

Evolutionary consequences of climate-induced range shifts in insects

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ABSTRACT

Range shifts can rapidly create new areas of geographic overlap between formerly allopatric taxa and evidence is accumulating that this can affect species persistence. We review the emerging literature on the short- and long-term consequences of these geographic range shifts. Specifically, we focus on the evolutionary consequences of novel species interactions in newly created sympatric areas by describing the potential (i) short-term processes acting on reproductive barriers between species and (ii) long-term consequences of range shifts on the stability of hybrid zones, introgression and ultimately speciation and extinction rates. Subsequently, we (iii) review the empirical literature on insects to evaluate which processes have been studied, and (iv) outline some areas that deserve increased attention in the future, namely the genomics of hybridisation and introgression, our ability to forecast range shifts and the impending threat from insect vectors and pests on biodiversity, human health and crop production. Our review shows that species interactions in *de novo* sympatric areas can be manifold, sometimes increasing and sometimes decreasing species diversity. A key issue that emerges is that climate-induced hybridisations in insects are much more widespread than anticipated and that rising temperatures and increased anthropogenic disturbances are accelerating the process of species mixing. The existing evidence only shows the tip of the iceberg and we are likely to see many more cases of species mixing following range shifts in the near future.

Key words: climate change, range shifts, breakdown of reproductive barriers, hybrid zones, introgressive hybridisation, adaptation, extinction, species persistence, genomics of hybridisation, insects.

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I. INTRODUCTION

Insects form integral parts of every ecosystem and are particularly responsive to environmental changes for three reasons. First, basic physiological functions such as locomotion, growth, and reproduction are directly influenced by ambient temperature (Deutsch *et al.*, 2008; Paaijmans *et al.*, 2013) and therefore even slight changes in annual temperature regimes can have profound effects on insect biodiversity. Second, many insects have short generation times coupled with high reproductive rates, which together allows them to adjust their population sizes rapidly compared to many vertebrates (Bale *et al.*, 2002; Gullan & Cranston, 2010). Third, the high mobility of some taxa means that they can undergo rapid range expansions (Settele *et al.*, 2008; Ott, 2010) and this enables them to colonise new areas shortly after they have become suitable. For these reasons, it has not come as a surprise that insect groups are modifying their distributions and abundances worldwide in response to rising global temperatures and anthropogenic changes (Parmesan, 1996; Parmesan *et al.*, 1999; Crozier, 2004; Karban & Strauss, 2004; Hickling *et al.*, 2005, 2006; Wilson *et al.*, 2005; Sánchez-Guillén *et al.*, 2013c, 2014c).

Several studies over recent years have documented such changes in insect distributions. Poleward shifts and expansions have been recorded for lepidopterans in Europe (Parmesan *et al.*, 1999) and North America (Parmesan, 1996) and for heteropterans, neuropterans, orthopterans and odonates in the UK (Hickling *et al.*, 2005, 2006; Hassall, Thompson & French, 2007; Ott, 2010). Specifically, Parmesan *et al.* (1999) showed that 22 of 35 European butterfly species (e.g. *Arashinia levana*, Fig. 1A) had shifted their ranges by 35–240 km over the last century. Similarly, a study by Hickling *et al.* (2005) showed that all but three of the 41 non-migratory odonate species in the UK had shifted their ranges northwards by 62–86 km (e.g. *Crocothemis erythraea*, Fig. 1B). Most recently, a meta-analysis by Chen *et al.* (2011) on butterflies (e.g. *Heliconius* spp., Fig. 1C) estimated a median range shift per decade of 16.9 km in latitude and 11.0 m in altitude for this group. Many other examples come from other taxa, such as from flight-capable heteropterans (e.g. *Phaneroptera falcata*, Fig. 1D) which are currently undergoing a northwards-directed range expansion (Böhme, Geissler & Wagner, 2011). Range shifts like these can result in significant economic losses, as seen in range shifts of pest species such as the pine processionary moth *Thaumetopoea pityocampa* (Fig. 1E) in France and the mountain pine beetle *Dendroctonus ponderosae* in the USA (Parmesan, 2006), and range shifts of disease vectors such as the heteropteran *Triatoma protacta* (Fig. 1F), which is the vector for Chagas disease. These studies together highlight that changes to insect distributions are widespread and that they occur globally.

Work investigating the evolutionary consequences of these range shifts has started to emerge and it is useful to classify them into one of two main patterns. First, range shifts can lead to range expansions and create new zones of sympatric overlap between formerly allopatric species, or second, they

can cause range contractions and isolate populations of a species and facilitate population divergence in allopatry. In the former scenario, *de novo* sympatric areas can create new species interactions leading to population divergence in mating characteristics, hybridisation, introgression and associated changes to biodiversity (Barton & Hewitt, 1985; Howard, 1993; Jiggins & Mallet, 2000; Redenbach & Taylor, 2003; Schwarz *et al.*, 2005; Secondi, Faivre & Bensch, 2006; Mallet, 2007; Ording *et al.*, 2010). Similarly, in the latter scenario newly created allopatric areas can facilitate population divergence due to the loss of species interactions, as seen in studies showing that species lose some of their ability to recognise heterospecifics following periods of allopatry (Rhymer & Simberloff, 1996; Mallet, 2007; Wellenreuther, Tynkkynen & Svensson, 2010). The short- and long-term ecological and evolutionary consequences of such range shifts can thus be pronounced, yet work evaluating the existing empirical evidence has been scarce.

Herein, we review how range shifts in insects can cause *de novo* sympatry and allopatry and discuss the effects of these new geographic settings on species interactions in terms of the short- and long-term consequences to species persistence, introgression and extinction. We summarise the empirical evidence for different processes and highlight areas that deserve increased attention in the future.

II. SHORT-TERM EVOLUTIONARY CONSEQUENCES OF RANGE SHIFTS: BREAKDOWN OF SPECIES BARRIERS

Range shifts can modify the sympatric overlap between species and as a consequence lead to an increase in the production of hybrids (Taylor *et al.*, 2006). Detailed studies of this phenomenon have already been conducted in cutthroat trout *Oncorhynchus* spp. (Rubidge & Taylor, 2004), flying squirrels *Glaucomys sabrinus* and *G. volans* (Garroway *et al.*, 2010), and grizzly (*Ursus arctos*) and polar bears (*U. maritimus*) (Kelly, Whiteley & Tallmon, 2010). However, examples of changes in heterospecific mating interactions are now also accumulating for several insect groups, namely hymenopterans, lepidopterans, odonates and orthopterans (Britch, Cain & Howard, 2001; James *et al.*, 2002; Kronauer *et al.*, 2011; Mallet, Wynne & Thomas, 2011; Sánchez-Guillén *et al.*, 2011). In the following sections, we discuss these findings in detail and place particular focus on the mechanisms that determine the extent of reproductive breakdown. The discussion of reproductive barriers is structured by employing the classic framework of the different temporal stages that occur during reproductive breakdown between species (Dobzhansky, 1937; Coyne & Orr, 2004).

(1) Breakdown of premating prezygotic barriers

Premating barriers between co-occurring species help to reduce or prevent hybridisation and its negative reproductive



Fig. 1. Insect species that are currently undergoing climate-induced range expansions. (A) The European butterfly *Arashinia levana* (photograph courtesy of Jürgen Ott) and (B) the European dragonfly *Crocothemis erythraea* (photograph courtesy of Jürgen Ott). (C) One representative of the American butterfly genus *Heliconius* (photograph courtesy of Adolfo Cordero). (D) The European heteropteran *Phaneroptera falcata*, a bug cricket capable of flying (photograph courtesy of Jürgen Ott). (E) The pine processionary moth *Thaumetopoea pityocampa* is a pest species (photograph courtesy of Walter Schoen) and (F) the heteropteran disease vector of Chagas disease *Triatoma protacta* (photograph courtesy of Guiehdani Villalobos).

effects. However, these barriers are *de facto* not necessary in the absence of sympatry and may be lost due to genetic drift, particularly if they are costly to maintain (Myers & Frankino, 2012). Indeed, several recent studies have documented a loss or reduction of premating barriers between species after populations of one or both species occur for some time in allopatry (Kronfrost, Young & Gilbert, 2007; Wellenreuther *et al.*, 2010; Myers & Frankino, 2012). It has further been shown that this loss of premating barriers can increase the likelihood of heterospecific matings and hybridisation upon secondary contact. For example, Gerhardt (2013) reported that geographic variation in the acoustic communication of grasshopper species following landscape alterations caused a breakdown of reproductive barriers between them. Specifically, sympatric and allopatric

populations of the field cricket *Gryllus fultoni* showed variation in song-calling properties, with sympatric females being more likely to discriminate against heterospecific songs (Gerhardt, 2013). Similarly, in a laboratory-based study Myers & Frankino (2012) demonstrated that sympatric *Drosophila pseudoobscura* and *D. persimilis* lost their premating recognition when maintained in allopatry for more than 50 years. Similarly, detailed experimental work on natural populations of two closely related European damselflies *Calopteryx splendens* and *C. virgo* showed that the likelihood of hybridisation was increased following an allopatric phase (Wellenreuther *et al.*, 2010). By comparing northern allopatric populations to southern sympatric populations Wellenreuther *et al.* (2010) found that allopatric populations of *C. virgo* had partly lost their ability to discriminate against *C. splendens* females. The

authors tested the consequences of this reduced premating isolation by moving *C. splendens* into the allopatric *C. virgo* zone and presenting females of the invading *C. splendens* to males of the resident *C. virgo*. In this simulated range expansion the authors showed that an increase in heterospecific matings in *de novo* sympatric sites occurred: males of the allopatric species clasped females of the invading species at a significantly higher rate compared with the naturally sympatric males. The fact that hybrids between these two species occur in nature (Tynkynen *et al.*, 2008) suggests that a higher likelihood of heterospecific matings would indeed result in increased species mixing. However, the scarcity of studies on this topic precludes determination of whether the loss of premating isolation following periods of allopatry is a general feature, although all studies conducted to date point in that direction.

Species mate preferences can have a genetic or a learned basis, or be based on a mixture of both. For a genetic basis, drift or selection can lead to the loss of the preference trait. Learning can occur through imprinting, in which learning during early life affects mating decisions once reproductively mature. A study on *Xiphophorus* swordtail fish showed that imprinting is typically based on parental phenotypic traits, such as visual or olfactory cues, resulting in the learner being able to discriminate its own species and even its own sex from other species (Verzijden, Culumber & Rosenthal, 2012). Mate preferences can also be learned when individuals are already mature through experiences with potential conspecific and heterospecific mates. Evidence for imprinting in insects is rare (Immelmann, 1975), partly because many species do not raise their young and thus no opportunity for imprinting exists. However, evidence for a role of learning later in life does exist for several species. For instance, males of at least three species of *Drosophila* fruit flies (Dukas, 2004) and males of *Calopteryx* damselflies learn to discriminate against heterospecific mates following courtship interactions (Svensson *et al.*, 2014). In species of damselflies with female-limited polymorphism, males learn to prefer the morph with which they had a successful mating experience (Fincke, Fargevieille & Schultz, 2007; Takahashi & Watanabe, 2010; Sánchez-Guillén *et al.*, 2013b). In some cases, individuals need experience with variations in phenotypes before expressing a preference. For example, female field cricket (*Teleogryllus oceanicus*) and female treehopper (*Enchenopa treehoppers*) become choosier with experience, yet this also depends on the quality of the male they interact with (Bailey & Zuk, 2008; Judge, 2010; Rebar, Zuk & Bailey, 2011; Fowler-Finn & Rodríguez, 2012). Likewise, female wolf spiders (*Schizocosa ocreata* and *S. roveni*) from polymorphic populations prefer ornamented males, but only after experiencing both ornamented and unornamented males (Hebets, 2003; Hebets & Vink, 2007). Finally, individuals can also learn from the experience of other individuals during mating interactions and can respond by copying the mate choice of others (Vakirtzis, 2011).

The strength of premating barriers acting between species further depends on whether the species' mate

preference is unidirectional or bidirectional. Sometimes species recognition is unidirectional, i.e. only the male or the female recognises its conspecific partner, leading to asymmetric premating isolation between species. One example of asymmetric isolation comes from the orthopterans *Orchelimum nigripes* and *O. pulchellum*, which occur allopatrically throughout most of their native range (Shapiro, 2001), but a limited area of geographic overlap occurs along the Potomac River in Washington D.C., USA. In these sympatric areas, *O. nigripes* females show a preference towards conspecific males, while *O. pulchellum* females show no clear preference towards males of either species. This lack of preference results in the gradual replacement of *O. pulchellum* in the hybrid zone by *O. nigripes* (Shapiro, 2001).

Unidirectional mating patterns can also be caused by mechanical isolation due to incompatibility between the primary and/or secondary genitalia and because of behaviours of the heterospecific male that may cause female rejection responses (Coyne & Orr, 2004). Numerous examples of asymmetrical mechanical isolation exist and the literature is particularly rich for coleopterans (Eberhard, 2002), dipterans (Coyne & Orr, 2004), lepidopterans (Lorkovic, 1958) and odonates (Paulson, 1974; Robertson & Paterson, 1982; Sánchez-Guillén *et al.*, 2014b). For example, in the damselflies *Ischnura elegans*, *I. graellsii* and *I. genei*, which partially overlap in their distributions, premating barriers break heterospecific copulations only in one direction, leading to asymmetric gene flow between species and hybrid formation (Sánchez-Guillén *et al.*, 2014b).

(2) Breakdown of postmating prezygotic barriers

When females mate with heterospecific males, direct costs can occur (Hochkirch, 2013; Svensson, 2013) and this can select for the evolution of postmating barriers. Empirical evidence for such costs has been demonstrated (Arnqvist & Rowe, 2005) from a few well-studied systems such as dipterans (Rice, 1996; Promislow & Kaeberlein, 2014) and coleopterans (Crudginton & Siva-Jothy, 2000; Eady, Hamilton & Lyons, 2007). In some of these species, such as *Callosobruchus maculatus* (Crudginton & Siva-Jothy, 2000; Eady *et al.*, 2007) and *Sepsis cynipsea* (Blanckenhorn, 2002) male genitalia have sharp pointed structures that damage the internal female genital tract.

Postmating barriers can, however, also evolve as a by-product of intraspecific sexual-selection dynamics, or alternatively, as a by-product of Bateson–Dobzhansky–Muller incompatibilities in the absence of gene flow. For example, genitalic spikes and toxic seminal proteins that damage females (Rice, 1996; Johnson, 2002; Lung *et al.*, 2002) have likely evolved as a by-product following intraspecific female–male arms races, and selected for rapid oviposition rates in intraspecific females (not just heterospecific females), all at a cost to female fitness in general (e.g. in *Drosophila melanogaster*). Such male morphological and physiological adaptations can decrease the immediate sexual receptivity of females and prompt spontaneous oviposition (Simmons, 2001), causing both intra- and interspecific females that have

engaged in matings with such males to experience (sometimes severe) fitness reductions.

Direct fitness benefits to females in terms of fecundity or survival could also arise if males of the hybridising species secure resources that females require. Under such a scenario, a female that mates with such a male would receive direct resource benefits following heterospecific pairings, even though the male is from another species. Whether these benefits outweigh the potential costs experienced by the mixing of two genomes is impossible to determine *a priori*, and the outcome is also affected by additional ecological parameters (e.g. such as mate-searching costs). This scenario has not been explored in insects so far.

(3) Breakdown of postmating postzygotic barriers

Hybrids from heterospecific matings are formed when no or only a partial reduction in egg and sperm compatibility is experienced (Coyne & Orr, 1989; Palumbi, 1999; Presgraves, 2002). Resulting hybrids can be either fertile or sterile. Fertile hybrids frequently show intrinsic isolation, ecological inviability and/or behavioural sterility because they cannot secure a niche and/or a mate, leading to intrinsic isolation and lower viability, sterility or even hybrid breakdown (Coyne & Orr, 2004). The production of unfit or sterile hybrids because of genetic incompatibilities is considered an evolutionary dead end (Haldane, 1922; Dobzhansky, 1937; Muller, 1942).

Postzygotic barriers are also frequently asymmetric, so that hybrids despite being fertile can only mate with one parental taxon, or alternatively, hybridisation can produce fertile offspring of only one sex (Rhymer & Simberloff, 1996). Empirical data for *Drosophila* and Lepidoptera (Wu, Johnson & Palopoli, 1996; Turelli & Begun, 1997; Presgraves, 2002; Tang & Presgraves, 2009) and other taxa (Orr & Turelli, 1996; Presgraves, 1998) show strong support for Haldane's rule, i.e. the observation that if one hybrid sex has decreased fitness or viability then this is typically the heterogametic sex (Haldane, 1922). By contrast, detailed investigations into Haldane's rule in some *Ischnura* (Odonata) species failed to find supporting evidence, despite the species showing partial F₂-hybrid sterility due to insemination or oviposition failure (Sánchez-Guillén, Wellenreuther & Cordero-Rivera, 2012; Sánchez-Guillén, Córdoba-Aguilar & Cordero-Rivera, 2013a).

Mating between heterospecifics can lead to direct fitness costs, since hybrid offspring commonly have reduced fitness (see Hochkirch, 2013). Examples of such costs include cases where sperm does not fertilize the eggs or has a reduced ability to do so (Howard, 1999; Marshall, Arnold & Howard, 2002). When hybrid formation is reduced, there is likely a discrepancy between the actual number of hybrids (typically low) and the frequency of heterospecific mating couples (which might be considerably higher), as seen for instance in recent studies of calopterygid damselflies. The number of observed hybrids in natural populations of *Calopteryx splendens* and *C. virgo* is around 0.1% (Tynkkyne *et al.*, 2008; Keränen *et al.*, 2013), whereas the number of heterospecific

pairs observed in the field is around 3.5% (Svensson *et al.*, 2007, 2010). The discrepancy might indicate either postmating prezygotic female choice and/or low viability of hybrid offspring (Svensson *et al.*, 2007, 2010). Situations with discrepancies like these can form the starting point of fruitful investigations into the underlying processes causing these patterns and future work may be able to establish the relative strengths of these two factors.

III. LONG-TERM EVOLUTIONARY CONSEQUENCES OF RANGE SHIFTS: HYBRID ZONES, INTROGRESSION, SPECIATION AND EXTINCTION

When species barriers are insufficient and hybridisation occurs, then the outcome of hybridisation can span from complete species isolation (Barton & Hewitt, 1985; Howard, 1993; Jiggins & Mallet, 2000; Redenbach & Taylor, 2003; Secondi *et al.*, 2006) to complete admixture (Schwarz *et al.*, 2005; Mallet, 2007; Ordning *et al.*, 2010). The position along this continuum is determined by a combination of intrinsic genetic factors that are determined by the extent of genetic incompatibilities and extrinsic factors related to the hybrid phenotype. When hybridisation does not lead to complete sterility among offspring, then parts of the genome can be introgressed between the species. For example, when a hybridisation event leads to fertile F₁ hybrids then they may backcross with at least one of the parental genotypes, thereby causing introgression. If hybrids of the heterogametic sex are inviable or sterile (Haldane's rule), introgression may still result from backcrosses with homogametic hybrids. If the resulting backcrossed individuals subsequently mate with the most similar parental genotype, novel genes and gene complexes can rapidly be introduced into the new genetic background (Barton, 2001). In addition to the establishment of hybrid and introgression zones, the long-term effects of heterospecific mating interactions can in exceptional circumstances also include the creation of novel species, for example when the resulting hybrid species preferentially mates only with other hybrids. The other side of the coin is that extensive introgression over time can lead to the disappearance of a parental species. Below, we outline in more detail how the creation of hybrid and introgression zones can be dependent on intricate morphological and mechanical factors, as well as long-term selective pressures. In addition, the factors leading to a reduction (extinction) and increase (speciation) in biodiversity are discussed.

(1) Intrinsic and extrinsic factors shaping the outcome of hybridisation

The consequences of hybridisation are species-specific and highly dependent on the level of reproductive isolation between species. Several studies suggest that the divergence time of reproductive isolation can be roughly calibrated using mitochondrial DNA (mtDNA) data, i.e. that a rough

'speciation clock' exists (Turelli & Orr, 2000). Evidence of a positive correlation between genetic divergence and reproductive isolation (mainly postzygotic isolation) comes from a wide range of lineages, including insects, lizards, birds and angiosperms (Coyne & Orr, 1997; Sasa, Chippindale & Johnson, 1998; Presgraves, 2002; Price & Bouvier, 2002; Moyle, Olson & Tiffin, 2004), strongly suggesting that mtDNA divergence between taxa can be used to predict hybridisation. Consistent with this correlation, Coyne & Orr (2004); Mallet *et al.* (2007) and Sánchez-Guillén *et al.* (2014a) found a negative correlation between mtDNA divergence and the proportion of hybrids in *Drosophila* fruitflies, *Heliconius* butterflies and *Ischnura* damselflies, respectively. The genetic threshold values that correlated with the occurrence of hybrids between taxa were similar in *Drosophila* (5%) (Coyne & Orr, 2004) and *Heliconius* butterflies (2–6%) (Mallet, 2005), but slightly lower in damselflies (1%) (Sánchez-Guillén *et al.*, 2014a). Despite the aforementioned evidence of a positive correlation between reproductive isolation and genetic divergence, it remains challenging to predict hybridisation rates and hybrid vigour based on the genetic distance between specific taxa (see Gourbière & Mallet, 2010).

Coyne & Orr (2004) highlighted the importance of extrinsic isolation, especially ecological postzygotic isolation, in nature. Extrinsic isolation is caused because hybrid genotypes are ecologically maladaptive in either parental environment. This reduced hybrid fitness results in negative epistatic interactions that are environmentally dependent (Schluter, 2000). In other words, when parental species are adapted to different environments and are showing distinct adaptive peaks, intermediate hybrids will fall in an adaptive valley between these peaks (Gavrilets, 2004). For instance hybrids between *Euphydryas* butterflies adapted to different host plants exhibited maladaptive behaviours, such as intermediate foraging and intermediate oviposition preferences (Mcbride & Singer, 2010). A solid demonstration of the contribution of extrinsic ecological factors requires experimental evidence such as demonstrated in the study by Egan & Funk (2009) where reciprocal hybrid backcrosses of *Neochlamisus* beetles were transplanted into different parental environments to demonstrate fitness trade-offs empirically.

(2) Hybrid zones

When species overlap spatially, stable and long-lasting hybrid zones can form as a consequence (although hybrid zones under non-environmental selection are inherently unstable) (Barton & Hewitt, 1985; Howard, 1993; Jiggins & Mallet, 2000; Redenbach & Taylor, 2003; Secondi *et al.*, 2006; Rosser, Dasmahapatra & Mallet, 2014). However, previously stable hybrid zones may become destabilised due to contemporary change (e.g. anthropogenic and climate fluctuations), as seen in some bird species (Engler *et al.*, 2013). Another possible scenario is that one of the two species, or possibly even the new hybrid cross, becomes more successful and displaces one or both of the parental species, and hybrid swarms are formed. Evidence for this latter scenario has

been gathered from butterflies (Mallet, 2007; Ordning *et al.*, 2010) and *Rhagoletis* fruit flies (Schwarz *et al.*, 2005).

Novel epistatic interactions in hybrid genomes (e.g. Bateson–Dobzhansky–Muller incompatibilities) are a key process to explain the origin of genetic barriers between populations and species (Coyne & Orr, 2004; Wu & Ting, 2004). However, evidence for disrupted epistatic interactions is often hard to gain, particularly in non-model species. Considerable work has investigated the Bateson–Dobzhansky–Muller model to demonstrate and verify incompatibilities. Support for predicted incompatibilities was found in genomic laboratory model species including *Drosophila sechellia* and *D. mauritiana* (Coyne & Orr, 2004; Wu & Ting, 2004; Masly & Presgraves, 2007) and in *D. melanogaster* and *D. simulans* (Brideau *et al.*, 2006). In general, incompatibility models can be based on any type of advantageous mutations in the different hybridising populations or species and can thus be coupled to environmental adaptations (Muller, 1942), meiotic drive (differential transmission of chromosomes: Johnstone & Hurst, 1996), as well as sexual selection and sexual conflict (Rice, 1998). Among those possible scenarios, mutations involved in sexual conflict (e.g. favourable mutations in males and counter-adaptations in females), including cytonuclear incompatibilities, have gained most interest in this context (Rice, 1998). It should be highlighted that a thorough understanding of the underlying mechanisms (i.e. how beneficial mutations within a lineage produce disadvantageous incompatibilities when combined in a hybrid background) is still lacking and requires further investigations. However, some progress has recently been made towards understanding 'speciation genes', for instance Tang & Presgraves (2009) found support for adaptive evolution at the nucleoporin 160 kDa (Nup160) gene of the fruitfly *Drosophila simulans* which interacts with the protein Nup96 of *D. melanogaster* and causes hybrid lethality.

(3) Introgression

An interesting perspective that has gained support over the past decade is that the mixing of genomes through introgressive hybridisation can be a potentially creative process (Hoffmann & Sgrò, 2011; Whitney *et al.*, 2015). This potential can be achieved through the transfer of adaptations among species to new environments (Ellstrand & Schierenbeck, 2000; Chakraborty & Datta, 2003; Arnold, 2004; Hoffmann & Sgrò, 2011; Casacuberta & González, 2013), which has for instance, been shown to increase species invasiveness (Ellstrand & Schierenbeck, 2000). During the process of rapid adaptive radiations, which typically occurs in geographically narrow regions, there is frequently a time span where species are connected by some degree of gene flow (i.e. parapatry). According to Seehausen's (2004) model, hybridisation between immigrant and resident species may help to elevate the response level that species can show to selection, thereby facilitating colonising populations to undergo rapid adaptive diversification through disruptive or divergent selection. As a consequence, resulting interspecific

hybrids often exhibit novel characters compared to their parental taxa, through a process called transgressive segregation (Rieseberg, Whitton & Gardner, 1999), which can help hybrids to exploit novel niches that parental species cannot utilise.

Numerous studies on insect species suggest that introgressive hybridisation is abundant in closely related species (see Table 1). The potential significance of introgressive hybridisation in adaptive evolution has been demonstrated experimentally by Lewontin & Birch (1966), by showing that hybrids of two Australian *Drosophila* fruit flies acquired adaptations that enabled them to expand their range. Pardo-Díaz *et al.* (2012) found evidence for the repeated introgression of adaptive alleles underlying wing colour diversity in the colourful and mimetic butterflies belonging to the *Heliconius* clade. Interestingly, the genome of *Heliconius melpomene* has recently been sequenced to investigate gene flow among multiple *Heliconius* species and races that are showing hybrid exchange of genes between the three co-mimics *H. melpomene*, *H. timareta* and *H. elevatus* (The Heliconius Genome Consortium, 2012). This new genomic information will likely shed more light on the role of hybridisation in the adaptive evolutionary radiation of this group (The Heliconius Genome Consortium, 2012). Models simulating the spread of adaptive alleles across species barriers during hybridisation have demonstrated that this may induce the invasion of formerly unoccupied habitats, resulting in the creation of hybrid lineages with new adaptive potential (Seehausen, 2004). Support for this model comes from a study on sculpin fish (*Cottus* spp.), where the emergence of a new lineage with increased fitness (compared to the parental species) has been observed (Nolte *et al.*, 2005; Nolte, Freyhof & Tautz, 2006). Moreover, studies on introgressive hybridisation in lepidopterans, dipterans and orthopterans (DeSalle & Giddings, 1986; Beltran, 2002; Shaw, 2002) have further implied that this process can play a role in the adaptive spread of genes (Roberts, Ser & Kocher, 2009) and in fuelling adaptive radiations (Dowling & Secor, 1997; Beltran, 2002). Two examples illustrating this come from *Dacus* fruit flies and *Solenopsis* ants. The first example concerns adaptations to extreme temperatures in hybrid fruit flies of *Dacus tryoni* and *D. humeralis* following a mutual range expansion (Lewontin & Birch, 1966) and the second example illustrates adaptation to low temperatures in hybrid ants (*Solenopsis invicta* and *S. richteri*) (James *et al.*, 2002) following a range shift of *S. invicta* into the range of *S. richteri* (Shoemaker, Ross & Arnold, 1994). The Argentinian ant *S. invicta* is native to South America but has become an important ecological and economic pest in the southern USA, where it coexists with *S. geminata* and several sub-species of the *S. xyloni* complex. Modelling of future distributions based on predicted temperature and precipitation scenarios indicates that *S. invicta* could extend further to the east and west coast of Mexico (Morrison *et al.*, 2004). Changes to insect distributions facilitated by global change scenarios, such as forecasted in this ant, can have far-reaching consequences for other species. For example, the plant community is negatively affected by the invasive ant

species *S. invicta* because it displaces the native seed-dispersing *Aphaenogaster rudis* ant species (Rodríguez-Cabal *et al.*, 2012). Overall, the diversity of possible outcomes suggests that the consequences of introgressive hybridisation are highly species and context specific and thus cannot be predicted *a priori*.

(4) Speciation and extinction

Examples of hybrid speciation span the diversity of insect groups (see Table 1). Bullini & Nascetti (1990) found evidence of hybrid speciation in four stick insect genera (*Bacillus*, *Lepytynia*, *Clonopsis* and *Carausius*), in the grasshopper *Warramaba virgo*, the planthopper *Muellerianella 2-fairmairei-brevipennis*, and in *Gymnopsis* and *Prosimulium* black flies. Additional data on hybrid speciation have recently been gathered in *Heliconius* butterflies (Salazar *et al.*, 2005; Mavárez *et al.*, 2006; Mallet, 2007; Kunte & Shea, 2011), *Pogonomyrmex* ants (Mavárez & Linares, 2008) and *Rhagoletis* fruit flies (Schwarz *et al.*, 2005). Both allopolyploid (whole-genome duplication) and homoploid (no change in chromosome number) hybrid speciation occur in nature, although the former seems to be more common (Rieseberg, 1997; Chapman & Burke, 2007), for example in phasmatopterans (Morgan-Richards *et al.*, 2009). Homoploid hybrid speciation has been documented in *Rhagoletis* fruit flies (Schwarz *et al.*, 2005) and in *Heliconius* (Salazar *et al.*, 2005; Mallet, 2007; Mavárez & Linares, 2008) and *Papilio* butterflies (Kunte & Shea, 2011).

The previous sections dealt with hybridisation as a potentially creative force in the diversification of lineages, nevertheless, hybridisation can also lead to extinction (Rhymer & Simberloff, 1996; Allendorf *et al.*, 2001). Local extinction through hybridisation depends on several ecological and genetic parameters such as competitive ability, fertility, adaptation to thermal stress and humidity (Wolf, Takebayashi & Rieseberg, 2001; Wellenreuther *et al.*, 2011), the strength of the reproductive barriers (Sánchez-Guillén *et al.*, 2012), the time of divergence between hybridising species (Mallet, 2007), the costs (direct and indirect) of hybridisation (Mallet, 2007; Svensson, 2013), and the size of the hybridising populations (Mallet, 2007). If hybridisation is followed by introgression, then the likelihood of extinction is increased (Huxel, 1999). Range-edge populations are prone to a higher extinction risk *via* hybridisation due to the typically low abundance and genetic variation of edge populations which could potentially prevent or weaken the evolution of reinforced mate preferences (Rhymer & Simberloff, 1996), although learned mate preferences could potentially offer evolutionary rescue.

Local extinctions of insect populations through hybridisation have been studied in butterflies, damselflies and crickets (see Britch *et al.*, 2001; Mallet *et al.*, 2011; Sánchez-Guillén *et al.*, 2011). Among these cases are the climate-induced hybridisation and introgression events documented in the ischnurid damselflies *I. elegans* and *I. graellsii* in northern Spain (Sánchez-Guillén *et al.*, 2011). Local extinctions of *I. graellsii* populations have been detected where *I. elegans* has recently colonised the area and subsequently displaced *I. graellsii*

Table 1. Representative studies showing different introgressive hybridisation processes following range shifts

Order	Lowest classification available	Climate-induced range shifts	Outcome	Reference
Coleoptera	Species: <i>Aphanarthrum glabrum</i> and <i>A. subglabrum</i>	—	Introgressive hybridisation	Jordal, Emerson & Hewitt (2006)
Diptera	Genus: <i>Carabus</i>	—	Introgressive hybridisation	Sota (2002)
	Genus: Anopheles	—	Introgressive hybridisation, insecticide resistance	Mallet (2005)
	Family: <i>Simuliidae</i>	—	Introgressive hybridisation, insecticide resistance	Mallet (2005)
	Family: <i>Simuliidae</i>	—	Introgressive hybridisation, hybrid speciation	Bullini & Nascetti (1990)
	Genus: <i>Rhagoletis</i>	—	Introgressive hybridisation, hybrid speciation	Schwarz <i>et al.</i> (2005)
Hemiptera	Species: <i>Limnopus dissortis</i> and <i>L. notabilis</i>	—	Introgressive hybridisation	Abe, Spence & Sperling (2005)
	Family: Planthopper	—	Introgressive hybridisation, hybrid speciation	Bullini & Nascetti (1990)
	Order: Phasmatodea	—	Introgressive hybridisation, hybrid speciation	Bullini & Nascetti (1990)
Hymenoptera	Species: <i>Solenopsis invicta</i> and <i>S. richteri</i>	Yes	Introgressive hybridisation, adaptation to low temperatures	James <i>et al.</i> (2002)
	Genus: <i>Neodiprion</i>	—	Introgressive hybridisation	Linnen & Farrell (2007)
	Species: <i>Heliconius cydno</i> and <i>H. melpomene</i>	—	Introgressive hybridisation	Bull <i>et al.</i> (2006)
Lepidoptera	Species: <i>Dacus tryoni</i> and <i>D. humeralis</i>	—	Introgressive hybridisation, adaptation to extreme temperatures	Lewontin & Birch (1966)
	Species: <i>Heliconius melpomene</i> , <i>H. timareta</i> and <i>H. elevatus</i>	—	Introgressive hybridisation, adaptation	The Heliconius Genome Consortium (2012)
	Species: <i>Helianthus annuus</i> and <i>H. debilis</i>	—	Introgressive hybridisation, herbivore resistance	Whitney, Randell & Rieseberg (2006)
	Species: <i>Limnitis a. arthemis</i> and <i>L. a. astyanax</i>	—	Introgressive hybridisation	Mullen & Andrés (2007)
	Species: <i>Papilio machaon</i> and <i>P. hospiton</i>	—	Introgressive hybridisation	Cianchi <i>et al.</i> (2003)
	Species: <i>Polygonatus artaxerxes</i> and <i>P. a. artaxerxes</i>	Yes	Introgressive hybridisation, local extinction	Mallet <i>et al.</i> (2011)
	Species: <i>Lycaeides m. melissa</i> and <i>L. m. samuelis</i>	—	Introgressive hybridisation	Gompert <i>et al.</i> (2006)
	Genus: <i>Bombyx</i>	—	Introgressive hybridisation, hybrid speciation	Astaurov (1969)
	Genus: <i>Grammia</i>	—	Introgressive hybridisation	Schmidt & Sperling (2008)
	Genus: <i>Heliconius</i>	—	Introgressive hybridisation, adaptive wing colour diversity	Pardo-Diaz <i>et al.</i> (2012)
	Genus: <i>Heliconius</i>	—	Introgressive hybridisation, hybrid speciation	Mallet (2007)
	Genus: <i>Papilo</i>	—	Introgressive hybridisation, hybrid speciation	Kunte & Shea (2011)
	Odonata	Species: <i>Mnais costalis</i> and <i>M. pruinosa</i>	—	Introgressive hybridisation
Species: <i>Ischnura elegans</i> and <i>I. graellsii</i>		Yes	Introgressive hybridisation, local extinction	Sánchez-Guillén <i>et al.</i> (2011)
Species: <i>Ischnura gemina</i> and <i>I. denticollis</i>		—	Introgressive hybridisation, local extinction	Leong & Hafernik (1992b)
Species: <i>Ischnura genei</i> and <i>I. elegans</i>		—	Introgressive hybridisation	Sánchez-Guillén <i>et al.</i> (2014a)
Orthoptera	Species: <i>Hemideina thoracica</i> (chromosome races)	—	Introgressive hybridisation	Morgan-Richards & Wallis (2003)
	Species: <i>Allonemobius socius</i> and <i>A. fasciatus</i>	Yes	Introgressive hybridisation, local extinction	Britch <i>et al.</i> (2001)
	Species: <i>Warramaba virgo</i>	—	Introgressive hybridisation, hybrid speciation	Bullini & Nascetti (1990)

through unidirectional introgression (Sánchez-Guillén *et al.*, 2011). Unidirectional hybridisation occurs because matings between *I. elegans* females and *I. graellsii* males are mechanically impeded (Monetti, Sánchez-Guillén & Rivera, 2002). Similarly, in the San Francisco Bay area in the USA the number of *Ischnura gemina* populations are decreasing because of unidirectional introgressive hybridisation with *I. denticollis* (Leong & Hafernik, 1992a; Hannon & Hafernik, 2007; Sánchez-Guillén *et al.*, 2014c). Another insect example of local extinctions through range shifts comes from two closely related species of argus butterflies: the northern brown argus *Aricia artaxerxes*, which is associated with limestone grasslands in northern Britain and the brown argus *A. agestis*, which is expanding its distribution northwards (Mallet *et al.*, 2011). Furthermore, the British endemic subspecies *A. a. artaxerxes* may suffer a global extinction as a consequence of introgression with the more warm-adapted *A. agestis* (Mallet *et al.*, 2011), but more studies are needed to evaluate this. Lastly, climate-induced hybridisation in the cricket *allonemobius fasciatus* in the Appalachian Mountains in the USA and Canada may also cause local extinction. In this case, the northward-expanding cricket species *A. socius* hybridises with *A. fasciatus* (Britch *et al.*, 2001). In the laboratory, and at least in one natural population, hybrids can be as fit or even fitter than either parental species (Britch *et al.*, 2001). Taking into account this pattern of hybridisation (Britch *et al.*, 2001) and the continual movement of *A. socius* northwards, it is possible that the current equilibrium between these species may be broken and that *A. fasciatus* could be replaced by its sister species *A. socius* in the Appalachian Mountains (Hughes, 2000).

IV. FUTURE OUTLOOK AND DIRECTIONS

Range shifts are leading to new distributions of insect species worldwide and the emerging studies document the ubiquitous potential short- and long-term evolutionary consequences for species persistence, introgression and extinction. Below we outline some particularly interesting research areas that deserve increased attention in the future: (i) the use of next-generation sequencing to investigate the process of adaptive genome mixing (Ekblom & Galindo, 2011; Twyford & Ennos, 2012) and (ii) the use of deterministic algorithms to generate species distribution models (Phillips, Anderson & Schapire, 2006). Following that, we (iii) briefly discuss the issues that emerge when the species that are undergoing a range shift involve insect pests and disease vectors.

(1) Unravelling the genomics of hybridisation and introgression

When hybridisation occurs between recently diverged but sympatric species, insights into the genetic underpinnings of reproductive isolation can be gained. Novel genetic combinations in recently originated hybrid zones allow the

study of the creation and maintenance of unique genetic combinations within ecological time frames (Fitzpatrick *et al.*, 2009). The identification of non-introgressed chromosome regions – candidates for ‘islands of divergence’ (Nosil & Feder, 2012) due to an accumulation of key speciation genes – is of particular importance, as these regions may contain genes responsible for reproductive isolation, e.g. genes coding for male traits or female preferences (prezygotic barriers), or Bateson–Dobzhansky–Muller incompatibilities (postzygotic barriers). Rieseberg pioneered this field with studies on *Helianthus* sunflowers, where strong adaptive introgression of morphological traits between hybridising *H. annuus* and *H. debilis* takes place (Kim & Rieseberg, 1999). A little less than a decade later, Rieseberg *et al.* (2007) were able to show that introgression in *Helianthus* also increases its invasiveness and were able to document this in *H. annuus*. The rapid development of fast and affordable sequencing technologies for DNA and RNA, in combination with the computational advancements of improved methods to analyse large volumes of data holds promise for unprecedented detail on the molecular patterns of adaptive evolution through introgression in different taxa (Rieseberg, Baird & Gardner, 2000; Seehausen, 2004; Dempewolf *et al.*, 2010; Song *et al.*, 2011; Crawford, Riehle & Guelbeogo, 2014), and progress on the genomics of introgression in insects is being made (The Heliconius Genome Consortium, 2012; Martin *et al.*, 2013; Clarkson *et al.*, 2014; Norris *et al.*, 2015). We think that this will be an exciting area for investigation in the future and has great potential to uncover the genomic processes facilitating or preventing species mixing.

(2) Forecasting range shifts

A widely applied tool to assess the ecological responses of species to predicted climate-change scenarios is Global Climate Models (GCMs) (Diffenbaugh & Field, 2013). GCMs usually consist of three-dimensional dynamical and physical models of the atmosphere, ocean, land surface and cryosphere. Modelling future projections of climate change requires forced scenarios of increasing greenhouse gases, among other factors, that are affecting global climate (Collins *et al.*, 2012). Additionally, the accuracy of predictive models to determine if a species will (or will not) expand its current distribution following environmental change depends on knowledge of its natural history, core biotic and abiotic requirements and the extent of niche conservatism (Holt, 1990; Hawkins *et al.*, 2006; Pearman *et al.*, 2007; Wiens *et al.*, 2010). However, even more specific models are required for some species. For instance, for pest species inhabiting forests, which are habitats where the climate consists of a multitude of complex factors, then BioSim software models are more appropriate, since they are able to incorporate both the available biotic information for a particular pest species as well as the key climate factors that determine seasonality (e.g. Régnière, Nealis & Porter, 2009). Climate projections, such as the maximum entropy modelling technique (MaxEnt) (Phillips *et al.*, 2006), and the

more recently developed maximum likelihood modelling technique (MaxLike) (Royle *et al.*, 2012; Fitzpatrick, Gotelli & Ellison, 2013) are the most frequently used models when mapping distributions of invasive species (Fitzpatrick *et al.*, 2007) and forecasting climate-induced range shifts (Lawler *et al.*, 2009).

Novel approaches to estimate real-time responses of insects to abiotic factors have also been developed recently, and the parameters that can be estimated with these approaches can then be used as realistic parameters in climate models. For example, insect monitoring with fluorescence light detection and ranging (lidar) techniques hold great promise to evaluate insect community responses to abiotic (e.g. ambient temperatures) as well as biotic (e.g. heterospecific species) factors (Brydegaard *et al.*, 2009; Guan *et al.*, 2010). Another technique, remote dark-field spectroscopy, is based on sunlight scattering and enables the measurement of whole insect ecosystem responses to environmental factors (Runemark *et al.*, 2012).

During the last 5 years, numerous studies forecasting climate-induced range shifts in insects have revealed the high potential that insects have to shift their ranges in response to climate warming. Some recent examples of potential climate-induced range shifts in insects include the coleopteran pine beetle *Dendroctonus brevicomis* (Evangelista *et al.*, 2011), the dipteran (pest) fly *Lucilia sericata* (Rose & Wall, 2011) and the sand fly *Phlebotomus perniciosus*, a vector for *Leishmania infantum* (Fischer, Thomas & Beierkuhnlein, 2011), the hemipterans *Magicada* spp. (Cooley *et al.*, 2013) and *Nabis pseudoferus* (Solhjouy-Fard & Sarafrazi, 2014), the hymenopteran ant *Pheidole megacephala* (Bertelsmeier, Luque & Curchamp, 2013) and bumblebees *Bombus* spp. (Pradervand *et al.*, 2014), lepidopterans (Kharouba & Kerr, 2010; Buckley, Butlin & Bridle, 2012) and several species of the order Odonata (Bush *et al.*, 2014; Sánchez-Guillén *et al.*, 2013c, 2014c). In the two recent studies on odonates (Sánchez-Guillén *et al.*, 2013c, 2014c), MaxEnt models were used to predict potential species distributions in response to future climate change scenarios and this was then combined with knowledge about the strength of reproductive barriers between species to predict future patterns of interspecific hybridisation. The MaxEnt models predicted partly or largely overlapping sympatric future distribution for 12 species out of a total of 42 species range comparisons, all of which are currently occurring parapatrically or allopatrically (Sánchez-Guillén *et al.*, 2013c; Fig. 2A for *Ichnura graellsii* and Fig. 2B for *I. elegans*). The lack of complete reproductive isolation between the majority of these modelled species is consistent with the finding that many odonates have radiated through non-adaptive mechanisms (e.g. sexual selection) and show negligible niche differentiation (Wellenreuther & Sánchez-Guillén, 2015), and highlights the potential dramatic increase of future hybridisation in this group. We foresee that the application of modelling techniques like the ones mentioned above have large potential in informing conservation efforts and policy makers.

(3) Biodiversity, insect pests and disease vectors, and their impact on human health and crops

Of particular concern is the spread of insect pests and disease vectors that have widened their range following anthropogenic change, e.g. due to the evolution of insecticide resistance (Feyereisen, Dermauw & Van Leeuwen, 2015; Liu, 2015), as well as through hybridisation and introgression with local species (Pimentel *et al.*, 2000). Their spread can have, among other concerns, both direct and indirect effects on human health, directly through disease vectors or indirectly through the modification of crop production in agriculture. Preventive actions and detailed modelling is possible in many cases because the economic importance of species means that many have been studied in detail and hence that reasonably good data regarding their distribution exist. Although in general, a warmer climate will tend to make the habitat more suitable for a broader array of species, including disease vectors and insect pests (see Hoberg, Brooks & Brooks, 2015), only the availability of accurate distribution data will allow generation of projections of predicted future geographic distributions of species, as seen for example in triatomine bugs (*Triatoma* spp.) which are the vectors for Chagas disease (caused by the protozoan, *Trypanosoma cruzi*). Distribution modelling predicts a considerable expansion of this species in North America due to increasing mean temperatures (Garza *et al.*, 2014). Two features of *Triatoma* biology warrant increased preventive actions to prevent an epidemiological outbreak. First, hybrids are relatively common (e.g. Correia *et al.*, 2013) and second, hybrids are more heavily infected with the protozoan that transmits Chagas disease (Herrera-Aguilar *et al.*, 2009). The availability of this information will hopefully prove useful to understand the environmental requirements of triatomine bugs so that effective management actions can be developed to counteract their continued spread and hybridisation in the future.

The spread of insect pests through human-induced invasions, climate warming and anthropogenic changes is another area of major concern. One classic example of such a spread is that of butterflies switching their plant hosts due to habitat alterations caused by agricultural practices (Singer & Wee, 2005; Singer & McBride, 2012). However, unlike insect vectors, there is no clear prediction of whether range modifications will always have a negative impact on local crop production. One reason for this is that natural enemies of insect pests are also affected by climate change, which will lead to asymmetric changes in competitive bottom-up and top-down effects (Aguilar-Fenollosa & Jacas, 2014). However, it is likely that the levels of interactions at higher trophic levels (e.g. herbivores and carnivores) will result in stronger negative effects in terms of insect abundance (Voigt *et al.*, 2003). This effect can negatively impact ecosystem services and, therefore, human welfare (e.g. Jones *et al.*, 1998). A second, and perhaps more important reason is that the dynamics of insect pests are affected by tritrophic interactions, since in addition to the biological control agents, the host plants are also part of the interaction. How climate warming and anthropogenic change will affect future costs of crops is still

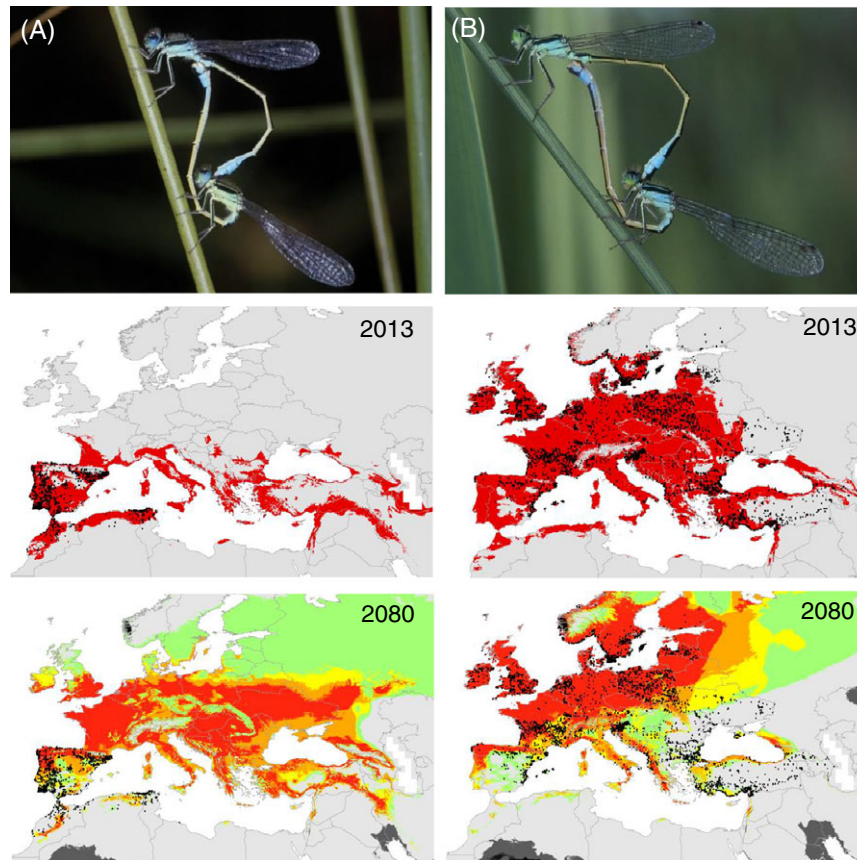


Fig. 2. Climate modelling to predict the extent of range overlap and future species interactions following range expansions. The figure shows the MaxEnt models of the current (2013) and the predicted (2080) distributions of the damselflies *Ischnura graellsii* (A) and *I. elegans* (B) (photograph courtesy of Adolfo Cordero). In the current (2013) distribution scenario, black pixels represent the presence data used to infer potential current distribution areas (in red). In the future distribution scenario (2080), black pixels represent presence data used to infer the future (2080) potential distribution; the number of binary models predicting the species according to four General Circulation Models (GCMs), for each pixel, is represented by green (one model), yellow (two models), orange (three models) and red areas (four models) (Sánchez-Guillén *et al.*, 2013c).

unclear, but given that many invasive insect pests originate from warmer climates than native pests, it is likely that we will see more pest outbreaks in the near future (Montserrat, Sahún & Guzmán, 2013).

V. CONCLUSIONS

(1) There is an urgent need quantitatively to assess the short- and long-term evolutionary consequences of climate- and anthropogenic-induced range shifts in insects. We reviewed the empirical evidence for altered species interactions following range shifts and showed that species mixing can have ubiquitous outcomes, sometimes increasing and sometimes decreasing species diversity. We suggest that these studies are just the tip of the iceberg and that future work will show that climate-induced hybridisation in insects is much more widespread than anticipated and that the rising temperatures and increasing anthropogenic disturbances are accelerating this process.

(2) Several recent advancements in techniques will allow researchers to understand and predict the consequences of different scenarios better. For example, next-generation sequencing techniques will allow researchers to investigate the genetic consequences of genome mixing in much more detail than ever before.

(3) Moreover, future studies combining field and laboratory experiments directed towards improving our understanding of the physiological, ecological and environmental requirements of insects may allow the construction of more mechanistic niche models to generate improved predictions of future range distributions. Such mechanistic studies may also deepen our understanding of the breakdown of reproductive barriers by quantifying the degree of isolation under various geographic settings in closely related species. With this information, we may be able to forecast how closely related species will respond to range shifts and hopefully this information will help to direct conservation efforts to preserve insect biodiversity in general.

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