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THE HIDDEN SIDE OF INVASIONS: MASSIVE INTROGRESSION BY LOCAL GENES

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Despite hundreds of reports involving both plants and animals, the mechanisms underlying introgression remain obscure, even if some form of selection is frequently invoked. Introgression has repeatedly been reported in species that have recently colonized a new habitat, suggesting that demographic processes should be given more attention for understanding the mechanisms of introgression. Here we show by spatially explicit simulations that massive introgression of neutral genes takes place during the invasion of an occupied territory if interbreeding is not severely prevented between the invading and the local species. We also demonstrate that introgression occurs almost exclusively from the local to the invading species, especially for populations located far away from the source of the invasion, and this irrespective of the relative densities of the two species. This pattern is strongest at markers experiencing reduced gene flow, in keeping with the observation that organelle genes are often preferentially introgressed across species boundaries. A survey of the literature shows that a majority of published empirical studies of introgression during range expansions, in animals and in plants, follow the predictions of our model. Our results imply that speciation genes can be identified by comparing genomes of interfertile native and invading species pairs.

KEY WORDS: **Bioinvasion, competition, hybridization, neutral model, organelle capture, spatial and demographic expansion.**

Molecular analyses have revealed that many related species share some elements in their genome, potentially due to the retention of neutral or balanced ancestral polymorphisms or to recent hybridization followed by introgression (Rieseberg et al. 1999; Machado et al. 2002; Charlesworth et al. 2005; Mallet 2005). Patterns of gene introgression are commonly thought to depend on the fitness of hybrids and their ability to backcross with parental species (Broyles 2002; Borge et al. 2005). Similarly, the observation that introgression is often asymmetrical between hybridizing species (Barton and Hewitt 1989; Orive and Barton 2002) seems to implicate selection as a cause (Lehman et al. 1991; Borge et al. 2005), with the more adapted alleles spreading from one species to the other (Barton 2001; Whitney et al. 2006). However, the spatial and dynamic contexts of introgression have rarely been considered, even though massive introgression has frequently been reported in species having recently colonized a new habitat (Melo-Ferreira et al. 2005; Rieseberg et al. 2007), thereby questioning the interpretations invoking selection. Hence, a model incorporating demographic details of species encounters might help decide if it is necessary to invoke selection (Ballard and Whitlock 2004; Rieseberg et al. 2007) or differences in relative species abundance (Cianchi et al. 2003) to explain actual patterns of introgression. An analysis of the introgression dynamics at neutral genes experiencing different effective rates of gene flow should also provide some hints to the actual mechanisms involved in asymmetric introgression.

Most models of hybridizing species have considered static hybrid zones, or they have insisted on the importance of selection to prevent or enhance introgression, without specifying a null model that would be valid for neutral markers (e.g., Huxel 1999; Ferdy and Austerlitz 2002; Tsitrone et al. 2003; Chan and Levin 2005). Nevertheless, it has been suggested that introgression of neutral genetic markers should affect mostly the advancing taxon as compared to the already established one (e.g., Baker 1948; Moran 1981; Barton and Hewitt 1985; Buggs 2007). For instance, in the context of moving hybrid zones, Buggs (2007) argued that "a moving zone will leave in its wake a tail of clines of unlinked neutral markers," which can be interpreted as introgression of genes from the native species into the colonizing one, as suggested by Moran (1981). This type of explanation appears rather intuitive: as the wave of advance spreads forwards, neutral alleles or traits will flow in the opposite direction, into the invading population, and the frequency of introgressed alleles will steadily increase behind the advancing wave front, until introgression is complete. However, in these previous studies, it was unclear if introgression was truly asymmetric from the native toward the invading species, or if introgression was symmetric but could only be tracked in the part of the range in which the native species was displaced by the invading (i.e., where the two species have been in contact). Moreover, the recent literature on hybridization between exotic and native species during biological invasions has focused on introgression into the native species, rather than on the expected direction of introgression (Huxel 1999; Epifanio and Philipp 2000; Wolf et al. 2001; Hall et al. 2006). As a consequence, no formal analysis has been performed to specify if introgression is generally biased toward the invading species or if introgression is affected by the coexistence of the two species. In the present study, we try to provide answers to these questions by explicitly considering the spatial dynamics of the invasion process.

Although several authors have studied population spatial expansions allowing for different dispersal kernels (see e.g., Mollison 1977; Shaw 1995; Bialozyt et al. 2006), and detailed models of genetic exchanges between local and incoming populations have been proposed at the intraspecific level (see e.g., Aoki et al. 1996; Barton 2000; Ackland et al. 2007), two-species models are still missing. There are clear analogies between the invasion of an occupied territory by a new population and the invasion of an advantageous allele in a population, because in both cases migrant individuals phenotypically distinct from local individuals are the vector of the invasion process. The spatial diffusion of an advantageous allele in a population has been investigated by Fisher (1937). Quite recently, the fate of neutral genes linked to a favorably selected mutant spreading in a continuously distributed population has been studied analytically (Barton 2000). This latter work has shown that only the genes located very close to a selected locus would hitchhike and get displaced away from their geographical origin with the wave (i.e., for $r/s << 0.1$, where r is the recombination rate and s is the selective advantage of the heterozygotes). Therefore, Barton's model predicts that most of the genetic background of a species should not be affected by the spatial expansion of an advantageous allele, but it is unclear to which extent this spatial model of hitchhiking in a single population could be extended to the case of an invading species interbreeding infrequently with a local species. Another intraspecific model that is also relevant for the study of interspecific introgression is the demic diffusion model (Ammerman and Cavalli-Sforza 1973). This model was introduced to explain the occurrence of allele frequency clines over a large portion of Europe by the progressive dilution of the gene pool of Neolithic farmers when they colonized the continent. Previous implementations of this model have shown that demic diffusion would lead to allele frequency clines for very small levels of admixture between invading and local populations (0.024%, as used in Rendine et al. 1986; Barbujani et al. 1995). Note however that allele frequency clines can also occur without any introgression after a spatial expansion (Currat and Excoffier 2005; Klopfstein et al. 2006; Travis et al. 2007). In connection to demic diffusion, Ackland et al. (2007) have recently extended Fisher's equations to model the wave of advance of a neutral trait associated to an advantageous (cultural) trait in humans. In line with previous theoretical work (Aoki et al. 1996), their simulations show that for low migration rates of the carriers of the beneficial technology, the diffusion of the beneficial trait can be quite distinct from that of the neutral trait. It thus suggests a possible disconnection between the diffusion of beneficial and neutral variation, in agreement with the work of Barton (2000) on genetic hitchhiking.

In previous models, the importance of intraspecific gene flow (among local or among invading populations) on introgression levels has not been investigated. Organelle genes typically experience reduced gene flow compared to nuclear genes, as a direct consequence of their uniparental and clonal mode of inheritance, both in animals (Birky et al. 1989) and in plants (Petit et al. 1993). Interestingly, organelle genes have long been shown to readily move across species barriers (e.g., Ferris et al. 1983; Powell 1983; Rieseberg and Soltis 1991; Whittemore and Schaal 1991; Bernatchez et al. 1995), but the reasons for this increased permeability are unclear.

In the specific context of human evolution, Currat and Excoffier (2004) have simulated the range expansion of modern humans into Europe already occupied by Neanderthals. They modeled interaction between these two taxa in the form of admixture and direct competition between populations, leading to the extinction of the Neanderthals. Although the goal of that study was to estimate the maximum level of Neanderthal genes into the modern human gene pool, these authors noted that the modern human population should present a large fraction of Neanderthal genes if admixture had been possible between the two species. Here, we propose to use similar spatially explicit simulations to further investigate the pattern of introgression at neutral loci resulting from the range expansion of a species into an already occupied territory. We model a range expansion process with and without competition with the local species, and we monitor introgression levels in invading and resident species as a function of their ability to interbreed. We then check our model predictions against published empirical studies of introgression for organelle and nuclear genes during range expansions in animals and plants.

Materials and Methods

SIMULATION OF SPATIAL EXPANSIONS WITH INTERBREEDING

Simulations were performed using a modified version of the SPLATCHE program (Currat et al. 2004) in a virtual world with 10,000 demes made up of haploid individuals and arranged on a two-dimensional lattice. Note that these haploid simulations apply equally well to diploid loci, but in that case population sizes do not represent the number of individuals (*N*) but the number of gene copies at those loci (2*N*). At the onset of each simulation, the whole world is already occupied by a local species. A new invading species appears in the lower left corner of the square world, in a deme arbitrarily located at position [5,5] on the lattice (see Fig. 1). This newly founded population then sends migrants to empty neighboring demes, which are logistically filled to their carrying capacity, and which send further migrants to adjacent demes, thus progressively colonizing the whole world (see Fig. 1). During and after this colonization process, the invading species can locally interact with the resident species by exchanging migrants through interbreeding and by competing with it for local resources. In more details, each intersection point of the lattice can harbor both a local and an invading deme, which can exchange genes by interbreeding. Here we define an introgression event as the transfer of a gene from the gene pool of one species to that of the other species. For simplicity, this event is supposed to occur in a single generation, although in reality it can take place over a few generations by hybridization and repeated backcrossing. Therefore, these interbreeding events should be viewed as effective interbreeding events. As discussed elsewhere (Currat and Excoffier 2004), the rate of interbreeding is assumed to be density-dependent. At any location of the lattice, the probability of a successful introgression event is thus defined as $A = \gamma\ (2N_iN_j)/(N_i + N_j)^2$, where N_i and N_j are the current deme densities of the two species. It results in the introgression of AN_i genes from species *i* to species *j*, whereas AN_j genes are transferred in the other direction each generation. In our model, the parameter γ is a general measure of the strength of barriers to gene flow between species. We do not explicitly model the nature of these barriers, but they could be either prezygotic (and γ could for instance be considered as a measure of disassortative mating), postzygotic (and γ would be a measure of the fitness of the hybrid individuals), or any combination of factors preventing the successful mating of members of both species. In any case, a γ value of 0 corresponds to a total absence of interbreeding between the two species, a γ value of 1 corresponds to random mating between the two species, and any value in between implies that mating is locally nonrandom between the two species. With this simple parameterization, we do not need to specify how mating is prevented or if it is controlled by one or several loci. Note however that the effect of genes involved in reproductive isolation on nearby neutral loci should decrease

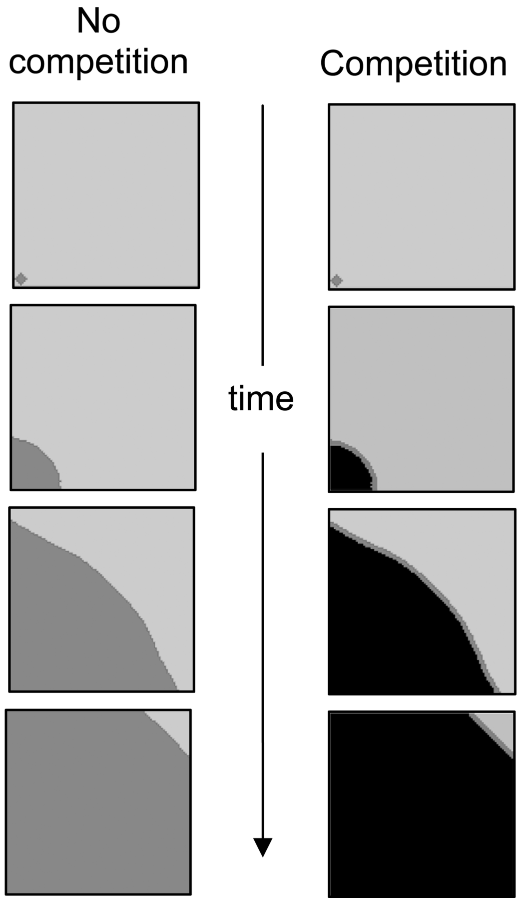

Figure 1. Schematic representation of the simulated invasion process with or without competition between the local and the invading species. Light gray and black pixels represent demes in which only the local or only the invading species occurs, respectively. Dark gray pixels represent locations where both species coexist. The first frame shows the situation after 40 generations. The three other frames depict the invasion process over time, depending on the demographic parameters reported in Table 1.

Table 1. Parameters of the simulated invasion scenarios. *K*: Carrying capacity. *Km*: Number of emigrants sent to neighboring demes of the same species at carrying capacity. The intrinsic rate of growth (*r*) was set to 0.5 in all cases. The cohabitation time is the average number of generations during which the two species coexist at a given location. The colonization time is the number of generations taken by the invading species to colonize the square world.

Scenario	Local species		Invading species		Cohabitation time	Colonization time
	K	*Km*	*K*	*Km*		
Competition						
C1	50	1	500	10	9.5–10.0	1495–1500
C2	50	1	5000	100	7.5–8.0	1240–1270
C3	500	10	5000	100	17.0–19.5	1140–1330
C4	50	10	500	100	10.0	540–570
C5	50	10	5000	1000	8.5	500–510
C6	50	1	100	10	19.0–23.0	1095–1270
C7	500	10	1000	100	29.0–32.0	735–1010
No competition						
NC1	50	10	50	10	1135–1150	680–715
NC2	500	10	500	10	705–790	1425–1500
NC3	500	100	500	100	1215–1245	505–555
NC4	50	10	500	100	1215–1225	540–555
NC5	500	100	50	10	1135–1170	645–715

monotonically with recombination distance (Barton and Bengtsson 1986). In other words, one would expect that the γ parameter would increase with distance from loci controlling the fitness of hybrids or disassortative mating. Assuming that γ values are identical in both species, deme densities are then updated as $N_i' = N_i(1 - A) + AN_j$ to reflect these episodes of interbreeding. Then, deme densities are logistically regulated (see Currat and Excoffier 2004) as $N_i'' = N_i'[1 + r(K_i - N_i' - N_j')/K_i]$, where K_i is the local carrying capacity of the *i*th population and *r* is the deme intrinsic rate of growth. Finally, migration can occur between neighboring demes of the same species, and deme densities are again updated as $N_i''' = N_i''(1 - m) + I_i$, where *m* is the probability of emigration, and I_i is the number of migrants received from the neighboring demes (four neighboring demes for central demes, and less for demes located on the border of the lattice). Note that at carrying capacity, each deme sends on average *Km* emigrants per generation to its neighbors. These updates are repeated over all demes for 1500 generations.

INVASION SCENARIOS

We studied seven scenarios (C1–C7) of invasion with competition between local and invading species as well as five scenarios without competition (NC1–NC5) (see Table 1). These scenarios explore the effects of differences in local carrying capacity (*K*) and number of migrants exchanged between neighboring demes of the same species (*Km*) on introgression levels. In scenarios with competition, the invading species has a competitive edge over the local one. This advantage is implemented by assigning it a larger carrying capacity, which eventually drives the local species to extinction (see Shigesada and Kawasaki 1997; Currat and Excoffier 2004 for details). In that case, interbreeding will only occur at the edge of the expansion wave, where the two species still coexist (see Fig. 1). An absence of competition implies that the two species occupy different ecological niches, and both will coexist and potentially interbreed until the end of the simulation.

COALESCENT SIMULATIONS

For each scenario and various levels of interbreeding γ, we performed 10,000 backward coalescent simulations to assess the final proportion of introgressed genes into a given species. For each coalescent simulation, we sample 40 genes in 25 equally spaced demes of the invading population for scenarios C1–C7 and in 25 demes (see Fig. 5) of the invading and of the local species for scenarios NC1–NC5. The ancestry of the samples is traced back in time on the simulated genealogies to infer the species' origin of these genes. The average fraction of genes originating from the other species is used as an estimator of the introgression level in each species. Note that for very small γ values, introgression levels can vary among the 25 demes and lead to clines from the introduction point toward the far end of the range (see Figs. 5 and 6).

LITERATURE SURVEY

We surveyed the recent literature for cases of significant introgression after a range expansion of one species into the range of another one. We looked for examples based both on chloroplast and mitochondrial markers and on nuclear markers. However, examples based on organelle markers were more frequent, because they are particularly abundant in the introgression literature and the specific origin of the lineages can be more easily inferred, thus making it possible to deduce the direction of the introgression. Among over 200 papers reporting introgression, many were restricted to recent zones of contact or to taxa showing only F_1 hybrids (hence without effective introgression). These cases were discarded because they do not correspond to the modeled process of range expansion with effective introgression measured over a large portion of the range of the species. A further difficulty was to objectively infer which species was resident and which one was invading. This information was sometimes unavailable, or the two species were thought to have both expanded, but it was unclear which one had arrived first. These ambiguous cases were also excluded.

Results

DYNAMICS OF THE INTROGRESSION

To understand the introgression process, it is instructive to monitor the dynamics of the interbreeding events at the wave front, where the invading species is initially at low densities. The change in deme densities upon invasion and the number of introgression events between the local and the invading species are illustrated in Figure 2 with or without competition between the two species. In both cases, local genes introgress the invading species when it is still at very low density. Therefore these few introgressed genes are amplified by the logistic growth of the invading population. This is in contrast with the situation of invading genes entering the local species, which is already at carrying capacity (without competition) or declining (with competition). Therefore, a single gene introgressing the invading population may be found at multiple copies when the invading population reaches its carrying capacity, which introduces a net asymmetry in effective introgression between the invading and the local population. Note that this asymmetry only occurs if interbreeding events are frequent enough to occur on the wave front, when the invading population is still at low density, which explains why the final introgression levels are symmetric for low interbreeding rates and become asymmetric with increasing interbreeding levels (see Fig. 3B). Large overall introgression levels in the invading population are therefore due to the progressive dilution of the gene pool of the invading species by the few interbreeding events occurring at the wave front (Chikhi et al. 2002). Note however that this dilution is greatly accelerated when one takes into account the logistic growth occurring in newly founded demes (Currat and Excoffier 2004). Therefore, as colonization proceeds, the gene pool of invading populations is increasingly diluted by resident genes, such that the invasion process is carried out by progressively more introgressed individuals, leading to higher introgression levels away from the source of the invasion (see Figs. 4–6).

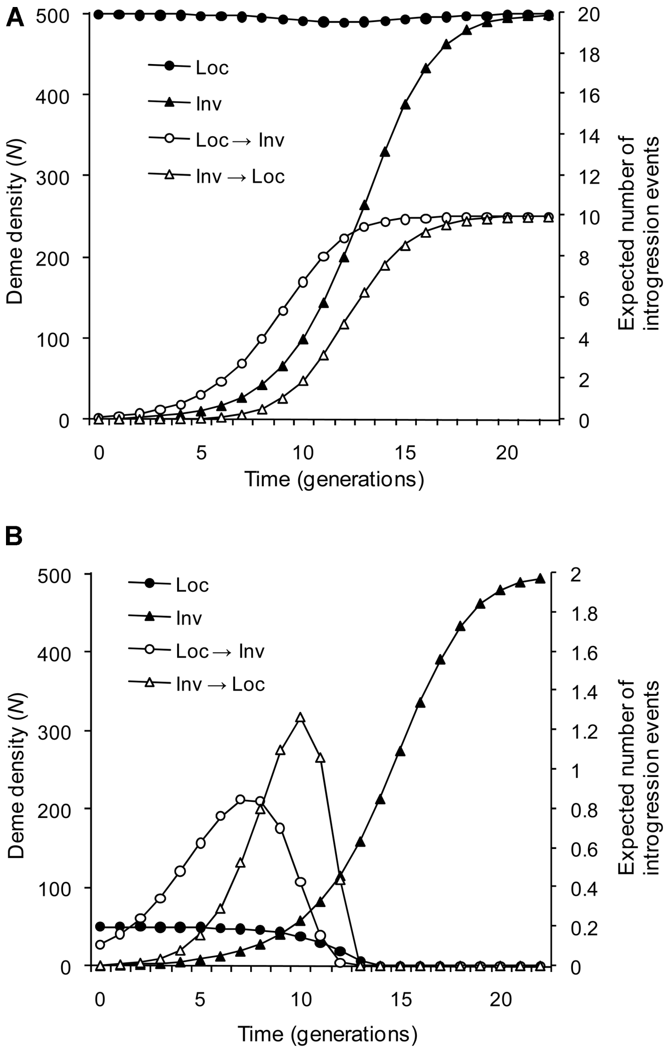

Figure 2. Illustration of the local demographic and introgression dynamics. We plot the evolution of population densities and introgression events over time at a given location of the lattice, assuming no migration from neighboring demes for simplicity. At generation zero, the local species is at carrying capacity, and the invading species appears. (A) Demographic parameters correspond to the scenario NC2 without competition and in (B) demographic parameters correspond to the scenario C1 with competition. In both cases, $\gamma = 4\%$. Note that introgression first occurs from the local to the invading species. Note that in (B) the number of introgression events is smaller than (A) due to the smaller population size of the local species (see Material and Methods). Loc → Inv: Introgression events from the local to the invading species. Inv → Loc: Introgression events from the invading to the local species.

INVASION WITH COMPETITION

When the resident and the invading species compete for local resources, the invading species progressively replaces the local species if it has a larger carrying capacity (Shigesada and Kawasaki 1997), but in our simulations it gets almost completely introgressed by local genes if more than 10% of effective

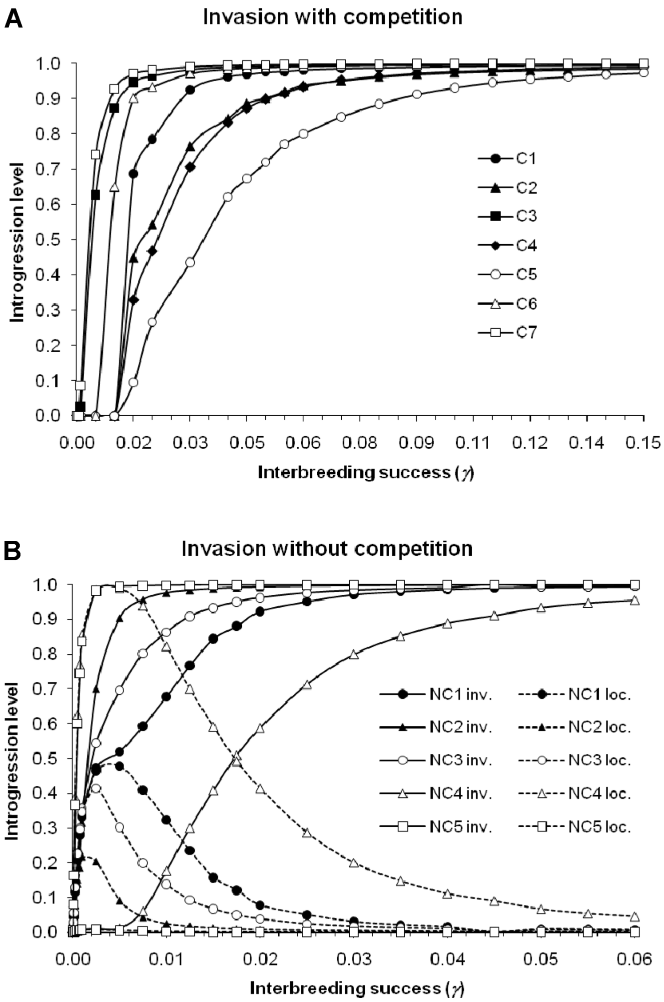

Figure 3. Proportion of genes introgressed into a given species as a function of the level of interbreeding (γ). (A) Cases with competition between a local and an invading species. (B) Cases without competition. loc. documents introgression level in the local species, whereas inv. documents the introgression level in the invading species. Reported rates are averages over 10,000 simulations. Case simulation parameters are those reported in Table 1. Interbreeding success can be considered as the fitness of genes transferred into a new background by interbreeding.

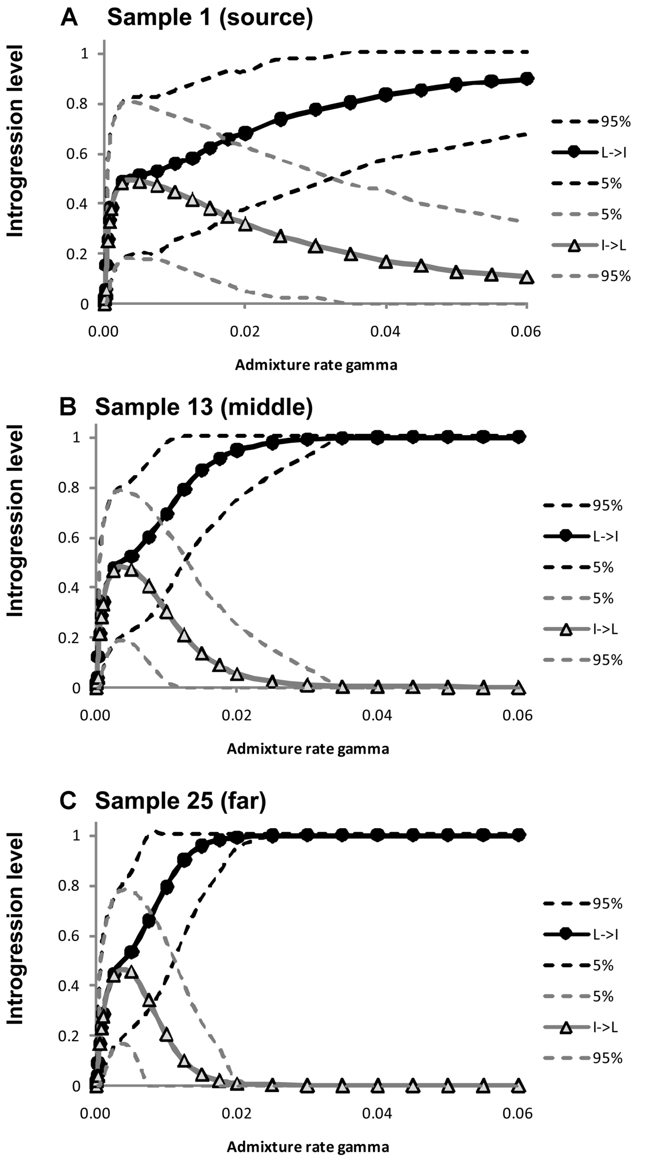

Figure 4. Variance in introgression levels across the invaded area. Proportion of introgressed genes in the invading species (black dots) and in the local species (gray triangles) for three samples located at various distances from the origin of the expansion. Sample 1 is located at the source of the expansion (pane A), sample 13 is in the middle of the invaded area (B) and sample 25 is most distant from the origin of the expansion (C). Dotted lines represent the limits of an empirical 90% confidence interval for introgression levels obtained from 10,000 simulations. The variance in introgression levels is particularly large close to the origin of the expansion and when the admixture rate (γ) between species is low. The introgression proportions have been obtained for scenario NC1 (Table 1).

interbreeding events are successful (Fig. 3A). Note that this 10% limit is rather arbitrary, as there are many scenarios for which complete introgression occurs for much lower interbreeding levels. It may be quite specific to our simulation sets, and the final level of introgression depends on where it is measured (e.g., see Fig. 5). Indeed, demes located further away from the source show higher levels of introgression, because more interbreeding events occured during the expansion at the wave front. Final introgression levels can actually reach up to 95% with as little as 3% interbreeding success (cases C1, C3, C6, and C7). Even when the invading species is 100 times more numerous than the local one, complete introgression of the invading species occurs when interbreeding rate (γ) exceeds 10% (cases C2 and C5). When the invading species is only two times more abundant than the local species, high levels of introgression also occur for moderate levels of interbreeding (cases C6 and C7). This is explained by the fact that the cohabitation period

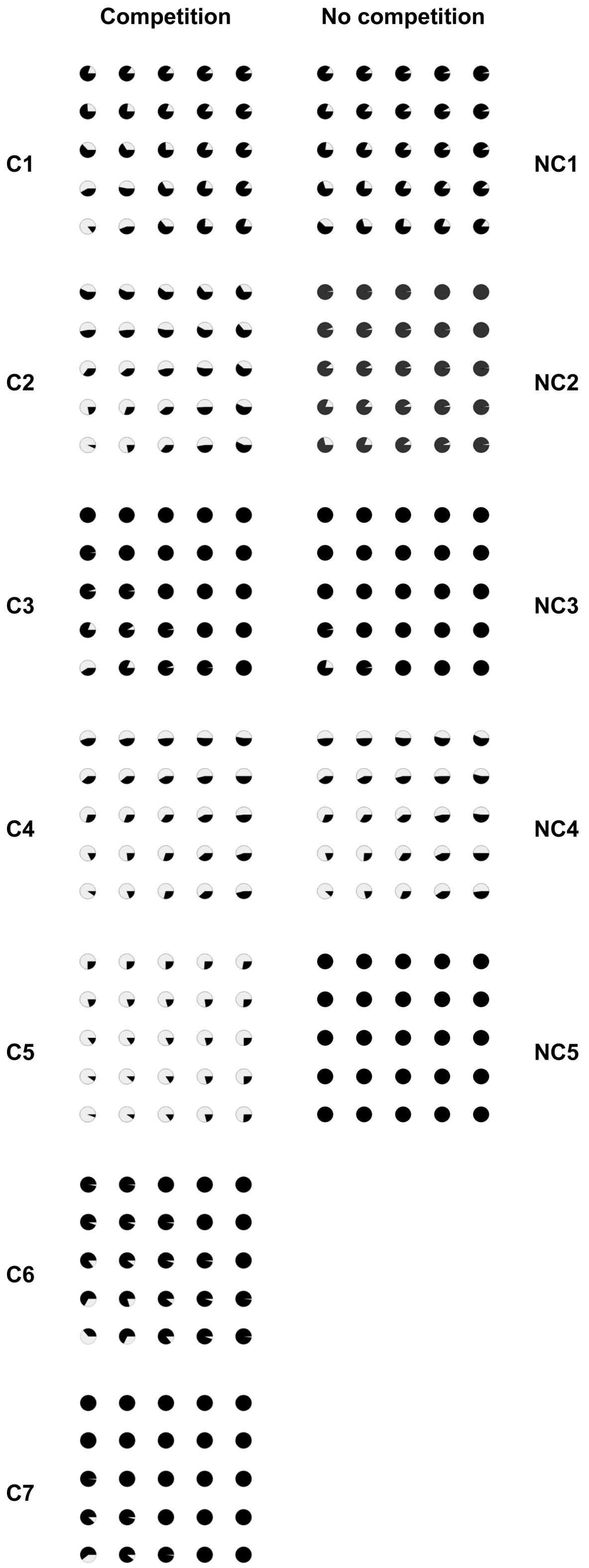

Figure 5. Spatial variation in introgression levels. Proportion of introgressed genes (black pie) in the invading species for each of the 25 simulated samples and for the 12 scenarios C1-C7 and NC1-NC5. Simulations were done by assuming that $\gamma = 0.015$. The source of the invading species expansion is close to the bottom left pie-chart (see Fig. 1).

at the wave front is longer for reduced competitive advantage of the invader (see Table 1), allowing for more interbreeding events to occur during this period. Overall, the final level of introgression is positively correlated with the interbreeding rate and the size of the local population (compare cases C2 and C3), and it is negatively correlated with the size of the invading population (compare cases C1 and C2 or C4 and C5). Introgression is also favored when gene flow between adjacent demes is restricted (compare cases C1 and C4, C1 and C6, as well as C2 and C5). This makes sense, because genes introgressed from the local population at the wave front will compete with migrant genes from the invading populations if gene flow is high, and will be thus less amplified by the logistic regulation. A similar negative effect of migration on the spread of new variants has been documented in the case of "allele surfing" in expanding populations (Klopfstein et al. 2006). Allele surfing refers to the spread of a previously rare allele during a range expansion. An allele can surf on a wave of advance, reaching high frequencies and occupying a large area, despite having no selective advantage (Edmonds et al. 2004; Klopfstein et al. 2006; Hallatschek et al. 2007; Travis et al. 2007). This phenomenon is due to high levels of genetic drift occurring at the wave front (Hallatschek and Nelson 2008). Because any allele can surf, there is a competition between all alleles present at the edge of the wave front for surfing. In case of large levels of gene flow between sub-populations of the invading species, introgressed alleles will compete more with alleles from the invading species, and will therefore be less likely to be propagated by the invasion process. This result is consistent with the observation that levels of introgression for uniparentally inherited markers such as mitochondrial (Bachtrog et al. 2006; Berthier et al. 2006) and chloroplast (Martinsen et al. 2001) DNA is higher than for nuclear markers, because maternally inherited genes typically experience less gene flow than nuclear genes (Birky et al. 1989).

INVASION WITHOUT COMPETITION

When the invading and the resident species do not compete and continue to coexist, reciprocal introgression can occur, but only at very low levels of interbreeding (Fig. 3B). For higher interbreeding levels, introgression patterns become similar to the competition case, with the invading species being completely introgressed by the genes of the local species. More specifically, introgression levels become asymmetric in our simulations at interbreeding levels of $\gamma > 0.5\%$, that is when interbreeding is frequent enough for hybridization events to occur on the wave front, as explained above. If interbreeding success level is slightly larger ($\gamma > 2\%$), the invading species gets massively introgressed, even when it is much more abundant than the local species (case NC4). Note finally that, as in the case of invasion with competition, most populations will have genes from mixed origins at many loci for low levels of interbreeding.

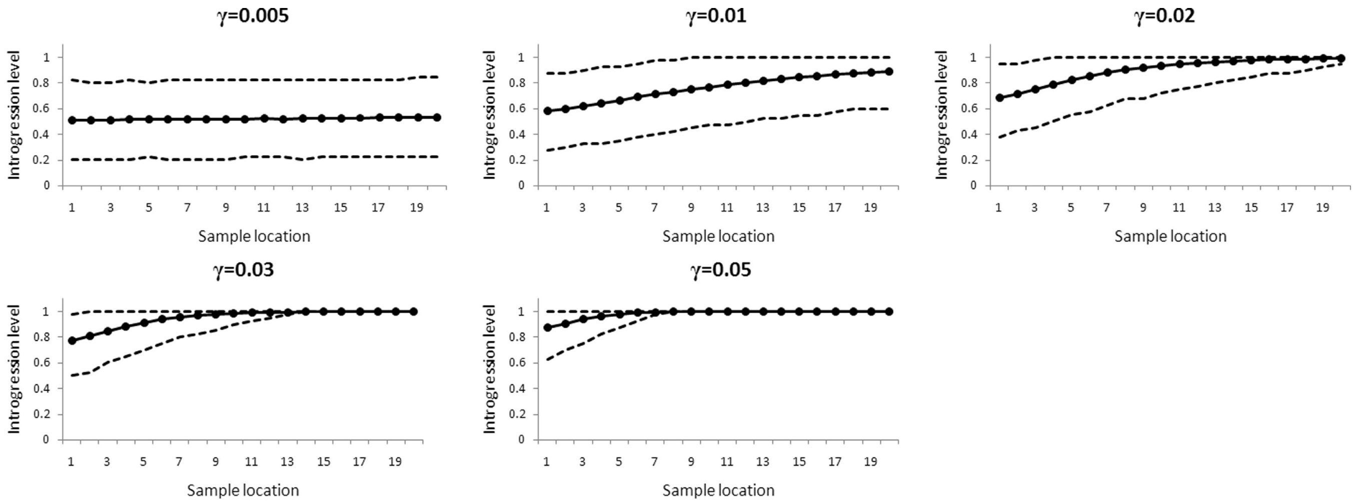

Figure 6. **Variation in introgression level into the invading population along the expansion path in absence of competition. The average introgression level is reported as filled circles for different interbreeding levels in 20 equally spaced demes located along the expansion path going from the lower left to the upper right of the simulated world. The modeled scenario corresponds to scenario NC1 in Table 1 and Figure 3B. The dashed lines correspond to the limits of a 90% empirical confidence interval obtained from 10,000 coalescent simulations. The expansion starts from deme 1. Note that a gradient of introgression is only visible over the whole transect for very limited levels of interbreeding ($\gamma = 0.01$).**

RECENT INVASION IN A SMALLER AREA

To study how the age of the invasion and the size of the invaded area affect the results, we have simulated the same 12 invasion scenarios reported above in a smaller world of 20 × 20 demes, and the introgression levels were measured after a shorter period of 200 generations. The results are reported in Table S3 and Figure S1 (see online Supplementary material). They are qualitatively very similar to those reported for a larger world and for an older invasion as reported in Figure 3, which confirms that our findings still apply to modern bioinvasions. However, rates of interbreeding need to be on average about four times larger than in the older invasion scenarios to reach similar levels of introgression. In our simulations without competition between the two species, the local species shows less than 5% of introgression and the invading species is massively introgressed when the effective interbreeding rate (γ) is larger than 10%, except when the invading species is much more numerous than the local species (scenario NC4*, see online Supplementary Figure S1B). Lower levels of introgression in the case of a recent and limited invasion are somehow expected, because introgression levels reported in online Supplementary Figure S1 are measured in demes much closer to the source of the invasion as compared to those measured in Figure 3. Indeed, more introgression events will have happened for the same rate of local interbreeding (γ) when measured far away from the source of the expansion, which also implies that larger levels of introgression are expected for invasions having occurred over large territories (see Figs. 4–6 and results below).

SPATIAL DISTRIBUTION OF INTROGRESSION

Although Figure 3 reports average introgression levels over the whole invaded area, it appears that local introgression levels can vary according to the geographic position, and most noticeably with distance from the introduction point. In Figure 4, we show the introgression levels for different rates of interbreeding in scenario NC1 at three different locations. As expected, similar interbreeding rates lead to larger final introgression levels at larger distance from the origin of the invasion. We can also see that the variance of observed introgression level is lower further away from the source. Although the average level of introgression is always equal or larger in the invading species than in the local species, the situation can be inversed when the introgression confidence intervals overlap in the two species, which happens for low rates of interbreeding (Fig. 4). In Figure 5, we present the spatial heterogeneity of average introgression rates for scenarios C1–C7 and NC1–NC5 in the case of low levels of interbreeding ($\gamma = 0.015$). This small γ value was chosen because it allows the observation of the genes of both local and invading species (see Fig. 3). With larger values of γ, the invading populations would mostly show genes from the local species. One can see that for this low level of interbreeding ($\gamma = 0.015$), introgression levels can drastically differ between the lower left demes (close to the source of invasion) and the upper right demes (farthest away from the source), like in scenarios C1–C3 and NC4. It implies that in practical cases, the measure of introgression levels can substantially vary depending on where sampling is performed. Additionally, one could predict that heterogeneous introgression levels measured across the range of a species should be indicative of low levels of interbreeding. Finally, we report in Figure 6 a more detailed study of the introgression levels in 20 demes located along a southwest-northeast transect for scenario NC1 and low levels of interbreeding ($\gamma =$ 0.5–5%). We can see that for $\gamma = 0.5\%$ the average introgression levels of local genes into the invading species are uniform over the transect and slightly exceed 50%, in keeping with Figure 3. For larger γ values, introgression levels steadily increase with distance from the source, and a gradient is observed over the whole transect only for $\gamma = 1\%$. For larger γ values, a gradient can be seen, but only over a much shorter section of the transect. It therefore appears that clines of introgression are only expected for a very narrow range of interbreeding levels. They should neither be expected for extremely low levels of interbreeding (because the rare interbreeding events will only occur beyond the front wave), nor for large interbreeding levels (because almost complete introgression will have occurred over most of the overlapping range of the species).

COMPARISON WITH EMPIRICAL DATA

Our modeling results are broadly consistent with empirical data. To test our predictions, we conducted a literature survey of patterns of introgression at mitochondrial or chloroplast DNA markers, which have been studied in a wide array of animals and plants. Among hundreds of papers reporting introgression of organelle DNA, we found 44 cases of introgression following range expansions where the resident and the invading species could be clearly identified (see online Supplementary Table S1), of which 12 were found in plants, eight in invertebrates, and 24 in vertebrates. In 36 cases (82%), introgression is highly asymmetrical and goes from the local to the invading species. Moreover, the invading species is often (70% of the cases) almost completely introgressed ($> 90\%$) by genes from the local species. Only seven cases (16%) report massive introgression in the reverse direction, and one case is ambiguous, as the direction of introgression varies depending on the region considered. The asymmetry of introgression still holds in current areas of sympatry, where the two species coexist (14 out of 19 cases involving predominantly sympatric species in online Supplementary Table S1, i.e., 75% of the cases). This suggests that introgression involving native and invading populations is a truly asymmetric process, and is not only found in the wake of moving hybrid zones. The prevalence of introgression is likely linked to past environmental and climatic changes to which many species respond rapidly by range shifts and expansions (Hewitt 2000), leading to secondary range overlap between species having evolved in isolation. This is especially true for temperate species that expanded postglacially into the range of more boreal species (e.g., Ballard and Whitlock 2004; Melo-Ferreira et al. 2005).

Numerous additional cases reporting massive or complete organelle DNA introgression are found in the literature, many of which could have been interpreted as evidence in favor of our model. However, these cases were not considered here, either because hybridization was too recent, because a clear evidence that a range expansion occurred was lacking, or because introgression was so pervasive that the specific origin of the organelle haplotypes could not be recognized (e.g., Dumolin-Lapègue et al. 1999).

Finally, note that we also identified 12 cases involving introgression of nuclear markers (reported separately in online Supplementary Table S2). In all cases, nuclear introgression was found to affect only or mostly the invading species. However, as all examples of nuclear introgression involve rapidly moving hybrid zones in which the resident species is displaced by the invading species, it was not possible to check if asymmetry was preserved in sympatry.

Discussion

We do not argue that range expansions and invasions explain all cases of introgression, because a number of factors are likely to complicate this general and simple scheme. The few cases that do not meet our expectations in Table S1 (see online Supplementary material) could be explained by various factors, such as selective processes (Ballard and Whitlock 2004; Whitney et al. 2006), asymmetric mating preference or behavior (Patton and Smith 1993; Roca et al. 2005), sex-biased gene flow (Petit et al. 2004), or sex-biased survival of hybrids (Haldane’s rule), which could all oppose (or amplify) the neutral trend (Barton 2001; Machado et al. 2002). Also, the fact that we have used parameters (carrying capacities, migration rates, rates of interbreeding) uniform over the whole species distribution may not be completely realistic. Indeed, environmental heterogeneity may affect the spread of the wave of advance (Klopfstein et al. 2006; Wegmann et al. 2006; Ackland et al. 2007; Travis et al. 2007), local differences in carrying capacities may change the cohabitation time (Table 1), which can affect the final rate of introgression, and interbreeding levels may themselves be affected by the levels of introgression. Note that in the latter case, if phenotypic convergence is correlated to levels of introgression, one would expect that interbreeding levels would increase with introgression, and that the invading species would converge toward the local species and therefore stop expanding. Moreover, even in case of uniform rates of interbreeding, the expected pattern of introgression is not always uniform over the whole invaded area (Fig. 5), and introgression levels have a relatively large associated variance, especially when the sampled deme is located close to the source of the invasion, or when the interbreeding rate is low (see Figs. 4 and 6). Finally, at least in principle, genes of the invading species that turn out to be adaptive in the local species could introgress and then spread in the local species. Our literature survey, however, underlines the commonness of the asymmetric introgression from the local to the invading species. Our simulation analyses assume that the studied markers are neutral, and the fact that most documented cases of organelle gene introgression follow our predictions is in keeping with the view that organelle genes mostly behave as neutral markers. We nevertheless anticipate that many more cases of massive or complete introgression of organelle DNA in plants and animals will fit the pattern predicted by our simulations when the dynamic of range expansion of the interacting species will be studied in more details.

We believe that our results have great significance as well as important implications. We illustrate this by listing seven important and often counterintuitive implications of our results.

First, our simulations show that it is not necessary to invoke selection (Ballard and Whitlock 2004; Rieseberg et al. 2007), unusual behaviors (Wirtz 1999), or differences in relative species abundance (Cianchi et al. 2003) to explain massive levels of introgression from a local to an invading species. Distribution shifts can also explain why introgression can be detected beyond current areas of sympatry, which is otherwise difficult to explain without invoking positive selection (Evans et al. 2006). Conversely, the absence of introgression from a local species into an invading species implies that interbreeding was virtually absent, as already pointed out in the case of modern humans that replaced Neanderthals across Europe (Currat and Excoffier 2004). We therefore propose that massive introgression in an invading species should not be considered as a sign of selection or disassortative mating but as the null expectation for neutral genes.

Second, our simulations not only document the introgression patterns expected when a species expands in an area colonized by a related species, but they also provide a simple explanation for this asymmetric gene flow. The asymmetry arises not only in the case of competitive interactions between species, where the resident species is eliminated by the invading one, but also in the absence of any competition in the area of sympatry. This asymmetry is due to a demographic imbalance between the two species at the wave front, where the invading species is at lower densities. As it has initially few available conspecific mates, it tends to be mainly involved in heterospecific crosses (Hubbs 1955). Subsequently, the genes from the resident population that have introgressed the invading species are amplified by the logistic demographic growth that occurs at the wave front of the invading population, resulting in a massive introgression of resident genes into the invader's gene pool.

Third, our findings suggest that the "pollution" of the gene pool of native species by interfertile invaders should be relatively limited, because introgression should mainly be from the local to the invading species (Figs. 2B and 3B). Hence, the risk incurred by the native species is primarily demographic and not genetic. In contrast with this finding, it has repeatedly been suggested that exotic plant species could threaten closely related native congeners through asymmetric hybridization and subsequent backcrossing (e.g., Brock 2004).

Fourth, our simulations show that introgression should be stronger for genes experiencing little gene flow with conspecific neighboring populations, which may partly explain the more frequent introgression of organelle genes compared to nuclear genes. At first sight, this result seems counterintuitive: the greater "interspecific gene flow" experienced by organelle genes compared to nuclear genes seems at odds with their reduced gene flow at the intraspecific level (Senjo et al. 1999). However, it does make sense, as pointed out above, because if intraspecific gene flow is low, genes from the local population that have introgressed in the invading population at the wave front will not be diluted by migrant genes from the invading populations and will thus become rapidly fixed in the gene pool of the invader following demographic growth.

Fifth, phylogenetic reconstructions based on markers showing high rates of introgression, such as organelle DNA markers, are likely to be incongruent with the history of the organisms (Clarke et al. 1996) and to show traces of reticulations due to the fossilization of ancient genomes in colonizing species. The genes belonging to the first population or species that has colonized an empty territory are indeed likely to persist over long evolutionary periods, and may still be found after the pioneer species itself has disappeared. Good illustrations of this process are the case of the introgression of mtDNA mountain hares into the Iberic hare, or that of the arctic charr into lake trouts (Wilson and Bernatchez 1998; Melo-Ferreira et al. 2005). Such patterns could easily be wrongly attributed to cases of sympatric speciation (Clarke et al. 1996, Jordal et al. 2006).

Sixth, our study could open the way to a method to detect which species first colonized a new territory, and which arrived later. We have shown that a strong asymmetry in the levels of introgression between the local and the invading species is expected. This asymmetry could be used in the future as a signature of past changes in species distribution. Barton and Hewitt (1985) made the same point in the case of moving hybrid zones, and pointed out that evidence will be most unequivocal when many neutral alleles from independent loci have introgressed, all in the same direction.

Seventh, genes from the resident species involved in local adaptation should easily introgress the invading species if they do not conflict with the invading phenotype (e.g., Rieseberg et al. 2007), but they should be difficult to distinguish from neutral genes that have also introgressed. Contrastingly, genes from the invading species will introgress the local species only if they are under very strong positive selection in that background. Simultaneously, genes of the invading species involved in phenotypic or behavioral differences with the local species must be under particularly strong positive selection to withstand introgression from the native species, as high levels of introgression genome-wide should result in phenotypic convergence. In the context of hybrid zones, Barton and Bengtsson (1986) have shown that if one assumes that the fitness of hybrids is controlled by a single locus, one should observe a reduction of gene flow in its vicinity by a factor $r\gamma/[(1-\gamma)+r\gamma]$, where r is the recombination distance to the selected locus, and γ is the fitness of hybrids. For instance, it means that with a 50% reduction in hybrid fitness, gene flow would be reduced approximately by a factor of 100, 1 cM away from the selected locus. In the case of a range expansion, one would therefore also expect to have similarly reduced levels of introgression around genes controlling the phenotypic integrity of the invading species. Hence, the study of nuclear diversity in invading species that have kept their phenotype despite massive introgression of genes originating from the pioneer species should offer a unique opportunity to discover DNA regions or speciation genes involved in phenotypic differences between species (Scotti-Saintagne et al. 2004; Lexer et al. 2007).

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Documented cases of cytoplasmic introgression after a range expansion.
Table S2. Documented cases of nuclear introgression after a range expansion.
Table S3. Parameters of the 12 recent invasion scenarios.
Figure S1. Proportion of genes introgressed after a recent expansion.

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