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Authors: Rheindt, Frank E., and Edwards, Scott V.

Source: The Auk, 128(4) : 620-632

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/auk.2011.128.4.620>

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PERSPECTIVES IN ORNITHOLOGY

GENETIC INTROGRESSION: AN INTEGRAL BUT NEGLECTED COMPONENT OF SPECIATION IN BIRDS

FRANK E. RHEINDT^{1,2,3} AND SCOTT V. EDWARDS^{1,2}

¹Harvard University, Department of Organismic and Evolutionary Biology, 26 Oxford Street, Cambridge, Massachusetts 02138, USA; and

²Museum of Comparative Zoology, 26 Oxford Street, Cambridge, Massachusetts 02138, USA

HYBRIDIZATION, OR THE act of reproduction between different species, is common in birds (Grant and Grant 1992) and can be an agent of adaptive evolution (Veen et al. 2001). When hybridization occurs, a species' genetic material may enter the gene pool of another and thereby introduce genetic novelty. This process is called "genetic introgression" (hereafter "introgression"; Anderson 1949). Although known for decades, the incidence of introgression in nature has long been underappreciated (e.g., Currat et al. 2008). Only recently have evolutionists come to regard it as an important and pervasive mechanism in speciation, in the maintenance of genetic diversity and in the introduction of advantageous novelty into the gene pool (Arnold et al. 1999, Noor et al. 2000, Seehausen 2004). In fact, genetic data now suggest that our own species may have undergone a complicated history of introgression with at least two extinct hominine lineages (Green et al. 2010, Reich et al. 2010). Another reason why introgression is an important topic is the impact of human-induced climate change, which is rapidly shifting vegetation boundaries and creating new hybrid zones, with little-known consequences for the genetic integrity of species (Mank et al. 2004, Brumfield 2010).

There has been a tremendous increase in introgression-related avian research since a comprehensive overview of the introgression complex between the Blue-winged Warbler (*Vermivora cyanoptera*) and the Golden-winged Warbler (*V. chrysoptera*) appeared in *The Auk* five years ago (Confer 2006). Here, we seek to fill a gap by summarizing the most important recent advances in avian introgression research and our current understanding of locus-specific differences in introgression dynamics, the detection of introgression, its directionality, and its relevance to conservation, phylogenetics, and speciation research.

INTROGRESSION PATTERNS DIFFER AMONG DNA CLASSES

Different DNA classes are expected to vary in their potential to introgress between species. One reason is "Haldane's rule," which predicts that heterogametic hybrid offspring are often less viable or fertile (Haldane 1922). The basis of Haldane's rule seems to lie in

the recessiveness of alleles that decrease hybrid fitness, such that, say, the ZW sex suffers more than the ZZ sex because Z-linked alleles causing postzygotic isolation tend to have greater cumulative effects when hemizygous than when heterozygous ("dominance theory"; Turelli and Orr 1995). In birds, females are the heterogametic sex (ZW), and experiments in ducks have empirically confirmed female hybrid inviability (Kirby et al. 2004). In the absence of positive selection, we can thus predict that mitochondrial DNA (mtDNA) and W-linked DNA, which are female-transmitted, are not as likely to introgress as Z-linked DNA and are even less likely to introgress than autosomal DNA.

In one of the earliest avian introgression studies, Tegelström and Gelter (1990) interpreted differences in interspecific divergence between mtDNA and nuclear DNA (nDNA) in a European flycatcher (*Ficedula*) hybrid zone as a sign of nuclear introgression. Even in the absence of introgression, divergence patterns between mtDNA and nDNA often differ because of the evolutionary properties of these DNA classes. However, the *Ficedula* hybrid zone has by now become a model system for the investigation of differential introgression among DNA classes, and Tegelström and Gelter's (1990) initial suspicions of species-wide nDNA introgression have been confirmed (Sætre et al. 2001, 2003).

Comparisons of the incidence of introgression between sex-linked and autosomal markers seem to demonstrate that the Z chromosome in *Ficedula* and other birds is particularly impermeable to introgression, perhaps more so than predicted by Haldane's rule (Sætre et al. 2003, Borge et al. 2005b, Carling and Brumfield 2008, Carling et al. 2010, Storchová et al. 2010). Flycatchers in the genus *Ficedula* exhibit plumage character displacement where species overlap, albeit at different regional intensities (Borge et al. 2005a). At the same time, their plumage characters and female-choice characters are Z-linked and under selection (Sætre et al. 2003, Sæther et al. 2007, Backström et al. 2010a). This simultaneous Z linkage, coupled with potentially reduced rates of recombination on the female Z chromosome, is a strong argument in favor of prezygotic factors playing a role in reduced Z introgression. This

³E-mail: frankrheindt@yahoo.com.au

is all the more plausible considering that Backström et al. (2010b) tested and rejected a competing hypothesis that rearrangements in the *Ficedula* Z chromosome account for its impermeability to introgression.

On the other hand, many other avian hybrid zones do not exhibit character displacement and may lack these special conditions of *Ficedula* gene arrangement. This suggests that postzygotic factors may be equally important in reducing levels of Z introgression. Indeed, Ellegren (2009) proposed an accelerated rate of adaptive divergence of Z-linked loci compared with autosomal loci (“large-Z effect”), suggesting that the Z chromosome is particularly impermeable to introgression because it holds a disproportionately high number of loci that may be subject to the dynamics of dominance theory (Turelli and Orr 1995). The large-Z effect is supported by recent work on a Z-linked locus involved in egg-laying characters: Carling and Brumfield’s (2009) study of a hybrid zone between two bunting species (*Passerina*) showed that the foreign allele (i.e., typical for the rarer species at any given locality in the hybrid zone) is selected against, prompting the authors to suggest that the Z chromosome may be a hotspot for “speciation genes” that are linked to reproductive isolation.

Many studies that have sampled both mtDNA and nDNA across avian hybrid zones have retrieved the pattern of increased nDNA versus mtDNA introgression predicted by Haldane’s rule. Mammals exhibit the opposite pattern, presumably because of their male heterogamety (Petit and Excoffier 2009). Disregarding cases of geographically widespread introgressive mtDNA sweeps for the moment, levels of mtDNA introgression in avian hybrid zones are often low or zero (Tegelström and Gelter 1990; Helbig et al. 2001, 2005; Sætre et al. 2001, 2003; Bensch et al. 2002; Crochet et al. 2003; Kvist and Rytönen 2006; Secondi et al. 2006; Martínez-Cruz and Godoy 2007; Vallender et al. 2007; Carling and Brumfield 2008; Rush et al. 2009) or are at least accompanied by equivalent levels of nDNA introgression (Brumfield et al. 2001, Gay et al. 2008, Rheindt et al. 2009). Studies on ducks in the genus *Anas* may show an opposite trend (McCracken et al. 2001; Kulikova et al. 2004, 2005; Peters et al. 2007)—similar to that in mammals—in that introgression appears to be more extensive in mtDNA than in nDNA. Petit and Excoffier (2009) accounted for this anomaly by invoking predominantly male-biased dispersal in ducks, which contrasts with female-biased dispersal modes in most other birds. Whether the incidence of mtDNA versus nDNA introgression in ducks really is different from that in other birds, and whether Petit and Excoffier’s (2009) explanation for this phenomenon is correct, remains to be tested with additional data sets that monitor both mtDNA and nDNA variation.

Dominance theory predicts reduced levels of introgression in avian mtDNA and sex-linked loci as compared with autosomal loci on the basis of the lower fitness of heterogametic hybrids (Turelli and Orr 1995). However, this prediction holds only for loci that are not otherwise under natural selection. The premise of neutrality is often violated, particularly for mtDNA, resulting in departures from the patterns expected for a strict Haldane’s process. As discussed below, positive selection can drive mtDNA introgression well beyond hybrid zones and lead to replacement sweeps across entire species distributions (Fig. 1).

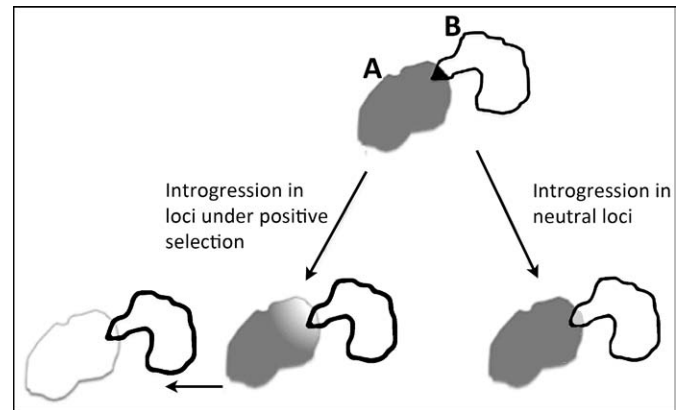


FIG. 1. Introgression scenarios for loci under neutrality and positive selection. Upper diagram depicts distributions of species A and B, with a stable hybrid zone in black. Under positive selection, the genotype of species B will sweep over the range of species A and replace the native genotype over time. Under neutrality, introgression will largely be restricted to the hybrid zone (indicated in light gray) in large populations. (Note that genetic drift can also account for neutral genetic sweeps in small populations).

POTENTIAL FOR INTROGRESSION DIFFERS AMONG AUTOSOMAL LOCI

Research into differences in introgression potential among autosomal, sex-linked, and mtDNA loci is an active field of inquiry in both model and non-model species. At the same time, studies on birds have played an important role in revealing large variation in the extent of introgression not only among distinct genomic compartments but also among autosomal loci themselves (e.g., Borge et al. 2005a, Kvist and Rytönen 2006, Secondi et al. 2006, Martínez-Cruz and Godoy 2007, Peters et al. 2007, Vallender et al. 2007, Carling and Brumfield 2008, Gay et al. 2008, Carling et al. 2010). For instance, among 13 autosomal loci sampled across a *Passerina* hybrid zone, Carling et al. (2010) detected differences of more than an order of magnitude in levels of haplotype and nucleotide diversity, attributing these to locus-specific differences in introgression. However, many previous studies have been restricted to a dozen or fewer nuclear markers, a level of sampling that makes it challenging to determine the causes of differences in introgression potential among autosomal loci. In addition, the representation of autosomal loci in hybrid zone studies may be biased by the preferential inclusion of markers that show strong clines, which can result in an ascertainment bias in the representation of genome-wide patterns (Brumfield et al. 2001, Yuri et al. 2009). Lastly, introgression—especially when diagnosed using few markers—can be difficult to differentiate with certainty from unusual patterns of shared ancestry, such as incomplete lineage sorting (see below). Therefore, we may currently underestimate the actual extent of differential introgression among autosomal loci.

Wilson et al. (1985) suggested that differential introgression may be a chance process determined by random lineage extinction. But considering consistent and potentially selection-related differences in introgression patterns between different DNA classes (see above), it is plausible to envisage that selective pressures may also account for locus-specific differences (Fig. 1). If

such pressures apply, genetic linkage may amplify the reduction or reinforcement of introgression from the selected locus to neighboring loci, as has been proposed by Harrison et al. (1987) for a cricket hybrid zone. This introgression linkage hypothesis has remained untested for birds in the era of Sanger sequencing but may soon be amenable to examination with the advent of second-generation sequencing platforms in avian evolutionary research. First insights from a mouse hybrid zone indicate that linkage disequilibrium seems to lead to *en bloc* introgression of neighboring loci but that recombination may be steadily breaking down these associations over time (Wang et al. 2011).

CLASSICAL INTROGRESSION ACROSS A HYBRID ZONE

The most direct way to study introgression is across a classic hybrid zone where two species come into contact and engage in variable levels of hybridization. Yet even in a hybrid zone it is challenging to identify patterns of DNA sharing as introgression. A large combination of marker types may be needed to identify individuals with introgressed DNA (Väli et al. 2010b).

Hybrid zones are often “tension zones” in which selection acts against the neutral diffusion of alleles across species (e.g., Kvist and Rytkönen 2006; Carling and Brumfield 2008; Gay et al. 2008, 2009; Irwin et al. 2009a; Mettler and Spellman 2009). Given constant ecological or reproductive conditions, a hybrid zone can be constrained to a narrow width by this mechanism, preserving the genetic integrity of the species on either side. Selection against hybrids is routinely attributed to female hybrid inviability via Haldane’s rule. However, there is mounting evidence that a variety of other factors may additionally put hybrids at a disadvantage. For instance, Leichty and Grier (2006) demonstrated sexual selection against hybrids in warblers (*Vermivora*), and Cicero (2004) suspected that adaptation to local environments may be an important factor in constraining a titmouse (*Baeolophus*) hybrid zone. In chickadees (*Poecile*) it may be either natural or sexual selection that accounts for reduced reproductive success in hybrids (Bronson et al. 2005). Both prezygotic and postzygotic factors may be important in constraining a hybrid zone, depending on the model species.

SHIFTING HYBRID ZONES AND HYBRID SPECIATION

Introgression often occurs at the front of immigration waves, where invaders will have a hard time finding partners of their own species. A special case of this process was demonstrated on Round Island in the Indian Ocean, which was recently invaded by an Atlantic and a Pacific species of petrel (*Pterodroma*), leading to a petrel population that possesses genetic affinities to both species (Brown et al. 2010). More typically, however, immigration waves are associated with a classical hybrid-zone scenario in which one species slowly pushes back the other in geographic space (e.g., Rohwer et al. 2001, Haig et al. 2004, Secondi et al. 2006, Gay et al. 2008). In most of these cases, pure individuals of the invading species move ahead past the center of the hybrid zone and leave behind an area of primarily hybrid birds.

In moving hybrid zones, introgression may occur at such a massive genomic scale that recipient populations can be considered the products of “hybrid speciation.” The crucial distinction between a population being subject to rampant introgression versus one that has become a new hybrid species seems to depend on

whether reproductive isolation toward both parental species is complete (Hermansen et al. 2011). Although this mode of speciation has long been contested in birds, Hermansen et al. (2011) recently demonstrated that the Italian Sparrow (*Passer italiae*) shares about an equal number of genotypes with both of its parental species, the House Sparrow (*P. domesticus*) and Spanish Sparrow (*P. hispaniolensis*), while being reproductively isolated from both. This seems to put the Italian Sparrow on the map as a good avian hybrid species. A second case of potential hybrid speciation involves the western Nearctic Audubon’s Warbler (*Setophaga auduboni*), which phenotypically resembles the Black-fronted Warbler (*S. [a.] nigrifrons*) from Mexico but shares its mtDNA and a hybrid zone with the eastern Nearctic Myrtle Warbler (*S. coronata*) (Brelsford and Irwin 2009, Brelsford et al. 2011, Milá et al. 2011). In terms of nuclear amplified-fragment-length-polymorphism (AFLP) markers, Audubon’s Warbler exhibits a gradient of decreasing Myrtle Warbler genotypes away from the hybrid zone. Further research will focus on the contact zone between Audubon’s and Black-fronted warblers to establish whether there is indeed reproductive isolation between them to warrant designating Audubon’s Warbler as a hybrid species, as opposed to a population that is conspecific with the Black-fronted Warbler, albeit variously admixed with Myrtle Warbler DNA.

On a continental level, hybrid zones often coincide geographically among different bird groups. Areas of congruence among several hybrid zones are called “suture zones.” The Great Plains suture zone, where eastern and western Nearctic sister species come into contact, is one of the most important (e.g., Carling and Brumfield 2008, 2009; Mettler and Spellman 2009; Carling and Zuckerberg 2011; Carling et al. 2011). Many hybrid zones are known to move; an interesting but untested hypothesis is whether members of a suture zone generally move in the same direction, thereby leading to a geographic shift of the entire suture zone (e.g., westward, as seems to be the case in the Great Plains; Carling and Zuckerberg 2011). The answer would have important implications for our insights into the role of environmental factors (such as climate change) in species replacement dynamics.

COMPLEX MULTIPLE INTROGRESSION

Hybridization has long been recognized as problematic in drawing species boundaries in plants, but it has been less of an issue in animals (e.g., Mayr 1996). Even so, some avian groups have low barriers to hybridization, and three of these are now known to be subject to complicated patterns of multispecies introgression. For instance, Darwin’s finches (*Geospiza*) form such a complex in which species may hybridize with various other members. Research on this important model system has revealed hybrid speciation (Grant and Grant 2009), the influence of climatic fluctuations on introgression (Grant et al. 2004), ecological speciation (de León et al. 2010), and the importance of introgression in the introduction of genetic novelty (Grant and Grant 2010). Hybridization is so extensive in this group that traditional species boundaries have been questioned (Zink 2002). The Mallard superspecies (*Anas diazi*, *A. fulvigula*, *A. rubripes*, *A. zonorhyncha*, and *A. platyrhynchos*) is another group that engages in complicated patterns of multispecies introgression (McCracken et al. 2001; Kulikova et al. 2004, 2005). Finally, eight species of gull in the genus *Larus* exhibit an intricate pattern of multispecies introgression (Liebers et al. 2004, Sternkopf et al. 2010; see also Pálsson et al. 2009).

Although the directionality of introgression and the identity of native genotypes in *Larus* have been partially untangled, the situation seems so complex that full definition will require nDNA sequence data from across many regions of the genome. All three examples (*Geospiza*, *Anas*, and *Larus*) demonstrate that avian introgression may involve multispecies hybrid swarms that often result in complicated phylogeographic patterns.

These three avian examples are probably not the only complicated introgression complexes. Similar but less well-studied groups are known in which hybridization combined with low mtDNA divergences predict some challenging analytical work ahead. These include seedeaters (*Sporophila*; Campagna et al. 2010) and pelagic birds such as skuas (*Stercorarius*; Techow et al. 2010).

ASYMMETRICAL INTROGRESSION AND GHOSTS OF INTROGRESSION PAST

Studies of several avian hybrid zones suggest that introgression can primarily be directed from one species to the other but not vice versa (e.g., Sætre et al. 2003, Grant et al. 2004, Borge et al. 2005a, Helbig et al. 2005, Storchová et al. 2010). In shifting hybrid zones, unidirectional introgression has almost universally been shown to occur from the “invadee” to the “invader” (Fig. 2), contradicting earlier assumptions that introgression usually extends into the range of the receding species (e.g., Rohwer et al. 2001, Secondi et al. 2006, Steeves et al. 2010). One potential exception to the pattern expected for asymmetrical introgression involves African doves (*Streptopelia*; den Hartog et al. 2010), in which hybrid populations have the nuclear background of the receding species (*Streptopelia vinacea*) but the mtDNA of the invader (*S. capicola*). On the basis of phenotypic similarity of hybrids with *S. vinacea*, den Hartog et al. (2010) interpreted this pattern as mtDNA introgression from the invader, a pattern that would disagree with the directionality reported in most other avian cases. However, because no phenotypically pure *vinacea* individuals seem to persist in the hybrid zone, this pattern could equally be interpreted as nuclear introgression into a population that is becoming increasingly similar to the invader. If true, this hybrid population would eventually turn into a phenotypic *S. capicola* with genomic remnants of the former inhabitant (*S. vinacea*), a pattern widely documented in other birds and animals and known as a “ghost of introgression past.”

How do ghosts of introgression past come into existence? If introgression is primarily directed at the invading species, we should be able to trace the DNA of invaded species back to regions that they formerly occupied as hybrid zones advance over time (Fig. 2). In birds, this pattern was first demonstrated in a study of the Hermit × Townsend’s warbler (*Dendroica occidentalis* and *D. townsendi*) hybrid zone by Rohwer et al. (2001), who showed that the receding Hermit Warbler left a trail of its past occurrence in the mitogenomes of Townsend’s Warblers that now occupy its former range (Fig. 2). There is no reason to suppose that Hermit Warbler mtDNA is selectively advantageous; otherwise it might by now have replaced native Townsend’s Warbler mtDNA over its whole range, not merely across the presumed former distribution of Hermit Warblers. This type of process may be widespread and is probably one of a few ways in which introgression can move far beyond hybrid zones without positive selection (Fig. 1). A study of warblers in the genus *Hippolais* suggests that the “foreign” genotype becomes most

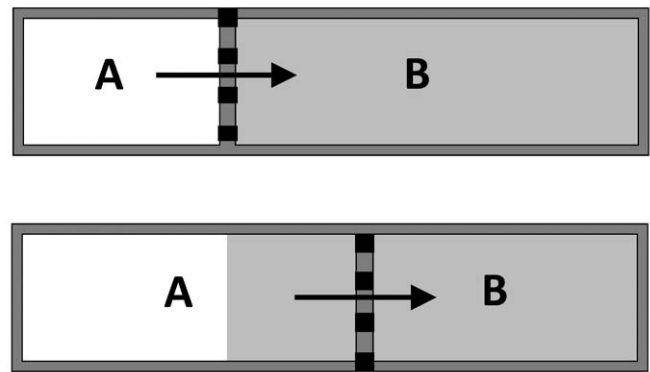


FIG. 2. Introgression scenario for a neutral locus in a moving hybrid zone. The stippled black line indicates the hybrid zone between species A and B. The arrow indicates the direction of hybrid zone movement. The white versus gray background colors indicate the genotype typical for species A and B, respectively. As the range of species A increases, species B leaves a genetic “ghost of its past range” through introgression.

abundant in areas that have just turned allopatric (i.e., after the local extinction of the receding species; Secondi et al. 2006).

The ghost-of-the-past phenomenon can be invoked to explain unusual patterns of character change across other avian hybrid zones such as that of manakins (*Manacus*; Brumfield et al. 2001), in which mtDNA and nDNA markers of *Manacus candei* reach almost 100 km into the range of birds that exhibit the plumage type of *M. vitellinus*. Similarly, Carling and Brumfield (2009) hypothesized that asymmetrical Z-linked introgression from *Passerina amoena* into *P. cyanea* may be a ghost of the past in the wake of a westward moving hybrid zone.

An intriguing prediction that arises from the ghost-of-the-past phenomenon is that some species may carry the “fossilized” genotype of another species that has long since died out (e.g., as a consequence of a moving hybrid zone that has run its full course and driven one of the species to extinction). Scenarios like this will be tricky to prove because the donor species is no longer there to compare against. These cases may especially apply to species that carry two distinct and private mtDNA lineages, such as the Savannah Sparrow (*Passerculus sandwichensis*; Zink et al. 2005), which may have received one of its distinct mtDNA haplogroups from another sparrow it has long since replaced.

WAVEFRONT DYNAMICS IN MOVING HYBRID ZONES

Numerous empirical studies point to unidirectional introgression into invading species, but are these results in agreement with theoretical considerations? Simulations by Currat et al. (2008) confirm substantial introgression of neutral loci into invading species across shifting hybrid zones. Their results imply that the most important arena for introgression in a newly forming hybrid zone is the wavefront of the invading species, where there is an initial demographic imbalance between a low number of invaders and a large number of invadees (Fig. 3). In this initial stage, sporadic hybridization may be sufficient to establish introgressing genotypes from the receding species in the small population of invaders. As the invading species increases and takes over, the frequency of the introgressed

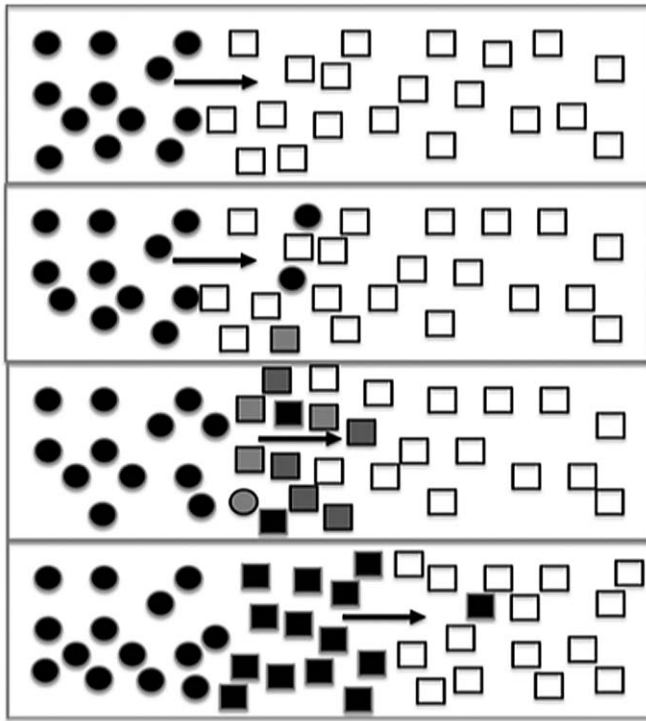


FIG. 3. A simplified version of Currat et al.'s (2008) "wavefront model" for a neutral introgressing locus with a different allele typical for either species. Each box is a successive snapshot of time. Species A (the invader) is black, species B (the invadee) is white, and hybrids are depicted in various shades of gray. Circles denote the native allele of species A at the introgressing locus (= allele a), and squares denote the allele initially native to species B (= allele b). (First panel) Expanding species A is establishing secondary contact with species B. (Second panel) Pure individuals of species A expand into the range of species B. The first hybrids may have either allele a or allele b, but in subsequent hybrid generations allele b is likely to predominate because bearers of allele a are in the minority at the wavefront of expansion. (Third panel) Pure (= white-colored) individuals of species B are becoming rare at the wavefront, as the range of the invader slowly expands. Nonetheless, the initial demographic inequality between rare invaders and common natives helps allele b to sweep to fixation at the wavefront. (Fourth panel) With time, the entire population of species B is replaced at the wavefront, although it leaves back certain alleles (such as the one depicted in this figure) in the new population of invaders via introgression.

genotypes is amplified by a founder effect (Fig. 3). Although selection on at least a limited set of loci must be involved in the expansion of one species at the expense of the other, Currat et al.'s (2008) "wavefront model" shows that selection need not be invoked as the main cause: demographic conditions at the wavefront permit thousands of introgressed neutral markers to surf to high frequencies.

GENETIC CONTAMINATION IN INTROGRESSION

A long-time concern is that introgression may lead to a loss of genetic integrity of native species whose ranges are invaded by newcomers. An early study by Gill (1997), for example, reported on a possible case of "cytonuclear extinction" in the receding Golden-winged Warbler, whose mtDNA may be rapidly replaced by that of

the expanding Blue-winged Warbler. However, follow-up studies in this system have been more optimistic: mtDNA introgression seems to be more or less symmetrical within most contact regions (Shapiro et al. 2004, Dabrowski et al. 2005), whereas foreign nDNA may predominantly move into the blue-winged invaders (Vallender et al. 2007), not into the golden-winged invadees. Although Vallender et al.'s (2007) hybrid zone samples were biased toward phenotypically pure Golden-winged Warblers (which were, on average, composed of 30% introgressed nDNA), the one phenotypic Blue-winged Warbler they examined was made up of 85% introgressed nDNA, which suggests much higher introgression rates into the invaders.

Because introgression often flows backward in a moving hybrid zone (Fig. 2)—akin to the exhaust fumes of a moving car—fear of genetic contamination of the native gene pool may often be unfounded, so long as there remain sizeable areas of native distribution where the shifting hybrid zone has not yet reached. The danger to receding species only arises once hybrid zones have moved close to the far end of the native species' distribution and are about to complete the replacement process. For example, Steeves et al. (2010) captured the very moment when a formerly widespread New Zealand species, the Black Stilt (*Himantopus novaezelandiae*), may have been pushed back to its last pure stronghold. The fact that this last pure population has weathered the massive recent intrusion of Common Stilts (*H. himantopus*)—while retaining virtually pure copies of native mtDNA and microsatellites—is perhaps not surprising against the background of the wavefront model (Currat et al. 2008). Sadly, however, the "pure zone" is now reduced to a few last river sections, and a discontinuation of active conservation management would lead to a further invasion of Common Stilts and a global extinction of the Black Stilt (Steeves et al. 2010).

The species replacement process of moving hybrid zones is a common evolutionary phenomenon, but it is plausible to assume that human impacts on the planet may accelerate the movement of existing hybrid zones or create new ones. On an evolutionary scale, our chances of witnessing rapid replacement events would be exceedingly low if humans had not caused them in the first place. A study of introgression in *Anas* documented how, within the span of only half a century, American populations of the Mallard (*A. platyrhynchos*) and the American Black Duck (*A. rubripes*) changed their microsatellite profile from highly distinct to near identical (Mank et al. 2004). In another case, Väli et al. (2010a) used a time series of samples over 16 years to demonstrate that the hybrid zone between two European eagles (*Aquila*) is >1,500 km wide and is moving rapidly eastward. At this pace, the completion of the replacement process is expected on a time scale of only tens to hundreds of years.

A very different but increasing conservation problem is presented by the artificial range-wide admixture of native populations with non-native individuals. In this situation, introgression is not restricted to the distributional margins as in the wavefront model, but instead is catalyzed by bouts of hybridization anywhere inside the range of a native species, such as following the release of exotics. S.-H. Li et al. (2010) documented such a case in Taiwan, where they found substantial range-wide nDNA introgression ($\leq 20\%$) into Taiwan Hwameis (*Leucodipteron taewanus*) from released Chinese Hwamei (*L. canorum*) cagebirds. Because hybrids showed almost no fitness reduction, prospects for the genetic integrity of the Taiwan Hwamei look bleak.

INTROGRESSIVE mtDNA SWEEPS

As discussed above, nuclear markers are known for their higher incidence of introgression across avian hybrid zones compared with mtDNA (in accordance with Haldane's rule). In apparent contrast, mtDNA is known for being among the most susceptible markers to introgressive sweeps, and mtDNA sweeps are reported to affect a wide range of bird species that are not currently known to engage in hybridization or populations of hybridizing species that are far from any hybrid zone. The phenomenon of mtDNA introgression was first documented in the early 1980s in flies (*Drosophila*; Powell 1983), mice (Ferris et al. 1983), and amphibians (Spolsky and Uzzell 1984). Subsequently, Australian birds provided early examples of avian mtDNA introgression (Degnan and Moritz 1992, Joseph and Moritz 1993). Since then, it has been detected in most bird families (see below). How can avian mtDNA be resilient to introgression across hybrid zones because of Haldane's rule on the one hand, but prone to introgressive sweeps on the other? Selection may be the answer.

When lacking a selective advantage, a rare foreign genotype will find it hard to introgress beyond a hybrid zone because genetic drift counteracts its spread (Fig. 1). If there is a fitness difference between two alleles, however, a foreign allele may rapidly run its course, potentially replacing the native one over its entire distribution (Fig. 1). Note that the directionality of wavefront dynamics no longer applies: whichever genotype has the selective edge will eliminate the other.

The sources of selective advantage behind mtDNA sweeps remain understudied, especially in the beginning stages, when a female F1 hybrid is required to introduce the novel and advantageous genotype into the recipient species. In many cases, Haldane's female hybrid inviability may not be absolute, and the occasional individual may manage to reproduce. On the other hand, paternal leakage of mtDNA may assist introgressive sweeps in the early stages. Paternal leakage is presumed to be rare but is difficult to detect. Skeptics of paternal leakage should note that the one reported instance in birds was in a hybrid tit (*Parus*) within a zone of documented introgression (Kvist et al. 2003).

Any locus under positive selection is capable of sweeping over the recipient's range and replacing its native genotype, so why is this phenomenon particularly relevant to mtDNA? Long considered a simple neutral phylogenetic marker (e.g., McKay and Zink 2009), mtDNA dynamics are now known to be much more complex than was assumed early on (Ballard and Whitlock 2004, Bazin et al. 2006). Because of its role in oxidative phosphorylation, mtDNA is the subject of frequent selective sweeps that instate genotypes with favorable metabolic properties (e.g., Niki et al. 1989), especially in organisms that occur across a variety of temperature regimes, ranging from humans and other mammals to sparrows in the genus *Zonotrichia* (Ehinger et al. 2002, Mishmar et al. 2003, Ruiz-Pesini et al. 2004, Fontanillas et al. 2005, Cheviron and Brumfield 2009). Frequent mtDNA sweeps explain the low level of mtDNA diversity that is often observed within species (Bazin et al. 2006). Consequently, incomplete lineage sorting (ILS) may be less of an issue in mtDNA as compared with nuclear markers not only because of its smaller effective population size, but also because selection can erase the lingering effects of ILS (Edwards 2009).

The adaptive importance of mtDNA in the colonization of new climatic regimes, especially in colder temperatures, would

predict that mtDNA sweeps should be more common at higher latitudes. This may be an overlooked factor in the debate about why tropical lowland birds are generally more deeply diverged whereas boreal or montane birds exhibit shallower mtDNA topologies (e.g., Weir and Schluter 2004). This hypothesis will be testable once genome-wide nuclear data become more widely utilized. Until then, it is conceivable that the lack of deep mtDNA diversification in many boreal and Arctic birds, such as redpolls (*Acanthis*; Marthinsen et al. 2008) and snow buntings (*Plectrophenax*; Maley and Winker 2010), may have a selective rather than a demographic basis, a hypothesis that can again be tested with multilocus nuclear data.

DIAGNOSING INTROGRESSIVE SWEEPS

The diagnosis of introgressive sweeps is in its infancy, because distinguishing ILS from introgression can be challenging (Funk and Omland 2003). Avian introgressive sweeps have typically been invoked when a locus (predominantly mtDNA) shows a robust and consistent phylogenetic signal different from those of other loci or phenotypic characters (e.g., Weckstein et al. 2001, Ödeen and Björklund 2003, Nittinger et al. 2007, Alström et al. 2008, Bellemain et al. 2008, Irwin et al. 2009b, Rheindt et al. 2009). In most of these cases, ILS is unlikely to explain the dichotomy between mtDNA and nDNA, often for reasons of deeply branching tree structure. Nevertheless, skeptics might argue that, in each case, invoking introgression is post hoc and cannot be considered a tested hypothesis in the scientific sense.

Various approaches have been proposed by which the hypothesis of introgression can be formally tested against that of ILS. In birds, Peters et al. (2007) championed an approach that involves a coalescent framework and applied it to a case of mtDNA paraphyly in two gadwall duck species (*Anas*). First they erected predictions about the time of divergence using either introgression or ILS as an explanation for mtDNA paraphyly; then they compared these predictions with estimates from nDNA (Fig. 4). This approach confirmed initial suspicions that mtDNA introgression is the likely cause of paraphyly. In more complicated "introgression complexes" (such as *Larus* gulls; Sternkopf et al. 2010), however, this approach may face challenges because it relies on the simplified assumption that the nDNA markers used as a comparative standard are immune to introgression. This is by no means the case (see Fig. 4B), although it seemed to create no bias in the less complex gadwall situation.

Another promising avenue for diagnosing introgression is one in which phylogenetic signal or divergence are contrasted not among different loci but among different populations and taxa. This approach requires comparing populations that are thought to be affected by introgression with those that are thought to be introgression-free (e.g., through allopatry). Grant et al. (2005) applied a simple but powerful version of this approach to Darwin's finches. To show that introgression has affected certain island populations of a species pair, they compared interspecific divergences between sympatric populations with those between allopatric populations, demonstrating that introgression has been pervasive in this radiation. Newer, more complex locus-based (as opposed to genetic-distance-based) versions of this approach have been elaborated for genomic data in introgression among recent lineages of

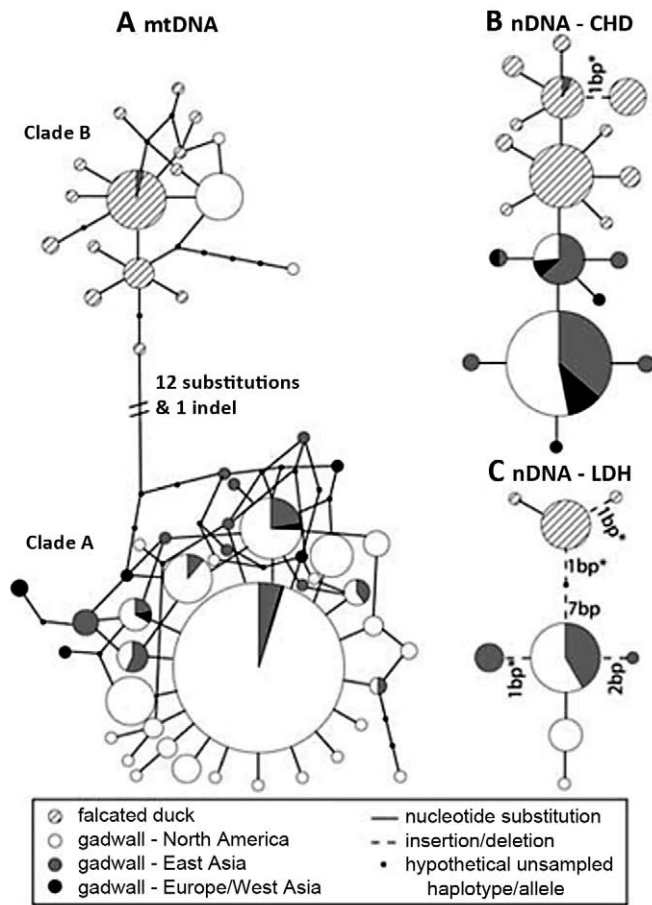


FIG. 4. Networks for one mitochondrial locus (mtDNA; panel A) and two nuclear loci (nDNA; panels B and C) in Gadwall (*Anas strepera*) and Falcated Duck (*A. falcata*). Circle area is proportional to the number of shared sequences (reproduced from Peters et al. 2007). Indel sizes are shown next to the corresponding branch where applicable. In panel A (mtDNA), the representation of Gadwall in a private haplotype cluster (clade A) as well as in a cluster dominated by Falcated Duck (clade B) is interpreted as introgression. Note, however, that the nDNA locus in panel B (which is used to test the hypothesis of mtDNA introgression) itself exhibits the signature of introgression.

humans (Green et al. 2010, Reich et al. 2010). The strength of these approaches in disentangling introgression from coalescence-based processes lies in their focus on loci that exhibit the ancestral (in this case, chimpanzee-like) genotype in the allopatric (i.e., African) human population, so that any apomorphy shared by the two (until recently) sympatric populations (the presumed donor and recipient) is likely to be introgressed. With the advent of genome-wide data in ornithology, this approach will soon be tested in birds.

CAN INTROGRESSION COMPROMISE PHYLOGENETICS?

Introgression is often invoked when two distinct but hybridizing species unexpectedly exhibit identical genotypes, especially in mtDNA (e.g., Weckstein et al. 2001, Irwin et al. 2009b, Rheindt et al. 2009; Fig. 5A), but this is merely the extreme point along a gradient of potential divergences resulting from introgression. If hybridization occurred in the past but has long since discontinued, we might

retrieve two species as distinct lineages but with shortened branch lengths (Fig. 5B). Such effects may have important implications for estimating divergence times, especially when a single marker is used. Dates based on the widely used mtDNA clock rate of $2\% \text{ Ma}^{-1}$ (e.g., Weir and Schluter 2008) have led to many important insights in ornithology. However, once second-generation sequencing becomes more widely established and multilocus dating becomes more refined, a re-examination may show some of these clock-based estimates to be too young, displaying instead the signature of introgression. For example, both intra- and interspecific sweeps could account for a resetting of mtDNA interspecific divergence to zero, so when an unusual but well-supported mtDNA pattern is detected, introgression should always be considered as a possible cause. Similar caution is needed when two or more species are lumped on the basis of identical mtDNA, especially when morphology, behavior, or both may indicate otherwise (e.g., Fuchs et al. 2007, Drovetski et al. 2009, Crottini et al. 2010). What these studies could be measuring is not the time since separation but the time since the last introgressive mtDNA sweep set the divergence clock to zero.

Introgression can only shorten branch lengths, not increase them back in time (Fig. 5). Many mtDNA studies, including the barcoding movement (Kerr et al. 2007, Tavares and Baker 2008, Johnsen et al. 2010), derive their conclusions from scanning data for atypically shallow or deep divergence dates. Although the deep divergences may well be reliable and are often subsequently supported by additional life-history data (see Kerr et al. 2007), the shallow divergences may sometimes represent artifacts of introgression. For instance, three region-wide barcoding projects (Kerr et al. 2007, 2009a, b) each documented a list of species characterized by non-diagnostic barcodes, and each list exhibits a high representation of species that are known to hybridize widely and in which introgression has been previously reported, such as ducks (McCracken et al. 2001; Kulikova et al. 2004, 2005; Mank et al. 2004; Peters et al. 2007), gulls (Liebers et al. 2004, Pálsson et al. 2009, Sternkopf et al. 2010), and seedeaters (Campagna et al. 2010).

A little-appreciated property of introgression is that it muddies not only branch lengths but also internal tree topologies. If a replacement sweep occurs between two non-sister species, the introgressive gene will yield a topology that erroneously shows them to be sisters (Fig. 5C). Brumfield et al. (2008) demonstrated this dilemma in a group of three *Manacus* species: despite the use of multiple loci, it was challenging to retrieve the true topology, given

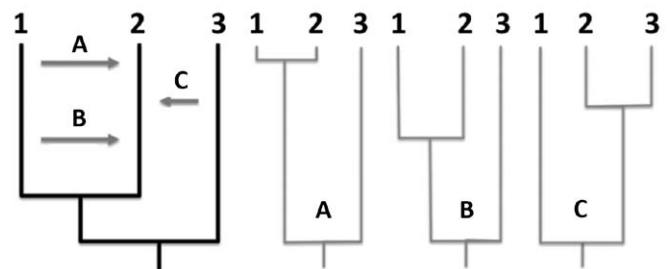


FIG. 5. Three introgression scenarios and the way they change gene phylogenies. The true species tree is black and depicts relationships among diverging lineages 1, 2, and 3. All trees are chronograms (i.e., branch lengths are proportional to time). Arrows represent introgressive sweeps into species 2 for three hypothetical loci. Gene trees for each introgressive locus are depicted in gray.

that introgression is known to occur in this lineage. A similar discrepancy between mtDNA- and nDNA-based relationship patterns involves three closely related and hybridizing orioles in the genus *Icterus* (Jacobsen et al. 2010, Jacobsen and Omland 2011). On the basis of 12 independent nuclear markers (K. E. Omland and F. Jacobsen unpubl. data), the Black-backed Oriole (*Icterus abeillei*) is now considered to be sister to Bullock's Oriole (*I. bullockii*), as traditionally assumed, and not to the Baltimore Oriole (*I. galbula*), whose mtDNA it shares. This result has implications for previous work based on the assumption of a sister relationship between *I. abeillei* and *I. galbula* (Kondo et al. 2008).

If a topology-changing introgressive sweep (Fig. 5C) occurred far back in time and both species have since diversified into several daughter species, the introgressive marker may give us a misleading branching arrangement at deep phylogenetic nodes. The most instructive non-avian case involves goats (*Capra*), which probably received an advantageous cold-adapted mtDNA haplotype from the distantly related tahrs (*Hemitragus*) through introgression (Ropiquet and Hassanin 2006). We are not aware of any case in which this potentially widespread but difficult-to-detect phenomenon has been demonstrated conclusively in birds. It had initially been invoked as one of several ways to explain the Red-winged Francolin's (*Scleroptila levaillantii*) unusual mtDNA affinity to morphologically dissimilar species (Crowe et al. 1992), but follow-up research by Bloomer and Crowe (1998) has repositioned *S. levaillantii* back near its traditional clade. A likely candidate for ancient hybridization may be the *Lanius excubitor* shrike complex: divided up by mtDNA phylogenies in ways that are challenging to reconcile with biogeographic and life-history data (Gonzalez et al. 2008, Klassert et al. 2008, Olsson et al. 2010), some of the "out of place" arrangements may be an artifact of introgressive mtDNA incursions in the ancestors of this radiation. Such suspicious patterns would be presented any time a single marker is used: multilocus data are useful because the additional loci corroborate or refute patterns found in individual loci and an ensemble picture can emerge.

HOW PERSVASIVE IS mtDNA INTROGRESSION IN AVIAN PHYLOGENETICS?

To determine how pervasive mtDNA sweeps are, it is helpful to examine cases that bear their signature, namely paraphyletic arrangements. Funk and Omland (2003) exposed introgression as one of three major sources of gene tree paraphyly, the other two being ILS and faulty taxonomy (the latter refers to a situation in which the accepted classification of a taxon is at odds with its true biological species status). The challenge lies in disentangling which of the three is causing a paraphyletic arrangement.

Joseph and Omland (2009) assigned most cases of Australian bird paraphyly to either introgression or ILS while questioning the importance of inadequate taxonomy. By contrast, McKay and Zink (2009), in a global review of 122 cases of bird paraphyly, attributed 56% to incorrect taxonomy, 16% to ILS, only 6% to introgression, and 22% to equivocal cases. They concluded that the low incidence of introgression in avian mtDNA paraphyly vindicates the superiority of mtDNA as a phylogenetic marker. However, McKay and Zink's (2009) interpretation of the causes of paraphyly

may have been compromised in two ways: (1) they often relied on the original authors' conclusions even though authors often overlook introgression, and (2) their diagnosis of faulty taxonomy was based on monophyletic subgroups (their fig. 1), although this pattern is easily mimicked by introgression in the past (Fig. 5B, C). We suggest that introgression may be a more widespread cause of avian gene (especially mtDNA) paraphyly than is commonly assumed. However, rigorous multilocus tests are needed to determine the extent to which introgression causes paraphyly.

INTROGRESSION IN SPECIATION RESEARCH: FUTURE DIRECTIONS

Classical allopatric speciation envisages the geographic separation of a lineage into two, which subsequently diverge over time (e.g., Mayr 1996). This dogma is implicit in most avian phylogenetic research in that genetic exchange after the initial split (i.e., introgression) is assumed to be negligible. Nonetheless, introgression may indeed be a standard component of initial differentiation (Machado and Hey 2003, Seehausen 2004), a hypothesis that can readily be tested with genome-wide data. Encouragingly, there has been a recent emergence of avian studies employing tools that allow for introgression to be taken into account during the initial stages of species separation (Joseph et al. 2009, Carling et al. 2010, J.-W. Li et al. 2010).

With the future availability of genome-wide data, another major goal in avian evolutionary research is the incorporation of climatic models into speciation and phylogeographic reconstructions (Hugall et al. 2002, Edwards et al. 2011). Introgression should be a vital component in these reconstructions: it is often driven by climatic change and shifting habitats. The past 3 million years have been characterized by a series of ~20 pan-continental glaciations, each lasting about 10–50 ka and separated by interglacials of slightly shorter duration (Lambeck and Chappell 2001, Siddall et al. 2003, Bintanja et al. 2005, Thompson and Goldstein 2005, Caputo 2007). With each of these glaciations or interglacials comes a cycle of range fragmentations caused by glaciers or rising sea levels, followed by a cycle of range expansions and secondary contact caused by retreating glaciers or falling sea levels (Fig. 6), resulting in cycles of differentiation, secondary contact, and introgression. The development of tools to incorporate these climatic fluctuations into reconstructions of genetic diversification should be a high priority on the agenda of evolutionary ornithologists.

For a long time, introgression has been viewed as an obstacle in the way of getting to the heart of the evolutionary process. A large body of recent insights shows that introgression may instead be an integral part of the evolutionary process. Research on human genetic variation based on an enormous battery of genomic resources has suggested that introgression may have been an important aspect in the evolution of *Homo sapiens* (Green et al. 2010, Reich et al. 2010). Similarly, introgression is thought to be an important part of the speciation process for other model species for which genome-wide data have been surveyed, such as *Drosophila* (Machado and Hey 2003, Kulathinal et al. 2009) or canids (Anderson et al. 2009). Technological innovations such as next-generation sequencing will soon put similar resources in the hands of evolutionary researchers of non-model species (e.g., Lerner and Fleischer 2010, Haig et al. 2011), promising exciting times ahead in the study of avian introgression.

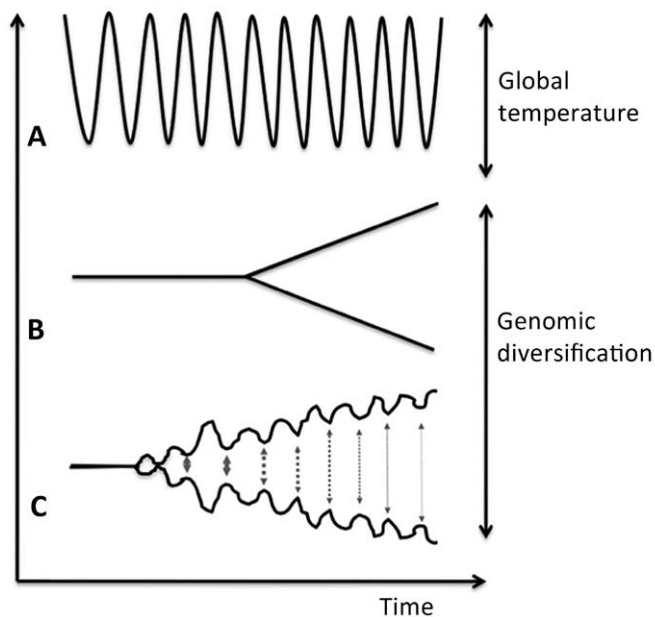


FIG. 6. Hypothetical speciation scenarios in the face of ongoing introgression. (A) A schematic representation of temperature during the last dozen ice ages. (B) The classical speciation model as assumed in most recent research. (C) A potentially more realistic scenario in which the two species become separated and increasingly diverge from one another with each ice age but revert to secondary contact and introgressive hybridization in each interglacial. The decreasing width of dark gray arrows represents a decline of interglacial introgression as the two species diverge over time. Note that model B will always assume a more recent time of speciation than model C. Note also that model C is depicted for species whose ranges become fragmented during glaciations, but it can equally be inverted to apply to species whose ranges become fragmented during interglacials (e.g., because of land fragmentation with rising sea levels, such as in the Greater Sunda Islands).

ACKNOWLEDGMENTS

This research was supported by a German Academic Exchange Service (DAAD) postdoctoral fellowship and by National Science Foundation grant IOS-0923088. We thank D. Irwin, R. Brumfield, B. Milá, and two anonymous reviewers for their valuable and constructive comments, which helped improve the manuscript.

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Received 27 September 2011, accepted 12 October 2011