

INVITED REVIEW

Impacts of climate warming on hybrid zone movement: Geographically diffuse and biologically porous “species borders”

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Abstract The ecology and evolutionary biology of insect–plant associations has realized extensive attention, especially during the past 60 years. The classifications (categorical designations) of continuous variation in biodiversity, ranging from global patterns (e.g., latitudinal gradients in species richness/diversity and degree of herbivore feeding specialization) to localized insect–plant associations that span the biospectrum from polyphenisms, polymorphisms, biotypes, demes, host races, to cryptic species, remain academically contentious. Semantic and biosystematic (taxonomical) disagreements sometimes detract from more important ecological and evolutionary processes that drive diversification, the dynamics of gene flow and local extinctions. This review addresses several aspects of insect specialization, host-associated divergence and ecological (including “hybrid”) speciation, with special reference to the climate warming impacts on species borders of hybridizing swallowtail butterflies (Papilionidae). Interspecific hybrid introgression may result in collapse of multi-species communities or increase species numbers via homoploid hybrid speciation. We may see diverging, merging, or emerging genotypes across hybrid zones, all part of the ongoing processes of evolution. Molecular analyses of genetic mosaics and genomic dynamics with “divergence hitchhiking”, combined with ecological, ethological and physiological studies of “species porosity”, have already begun to unveil some answers for some important ecological/evolutionary questions. (i) How rapidly can host-associated divergence lead to new species (and why doesn’t it always do so, e.g., resulting in “incomplete” speciation)? (ii) How might “speciation genes” function, and how/where would we find them? (iii) Can oscillations from specialists to generalists and back to specialists help explain global diversity in herbivorous insects? (iv) How could recombinant interspecific hybridization lead to divergence and speciation? From ancient phytochemically defined angiosperm affiliations to recent and very local geographical mosaics, the Papilionidae (swallowtail butterflies) have provided a model for enhanced understanding of ecological patterns and evolutionary processes, including host-associated genetic divergence, genomic mosaics, genetic hitchhiking and sex-linked speciation genes. Apparent homoploid hybrid speciation in *Papilio* appears to have been catalyzed by climate warming-induced interspecific introgression of some, but not all, species diagnostic traits, reflecting strong divergent selection (discordant), especially on the Z (= X) chromosome. Reproductive isolation of these novel recombinant hybrid genotypes appears to be accomplished via a delayed post-diapause emergence or temporal isolation, and is perhaps aided by the thermal

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landscape. Changing thermal landscapes appear to have created (and may destroy) novel recombinant hybrid genotypes and hybrid species.

Key words cryptic species, divergence hitchhiking, ecological speciation, host associated divergence, mosaic genomes, range limits, recombinant hybrid species, phylogeography, polyspecialists, species boundaries

The search for pattern in ecology (taxonomic and geographic “latitude”)

The discovery of pattern in nature is perhaps the ultimate challenge for ecologists, and one of the most gratifying aspects of their work. John Lawton has said (1991): “Without patterns in nature to guide us, we risk being overcome with detail”. One fruitful place to look for patterns in nature is to examine gradients of different types. Examples might include: latitudinal gradients, such as comparing temperate and tropical species diversity, altitudinal gradients in species composition (Hodkinson, 2005), or adaptations or changes along temporal gradients (seasonal or phenological) and other environmental gradients (e.g., desiccation, Gilchrist *et al.*, 2008; or photoperiods, Bradshaw & Holzapfel, 2007, 2008) driving species adaptations and even speciation (Doebeli & Dieckmann, 2003). Recent studies have shown that some specialized species lack genetic variation in key traits, which constrains their ability to adapt to conditions beyond their current range, such as climate changes (Kellerman *et al.*, 2009; Merila, 2009). Others suggest that necessary variation for detoxification in specialized species may be retained for millions of years (Mao *et al.*, 2007; Scriber *et al.*, 2008b). Understanding the continuous ecological variation (i.e. gradients) from feeding specialists to generalists, and the existence of an evolutionary continuum in host-associated divergence, from polymorphisms through biotypes, local demes, and host races, to cryptic species (and post-speciational divergence, Nosil *et al.*, 2009a) is fundamental for useful classification of insects. The local dynamics of “species diagnostic traits” (markers) across hybrid zones has proven to be genetically discordant with independent (not concordant) trait movements. Ecological genetics, “species” status dynamics, and evolutionary “plasticity” of host associations have emerged with homoploid (recombinant) “hybrid speciation” in animals as recent foci for climate-mediated evolutionary change (Seehausen, 2004; Gay *et al.*, 2008; Mavarez & Linares, 2008). Swallowtail butterflies (*Papilio*) have provided a rare long-term historical study system of a hybrid zone that can be used for intensive temporal analyses of geographically broad (extensive) hybrid zone multi-trait tran-

sects, and will be reviewed here. They provide a valuable system for examining the gene flow, local selection, differential introgression, multi-trait ecological divergence and incipient speciation (Parmesan *et al.*, 2005; Sagarin *et al.*, 2006; Buggs, 2007; Eckert *et al.*, 2008; Nosil, 2008; Nolte & Tautz, 2010; Ohshima & Yoshizawa, 2010; Payseur, 2010), possibly resulting from regional climate warming.

Geographically diffuse and biologically porous “species borders” may be common

The strength of selection diverges continentally, regionally, locally and within single populations (Scriber, 1996b, 2002a, 2002b; Thompson, 2005; Cogni & Futuyma, 2009; Laine, 2009). Genetic variation even in a single tree species across its range can drive geographical mosaics of forest communities beyond the insect herbivore trophic level (Whitham *et al.*, 2003; Barbour *et al.*, 2009). Analysis of the entire geographic range for a butterfly has also revealed cryptic species which had allopatric origins, but that were discovered in sympatry (McBride *et al.*, 2009). This discovery of specialized species inside more generalized taxa is not uncommon, especially in the tropics (e.g., Berkov, 2002; Hebert *et al.*, 2004; Smith *et al.*, 2006; Burns *et al.*, 2008). A comprehensive geographic scale of analysis is the key to understanding local, recent and historical evolutionary divergence and speciation, as well as for invasive species ecology, but we know very little about differences across the entire geographic range of any insect herbivore or plant species (Johnson & Scriber, 1994; Scriber, 2002a, 2002b; McGill & Collins, 2003; Hampe & Petit, 2005; Sagarin *et al.*, 2006; Hellmann *et al.*, 2008; Eckert *et al.*, 2008). The dynamics of evolutionary change includes diverging (incipient speciation via host races), merging (de-speciation), or emerging genotypes/species (e.g. hybrid species) across hybrid zones (Bridle & Vines, 2007; Nosil *et al.*, 2009a, 2009b; Nolte & Tautz, 2010; Payseur, 2010; Rieseberg, 2010).

The modes of selection may differ in central versus edge species (Hoffmann & Blows, 1994; Case *et al.*, 2005; Bridle & Vines, 2007; Kawecki, 2008). Indeed, to

understand the impacts of global climate change upon ecological and evolutionary processes, and the significance of climate in determining current geographic species borders and future range limits (Parmesan, 2006; Pelini *et al.*, 2009), we must examine historical biogeography as well as dynamic selection pressures locally, across the entire species range (Hoffmann & Blows, 1994; Scriber, 2002a, 2002b; Doebeli & Dieckmann, 2003; Parmesan *et al.*, 2005; Thompson, 2005; Sexton *et al.*, 2009). The relative importance of recent versus historical factors molding the variation in genetic diversity geographically across ranges must be assessed to understand significance of local adaptations (Eckert *et al.*, 2008; Gaston, 2009).

Long-term multi-trait studies (>30 years) across the entire range of a species, before and after the shift in climate, are not surprisingly, extremely rare (Parmesan *et al.*, 2005; Sexton *et al.*, 2009), and even more scarce for hybrids across natural hybrid zones (Arnold & Hodges, 1995; Buggs, 2007; Gay *et al.*, 2008; Petit & Excoffier, 2009; Payseur, 2010). However, the North American tiger swallowtail butterflies (*Papilio* spp.) provide such a long-term model system that has been studied extensively and intensively for multi-trait adaptations (Scriber *et al.*, 2003, 2008a), and will be an important example of understanding the evolution of geographic range limits (Gaston, 2009; Sexton *et al.*, 2009) and the genetic basis of rapid evolution and adaptation at species borders, including hybrid zones with divergence due to climate change (Mussolin, 2007; Mullen *et al.*, 2008; Petit & Excoffier, 2009; Loxdale, 2010; Rodriguez-Trelles & Rodriguez, 2010).

From biogeography to micro-allopatry

The “abundant center hypothesis” suggests abundant populations exist in the center of a species range but decline near range edges (Sagarin & Gaines, 2002; Gaston, 2003; Sagarin *et al.*, 2006; Hellmann *et al.*, 2008; Kawecki, 2008). However, the evidence for decreased abundance and fitness (or genetic diversity, Eckert *et al.*, 2008) at the edges is lacking (Sexton *et al.*, 2009). Genetic variation can decline toward expanding range margins or not, but fragmentation of habitat at these margins reduces diversity in both cases, especially in specialist butterflies (Hill *et al.*, 2006). Local adaptations to climate change can be rapid, particularly at range margins (Thomas *et al.*, 2001; Bradshaw & Holzapfel, 2007; Buggs, 2007; Gay *et al.*, 2008; Knowles, 2009; Mercader *et al.*, 2009a; Loxdale, 2010; Rodriguez-Trelles & Rodriguez, 2010). Phylogeography is an emerging field that concerns the processes underlying interactions between spatial and temporal aspects of genetic diversity (Knowles, 2009).

The tiger swallowtail (*Papilio glaucus*) species group has a huge distribution across nearly all of North America from central Alaska to Central America (Kukal *et al.*, 1991; Ayres & Scriber, 1994; Scriber, 1996a) and has been studied in our laboratory for 40 years (Scriber *et al.*, 2003, 2008a). Long-term studies of this *Papilio* group has provided many of the important features needed (see Parmesan *et al.*, 2005) for studies of species borders and range-limiting factors before and after climate warming events of the past decade (including dynamic hybrid zones). Parmesan (2006) concludes that “for species level evolution to occur with climate change, either appropriate novel mutations or novel genetic architecture (new gene complexes) would have to emerge in response to selection”. The recently described mountain swallowtail butterfly (*P. appalachiensis*, Pavulaan & Wright, 2002) and the delayed “late flight” hybrid swarm appear to reflect just such a novel gene complex, suggesting recombinant hybrid speciation (Coyne & Orr, 2004; Scriber & Ording, 2005 and discussion below). It is still not clear what the roles of thermal adaptations (e.g. Ldh allozymes, lactate dehydrogenase, Schulte *et al.*, 1997) and photoperiod responses may be in allochronically delayed reproductive cycles (e.g. Tauber & Tauber, 1977; Tauber *et al.*, 1977; Bradshaw & Holzapfel, 2007). However, it appears that recombinant hybrid introgression on the Z (= X) chromosome is involved in other Lepidoptera (e.g. European corn borer, Glover *et al.*, 1992; Dopman *et al.*, 2005) as well as the *Papilio* (Rockey *et al.*, 1987a, 1987b; Scriber *et al.*, 1991b, 2008a). Loci involved in local adaptation may have decreased recombination (see below).

Papilionidae: A model system for ecological monophagy and evolutionary specialization over large geographic regions with independent introgressive movement of species diagnostic traits

The swallowtail butterflies (Papilionidae family) serve as the foundation of this review since they have provided a model system for examination of multiple levels of biological organization from latitudinal gradients in global species richness, through behavioral, biochemical and genetic divergence at local levels (Scriber *et al.*, 1995a). Globally, these species are well-recognized, and their host affiliations and life histories are probably as well known as for any family of butterflies (Tyler *et al.*, 1994; Scriber, 1973, 1984, and references therein). The North American tiger swallowtail (*Papilio glaucus*) species group in particular, being the most polyphagous of all 570+ species

of Papilionidae as well as an extreme Lauraceae specialist for a sister group (Munroe, 1961), provides insights into many of these questions, from evolutionarily ancient “key innovations” (Nitao, 1995; Berenbaum *et al.*, 1996) for allelochemical detoxification among major phylogenetic lineages, to local specialization inside hybrid zones. Driven by high rates of recombination on the Z (= X) chromosome and strong divergent selection inside a thermally defined and dynamic hybrid zone (Scriber & Ordington, 2005; Putnam *et al.*, 2007) we may also soon identify the Z-linked post-diapause delay factor (pdd) that has resulted in rapid temporal reproductive isolation and incipient hybrid speciation in *Papilio glaucus* and *P. canadensis* (Scriber *et al.*, 2008a; Ordington *et al.*, 2010; see also Dopman *et al.*, 2005 for a similar potential “speciation gene”).

While often considered a model for the potential chemically driven coevolution or co-speciation between insect herbivores and plants (Dethier, 1954; Ehrlich & Raven, 1964; Berenbaum, 2001; Cornell & Hawkins, 2003; Murphy & Feeny, 2006; Berenbaum & Feeny, 2008), the Papilionidae have also provided a model system for the investigation of hybridization (Ae, 1979, 1995; Sperling, 1990, 2003; Aubert *et al.*, 1996; Cianchi *et al.*, 2003; Scriber, 2007; Scriber *et al.*, 2003, 2008a) which may involve climate-driven genetic introgression of some, but not all, of the species-diagnostic traits (Scriber, 2002a, 2002b; Scriber *et al.*, 2008a; Figs. 1 & 2). For example, hybrid introgression has recently extended the abilities of *Papilio* populations north of the hybrid zone to detoxify tulip tree leaves (Fig. 3) despite the fact that this tree species has not moved northward from the center of the historical hybrid zone (Scriber, 2002b; Scriber *et al.*, 2003; Mercader *et al.*, 2009a). This detoxification ability is an autosomal trait, as with larger wing lengths and other morphological traits (e.g. narrower hindwing bands) that have introgressed rapidly northward (Scriber, 2002b). The geographic pattern of recent warming (see thermal landscapes 1990–1999 (Fig. 4) compared with 2007 (Fig. 2) corresponds to the earliest signals of genetic introgression detected in the Midwest (Donovan & Scriber, 2001). Some Z-linked traits such as diagnostic allozyme Pgd (Fig. 4), and the melanism enabler gene (*s*–, Scriber *et al.*, 1996) have also moved rapidly northward while other Z-linked traits such as Ldh allozyme, and the gene for bivoltine potential (non-diapause, *od*–) have moved very little (Fig. 2). Even less “mobile” are the *glaucus*-type mitochondrial DNA (mtDNA), which has remained close to the southern edge of the historical hybrid zone (Fig. 5; Stump *et al.*, 2003; Ordington *et al.*, 2010) and the W (= Y) linked melanism gene, *b*+, for dark (mimetic) females (Fig. 6).

From such recent genetic divergence, allochronically mediated homoploid hybrid recombinant speciation may have resulted (Scriber & Ordington, 2005; Putnam *et al.*, 2007; Ordington *et al.*, 2010). This mode of speciation has been rare in animals (Coyne & Orr, 2004; see also Mavárez & Linares, 2008). Wu (2001) emphasizes that it is not the complete genome, but rather the gene that is the unit of species differentiation, and that “speciation genes” have direct effects on differential adaptations. This key speciation gene may be the Z-linked “delayed diapause development” gene in both the European corn borer (Dopman *et al.*, 2005) and *Papilio glaucus*/*P. canadensis* hybrids (Ordington *et al.*, 2010). However, other “species diagnostic trait” selection factors are likely at the hybrid zone (e.g. thermal stress; Scriber *et al.*, 2002; Mercader & Scriber, 2008a; J.M. Scriber, M.L. Aardema, E. Maher & R. J. Mercader unpubl. data), differential predation (Brower & Brower, 1962) or pleiotrophic effects of melanism (True, 2003; J.M. Scriber & H. Romack, unpubl. data), as well as sexual selection factors (e.g., pheromones and mating preferences, host races, etc., Thomas *et al.*, 2003).

In addition to broad-purpose polyphagous genotypes, swallowtail butterfly species provide examples with old long-term (i.e. “ancient”) angiosperm specializations (Feeny, 1995; Scriber *et al.*, 2008b) as well as recent climate change-driven “polyspecialists” (Fox & Morrow, 1981; West-Eberhard, 2003; Mercader *et al.*, 2009a; Nylin & Janz, 2009). As such they have shown the capacity for expansion of diet breadth to include new plant families in long-standing family specialists (specialized for millions of years; Zakharov *et al.*, 2004a, 2004b; Scriber *et al.*, 2006, 2007; Nyman, 2010). They have also recently diverged inside the hybrid zone and express very local host preferences in hybrids of generalist species (Mercader *et al.*, 2009a). These results with both ancient and neospecies of *Papilio* both provide strong support for the “oscillation hypothesis of speciation” (i.e. generalists derived from specialists derived from generalists, Janz & Nylin, 2008). However, asynchronous radiations in plants and animals also suggest that co-speciation events may be generally rare in insect–plant interactions (Jermy, 1993; Scriber, 2002a; Percy *et al.*, 2004). For example, adaptive radiation in the Pieridae butterflies may be via repeated colonization and specialization rather than co-speciation (Braby & Trueman, 2006; but see Wheat *et al.*, 2007). Furthermore, the possibility that these Lauraceae-feeding specialists lose ancestral host use abilities as they specialize (i.e., burning their ecological/evolutionary bridges behind them) appears to have some support in Lauraceae-specialized *P. troilus* and *P. palamedes* (Scriber, 2005, 2010; see also Nitao *et al.*, 1991a; Cohen *et al.*, 1992;

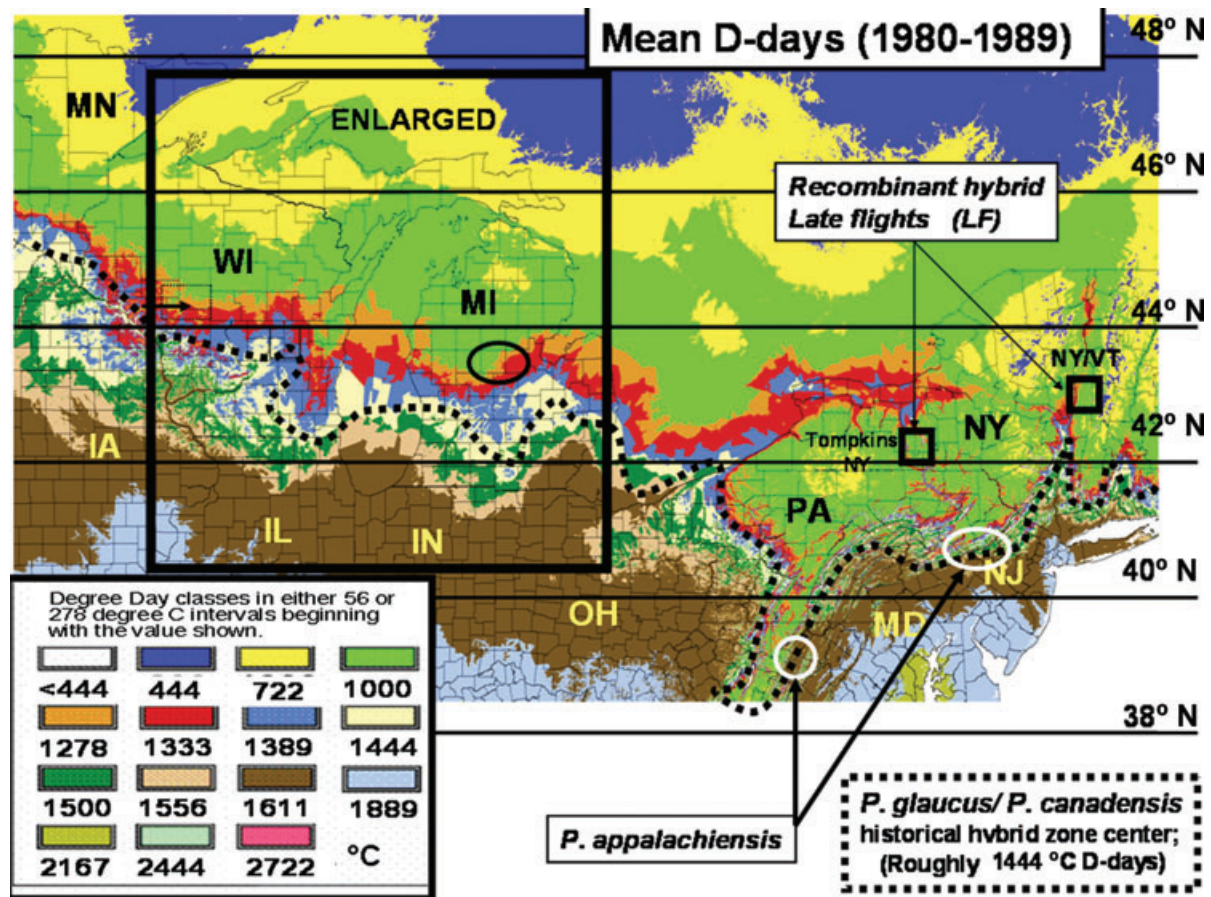


Fig. 1 Thermal landscape presented as the mean degree-day accumulations during the 1980–1989 period in the Great Lakes region of North America. The center of the thermally defined hybrid zone (dotted line) corresponds to the ecotone between boreal and temperate deciduous forest biomes and also represents the suture zone of hybrid interaction for many insects (Remington, 1968; Scriber & Lederhouse, 1992). The color intervals are narrower for the areas between 1 278–1 611°C (2 300–2 900°F) degree-days (D-days), corresponding to the historical hybrid zone of the bivoltine *Papilio glaucus* and univoltine *P. canadensis*. The putative *P. appalachiensis* hybrid species in West Virginia and Pennsylvania is found inside this hybrid zone, on the warmer side. Delayed flights of hybrid recombinants (indicated by squares) have been examined in central New York (1970–1985) and in southwest Vermont (1999–2009). The Wisconsin and Michigan part of this map is enlarged in Fig. 2.

Lederhouse *et al.*, 1992; Frankfater & Scriber, 1999, 2003; Scriber *et al.*, 2008a). However, these Lauraceae feeders have the most efficient food processing larvae of all Lepidoptera tested to date, and they strongly support the “feeding specialization/physiological efficiency and/or fast-growth hypothesis” (Dethier, 1954; Scriber & Feeny, 1979; Singer, 2001; Scriber, 2005). Oddly enough, the overspecialized *P. troilus* is the sister group of *P. glaucus*, the most polyphagous of 570+ species of Papilionidae (Hagen & Scriber, 1991; Sperling, 1993; Scriber, 2010).

Ecological speciation and the evolution of host races/cryptic species

Until relatively recently, it has been largely accepted that “ecological speciation” (focusing on the role of ecology, rather than geography) is likely to be the rule rather than the exception in genetic divergence/evolutionary speciation (Howard & Berlocher, 1998; Via, 2001; Coyne & Orr, 2004; Dieckmann *et al.*, 2004; Thompson, 2005; Funk *et al.*, 2006; Nosil, 2008; Schluter & Conte, 2009; Via, 2009; but see Futuyma, 2008). Geographical

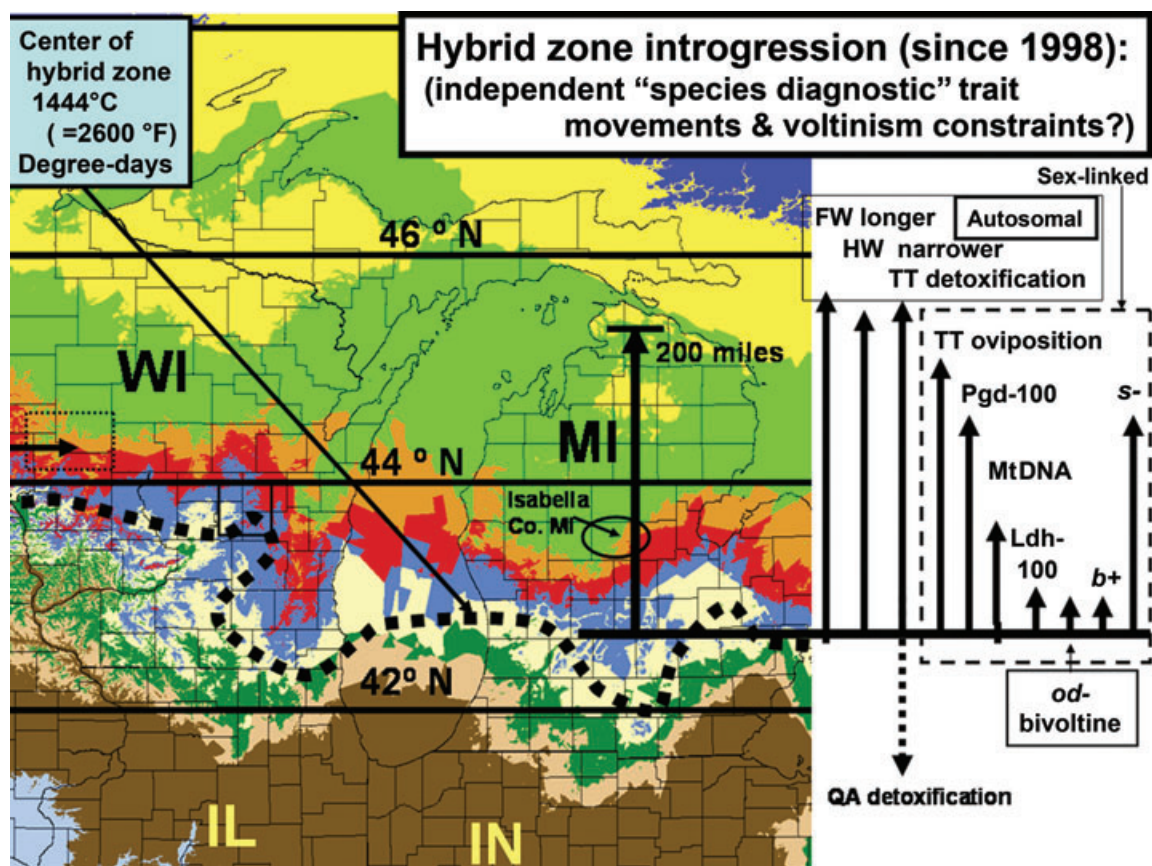


Fig. 2 “Species diagnostic” traits for *P. canadensis* and *P. glaucus* with respect to the historical hybrid zone center location (dotted line). On the left are autosomally determined traits including hindwing band width (HW), forewing length (FW), tulip tree detoxification and neonate survival (cf. Fig. 3), quaking aspen survival and Hk-100 allozymes autosomal but not shown (Hagen & Scriber, 1991; Scriber, 1994). On the right some diagnostic Z (= X)-linked traits include oviposition preference profile of *P. glaucus*, Pgd-100 and Ldh-100 allozymes, and dark melanic enabler (*s*–; see Fig. 5). Also, the mitochondrial DNA (Stump *et al.*, 2003; Fig. 7), and the Y-linked gene for dark (*b*+) are generally believed to be maternally inherited (but see Andolfatto *et al.*, 2003). Close linkage of the *glaucus*-like non-obligate (facultative) diapause control (*od*–) permits bivoltine potential where degree-days exceed 1444°C (= 2600°F). Little northward movement of *glaucus*-like mtDNA has occurred to date (Ording *et al.*, 2010).

speciation dichotomies between sympatry and allopatry are not easily determined (Berlocher & Feder, 2002), and invoking “micro-allopatry” concepts may simply further confuse the issue (Fitzpatrick *et al.*, 2008; Mallet *et al.*, 2009). “Host-associated divergence” in phytophagous insects (including important geographic aspects) has been central to many studies during the past century (e.g. Bush, 1975), but now we have the necessary genetic tools to examine the genome for selected and less selected traits. Generally such divergence is presumed to contribute to speciation when the selection against their hybrids is high (Schluter, 2001), but evidence of homoploid hybrid speciation and adaptive novelties in hybrids has altered this perspective (Arnold, 1997; Mavarez & Linares, 2008).

For evolutionary biologists the spectrum from non-genetic polyphenisms (Shapiro, 1976), through polymorphisms, biotypes, locally specialized demes, geographical races, host races, cryptic species and generally recognized species (or “recognized discontinuities”, J. Fordyce, pers. comm.) has been difficult to partition or categorize, and remains academically unsettled (Dethier, 1954; Fox & Morrow, 1981; Denno & McClure, 1983; Diehl & Bush, 1984; Cobb & Whitham, 1993; Harrison, 1998; Howard & Berlocher, 1998; Mopper & Strauss, 1998; Berlocher & Feder, 2002; Dres & Mallet, 2002; Scriber, 2002b; Sperling, 2003; Porter & Levin, 2007; Tilmon, 2008). New molecular genomic techniques have given some insight and elicited considerable excitement

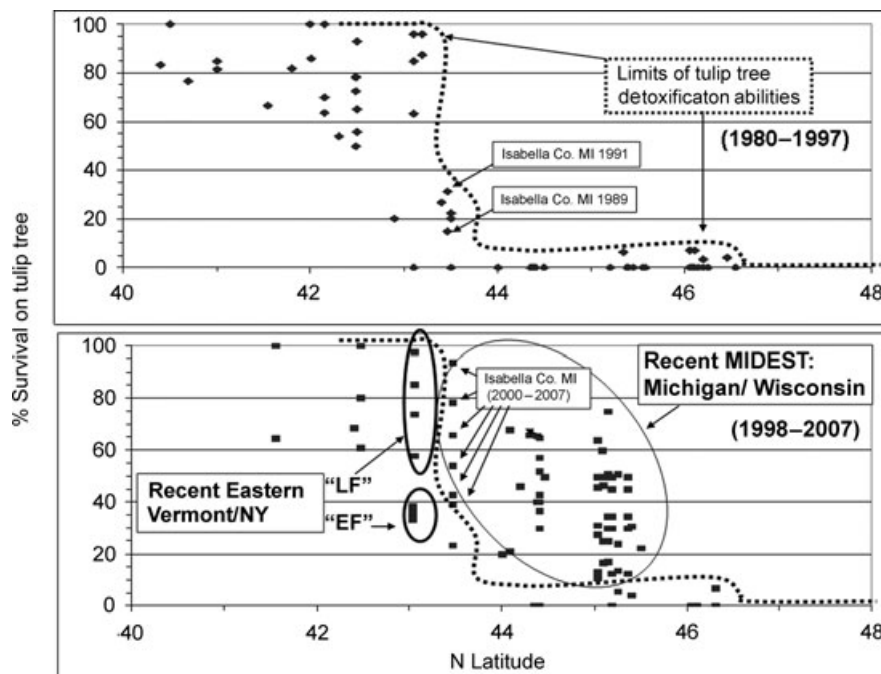


Fig. 3 The neonate larval survival on tulip tree (*Liriodendron tulipifera*; Magnoliaceae) leaves (no-choice arena) as a function of latitude for the period before and after 1998 in midwest USA. Each dot represents the mean of the family means for a particular county in a particular year for Wisconsin, Michigan, New York, and Vermont and Ohio (more than 4 000 larvae from a total of 216 families in split brood assays, with half on quaking aspen). The infusion northward of tulip tree survival (autosomally based capacity to detoxify) in the recent decade is highlighted for the Eastern (Battenkill River of New York/Vermont, “EF” and “LF”) and the midwest (Isabella Co central Michigan) populations. Quaking aspen detoxification abilities (also autosomally controlled, Scriber, 1986) have been much slower to move southward (not shown; see Scriber, 2002b).

about finding the genetic basis of ecological divergence and speciation (Wu, 2001; Hey, 2006; Putnam *et al.*, 2007; Gompert *et al.*, 2008; Nosil *et al.*, 2009a, 2009b; Via, 2009; Kane *et al.*, 2009; Maroja *et al.*, 2009a).

The role of host plant specialization in ecological speciation has been evident in several species, but the particular mechanisms of host-associated divergence remain complex in some cases, and elusive in most (Berlocher & Feder, 2002; Abrahamson & Blair, 2008). For example, the general lack or strength of correlation between the oviposition preference and the larval performance on different hosts has been variable for several reasons (Wiklund, 1975; Thompson, 1988; Agosta, 2006; Craig & Itami, 2008; Mercader *et al.*, 2008; Friberg & Wiklund, 2009; but see Berenbaum & Feeny, 2008). The Aristolochiaceae-feeding swallowtails are generally considered tightly coevolved with this family and basically feed on nothing else (Scriber, 1984), but there is variability in the particular *Aristolochia* species selected locally (Rauscher, 1995; Weintraub, 1995; Silva-Brandao & Solferini, 2007). This point is exemplified by

the endangered Richmond birdwing *Ornithoptera richmondia* near Brisbane in Australia which is threatened by the introduced *Aristolochia elegans* (originally from Brazil) with chemicals that still elicit oviposition, but has others toxic to the larvae (Straatmann, 1962b; Sands & Scott, 1997). This interaction is a dilemma for butterfly conservation ecologists, but may provide an excellent study system for examining the rate of larval adaptation to the currently toxic choice (“mistake”) of adult females. Determining the differential aristolochic acid profiles might elucidate causal factors and potential mechanisms involved.

Host-associated divergence (cryptic species and speciation); recent multi-trait studies with insects

Ecological and evolutionary processes that drive diversification, dynamics of gene flow, reproductive isolation, speciation and local extinctions involve

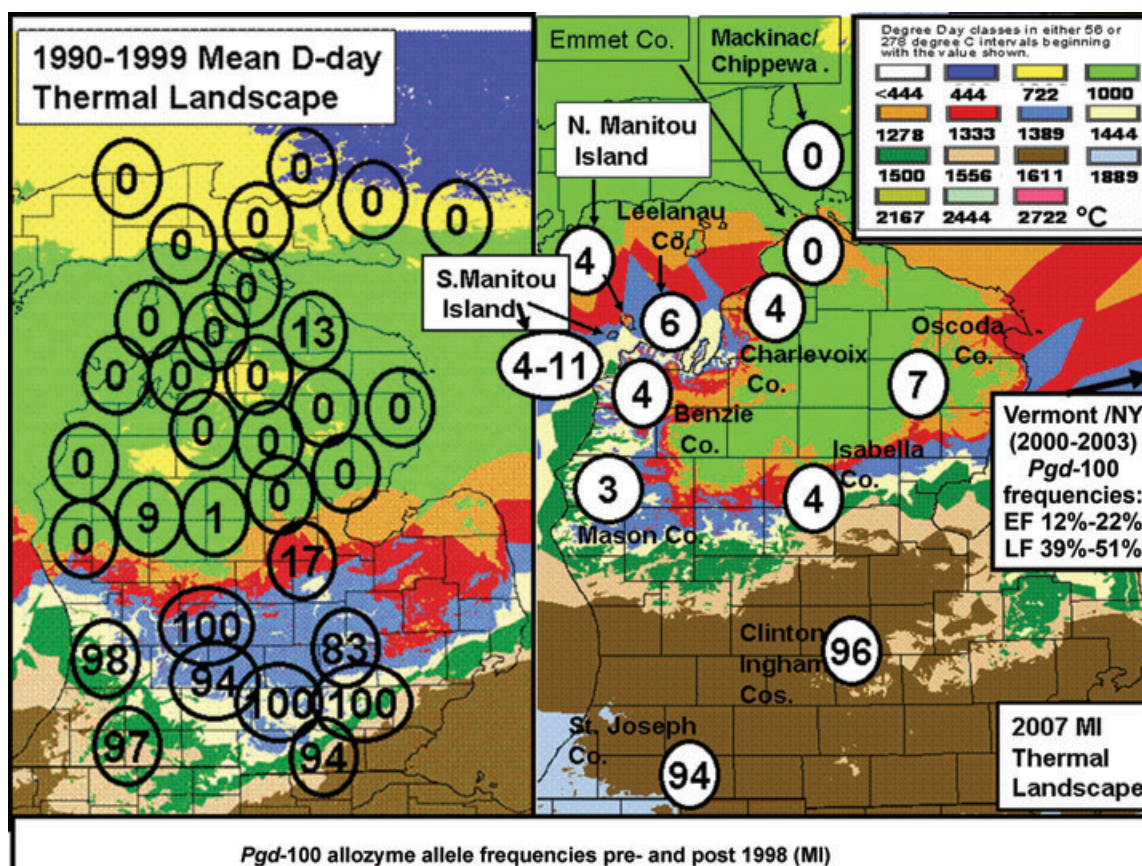


Fig. 4 Allozyme alleles, *Pgd*-100 (Z-linked and *P. glaucus* diagnostic) before 1998 and during the subsequent years. Thermal landscape of 1990–1998 and recent 2007 are presented for comparison (Hagen & Scriber, 1989, 1991; Hagen *et al.*, 1991; Scriber, 1996a; Ording, 2001; Stump *et al.*, 2003). To the east (Battenkill River region of New York state and Vermont) the late flight hybrid swarm (LF) shows significant recent evolutionary change in the frequency of *Pgd*-100 (see also Fig. 4).

community ecology, phytochemical constraints, mating behavior and molecular mechanisms. Local adaptations depend on scale (Cogni & Futuyma, 2009). With regard to host-associated divergence, the search for “key innovations” and “speciation genes” has produced interesting results for insects and swallowtail butterflies in particular. However, various combinations of causal mechanisms (host races, habitat selection, pheromones, sexual selection and allochrony) may be involved in speciation, including recently recognized “homoploid (recombinant) hybrid speciation” in animals. These are briefly reviewed below. The “oscillation hypothesis” for speciation and adaptive radiation (from specialists to generalists and back, Janz & Nylin, 2008), has received support from assays of ancient angiosperm specialists (Scriber *et al.*, 2008b, 2008c) as well as from recent neospecies and hybrid species (below).

1. Sympatric host-associated divergence in genetics, morphology and phenology can be rapid, as seen

in yucca moths (Groman & Pellmyr, 2000; Thompson, 2009), soapberry bugs (Carroll *et al.*, 1998, 2005; Carroll, 2007), fruit flies (Berlocher & Feder, 2002; Feder *et al.*, 2003), *Drosophila* (Carsten *et al.*, 2005; McBride, 2007; Matzkin, 2008), pea aphids (Caillaud & Via, 2000; Via & Hawthorne, 2002), leaf beetles (Funk & Nosil, 2008), walking sticks (Nosil, 2007), and in Lepidoptera (Singer & Thomas, 1996; Zangerl & Berenbaum, 2003). These co-adapted radiations may carry over to the parasites (enemies) of the herbivores (Abrahamson & Blair, 2008; Forbes *et al.*, 2009). It may be that if parental species with differential adaptations to pathogens exist (as seen in detoxification differences, Scriber *et al.*, 1989, 1999), then “hybrid vigor” (as seen in lab crosses, Scriber *et al.*, 2003) may be partly due to higher pathogen resistance in hybrids relative to parental species (see also Moulia, 1999; Moulia *et al.*, 1995). This possibility could be addressed using known hybrids and backcrosses challenged

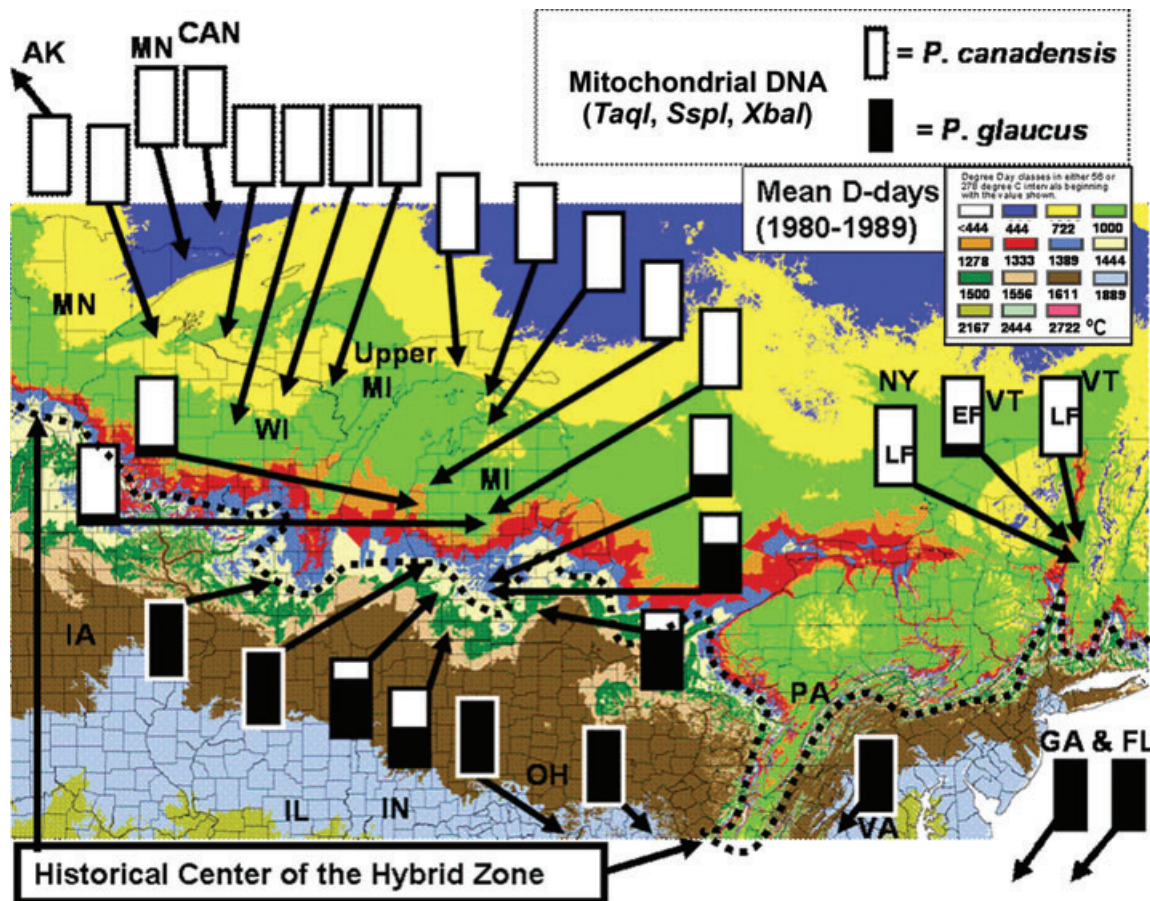


Fig. 5 Proportion of mitochondrial DNA (mtDNA: *TaqI*, *XbaI*, *SspI*) in various populations in the midwest and eastern USA. The number of individuals examined for mtDNA were: 4, Fairbanks, Alaska (AK); 12, Thunder Bay, Canada (CAN); 12, Cook Co., Minnesota (MN); 1 each from Bayfield, Lincoln and Forest Co., Wisconsin (WI); 2, Dane Co., Michigan (MI); 12, Ontonagon Co., MI; 12, Dickinson Co., MI; 1 each from Mackinac and Emmet Cos., MI; 13, Charlevoix Co., MI; 12, Mason Co., MI; 16 Isabella Co., MI; 15 Clinton Co., MI; 4 Washtenaw Co., MI; 1, Adams Co., Ohio (OH); 2, Lawrence Co., OH, 2 Wise Co., Virginia (VA); 4 Clarke Co., Georgia (GA); 4, Highlands Co., Florida (FL); 1 Washington Co., New York (NY); 32 "EF" and 35 "LF" Battenkill River population (from Stump *et al.*, 2003; Ording *et al.*, 2010; R. Mercader, A. Stump; R. Hagen and J.M. Scriber, unpubl. data).

with various pathogens (e.g., viral, fungal, bacterial, etc.).

Host shifts that occur from wild plants onto crop plants (e.g., the Colorado potato beetle from nightshades to potatoes) generate significant attention. In California Shapiro and Masuda (1980) describe such a potential shift after 1918 of the anise swallowtail, *P. zelicaon*, to economically significant *Citrus* (Rutaceae family) from weedy sweet fennel (Apiaceae) plants. The potential for multiple generations is an associated and interesting ecotypic response of fennel feeding, while the *Citrus* race is univoltine. Although *Citrus* is not a better host for growth, survival or fecundity, it apparently allowed butterfly expansion into areas where fennel did not occur.

Host-associated differentiation in goldenrod gall midges may constitute cryptic species (Dorchin *et al.*, 2009). A similar level of divergence to host-specific cryptic species was suggested for feather-feeding lice (Malenke *et al.*, 2009). A purportedly generalized tumbling flour beetle may be comprised of host-specialized cryptic species (Blair *et al.*, 2005). The outbreaks of red pine-feeding populations of sawflies, *Dioryctria zimmermani* (Grote) in Wisconsin, turned out to be a cryptic species, the red pine shoot moth, *D. resinosa* (Mutuura) (Scriber & Hainze, 1987; see also Nymen *et al.*, 2006).

There was no indication that host affiliations of the specialized or oligophagous *Yponomeuta* species had any impact on mating preferences between host races (Bakker

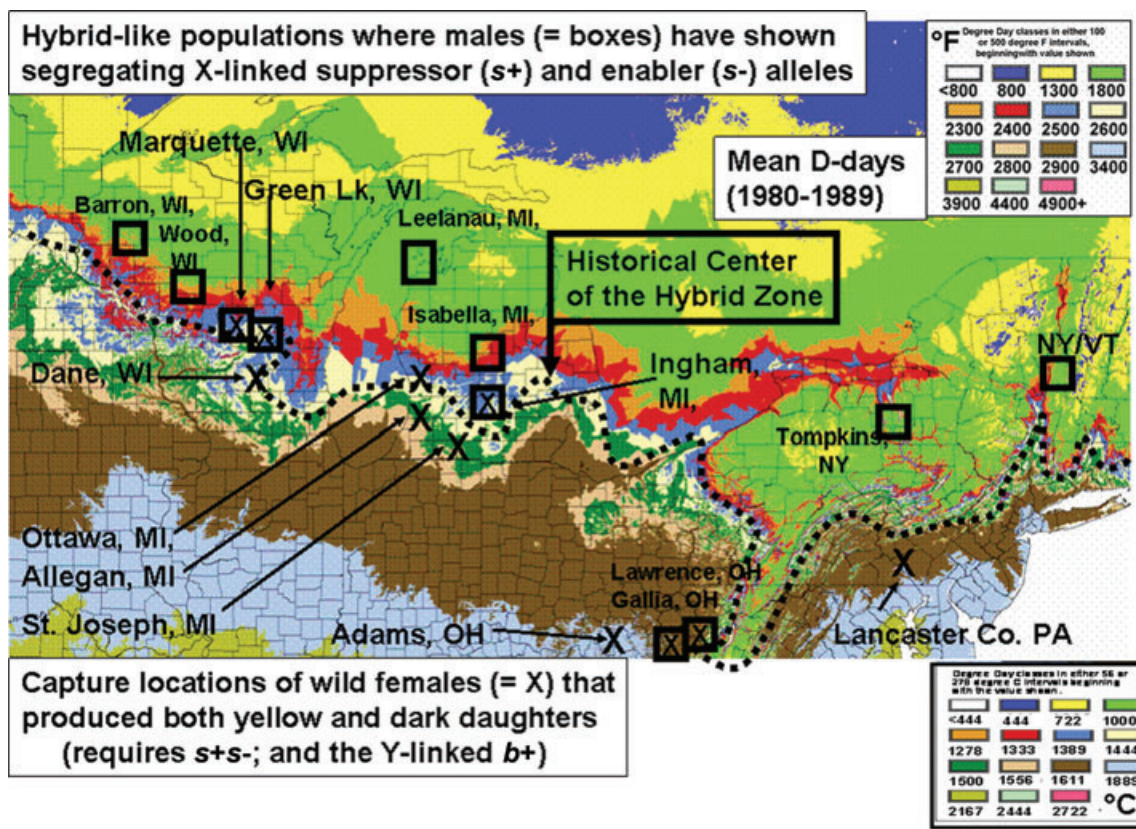


Fig. 6 The historical records for males showing segregating Z-linked suppressor (s+) and enabler (s-) alleles extend from the warm edge to the colder edge of the thermally defined hybrid zone. Wild-captured females showing both yellow and dark daughters (requiring s+ and s- from the father, and the W-linked b+ melanism gene from the mother) are only seen at the center of the hybrid zone and toward warmer summer degree-day totals. The dotted line (center of historical hybrid zone) closely reflects the northern limits to dark female records (Scriber *et al.*, 1996; J.M. Scriber & M.L. Aardema unpubl. data).

et al., 2008). Changes in the insect nervous system that functionally change plant recognition and host plant specificity may represent autonomous evolutionary events, and as such may be intrinsic to the genome (and not evoked by ecological selection, Jermy, 1993). However, selection on specialists may also favor chemosensory function and evolution in fruit flies as shown in odorant-binding proteins (permitting toxin avoidance in specialists) but nonetheless, these may also be lost more rapidly than in generalist relatives (Whiteman & Pierce, 2008).

Different degrees of reproductive isolation from natural and sexual selection (often with a mixture of pheromones, host races and temporal divergence; see below) or varying modes of inheritance (Nygren *et al.*, 2006) occur with various insect host races (Scriber, 1983; Pashley, 1986; Feder *et al.*, 1994; Harrison & Bogdanowicz, 1995; Dres & Mallet, 2002; Wood & Keese, 1990; Funk, 1998; Wood *et al.*, 1999; Blair *et al.*, 2005; Nosil & Mooers, 2005; Nosil *et al.*, 2002; Nosil, 2007; Dworkin & Jones, 2008;

Frantz *et al.*, 2009; Messina *et al.*, 2009) and pluralism in speciation mode may exist (Xie *et al.*, 2007; Fitzpatrick *et al.*, 2008). Parapatric habitat (altitude) adaptation may be fundamentally important for *Heliconius* butterfly speciation (Arias *et al.*, 2008). Despite the well-documented scarcity of host-shift-associated speciation in *Euphydryas* spp., multi-trait divergence in other traits does occur (Singer & McBride, 2010).

2. Divergence with host races and pheromones Sexual selection has undergone strong stabilizing selection in many different animals (hence the effective isolating mechanisms), but in Noctuid moths, interspecific selection may have also contributed to the diversification of sexual signals such as pheromones (Groot *et al.*, 2008; Gould *et al.*, 2009). Emelianov *et al.* (2001) have shown pheromone differences between larch and pine races of the larch budmoth, *Zeiraphera diniana*. The rice strain (race) and corn strain (race) of the fall armyworm, *Spodoptera frugiperda* differ in their pheromone blends from

virgin females and may play a role in divergence/isolation (Groot *et al.*, 2008; Lima & McNeil, 2009). Symonds *et al.* (2009) suggest that different sex pheromones associated with male Tephritidae may be closely associated with rapid changes in host plant use. Chemosensory speciation may include pheromones, but also other chemically based behaviors (e.g. habitat choice, Smadja & Butlin, 2009).

The European corn borer (ECB), *Ostrinia nubilalis*, in Europe colonized maize (*Zea mays*) after its introduction 500 years ago, and two sympatric host races exist in France, with one on maize and one on mugwort (*Artemisia vulgaris*, Thomas *et al.*, 2003) or hop (*Humulus lupulus*, Malausa *et al.*, 2008). Both of these races are physiologically adapted to their respective hosts (Calcagno *et al.*, 2007). The colonization of maize resulted in a delay in emergence of adults and an escape from enemies that attacked the hop and mugwort borer race (Thomas *et al.*, 2003). In central New York state a delayed univoltine race also occurs temporally between the two races of bivoltine *Ostrinia nubilalis* (Eckenrode *et al.*, 1983; Roelofs *et al.*, 1985). Although the French host races differ in pheromones (maize race with Z-pheromone; mugwort race with E-pheromone), differential voltinism is not a factor in their isolation (Thomas *et al.*, 2003) as in the USA (see below).

Tight linkage of male response to the pheromone differences between races and developmental timing regulation with the *Tpi* allozyme locus on the Z (= X) chromosome may have enhanced the rate of development of premating barriers between the European ECB races (Thomas *et al.*, 2003). Based on additional studies using microsatellite markers, it was suggested that the two *Ostrinia* taxa have sufficiently diverged genetically and should be considered sibling species rather than host races (Malausa *et al.*, 2007). The mugwort/hop race is called *O. scapularis* but the maize race, *O. nubilalis* still sometimes uses hop (Malausa *et al.*, 2008). Hop plants (and corn plants) in the USA also appear to be the common denominator for two stalk-boring *Hydraecia* species (one native and one introduced) that have recently become sympatric and may potentially hybridize naturally on corn in the Great Lakes region (Giebink *et al.*, 1984; Scriber & Hainze, 1987) hybrid zone (or suture zone, Remington, 1968).

Roelofs *et al.* (1987, 2002; see also Pelozuelo *et al.*, 2004) described the Z-strain and E-strain pheromone ecotypes of the ECB, *Ostrinia nubilalis*, with production of the attractant “pher” (autosomal) and the respective responses of males “resp” which is X (= Z)-linked. These strains had earlier been shown to reflect different host, favorite host use and different voltinism patterns (Showers, 1981; Eckenrode *et al.*, 1983). Scriber and Lederhouse

(1992) reviewed these and similar voltinism/host plant transitions and thermal constraints across the Great Lakes transition zone in *Hyalophora* spp. silkmoths, *Callosamia* spp. silkmoths, *Hydraecia* spp. of hop vine borer and potato stem borer *Limenitis* butterflies and *Papilio* butterflies. The univoltine strain of ECB that flies in mid-July (as does the “late flight” of *Papilio glaucus*/*P. canadensis* hybrids, Scriber & Ordning, 2005; Scriber *et al.*, 2008a) is also a hybrid-like mix genetically (Dopman *et al.*, 2005) and has been shown to reflect differences in post-diapause development time, which is being controlled by a major factor on the Z (= X) chromosome for both the *Papilio* and the ECB (Rockey *et al.*, 1987a, 1987b; Glover *et al.*, 1992). As found in *Papilio* (Hagen & Scriber, 1989; Scriber, 1994; Putnam *et al.*, 2007), so too the *Tpi* allozyme locus is closely Z-linked with diapause regulation in corn borers (Dopman *et al.*, 2005).

3. Divergence with sexual selection (and mimicry) In *Heliconius* butterflies, the mimicry coloration was shown to be important in divergence of a hybrid species (Mavarez *et al.*, 2006) and in the incipient speciation of *H. erato chesteronii* which maintains high integrity despite substantial amounts of hybridization (Arias *et al.*, 2008). The mate preference gene and wing color preference cue are linked closely in *Heliconius* butterfly species, and thus favors transferal of both, and coordination between sexual and natural selection processes (Kronforst *et al.*, 2006).

The fastest rate of evolution in arthropods was reported for forest-dwelling grasshoppers in Hawaii (Mendelson & Shaw, 1996; see also Kaneshiro, 1988). Sexual selection has been identified as driving forces in other cases (Butlin, 1996; McNett & Crocroft, 2008; Oneal *et al.*, 2009; reviewed by for other insects and animals, see also Panhuis *et al.*, 2001; Vines & Schluter, 2006).

“Cryptic sexual selection” (in multiple-mating females) rather than “last male sperm precedence” of some insects may occur by females “choosing” the sperm with which they fertilize eggs as in dung flies and crickets (Ward, 2002). However, conspecific sperm selection (cryptic sexual selection) in cases of a female with interspecific matings (Howard *et al.*, 2002), was not consistently observed in experimental multiple-mated interspecific *Papilio* hybrids (Stump & Scriber, 2006).

Differential (asymmetrical) mate preferences of males (using size-matched, virgin females of tiger swallowtail butterflies) in the *Papilio* hybrid zone may also contribute to asymmetrical introgression (Deering & Scriber, 2002; see also Wirtz, 1999). Deering and Scriber (2002) showed that female interspecific attractiveness (newly emerged, size-matched, tethered virgins) to wild male tiger swallowtail butterflies was asymmetrical, with the *P. glaucus* females preferred by both the *P. canadensis* males (83%

in northern Michigan) as well as *P. glaucus* males (97% in Florida). Asymmetrical gene flow in a hybrid zone of field crickets may be due in part to differential parental female refusal of hybrid males or differences in the time to mate with conspecifics and heterospecifics (Maroja *et al.*, 2009a, 2009b).

4. Host-associated divergence with natural enemies

Murphy (2004, 2007) has shown that in the presence of natural enemies, *Papilio machaon alaska* has highest survival on novel host plants, but in the absence of predation the ancestral host is best and host races seem unlikely. Additional local host favorites appear driven by differential predation (Gratton & Welter, 1999; Müller & Arand, 2007; Zovi *et al.*, 2008; Wiklund & Friberg, 2008; Forbes *et al.*, 2009). In mice, the F-1 hybrids are more resistant to pinworm parasites (hybrid vigor) than were the parental species (Mouliia, 1999). However, backcrossed and recombinant genotypes were more susceptible, perhaps because of the breakup of co-adapted gene complexes of the immune response system (Mouliia *et al.*, 1995). Little is known about how pathogens or phylloplane microbes such as *Bacillus* bacteria (or other viruses, fungi) directly or indirectly affect insect plant interactions and differential survival of hybrid versus parental species (Scriber, 2001; Smilanich *et al.*, 2009) or genetically manipulated populations (Marec *et al.*, 2005). And it may be that lab-reared hybrid *Papilio* have a type of “hybrid vigor” in pathogen resistance (J. Scriber, unpubl. data). This may be an important understudied area deserving attention in theory and practice (e.g., insect management and conservation, Scriber, 2004). The concept that disease should be less intense at range edges does not take into consideration those pathogens that sterilize but don't kill (Antonovics, 2009) or those that alter sex-ratios and mtDNA selective sweeps after introgressive hybridization in their insect hosts (e.g., *Wolbachia*, Gompert *et al.*, 2008) and need to be considered.

When 70 species of Lepidoptera were offered to predatory ants, the prey chemistry was the best predictor of rejection by ants (most noxious chemistry was rejected) and the second best predictor of rejection was diet breadth of the caterpillars; specialists were rejected more frequently than generalists (Dyer, 1995), but instars can differ in defenses (Frankfater *et al.*, 2009). These findings are in line with the “plant apparency” concept of Feeny (1976), where specialists are able to detoxify and/or sequester nasty chemicals from their host plant leaves, perhaps better than generalists (see also Sime & Brower, 1998). Specializing on particularly suitable host plants may aid in protection from general enemies (as well as aid in fast growth) but host-specific enemies may also favor broader host range where thermal constraints are relaxed in re-

gard to the voltinism/suitability hypothesis (Scriber & Lederhouse, 1992).

5. Divergence with allochronic isolation Host races of the apple maggot fly, *Rhagoletis pomonella*, show differences in the depth and timing of diapause on hawthorn and apple, resulting in fruiting synchrony with the respective hosts, and which may contribute to divergence/isolation of the races (Feder & Filchak, 1999; Filchak *et al.*, 2000). Seasonal allochrony has also played a role in divergence of *Enchenopa* treehoppers (Wood & Keese, 1990; Wood *et al.*, 1999), field crickets (*Acheta* spp.; Alexander & Bigelow, 1960); 13- and 17-year cicadas (*Magicalicada* spp.; Simon *et al.*, 2000; Cooley *et al.*, 2001); yucca moths (*Tegeticula* spp.; Groman & Pellmyr, 2000); *Pemphegus* aphids (Abbot & Withgott, 2004), *Eurosta* goldenrod gall makers (Horner *et al.*, 1999) and pine processionary moths (*Thaumetopola* spp.; Santos *et al.*, 2007).

Allochronic emergences may be involved in other insects (Cooley *et al.*, 2001; Yamamoto & Sota, 2009; Whipple *et al.*, 2009). Allochronic mating and flight activity has been seen in regard to pheromone release by female *Callosamia* species silkmoths (Scriber, 1983) and in different host-associated strains in other moths (Ueno *et al.*, 2006; Schoefer *et al.*, 2009). Allelic substitutions at two unlinked autosomal loci cause important differences in photoperiod responses and result in seasonal asynchrony in interspecific hybrids of lacewings (*Chrysopa carnea* and *C. downesi*; Tauber & Tauber, 1977; Tauber *et al.*, 1977). This and the single pair of alleles adapting them to two habitats have produced sympatric speciation.

A model of recombinant homoploid hybrid speciation based on allochronic isolation has been presented (Scriber *et al.*, 2008a). False second generation flights in mid-season (July) of the ECB (Eckenrode *et al.*, 1983) as well as the recombinant hybrid late flight of *P. glaucus/P. canadensis* butterflies (Hagen & Lederhouse, 1985) were discovered in central New York state. These false second generation flights are really delayed emergence of univoltine genotypes that emerge as adults between flights of the two generation races of ECB (Roelofs *et al.*, 1985) and the parental *Papilio* species; *P. glaucus* and *P. canadensis* (Ording *et al.*, 2010).

Furthermore, the genetic basis of this delayed post-diapause development in these univoltine mid-season “late flights” has been located on the Z (= X) chromosome of both ECB and *Papilio*, and may be closely affiliated with, or in fact serve as, “reproductive isolation genes” or “speciation genes”. The delayed diapause development gene in ECB larvae (*Pdd*, Glover *et al.*, 1992) combined with Z-linked genetic differences in the sensitivity to day-length (regulating diapause induction and

development rates (Stengel & Schubert, 1982) and different pheromone responses of males, *Resp*, Z-linked (Roelofs *et al.*, 2002), may have led to the reproductive isolation between host races (Thomas *et al.*, 2003; Dopman *et al.*, 2005). The *Papilio* species do not use sex pheromones (Deering & Scriber, 2002) as observed in the univoltine and both bivoltine ECB races (see above).

It is interesting that the allozyme locus for *Tpi* is tightly linked to both the *Pdd* gene and the *Resp* pheromone response gene in ECB (Glover *et al.*, 1990), since similar Z-linkage of *Tpi* and recombinant late flight (i.e. post-diapause delayed development) also occurs in *Papilio* hybrids. The photoperiod insensitivity that produces obligate diapause (even under short photoperiods) in *P. canadensis* (*od+*, Hagen & Scriber, 1989), may also do so in the hybrid late flight swarm, and in the putative hybrid species (*P. appalachiensis*). This obligate diapause in univoltine genotypes is linked closely with *Ldh*-40 and or 80, allozyme alleles found in *P. canadensis*, not in *P. glaucus* (Scriber & Ording, 2005). The Z-linked facultative diapause found in *P. glaucus* is controlled by an *od-* allele and this is closely linked to the *Ldh*-100 allozyme in *Papilio* (Ording, 2008).

We suspect that high rates of recombination on the X-chromosomes (Putnam *et al.*, 2007) and strong divergent selection, including voltinism capacity (Scriber & Ording, 2005) inside the thermally defined hybrid zone may account for the genetic divergence observed in these delayed post-diapause emergers with recombinant hybrid genotypes in Vermont late flights (Ording *et al.*, 2010) and the resulting potential hybrid species seen in the Appalachian Mountains (*P. appalachiensis*, Pavulaan & Wright, 2002; Scriber *et al.*, 2008a). Any trait combinations on the Z-chromosome with the direct development (non-diapause) gene (*od-* and the closely linked *Ldh*-100 allele) would be eliminated by intense ecological selection inside the hybrid zone, because all direct developers trying to complete a second generation would fail (Scriber & Lederhouse, 1992; Scriber *et al.*, 2008a; Table 1). Close linkage of facultative diapause regulation (*od-* gives bivoltine potential) and the *Ldh*-100 allozyme may explain why such a sharp step cline in *Ldh*-100 frequencies are observed at the warmer side of the hybrid zone, where offspring of any direct developing pupae would fail to pupate before winter (Scriber *et al.*, 2008a). Interspecific laboratory backcrosses have shown that direct developing individuals do have a very high correlation of >95% with *Ldh*-100 alleles, whereas diapausers are more closely associated with the *canadensis*-like *Ldh* 40 or *Ldh*-80 (Ording, 2008). These direct developers (various recombinant backcross genotypes) would have been eliminated anywhere in the hybrid zone with fewer than

the 1444°C (2600°F) degree-days needed to complete two generations (Figs. 1 & 2).

The “divergence hitchhiking” (Via, 2009) in the *Papilio* genome has shown initial discordances that reflect recombinant genotypes with some regions of the genome (especially on the Z-chromosomes) showing different historical divergences (Scriber & Ording, 2005; Putnam *et al.*, 2007; see also Andolfatto *et al.*, 2003; Galtier *et al.*, 2009 for mitochondrial DNA and W (= Y)-chromosome independence). The Z-linked gene locus suppresses/enables (*s+/s-*) the expression of the W chromosome melanic (mimetic) black wing color (*b+*) in females of *P. glaucus*. Interspecific introgression, producing some broods with both dark and yellow females, has been detected along the hybrid zone from Wisconsin to Vermont (Scriber *et al.*, 1996; Fig. 6). The suppressor/enabler locus on the Z-chromosome may correspond closely (or directly involve) the tyrosine hydroxylase gene (*TyH*) that we have also identified on this chromosome (Putnam *et al.*, 2007). In melanic females, black melanin replaces the background yellow papiliochrome (Koch *et al.*, 1998) with a key enzyme involved (called “BAS”; Koch *et al.*, 2000a, 2000b) which shunts, or suppresses dopamine from the melanin pathway into the production of yellow papiliochrome pigment, as a likely response to the Z-linked suppressor (*s+*, Hagen & Scriber, 1989) gene products. Tyrosine hydroxylase (*TyH*) or closely linked factors are involved in production of dopa (which is common to both pathways, Koch *et al.*, 2000a, 2000b), and late conversion of tyrosine into melanin may result in incomplete penetrance in females (intermediate, “cinnamon” coloration, where yellow scales are brownish, Scriber *et al.*, 2009a, 2009b) due to differential interpretation of patterning signals by females (Ffrench-Constant & Koch, 2003).

Differential introgressive movements of other Z-linked “species diagnostic” traits may have occurred (see Fig. 2) such as oviposition preferences (Scriber *et al.*, 1991b; Scriber, 1993; Mercader & Scriber, 2007, 2008b), diapause regulation (Rockey *et al.*, 1987a, 1987b), post-diapause emergence delays (*Pdd*; in *Papilio* recombinant hybrids, Scriber *et al.*, 2008a; which may be very closely linked to *Tpi* allozyme, as in the European corn borer; Dopman *et al.*, 2005). The Z-linked allozymes *Pdg* and *Ldh* appear to provide unique diagnostic alleles for *P. glaucus*, *P. canadensis*, and the hybrid species *P. appalachiensis* (Hagen *et al.*, 1991; Scriber & Ording, 2005). The Haldane effect in certain *P. glaucus*/*P. canadensis* recombinant hybrid female pupae (especially those with the *canadensis*-type allozyme alleles of *Ldh*-80/40 and *Pgd*-125/80; Hagen & Scriber, 1995; Ording, 2008) may also involve specific Z-linked loci.

Table 1 Emergence of various experimental laboratory pairings of Vermont early (EF, = *P. canadensis*) and late flight (LF, = hybrid swarm) individuals reared under long day (18 : 6 h) photoperiods throughout larval and pupal stages (except * = field-reared late summer).

Genotype/Family (Female × male)	Sons		Daughters		Dead
	Direct	Diapausers	Direct	Diapausers	
Dark (Pg) × LF					
19003	11	2	0	1 dk	(2)
19019	31	7	0	4 dk	(7)
22362*	0	0	0	1 dk	(0)
22376*	0	4	0	6 dk	(0)
LF × LF					
19036	3	5	2 yel	4 yel	(1)
19072	0	6	0	5 yel	(2)
19075	0	11	0	6 yel	(1)
LF × Pg					
19038	17	7	6 yel	0	(1)
19040	38	7	41 yel	0	(3)
Pc (EF) × Pg					
19008	28	4	21 yel	1 yel	(3)
19031	8	0	3 yel	2 yel	(0)
19042	3	0	6 yel	0	(0)
20019	2	3	4 yel	3 yel	(1)

*Dark includes intermediate (cinnamon) color as Scriber *et al.* (2009b).

Direct developing (non-diapause) yellow daughters (yel) reflect presence of the Z-linked *od*— (while diapausing daughters reflect the *od*+ allele). Lack of dark daughters (dk) for LF × Pg and EF × Pg (with a *P. glaucus* father) reflects lack of the W-linked *b*+ allele for melanism since it would otherwise be expressed with the enabler *s*— allele (Scriber *et al.*, 1996). The dark Pg × LF father produces dark daughters and shows presence of the enabler *s*— allele in all 4 of these hybrid swarm male fathers (who apparently passed the obligate diapause gene *od*+ to daughters).

The “species boundary” between these *Papilio* taxa (*P. glaucus*, *P. canadensis*, *P. appalachiensis*) may be viewed as a continuum, separating at different latitudes/altitudes, depending on the particular “diagnostic” trait selected (Fig. 2). Under varying spring temperatures, the *P. appalachiensis* type (and recombinant hybrid prototypes) separate via different emergence dates on the warm side of the hybrid zone from *P. glaucus* and on the cooler side of the hybrid zone from *P. canadensis* (Scriber *et al.*, 2008a; Ordning *et al.*, 2010). The autosomal traits have moved faster (further since 1998) than the sex-linked (Z- and W-linked) diagnostic traits (Fig. 2). However, the previously absent Z-linked *Pgd*-100 allozyme allele rapidly reached 50% in the Vermont late (false-second) flight during the 1998–2003 period (while the Z-linked *Ldh*-100 frequency remained at zero, Scriber & Ordning, 2005). Evolution has been suggested as faster for traits on the X (= Z) chromosome (Sperling, 1994; Pashley-Powell, 1998;

Mank *et al.*, 2007; Qvarnström & Bailey, 2008) and the strong divergent selection driving hybrid speciation and genomic discordance (Putnam *et al.*, 2007) in these *Papilio* appears to be focused on the Z-chromosome (Scriber *et al.*, 2008a; Fig. 8).

6. Hybrid zones and hybrid species Some species hybridize, creating an evolutionary continuum and causing taxonomic/conservation issues (as well as difficulty with the ecological continuum for feeding specialization). Despite the possibility that multi-species communities could collapse into hybrid swarms (Seehausen *et al.*, 2008), hybrids and introgression do not always represent evolutionary dead-ends as suggested by Rhymer and Simberloff (1996). In fact, it has been recognized that divergence to species status can be accompanied with extensive gene flow (Sperling, 1993, 1994, 2003; Kronforst, 2008; Nosil, 2008). Traits that are selected during hybridization have been reviewed for 11 Lepidoptera taxa pairs of strains or species and 39% were X (= Z) linked

with 10% maternal or Y (= W)-linked (Sperling, 1990; Pashley-Powell, 1998; Vicoso & Charlesworth, 2006). Mitochondrial DNA can also be biparental and with recombination (in patriline, and not simply maternally inherited), and such “paternal leakage” has been observed in *P. glaucus* (Andolfatto *et al.*, 2003) and hybrid cicadas (Fontaine *et al.*, 2007). Such biparental inheritance of mitochondrial DNA and later recombination has made some phylogenetic analyses and historical (molecular) dating of lineages more complicated for biosystematists (Satta *et al.*, 1998; Sackton *et al.*, 2003; Piganeau *et al.*, 2004). Such mtDNA introgression needs to be considered seriously in assessing mito-nuclear discordance and before conclusions can be rigorously drawn from analyses of selective sweeps (Gompert *et al.*, 2008). For example, selection-mediated introgression of the W (= Y) – chromosome in *P. glaucus* (which has the b+ allele for melanic female wing color; Scriber *et al.*, 1996; Fig. 2) could result in the spread of associated mt-DNA alleles, but paternal leakage alters this expectation (Andolfatto *et al.*, 2003). Hybrid plant populations also selectively filter gene introgression between some species (Martinson *et al.*, 2001) and insect pathogens such as *Wolbachia* (endoparasitic bacteria) may differentially select against certain mt-DNA haplotypes and contribute to mito-nuclear discordance (Gompert *et al.*, 2008).

For delineating species boundaries, use of many traits and molecular markers is advised (Luebke *et al.*, 1988; Hewitt, 2001; Hoffmann & Blows, 1994; Lushai *et al.*, 2005; Roe & Sperling, 2007; Scriber, 2007; Payseur, 2010; Winter & Porter, 2010). This independent trait movement also requires serious attention from bioclimatic modelers, since species traits not species, may move (Pöyry *et al.*, 2008; Pellini *et al.*, 2009; Ohshima & Yoshizawa, 2010). Ancient hybridization may also be a characteristic for Lepidoptera, including *Papilio* (Sperling & Harrison, 1994; Scriber, 2007), and it may be confused with recent divergence unless appropriate genomic analyses are made (Putnam *et al.*, 2007; Maroja *et al.*, 2009a; Nolte & Tautz, 2010).

Hybrid speciation

Interspecific hybridization has been recognized as more common than expected (e.g. polyploidy in plants) and can contribute to novel genotypes and adaptive radiations (Arnold, 1997, 2006; Seehausen, 2004). Sympatric/parapatric interspecific hybridizations of animals, including some Lepidoptera species, have been long recognized (Remington, 1968; Platt & Brower, 1968; Collins, 1984; Dowling & Secor, 1997; Cianchi *et al.*, 2003; Scriber *et al.*, 2003; Emelianov *et al.*, 2004;

Mavarez *et al.*, 2006). Of the genus *Papilio*, ($n = 216$ species) 6%–15% hybridize naturally (Sperling, 1990; Presgraves, 2002). Homoploid hybrid recombinant divergence of complex genotypes (Coyne & Orr, 2004) and subsequent hybrid speciation (in the face of gene flow) have also recently been recognized as feasible in some cases for phytophagous insects (Scriber & Ording, 2005; Schwarz *et al.*, 2005, 2007; Gompert *et al.*, 2006; Putnam *et al.*, 2007; Scriber *et al.*, 2008a; Nolte & Tautz, 2010; Mavarez & Linares, 2008). Indeed, analysis of such mosaic genomes in host races of pea aphids suggests that large genomic regions around the trait loci that were divergently selected may be protected from interracial (and presumably in other interspecific) recombination by a process called “divergent hitchhiking” (Via, 2009). It has been predicted that the number of genomic regions at which gene flow is blocked for hybrids should increase with divergence times (Payseur, 2010). This possibility is under investigation with the tiger swallowtail butterfly species, *Papilio glaucus*, *P. canadensis*, and their hybrid swarms across the hybrid zone from Minnesota to New England and Georgia (Putnam *et al.*, 2007; Scriber *et al.*, 2008a; Mercader *et al.*, 2009a; K. Kunte, C. Shea, M.L. Aardema, J.M. Scriber, P. Andolfatto, T. Juenger, L.E. Gilbert, M.R. Kronforst [2010] ‘Sex chromosome mosaicism and hybrid speciation among tiger swallowtail butterflies’ [in review]; see Fig. 1). Distinguishing between secondary introgression of putatively neutral genes and hybrid speciation may not be a simple task, but as we better define the allelic combinations and key loci that may enhance reproductive isolation, we should get a clearer picture of gene genealogies and detect potential repeated hybridization events from ancient populations (Mallet, 2007; Nolte & Tautz, 2010).

Adaptive trait introgression in *Papilio* reflects divergent selection and mosaic genomes

Although rare, “adaptive trait introgression” of some loci across a natural zone of interspecific hybridization has been reported for sunflower species (*Helianthus* spp., Kim & Rieseberg, 1999), Iris species (Martin *et al.*, 2006) and mice (*Mus* spp., Payseur *et al.*, 2004; Teeter *et al.*, 2008). In these cases, other loci show “restricted interspecific introgression” and fail to cross the “species border” in the hybrid zone (Payseur, 2010). Such differential introgression creates “mosaic hybrid genomes” from divergent ecological selection pressures (Via & West, 2008; Arnold & Martin, 2009). The introgressive movement of autosomal alleles further than Z-linked or mitochondrial haplotypes in birds are consistent with Hal-

dane's rule, but reinforce the need to examine many traits across the hybrid zones (Carling & Brunfield, 2009). We have shown similar trends in our long-term transect studies across the *P. glaucus* and *P. canadensis* hybrid zone (Scriber *et al.*, 2003). Strong divergent selection on parts of the Z-chromosome has been detected using two Z-linked allozymes (Ldh and Pgd, Scriber & Ording, 2005) and molecular analyses (Putnam *et al.*, 2007). Differential "species diagnostic trait introgression" (Fig. 2) may have been driven by strong selection on novel genotypes produced inside the hybrid zone, resulting in a post-diapause delayed emergence of these recombinant genotypes (Scriber *et al.*, 2008a).

Constraints on movement of bivoltine *Papilio* genotypes (*od*— control on the Z (= X)-chromosome) to any location on the thermal landscape with fewer than 1 444°C (= 2 600°F) degree-days (Scriber & Lederhouse, 1992) correspond precisely with the northern limits of the Z-linked Ldh-100 allozyme (Figs. 1 & 2). Other rapidly and extensively moving species diagnostic traits such as tulip tree detoxification abilities (Fig. 3), adult size (wing lengths, Scriber, 1994) and narrow *glaucus*-like hindwing black bands in the anal cells (Luebke *et al.*, 1988; Scriber, 2002b) are autosomally controlled (Fig. 2). However, Z-linked *glaucus*-like oviposition preference rankings (Mercader & Scriber, 2005, 2007, 2008b) and the Pgd-100 allozymes (Scriber *et al.*, 2008a) have also moved extensively and rapidly across the historical hybrid zone at several locations (including Michigan, Fig. 4). The *glaucus*-type Z-linked enabler of melanism (*s*—, Scriber *et al.*, 1996) has been detected further north than the W-linked gene for melanism potential (*b*+, Figs. 2 and 6; see below). Mitochondrial DNA of the *glaucus*-type has moved slightly northward in central Michigan, but most field-captured hybrid zone specimens possess the mt-DNA of *P. canadensis* (Stump *et al.*, 2003), even in the late flight hybrid swarm at Vermont (Ording *et al.*, 2010; Fig. 5). Thermal constraints on southward movement of *P. canadensis* have been suggested (Scriber *et al.*, 2002; Mercader & Scriber, 2008a).

The asymmetrical hybrid viability that characterizes many hybrids (Darwin's corollary) and faster mt-DNA evolution in the maternal parent tend to produce less viable F-1 hybrids, possibly due to genetic incompatibilities between mitochondrial and nuclear genes (Bolnick *et al.*, 2008). Asymmetric mito-nuclear incompatibilities may contribute to the introgression asymmetries between hybridizing pairs (Wirtz, 1999; Chan & Levin, 2005; Carling & Brunfield, 2009). Fitness effects of mtDNA are different in males and females (Gemmell *et al.*, 2004). The rapid evolution of mt-DNA versus nuclear DNA and mitochondrial mutations that affect male fitness are passed

on to the next generation and are invisible to selection, leading to more rapid divergence and mito-nuclear disruption, which could be greater in hybrids (Burton *et al.*, 2006). This may be involved here with the slow northward movement of the *glaucus*-like mt-DNA (Stump *et al.*, 2003; Ording *et al.*, 2010; Fig. 2). It has recently been revealed that, despite their cheapness and ease-of-use, mtDNA analyses do not always reflect maternal inheritance (Andolfatto *et al.*, 2003; Fontaine *et al.*, 2007), are not neutral in regard to selection, are not free of recombination, and do not provide as good a molecular clock as was hoped for or as is still believed by many (reviewed by Galtier *et al.*, 2009). As a result systematics and species delineation requires many trait analyses, including morphological, behavioral and ecological aspects (see also Ohshima & Yoshizawa, 2010).

In a survey of 44 cases of introgression following range expansions, 82% of these studies showed extensive introgression from the resident into the invading species (Currat *et al.*, 2008). However, in *Papilio* (below) we see introgression of several traits into the local resident species (in the cooler side of the historical hybrid zone; Fig. 2) from the "invading" southern species since climate warming, but mt-DNA remains mostly that of the resident species, *P. canadensis* (Ording *et al.*, 2010). Similarly, the W (= Y) chromosome trait *b*+ for melanic female wing color has not introgressed beyond the warmest side of the hybrid zone (Figs. 2 & 6). Strong divergent selection on the X-chromosome has been postulated (Scriber & Ording, 2005) but intrinsic (Haldane's effects in recombinant hybrid female pupae) as well as extrinsic (thermal constraints and selection against the *od*—, facultative diapause) factors appear to be involved in the steep non-concordant allozyme clines across the historical hybrid zone (Scriber *et al.*, 2008a). Whether any of the other "invader" genes (Fig. 2) have selective advantages in the local resident background (e.g. Kim *et al.*, 2009) is under investigation. It is deduced that genes would introgress from the invading species into the local species only under strong selection (Currat *et al.*, 2008).

"Why" (= "W") chromosomes move slowly across the hybrid zone!

Constraints on movement of dark melanic females of *P. glaucus* appear to have been intense, with northern range limits to the dark (mimetic) morph basically delineated at precisely the center of the thermally defined historical hybrid zone for the past 13 decades (indicated by the dotted line in Figs. 1 and 2; Scriber *et al.*, 1996). Several hypotheses exist for this

sharp delineation of dark female distribution, including the close northern range limit match of the model (*Battus philenor*; Brower & Brower, 1962; Platt & Brower, 1968), as well as the suppression of melanism by the Z-linked ($s+$) suppressor in essentially all *P. canadensis* which occur on the cooler side of the hybrid zone (Scriber *et al.*, 1996). Pleiotrophic gene action for or against dark morphs (True, 2003) and differential sexual selection (male mate preferences at the hybrid zone; Deering & Scriber, 2002) are unlikely to be major factors (J.M. Scriber & M.L. Aardema, in prep.). Since the 1998 climate warming, a few records of isolated individual dark females have appeared further north than usual (a rare “blow-in” on a storm front was suspected as in Michigan’s Upper Peninsula; Scriber *et al.*, 1998).

Both the Z-linked enabler gene ($s-$) and the W-linked melanism gene ($b+$) must be present for the dark female morph to be expressed (Scriber *et al.*, 1996; Figs. 2 and 6). The genetic incompatibilities (and Haldane’s effects) of certain introgressed hybrid genotypes (recombinant females with either or both Z-linked “*canadensis*-like” allozyme alleles, *Ldh* or *Pgd*) have been examined in experimental backcrosses (Hagen & Scriber, 1995) but the melanism gene ($b+$) does not play a conspicuous role in dark or yellow morph bias. While the Z-linked dark enabler ($s-$) appears to have naturally moved readily via introgression, the melanism allele ($b+$) on the W-chromosome has not (Fig. 6).

Laboratory crosses also suggest that the X-linked $s-$ gene moved independently (and further than) the Y-linked $b+$ gene for melanism

Pairings of virgin dark morph *P. glaucus* females with wild males from the late flight Battenkill Vermont hybrid swarm in Vermont (Table 1; top) resulted in 43 non-diapause males but no females (all hybrid daughters diapaused and were all dark morph adults upon emerging the next year). Combined with the absence of any dark female records within 130–300 km, this strongly suggests that the X-linked enabler allele ($s-$) has recently moved further (faster?) across the historical hybrid zone than the Y-linked dark gene ($b+$).

Two virgin late flight (LF) yellow females with ($b-$) (i.e., families 19038, 19040; Table 1) mated to *P. glaucus* males ($s-$, $s-$) produced 44 non-diapause sons and only yellow daughters ($n = 36$, also non-diapause types). Also, three families (19036, 19072, 19075) of yellow morph LF females mated to LF males from the same VT/NY border population produced only yellow daughters. These results suggest that LF females may have lacked the Y-linked $b+$ gene (since the $s-$ enabler gene was present

in the LF population, and some dark daughters might be expected). However, no dark daughters from four other Vermont early flight (EF) \times *P. glaucus* father families (19008, 19031, 19042, 20019; Table 1) were evident, also suggesting that no dark gene ($b+$) has yet made it into this population.

Odd segregating families with dark and yellow morph females (non-Mendelian; Scriber & Evans, 1987) and occasional aberrant color forms or gynandromorphs (Scriber *et al.*, 2009a, 2009b) attest to the unique genetics of Lepidoptera (Robinson, 1971; Blanchard & Descimon, 1988). Bilateral phenotypes have also been described for larval and pupal stages of *Papilio* (Scriber & Hagen, 1990).

Lepidoptera have unique chromosomes and genetic processes

In addition to many types of mimicry in the Papilionidae (monomorphic, dimorphic, female-limited, etc., Kunte, 2009), such mimetic forms have originated independently in many of the 50+ mimetic species of *Papilio* (Zakharov *et al.*, 2004a, 2004b). Sex-determining chromosome types have females as the heterogametic sex (ZW) and males homozygous (ZZ), unlike most animals (Charlesworth, 1996). Since synaptic chromosome pairings are lacking in the heterogametic sex, female Lepidoptera lack crossing-over (genetic recombination) and meiosis is achiasmatic (Marec *et al.*, 2001, 2005). A consequence of non-recombination on the W chromosome is that genetic changes accumulate there, independently of its homolog (the Z chromosome; Charlesworth & Charlesworth, 2000). Lepidoptera have holokinetic (= holocentric) chromosomes that lack the large distinct primary constrictions (centromeres), and their kinetic activity is instead distributed along most of the chromosome (not just at the centromere, as in Diptera, etc.). Unlike the W chromosome, the Z-chromosomes of Lepidoptera have transcriptionally active euchromatin and are rich in genes (Traut, 1999; Scriber, 1994; Sperling, 1994; Pashley-Powell, 1998). Instead, heterochromatin (which is female-specific) characterizes the W (= Y) chromosome and few genes are found on it (Traut & Marec, 1997). Thus far, these include egg-size determining gene in *Bombyx mori* (Kawamura, 1988); a homologue of the period gene in *Antherea pernyi* (Gotter *et al.*, 1999) and the melanism gene ($b+$) in *P. glaucus* (Clarke & Shepard, 1962; Clarke *et al.*, 1976; Traut *et al.*, 1999; Scriber *et al.*, 1996).

As the Y (= W) chromosomes become genetically inert (independent of their X, = Z chromosome homolog) they tend to collect transposable elements as a “graveyard”

(Steinemann *et al.*, 1993; Kjellman *et al.*, 1995). Accumulation of retrotransposable elements may accumulate on the W chromosome because of the lack of crossing over or because mutation rates are predicted to be lower with in the W chromosome (with lower rates of cell division in oogenesis than in spermatogenesis, which has higher cell division rates; Goldsmith *et al.*, 2005). Insertion of conditional lethals onto the W chromosome to kill all females of pest Lepidoptera may be feasible and has been started in sterile insect management programs (Marec *et al.*, 2005).

The odd segregation with mostly dark (melanic morph) daughters from yellow mothers of *P. glaucus* and *P. canadensis* (neither of which should possess the *b+* gene on the W chromosome, Scriber & Evans, 1987), may now have an explanation. Either the common male mate to these two females carried and somehow transferred this gene to both female mates, or else a piece of the W chromosome with the *b+* gene may in the past have broken off and attached to an autosome or to the male Z chromosome in the father's ancestors. Such translocation possibilities have been reported in Mediterranean flour moths (Marec *et al.*, 2001).

Chromosome evolution among the Papilionidae has been largely inactive overall, or restricted to relatively small changes at few loci as suggested by the minimal karyotypic variation of 105 species tested thus far (modal number of $n = 30$, Emmel *et al.*, 1995). Emmel *et al.* (1995) suggest that "the species characters depend on variation in relatively few loci, and the majority of genes have probably persisted in relatively undisturbed sequences on these same chromosomes for 30–48 million years". Although lepidopteran chromosomes have been shown to be more resistant to ionizing radiation than other insects (LaChance & Graham, 1984) and may involve an inducible cell and/or DNA repair process (Koval, 1996), it is unclear if these have anything to do with their evolutionarily stable chromosome numbers. This chromosome biology may also help explain the fact that many interspecific crosses of swallowtail butterflies with diverse phenotypes (both closely and distantly related) have relatively minor chromosomal abnormalities and produce viable hybrid offspring (e.g., Scriber *et al.*, 1991c, 1995b). The analysis of interspecific hybrid genetic incompatibilities (egg viability, pupation and eclosion success) has generally reflected taxonomic distance (Ae, 1979, 1995; Hagen & Scriber, 1995). The species boundaries between *Papilio rutulus* and *P. eurymedon* of the *P. glaucus* group are clear in morphological and ecological distinctions, but not in mtDNA (Sperling, 1993). Allozyme differences are also greater in the Mexican swallowtail, *P. alexiares*, than mtDNA differences with *P. glaucus*, suggesting significant divergence of nuclear genes (Hagen & Scriber, 1991;

Sperling, 1993). Traditional species boundaries and those from mtDNA haplotypes do not always correspond, and thus the need for multi-trait analyses.

Hybrid species

Animal speciation has generally assumed splitting of a single lineage into an ancestral and a derived species. Hybrid speciation (a neospecies from two distant lineages or parental species) is rare (Dowling & Secor, 1997; Coyne & Orr, 2004; Gross & Reiseberg, 2005). Homoploid hybrid speciation is the creation of a lineage without a change in chromosome number (Mavarez & Linares, 2008; see also Nolte & Tautz, 2010).

Homoploid hybrid recombinant genotypes (prototypes of hybrid species) have been likened to "hopeful monsters" (Mallet, 2007) that are unlikely to survive competition from their parental species. Unfortunately, Mallet (2007), Seehausen *et al.* (2008) and mathematical modeling of hybrid speciation probabilities (Duenez-Guzman *et al.*, 2009) all fail to recognize that recombinant hybrid species may also arise by allochronic separation from both parental species (not just spatial separation). Such allochronic isolation has been shown for homoploid recombinant hybrids in the North American Great Lakes region *Papilio* hybrid zone (see Scriber & Ording, 2005; Scriber *et al.*, 2008a; Ording *et al.*, 2010). In addition to allochrony, other suspected cases of hybrid speciation in insects (see details below) show extreme habitat differences, host races, sexual selection (e.g. wing color) or species-specific pheromones and/or responses (or some combination of these) which may provide necessary isolation from parental types (Coyne & Orr, 2004; Mavarez & Linares, 2008).

If species are recognized as multi-locus "genotypic clusters", rather than completely isolated and unique entities with special qualities to differentiate them from races or genera, we have potential for considerable interspecific introgression and gene flow without loss of "species" status (Sperling, 2003; Coyne & Orr, 2004). Recognizing the reality of a continuum in genetic variation among polymorphic phenotypes (Leimar, 2009), genotypes, races, cryptic species, or "recognized discontinuities" (Diehl & Bush, 1984; J. Fordyce 2009 pers. comm.) is important. Hybrids are complicated because the interface between two species may be a mosaic geographically and genetically (Arnold, 1997; Harrison, 1998; Thompson, 2005; Mavarez & Linares, 2008; Ohshima & Yoshizawa, 2010; Payseur, 2010) and because it is debatable as to which "magic threshold" of gene flow would be necessary to produce a merged single "genotypic cluster" or a "good" species (Mallet, 2007).

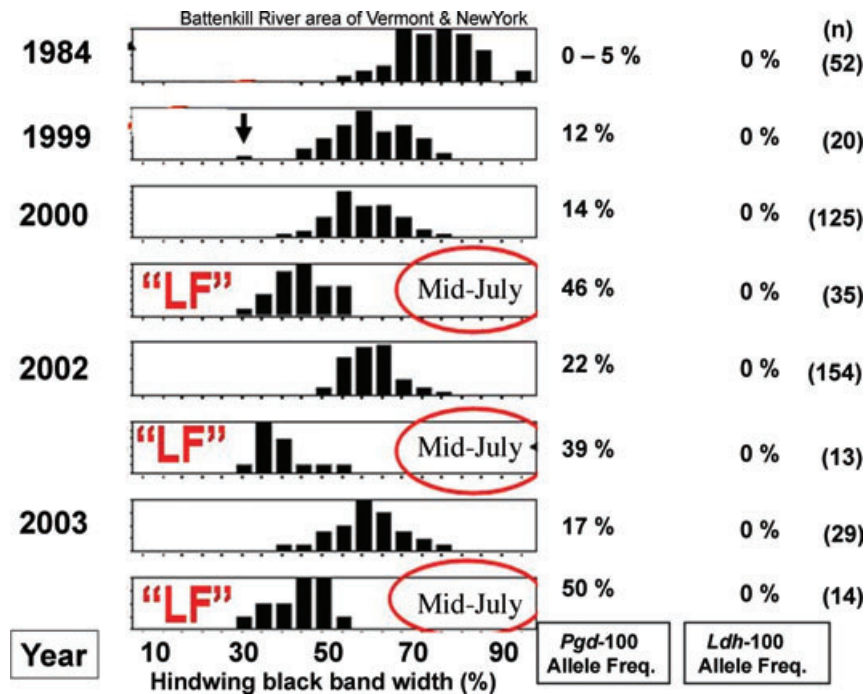


Fig. 7 The individual frequencies of male hind wing (HW) band widths in the same Battenkill River area of the Vermont/New York border, with corresponding diagnostic allozyme alleles shown. The first occurrence of the July late flight (LF) was a single individual captured in mid-July 1999 with a narrow black band (indicated by an arrow). The late flight had higher levels of introgression in the *glaucus*-like *Pgd*-100 and has been characterized as an interspecific hybrid swarm (or incipient homoploid hybrid species) with recombinant X-chromosome traits, several being “diagnostic” for the parental species (see also Fig. 8).

Even less accepted by taxonomists and systematists has been the idea that “hybrid species” could arise inside a hybrid zone (Coyne & Orr, 2004). However, divergent ecological selection as seen in the *Papilio* hybrid zone (Scriber *et al.*, 2008a), contributes to heterogeneous genomic divergence producing various “genomic islands” of divergence and a “genetic mosaic”. Genetic (genomic) hitchhiking during ecological selection may contribute to rapid fitting of the available niches (Nosil *et al.*, 2009a, 2009b; Via, 2009). Probable animal hybrid speciation was also reported in 2005 for the mountain swallowtail butterfly, *Papilio* (= *Pterourus*) *appalachiensis* (Pavulaan & Wright, 2002) from *P. glaucus* and *P. canadensis* parents where species-diagnostic Z-linked allozymes were mixed (fixed for alternative alleles, Scriber & Ording, 2005). The recombinant *P. appalachiensis* has many hybrid-like traits (morphological, physiological, detoxification chemistry and biochemical factors, Scriber *et al.*, 2008a; Mercader *et al.*, 2009a) but it is the post-diapause developmental delay that makes this recombinant genotype reproductively isolated, as with the late flight in Vermont (Figs. 7 & 8).

In *Papilio* this allochronic separation may be enhanced by a “thermal niche” (1 444–1 611°C degree-days annually) such as that found only on the warmer side of the hybrid zone (Figs. 1 & 2). Thus this *P. appalachiensis* (mountain swallowtail) represents a genetically distinct (Scriber & Ording, 2005), morphologically identifiable population of hybrid-like individuals, with recombinant Z chromosomes reflecting discordant DNA (Putnam *et al.*, 2007), with males and females that appear reproductively isolated from the parental species by allochronic adult flight times (Ording *et al.*, 2010), and that occupies a unique “thermal niche” inside the hybrid zone (Scriber *et al.*, 2008a). In most “species” definitions (Harrison, 1998), this homoploid hybrid species would fit (Mavarez & Linares, 2008). In fact, it seems that these various genotypes (morphospecies) have been produced in laboratory backcrosses, with extensive recombination and co-segregating diapause and wing traits (Scriber *et al.*, 2008a; Ording, 2008).

In more than 40 000 multichoice oviposition events of the polyphagous North American *P. glaucus* and *P. canadensis*, the primary difference was limited to a

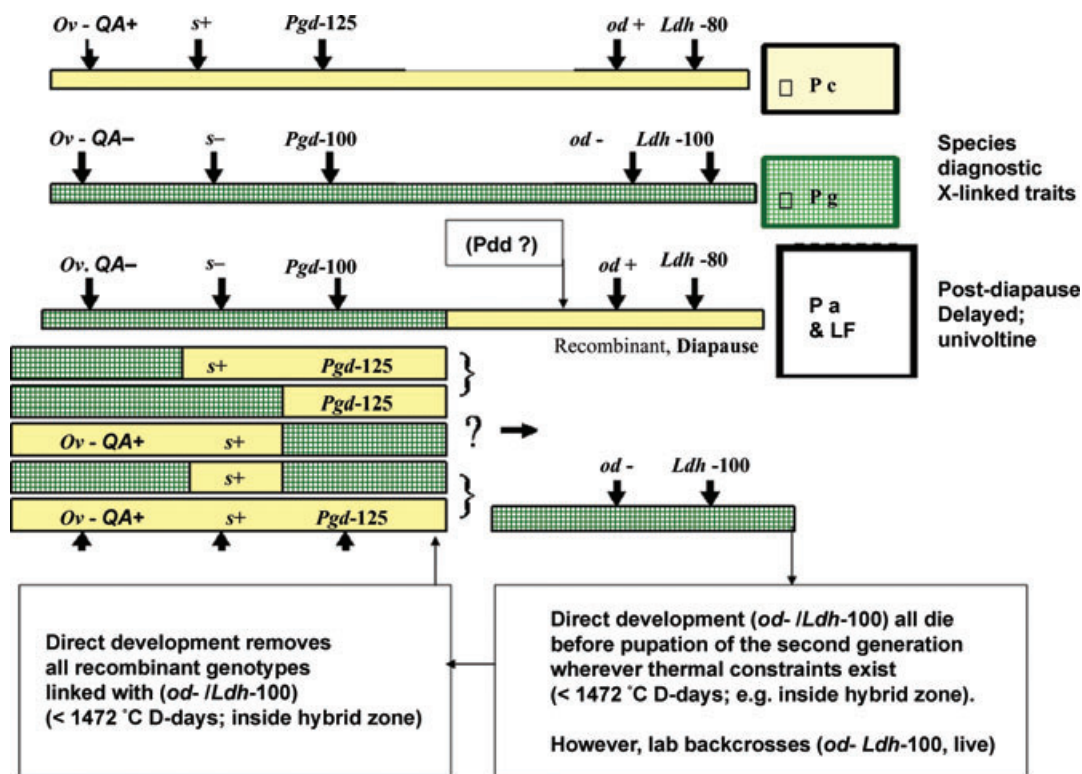


Fig. 8 Z-chromosome cartoon with selected traits known to occur in *P. glaucus* (Pg), *P. canadensis* (Pc) and the recombinant genotypes of the late flight (LF) from Vermont and *P. appalachiensis* (Pa), both with the post-diapause delay (pdd). The *od+* results in obligate diapause (univoltinism) for all females (hemizygous) and most males (heterozygous) and may be necessary for the post-diapause delay. *Ldh-100* is found basically fixed for the multivoltine *P. glaucus* and closely linked to *od-* (facultative diapause; non-diapause). All genotypes of recombinant hybrids possessing the *od-* gene and the closely linked *Ldh-100* allele (including Z-linked dark melanism suppressors/enablers = *s+*/*s-*, differential oviposition preferences, and other traits; Scriber, 1994; Putnam *et al.*, 2007) would be eliminated by failure to reach the diapausing pupal stage in second generation inside the thermally defined hybrid zone. However, in the laboratory backcrosses, we find these individuals direct-develop without diapause under long day photoperiods (and have very close linkage with *Ldh-100*; Ording, 2008).

Z-linked shift in host rank hierarchy caused by acceptance of quaking aspen (Salicaceae) and reduced specificity for tulip tree (Magnoliaceae, Mercader & Scriber, 2005, 2007; Mercader *et al.*, 2008) which is toxic to *P. canadensis* and *P. troilus* groups (Nitao *et al.*, 1991b; Scriber *et al.*, 1991a; Frankfater *et al.*, 2005). A lack of the Z-linked aspen acceptance (Scriber *et al.*, 1991b) in the allochronically distinct hybrid swarm late flight (Scriber *et al.*, 2008a; Ording *et al.*, 2010) was found, probably due to introgression from the parental, *P. glaucus* (Mercader & Scriber, 2007, 2008b; Fig. 1). In the eastern hybrid zone, the hybrid swarm reflects the identical oviposition preference hierarchy of the introgressing parental species, *P. glaucus*. However when the favored hosts tulip tree (Magnoliaceae) and hop tree (Rutaceae), are absent (as in the hybrid zone at this location), a secondary host of

both parental species is favored (ash, *Fraxinus* species of the Oleaceae, Mercader *et al.*, 2009a). This may represent the beginnings of a host shift or host race, but unlike the case with the host shift to *Lonicera* leading to evolutionary divergence in *Rhagoletis*, a potential host shift to ash (*Fraxinus* spp.) trees by the recombinant hybrid genotypes inside the *Papilio* hybrid zone is likely to be the result of ecological divergence (allochronic delayed post-diapause emergence of recombined hybrid genotypes) not its cause (Mercader *et al.*, 2009a).

Other recent examples (hybrid zones and homoploid hybrid speciation)

In 2005, a host shift to an invasive honeysuckle plant (*Lonicera* spp.) was credited with catalyzing rapid hybrid

speciation in *Rhagoletis* spp. (the *Lonicera* fly: Schwarz *et al.*, 2005). Homoploid recombinant hybrid speciation is accompanied without a change in chromosome number (Coyne & Orr, 2004), and a unique mixture of species-specific allozyme alleles indicated that this “*Lonicera* fly” was formed by hybridization of the blueberry maggot (*R. mendax*) and the snowberry maggot (*R. zephyria*, Schwarz *et al.*, 2005, 2007).

Putative hybrid speciation in *Heliconius* butterflies in Colombia was not due to host races or pheromones, but may have involved visual color differences leading to assortative mating of hybrids of *H. heurippa* and its parental species *H. melpomene* and *H. cydno* (Mavarez *et al.*, 2006). This behavior, combined with some geographic isolation and some post-zygotic isolation (with intermediacy in some traits), led to speculation that a hybrid origin may be involved for *H. heurippa*.

In *Lycaeides* (Gompert *et al.*, 2006) extreme alpine habitat conditions may have played a major role in development of a reproductively isolated homoploid hybrid species from two parental species. The highest elevation alpine populations are a genetic mosaic of the two parentals and is not compatible with the bifurcating speciation concept, since no F-1 primary hybrids could be found (Gompert *et al.*, 2006), as was the case with the late flight hybrid swarm of *Papilio* (and *P. appalachiensis*, Scriber & Ording, 2005).

A classical hybrid zone interaction between *Limenitis arthemis arthemis* and *L. a. astyanax*: Platt & Brower, 1968) has shown asymmetrical gene flow, mostly from the southern mimetic populations into the northern non-mimetic populations (Mullen *et al.*, 2008). Barriers to gene exchange were incomplete, but different wing pattern phenotypes appear to reflect a complex history of divergence and gene flow between two lineages that were not completely isolated. In Sardinia and Corsica there are low levels of introgression of sex-linked traits and mitochondrial DNA with more introgression in autosomal loci in hybrids between *Papilio hospiton* and *P. machaon* (Cianchi *et al.*, 2003).

These systems may represent additional examples of natural selection acting to produce divergence with gene flow (Caillaud & Via, 2000; Hawthorne & Via, 2001; Feder *et al.*, 2003; Emelianov *et al.*, 2004; Turner *et al.*, 2005; Bull *et al.*, 2006; Kronforst *et al.*, 2006; Michel *et al.*, 2006; Funk *et al.*, 2006; Machado *et al.*, 2007; Putnam *et al.*, 2007; Egan *et al.*, 2008; Nosil, 2008; Nosil *et al.*, 2002, 2009b; Via, 2009; Ohshima & Yoshizawa, 2010; Payseur, 2010). For most researchers the “species boundary” has been recognized as a gradient in the degree of reproductive isolation (from one panmictic population to reproductively isolated multi-trait clusters). Divergence

with gene flow is clearly becoming more recognized in the past few years, and defining species using “complete” reproductive isolation should now be replaced with the concept of “recognizable discontinuities” or stable clusters of phenotypes that remain distinctive in the face of gene flow and hybridization (Barton, 2001; Harrison, 1998; Sperling, 2003; Mullen *et al.*, 2008; Nolte & Tautz, 2010). Implications of independent genetic introgression of individual autosomal, sex-linked and mtDNA traits has not been adequately addressed in consideration of “species borders” (Parmesan *et al.*, 2005) or species movements under climate change (Parmesan, 2006). It is time to recognize “invasive traits” may be at least as significant in their impact as “invasive species”.

Independent movement of species diagnostic traits as in *Papilio* (Scriber, 2002a; Scriber & Ording, 2005; Putnam *et al.*, 2007; see Fig. 2) with global warming (and not just species movement, Parmesan *et al.*, 2005; Parmesan, 2006) shows porous species borders across a hybrid zone (Zakharov & Hellmann, 2008; Gompert *et al.*, 2008). Nonetheless, the immediate isolation of interspecific univoltine *Papilio* hybrid recombinant genotypes with delayed post-diapause emergence times could provide almost instant reproductive isolation (Scriber *et al.*, 2008a; Ording *et al.*, 2010; Figs. 7 & 8). This scenario with segregating adult emergence times (*glaucus*-like direct development; *canadensis*-like early post-diapause emergence, and the *appalachiensis*-like delayed post-diapause emergence, Ording, 2008) can be created in laboratory backcrosses. However, the fate of this LF genotype or hybrid species of *P. appalachiensis* outside the thermal niche (1 444–1 611°C degree-days, or 2 600–2 900°F degree-days; see Fig. 1) remains unclear. It is feasible that the warming temperatures in the southern Appalachian Mountains of North Carolina and northern Georgia (Fig. 9) could drive the *Papilio* “*appalachiensis*” genotype/species up the mountain tops to extinction (Hodkinson, 2005; Mercader & Scriber, 2008a), or that gene swamping from the bivoltine (and now trivoltine) *P. glaucus* populations from lower elevations (Peterson, 1995; Scriber *et al.*, 2008a) in that region might blur or eliminate this unique “hybrid genotype” (a morphologically identifiable, genetically distinct, temporally isolated univoltine population), especially with further climate warming.

To evolutionary ecologists, the arbitrary “taxonomic” differences between host races (or partially isolated subspecies) and cryptic species (that are essentially reproductively isolated) are neither significant nor the most interesting issues. The ecological and evolutionary processes producing this divergence continuum (and coevolutionary mosaics) are the scientifically attractive issues

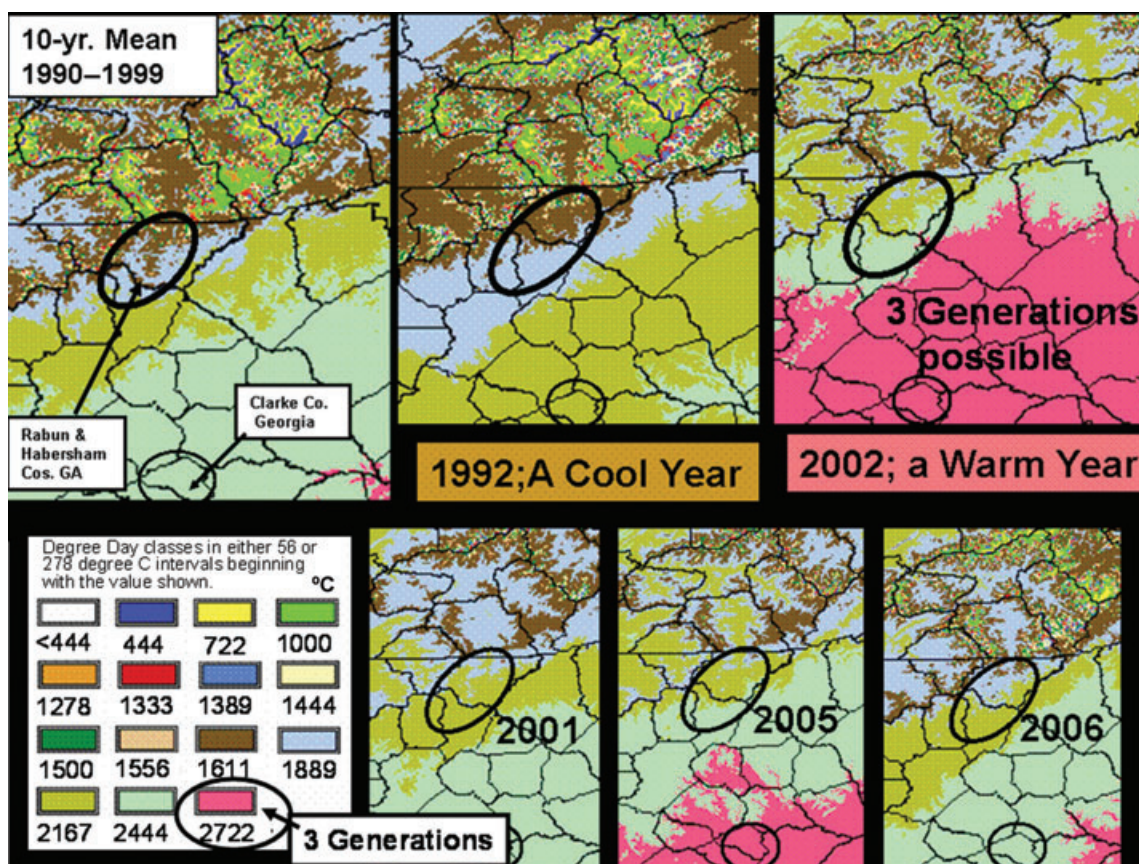


Fig. 9 Thermal landscapes (seasonal total degree-days) in the southern Appalachian Mountains (Rabun/Habersham Cos. in northern Georgia, where type specimens of *P. appalachiensis* have been described by Pavulaan & Wright, 2002; cf. Fig. 1) for 1990–1999, 1992 (a cold year), and for several warmer years (2001, 2002, 2005, 2006).

(Mavarez & Linares, 2008; Gould *et al.*, 2009; Payseur, 2010). In this regard, the biodiversity generation with herbivorous insects and their host plants remains fascinating. One of the most exciting new hypotheses regarding the generation of biodiversity is the “oscillation hypothesis” (Janz & Nylin, 2008; see below).

Oscillation hypothesis and ancient specialists

The concept that host specialization such as that driven by adaptive radiations can lead to “evolutionary dead ends” has been recently challenged (Kelly & Farrell, 1998; Termonia *et al.*, 2001; Nosil, 2002; McCoy *et al.*, 2005; Stireman, 2005; Yotoko *et al.*, 2005; Winkler & Mitter, 2008; Mercader *et al.*, 2009a; Nyman, 2010) by studies showing the occurrence of polyphagous plasticity and the “polyspecialist” concepts (Nylin & Janz, 2009; Nylin & Wahlberg, 2009). The oscillation hypothesis (Janz *et al.*, 2006; Janz & Nylin, 2008; Nylin & Janz, 2009; Nylin & Wahlberg, 2009) suggests that specialized lineages may

produce generalists that may subsequently specialize again, especially if enhanced by geographic fragmentation or assortative mating, and that “diversity of host use is driving species richness, rather than the reverse” (Janz *et al.*, 2006). Transition rates between specialists and generalists suggest that specialization is not an evolutionary dead-end (Nosil, 2002). It was noted that the Nymphalidae butterflies have maintained behavioral/biochemical abilities to use ancestral hosts over long time periods allowing recolonization (Nylin & Janz, 2009). With the exception of *P. troilus* on Lauraceae (Cohen *et al.*, 1992; Nitao *et al.*, 1992; Carter *et al.*, 1999; Scriber *et al.*, 2001), the Papilionidae generally support the oscillation hypothesis. In the Papilionidae, several recent studies show similar trends in which long-time family specialists on ancient Angiosperm families such as the Rutaceae, Monimiaceae, Annonaceae and Magnoliaceae are able to use additional host plants from several other families (Scriber *et al.*, 2006, 2007, 2008b; Larsen L. *et al.*, 2008). Nylin and Janz (2009) point out that differentiation between

“polyspecialists” and “general purpose genotypes” will require additional studies of the physiological and behavioral traits conveying host specialization/generalization. Recently, Mercader *et al.* (2009a) have shown that potential “ash-race” oviposition preferences inside the hybrid zone may quickly appear in hybrid recombinants of two polyphagous *Papilio* species (local specialization with Z-linked hierarchy rank order oviposition preferences). In these hybrids the larval detoxification abilities (autosomal performance traits) are intermediate for Magnoliaceae and Salicaceae host species (Scriber *et al.*, 1989). Both preference and performance traits can be readily passed to new recombinant genotypes (or potential homoploid hybrid species; Scriber & Ordning, 2005). The evolution of an “ash-feeding host race” inside the hybrid zone (that lacks tulip tree and hop tree favorites) suggests local specialization arising from generalist parental species, but at the same time these recombinant hybrids of the late flight and *P. appalachensis* also reflect wider host potential because larval hybrids have both the Salicaceae and Magnoliaceae host detoxification enzymes (Scriber *et al.*, 1989, 1999; Scriber & Ordning, 2005). The derivation of the polyphagous *P. glaucus* and *P. canadensis* from the oligophagous Rutaceae-feeding *P. multicaudatus* was due to a few mutations in the cytochrome P-450 enzymes, which allowed host range broadening without loss of ancestral detoxification abilities (Li *et al.*, 2002, 2004; Mao *et al.*, 2007).

Summary: From ancient angiosperm associations to geographically local and genetically variable mosaics

The dynamic process of host range evolution for herbivorous insects has fascinated ecologists for centuries, yet because of natural variation among and within species and their geographical, allelochemical and thermal landscapes, combined with an impressive array driving factors shaping global biodiversity, we remain basically unable to easily discern any overriding general organizational global patterns for insects (Scriber, 2002a, 2002b). It has been recognized that phenotypes of both plants and herbivores vary with adaptations of local populations, producing geographical mosaics (Scriber & Lederhouse, 1992; Thompson, 1994, 2005; Scriber, 1996b, 2002a; Mopper & Strauss, 1998; Gavrillets, 2004), including evolutionary “sky islands” (DeChaine & Martin, 2004) as well as phytochemically-defined plant “islands” (Nyman, 2010) and real islands such as Great Lakes islands (Ordning, 2001). The underlying genetic framework also involves genomic mosaics and phenotypic/ecological

plasticity (Thompson, 2005; Putnam *et al.*, 2007; Via, 2009). Taxonomic classification of somewhat isolated evolutionary clusters (species) and the categorization of specialists and generalists at various levels of taxonomic designation have been proven to be an elusive quest (Arnold, 1997; Sperling, 2003; Coyne & Orr, 2004; Fitzpatrick *et al.*, 2008; Scriber, 2010). However, while unresolvable theories and unnecessary semantics persist, the mechanistic processes involved in generating this dynamic web of ecological and evolutionary interactions remain of fundamental interest to most. Nonetheless, taxonomic compulsion persists for attempts at categorical systematic criteria imposed over a continuum (i.e., how much gene flow can there be with hybridizing species before they are not considered “real” species, but rather subspecies, geographical races, ecotypes, demes, host races, cryptic species, sibling species or sister species, etc.; see Berlocher & Feder, 2002; Dres & Mallet, 2002). Sometimes the criteria for successfully delineating the taxonomic borders of species simply do not exist (de Queiroz, 2005; Hey, 2006). Deciding at which point divergent lineages might be considered species has been generally focused on older splits (sometimes perceived as “good” species) but incipient species and hybrid species enhance understanding of the mechanisms of speciation and are especially valuable (Nolte & Tautz, 2010). Furthermore, while spatial roles are fundamental in diverging taxa, arguments over the definition of sympatry or “micro-allopatry” continue (Mallet *et al.*, 2009). Whether or not we define divergence into ‘ecological’ (rapid) and ‘evolutionary’ timescales (Gingerich, 2001), both ends of this timescale are involved (Eckert *et al.*, 2008; Loxdale, 2010; Payseur, 2010). While host-associated divergence in phytophagous insects has been shown to be somewhat common, ecological speciation in parasitic species on animals may be even more common, since it almost always is both the food source and breeding site (De Meeus *et al.*, 1998; McCoy *et al.*, 2005; Kempf *et al.*, 2009).

During ecological speciation the genomically localized heterogeneity among loci brought about by strong divergent selection may initiate incipient species or genotypes (and the quantitative trait loci involved in reproductive isolation may look like a “genetic mosaic” with “divergence hitchhiking” of closely linked traits (Via & West, 2008; Maroja *et al.*, 2009b; Via, 2009). Gene exchange in other regions of the genome may continue with low levels of differentiation occurring (Wu, 2001; Smadja *et al.*, 2008). How porous the “species boundary” can be with interspecific hybridization (still retaining species status) has been the subject of contention (reviewed in Sperling, 2003; Galtier *et al.*, 2009). Recent studies suggest that neospeciation (incipient species) as well as long

persistence of such introgressive porosity occurs with extensive gene flow during speciation more than previously believed (Hey, 2006; Bolnick & Fitzpatrick, 2007; Kronforst, 2008; Nosil, 2008; Niemiller *et al.*, 2008; Scriber *et al.*, 2008a; Ohshima & Yoshizawa, 2010).

Host-affiliated divergence may play an important role in speciation (Tilmon, 2008), with host-associated races of insect herbivores being prominent points of interest because of the potential for partial reproductive isolation they provide (see above and Nosil *et al.*, 2009a, 2009b; Peccoud *et al.*, 2009). Study of the causes of reproductive isolation between ecological races may help us to get a peek at the early barriers to gene flow before such isolating mechanisms become obscured by additional species differences that could subsequently arise (Stelkens & Seehausen, 2009; Ording *et al.*, 2010). The mosaic nature of the genome during these early stages (“genomic islands of divergence”) has become an important focus for future work (Laine, 2009; Nosil *et al.*, 2009a, 2009b; Via, 2009). However, even though spatial genetic variance has been recognized for decades (Storfer *et al.*, 2007; Excoffier *et al.*, 2009), we still know little about how this diversity originates, making trait analyses and their causal ecological mechanisms such as host affiliations, thermal constraints and sexual selection, especially important.

It is clear that independent, non-concordant “diagnostic trait” movement across the historical *Papilio* hybrid zone (Fig. 2; see also Maroja *et al.*, 2009a) illustrates the need for multiple indicators in their systematic biology and presents difficulties for determining the extent of “hybrid zone movement” (Buggs, 2007). To delineate “species boundaries”, mtDNA is insufficient (Galtier *et al.*, 2009), and morphology, behavioral assays, ecological analyses and molecular genomics will be essential. For example, recent examples of divergence with gene flow have been reported for *Drosophila* by Wang *et al.* (1997), for the European corn borer (Dopman *et al.*, 2005), for *Heliconius* butterflies (Bull *et al.*, 2006), leaf beetles (Egan *et al.*, 2008), pea aphids (Via, 2009), crickets (Maroja *et al.*, 2009a, 2009b), as well as *Papilio* tiger swallowtails described here (Bossart & Scriber, 1995; Scriber & Ording, 2005; Putnam *et al.*, 2007). Such local adaptations and divergence will vary with climate, and may be significantly constrained with regard to differences in thermal tolerances of tropical versus high latitude (Deutsch *et al.*, 2008; Hoffmann, 2010; Scriber, 2010).

In addition to gene flow and natural selection, phenotypic plasticity, maternal effects, and sexual selection all impact population dynamics, speciation, community interactions, ecosystem function and phylogeography of herbivorous insect communities (Hewitt, 2001; Whitham *et al.*, 2003; Scriber, 2004; Carroll *et al.*, 2007; Case *et al.*,

2005; Barbour *et al.*, 2009; Thompson, 2009; Hoffmann, 2010). The swallowtail butterflies of the Papilionidae have provided a useful model system for investigating ecological and evolutionary processes and outcomes at mosaic genome levels (as well as globally) and illustrate ancient angiosperm associations as well as local specialization and recent hybrid speciation processes (K. Kunte, C. Shea, M.L. Aardema, J.M. Scriber, P. Andolfatto, T. Juenger, L.E. Gilbert, M.R. Kronforst [2010] ‘Sex chromosome mosaicism and hybrid speciation among tiger swallowtail butterflies’, in review). While local host plant adaptations occur in some populations of polyphagous *Papilio* species, gene flow clearly continues for many traits, suggesting decreased adaptive divergence with more gene flow (Bossart & Scriber, 1995). However, adaptive divergence inside the hybrid zone has also decreased gene flow via temporal delays in post-diapause emergences of the late flight (recombinant LF) populations and in *P. appalachiensis* (Scriber & Ording, 2005; Ording *et al.*, 2010). Such interactions between adaptive divergence and gene flow are complex and may occur simultaneously when ecological factors (natural or sexual selection) drive diversification (Nosil & Crespi, 2004; Hey, 2006; Räsänen & Hendry, 2008). This review has recognized historical concepts but also reflects some of the impetus created in recent genetic advancements in understanding the genomic dynamics of and ecological/evolutionary divergence in insect–plant interactions.

Acknowledgments

This review reflects decades of personally treasured friendships and assistance from colleagues in the insect–plant interactions field of study. The Papilionidae research from our laboratory was supported by such academic synergism and also in part by the National Science Foundation (DEB-9201122; DEB-9510044; DEB 0716683; DEB 0918879) and the Michigan Agricultural Experiment Station (Project # 01644). I wish to thank all laboratory members and friends for their enthusiasm and assistance over the years, and most recently, Matthew Aardema, Rodrigo Mercader and Gabe Ording. Special thanks are extended to one particularly helpful reviewer.

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Accepted July 23 2010