurisilva patches and is more specialized ecologically, which could suggest that this species has a lower adaptive potential to adapt to new conditions. The significant decline in performance for peak fecundity shown by *D. madeirensis*, the fact that this species also showed an absence of evolutionary trend for age of first reproduction and had a slower rate of improvement in early fecundity lends some support to this hypothesis. Inbreeding is not a likely explanation in this case, as the populations of *D. madeirensis* were established using a large number of wild-caught individuals, and were maintained in outbred conditions with a large number of individuals.

Overall, the experimental evolution of early fecundity indicates adaptation to the new conditions in both species but the rate of improvement is faster in the generalist widespread species *D. subobscura*. On the other hand, *D. madeirensis* shows signs of a possible failure to adapt to the new environment; these two factors resulted in further divergence between the two species during the process of adaptation to captivity (Rego *et al.*, 2007b).

Climate change - what do we know about *Drosophila madeirensis* and *D. subobscura* thermal traits?

Drosophila subobscura is considered a cold-adapted species with a thermal range between 6 and 26°C (Moreteau *et al.*, 1997) and a thermal optimum of 18°C (Krimbas, 1993). In spite of the fact that this species can attain normal development at 26°C, 8°C above its presumed thermal optimum, there is some indication that it may face fitness problems at lower temperatures. For instance, exposure to 25°C can induce male sterility in this species (Krimbas, 1993). Behavioral assays revealed that this species shows a thermal preference of 16.6°C when placed in a linear thermal gradient (Rego *et al.*, 2010) and a similar value was obtained when using interconnected population cages set at different temperatures allowing flies to move freely between the different temperatures (Davis *et al.*, 1998). The populations used in these two studies were from different geographic origins: mainland Portugal (Rego *et al.*, 2010) and France (Davis *et al.*, 1998). Further evidence that thermal preference in *D. subobscura* does not vary according with the population geographical origin was obtained from comparisons between *D. subobscura* populations from mainland Portugal and from

Madeira Island (Rego, Dolgova & Santos, unpublished results). However, these results are merely indicative as the geographical range covered in these studies is much smaller than the total range of this species.

A comparison of the thermal preference of *D. subobscura* and *D. madeirensis* also using thermal gradients revealed that the endemic species prefers lower temperatures (Rego, Dolgova & Santos, unpublished results). This corroborates the notion that *D. madeirensis* is also a cold adapted species and suggests that this species might have a lower thermal range than its widespread congener.

Rego and co-workers (2010) also analyzed stress resistance to high temperatures studying knockout temperature in *D. subobscura*, i.e. the temperature that induces loss of “conscience” due to heat stress. Their results show that 34.4°C was the average knockout temperature, with females showing a higher resistance to the heat stress (Rego *et al.*, 2010). A similar analysis was done comparing *D. madeirensis* and *D. subobscura* revealing that *D. madeirensis* resisted on average less than its close relative (Rego, Dolgova & Santos, unpublished results), reinforcing the idea that this species probably has a lower thermal range and is less tolerant to heat stress. This is in accordance with previous studies comparing several *Drosophila* species with contrasting distributions, which revealed significant differences between widespread and localized species in terms of desiccation and cold resistance, with species with restricted distributions showing smaller tolerance ranges (Kellerman *et al.*, 2009). Further, the quantitative genetic variation for these traits was significantly lower in the species with narrow distributions suggesting lower adaptive potential (Kellerman *et al.*, 2009).

Comparing thermal preference of flies from both species reared at 18°C and 22°C revealed that the ones developed at 22°C tended to choose higher temperatures in a thermal gradient. A similar comparison for heat resistance gave the opposite result, i.e. on average flies reared at the lower temperature showed higher stress resistance (Rego, Dolgova & Santos, unpublished results). This suggests that the two thermal traits are independent which is in accordance with previous work on *D. subobscura* (Dolgova *et al.*, 2010; Rego *et al.*, 2010). The results also indicate that both species may lack the variation to increase resistance to heat stress. However, it could also reflect that a developing temperature of 22°C is stressful and may disrupt the mechanisms to cope with heat tolerance. Santos and collaborators (2006) found evidence that a developmental temperature of 22°C increased fluctuating asymmetry in *D. subobscura*, a sign that this temperature disrupts development in this species. This coupled with the fact that both species are more difficult to maintain at 22°C, in particular *D. madeirensis* (personal

observation) reinforces the notion that this developmental temperature could be stressful for both species and affect their heat tolerance.

Implications for response to environmental change in the system *Drosophila madeirensis* - *D. subobscura*

Empirical studies on how species with different ecological requirements adapt to captivity, particularly ones comparing their evolutionary trajectories, are still generally lacking. An important information to retain from the study of Rego and colleagues (2007b), is that generalizations about the adaptive potential of different species can be misleading, even for closely related ones as in this case. This finding can have important implications for conservation; in the case of captive breeding programs it is relevant because some species might be unsuitable for this type of intervention, failing to thrive in captivity due to an inability to adapt to such radical changes. On the other hand, it also has implications when planning for protected areas. For instance, if different species show different adaptive potential or even lack the ability to adapt in relevant traits to environmental/climate change, the planning and management of protected areas should take this in consideration and include additional areas or ecological corridors that allow species to change or shift their current ranges in search of more suitable conditions, another possible solution being managed translocations to 'keep pace with' climate change trying to maximize genetic diversity and thus adaptive potential (Frankham, 2010).

The preliminary results of Rego and collaborators (2010, unpublished results) analysing thermal traits in the species pair *D. madeirensis* and *D. subobscura* indicate that the endemic species prefers lower temperatures and is less tolerant to heat stress. The fact that this species also showed no capacity to increase thermal resistance through a plastic response seems to bear ill omens regarding its ability to adapt to climate change, but more information is needed to clarify this issue, namely on quantitative genetic variation for traits relevant for thermal adaptation and on their evolutionary trajectories.

Another interesting point is how climate change might affect hybridization between *D. madeirensis* and *D. subobscura*. These species are sympatric on Madeira Island and as we said before, it is possible to obtain fertile and viable hybrids from both cross directions, and there is also some evidence that hybrids occur in nature (Khadem *et al.*, 2001). Climate change has already increased hybridization between several species (Mercader *et al.*, 2009;

Garroway *et al.*, 2010; Kelly *et al.*, 2010). In *D. madeirensis* females are more resistant to thermal stress than males (Rego, Dolgova & Santos, unpublished results), and in the laboratory hybrids are more easily obtained when *D. madeirensis* is the mother species (Khadem & Krimbas, 1991, 1993; Papacit *et al.*, 1991; Rego *et al.*, 2006, 2007a). A rise in temperature could lead to habitat reduction and fragmentation and facilitate hybridization by reducing the number of conspecifics available for reproduction and promoting more frequent encounters between these two species.

An important thing to consider when trying to predict the possible impact of climate change on *D. madeirensis*, is the effects of global warming on its habitat. As we mentioned before this endemic fly is associated with Laurisilva, a particular type of laurel forest with a high degree of humidity and low to moderate temperatures. In the case of *D. madeirensis*, in the end it might not matter if this species can endure and adapt to higher temperatures, if the forest it depends on does not. The available predictions on the impact of global warming on Laurisilva are contradictory: one study indicating that this habitat will shift its distribution to areas of higher altitude (Cruz *et al.*, 2008) while another indicates that this forest will suffer greatly with the predicted rise in temperature and will consequently contract its range on Madeira Island (Petit *et al.*, 2008). However, both studies agree on one important point: the predicted changes in temperature will have an important impact on Madeiran endemics survival.

The future...

Understanding how species react to environmental changes, including human induced global warming, is fundamental for effective conservation measures and is one of the greatest challenges of this century. In the best case scenario species will have adaptive potential to either adapt to the new settings *in loco* or to shift their distribution to areas presenting more suitable conditions. But what will happen when there is “no place to go”? Islands are particularly vulnerable to the impact of climate change: being isolated, and in many situations with their native habitats highly fragmented, migration to more suitable circumstances may be difficult or impossible. The problem is further increased by the fact that many island endemics have low dispersal capability due to adaptations to island life and may not be able to cope with the direct and indirect changes induced by global warming. Also many islands present a low diversity of habitats and frequently these are exclusive, so insular specialist species have

virtually “no place to go” if their habitats do not withstand the effects of climate change on the long run.

In recent years several efforts have been made to predict the effects of global warming on biodiversity. However, this is not a simple task. The impacts of global warming are being estimated based on the association between temperature changes and species range shifts, or changes in migration patterns or species phenology. Bioclimate modeling usually relies on models made at the species level and includes for the most part only climatic factors. However, global climate change is more than simply about temperature, as weather patterns, rhythms and intensities will also change. These large-scale effects are strongly synergistic with other, local effects, such as pollution and landscape fragmentation (Samways, 2005).

So far, we are only glimpsing the consequences of climate change. By concentrating on one species, bioclimate models ignore how interactions with other species, like predators, preys, parasites, hosts or invasive species, and their changing surroundings, might influence the outcome of climate change. Further, these models disregard important factors like the adaptive potential of organisms to new conditions or the limits to their dispersive capability (Hampe, 2004). However, to be able to predict the consequences of increasing temperature we also need an indication of the ability that species have to adapt to this change. So it is necessary to supplement the predictive models with information on species biology and evolutionary trends whenever possible. Thermal adaptation is thus a fundamental part of future models predicting the impact of increased temperature. Further studies are needed to understand the dynamics of thermal adaptation and its limits, particularly studies focusing on different thermal traits and other relevant traits, like desiccation resistance, are needed to have a clearer picture of the way different species might react to climate change.

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