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BIODIVERSITY VIEWPOINT

Biological invasions at the gene level

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ABSTRACT

Despite several recent contributions of population and evolutionary biology to the rapidly developing field of invasion biology, integration is far from perfect. I argue here that invasion and native status are sometimes best discussed at the level of the gene rather than at the level of the species. This, and the need to consider both natural (e.g. postglacial) and human-induced invasions, suggests that a more integrative view of invasion biology is required.

Key words

Alien, genetic assimilation, gene flow, homogenization, hybridization, introgression, invasibility, invasiveness, native, *Quercus*, *Spartina*.

INTRODUCTION

Biological invasions are among the most important driving forces of evolution on our human-dominated planet. According to Myers & Knoll (2001), distinctive features of evolution now include a homogenization of biotas, a proliferation of opportunistic species, a decline of biodisparity (the manifest morphological and physiological variety of biotas), and increased rates of speciation in some groups prospering in human-dominated systems. For the most part, progress towards integrating evolutionary biology into invasion biology is very recent (for reviews see Levin, 2000, 2003, 2004; Mooney & Cleland, 2001; Sakai *et al*., 2001; Hänfling & Kollmann, 2002; Lee, 2003; Schaal *et al*., 2003; Petit *et al*., 2004a), following a few isolated efforts (e.g. Barrett & Husband, 1990; Abbott, 1992 and references therein). As a consequence, the synthesis is far from perfect. Although there is widespread agreement that biodiversity spans levels of organization ranging from ecosystems to genes (e.g. Frankel *et al*., 1995), many recent treatments of biological invasions seem to still ignore or minimize this genetic dimension. In particular, despite this recent focus on evolutionary processes, it is not widely perceived that biological invasions also include the introduction of alien genotypes and alleles.

Considering biological invasions at the gene level could solve some terminological difficulties in the field and help address questions at the appropriate level of biological organization. Here, I discuss several points destined to emphasize the genetic dimension in invasion biology, focusing on plants. I suggest that it might sometimes be more relevant to discuss the question of native vs. alien status at the levels of genes, rather than at the species level, using hybrid taxa as a case in point. There is indeed a growing body of information on hybridization and introgression during plant invasions, which seems to be facilitated by the particular genetic system of plants. Although great attention has been paid to the formation of new hybrid taxa, introgression more often results in hybrid swarms or in 'genetic pollution', which is best examined at the gene level. Under this perspective, translocations of individuals and even movement of alleles within a species' range (e.g. following selective sweeps) should equally be recognized as an important (if often cryptic) component of biological invasions. Throughout, rather than stressing the peculiarities of human-induced invasions, I point out the similarities with natural invasions, with the hope that this may further contribute to the integration of invasion studies into evolutionary biology. Altogether, these examples call for a broader, more integrative view of invasion biology.

WHAT IS A NATIVE? THE CASE OF HYBRID TAXA

'Native' hybrid taxa with alien parents?

In a recent effort to clarify communication between taxonomists and ecologists, Pyšek *et al*. (2004) made several suggestions regarding terminology in the field of plant invasions. The idea was to harmonize the classification of taxa in floras, which should facilitate the identification of the determinants of invasiveness or invasibility in future comparisons. One difficulty encountered involves the case of hybrid plants resulting from the cross between a native and an alien plant (or between two alien plants that could not cross before). Should these hybrid taxa be considered as 'natives' to the new territory, given that they originated there and lack any alternative native range, or should they be considered 'aliens' given that they came into existence as a consequence of a human introduction?

Vermeij's agenda: invasion as a natural process

Pyšek *et al*. (2004) propose to reserve the term 'invasion' to situations where the distribution and abundance of plants change as a result of human activities. They further argue that since invasions are a human-related phenomenon, the 'had-it-not-been-for-people' reasoning is more appropriate for the definition of what is a native plant than the 'where-it-evolved' approach. Consequently, hybrids having at least one alien parent should not be considered as natives since they would not be present without human intervention. In other words, the anthropocentric viewpoint is given precedence over the biogeographical viewpoint. I have suggested elsewhere with several colleagues that anthropocentric views should be avoided when studying biological invasions. In particular, we proposed to use identical terms to describe artificial and natural invasions, as this should help integrate the fields of palaeoecology and invasion biology (Petit *et al*., 2004a). Richardson *et al*. (2000a) have also lamented that invasion ecologists frequently make use of anthropocentric concepts such as aggression or attack. He has further pointed out that, as the spatial scales of 'palaeoinvasions' and 'neoinvasions' are often comparable and the context is always clear, the term 'invasion' is appropriate for palaeoecological studies. This usage conforms to that of Elton (1958), who used the term 'invaders' with reference to the intermixing of faunas during the Pliocene (although he maintained a strong dichotomy between natural and artificial invasions, see Davis *et al*., 2001), and to that of many other early authors cited in Richardson *et al*. (2000a). Vermeij (1996) has emphasized that invasion biology should be viewed as an integral part of ecology and evolutionary biology (see also Davis *et al*., 2001), but progress in this direction has been impeded by the lack of a common language with the flexibility to describe the same processes in different contexts. Some palaeoecologists have now rehabilitated the word invasion and use its derivatives invasiveness and invasibility in the context of post-glacial colonization (see, e.g. Pielou, 1991; Jackson, 1997; Davis *et al*., 1999; Parshall, 2002; Lyford *et al*., 2003), facilitating interdisciplinary exchanges (Rejmánek, 1999). Despite the fact that most ecologists currently equate invasion with the dynamics of alien species (Richardson *et al*., 2000a), the advantages of applying this term to natural range expansions seem to outweigh the disadvantages (Petit *et al*., 2004a).

Alien and native genes

If we allow the biogeographical viewpoint to take precedence over the anthropocentric viewpoint, is it not inescapable that these hybrid taxa should be dubbed natives, whether we like it or not? Although I agree with this, I would point out that the whole argument exists only by virtue of a focus on higher categories (the hybrid taxa, considered as real entities), which may not always be the most relevant category (e.g. for management purposes). As long as the genome of one individual includes alleles that can clearly be shown to have evolved in an alien territory and to have invaded the new territory as the direct or indirect consequences of human activities, then the plant itself can no longer be considered as fully native (although the higher category to which it belongs may be considered so). A 'gene view' of the native status is therefore not only possible but necessary if we want to avoid this dilemma. This view is not unlike the 'genic view' of speciation, which shifts the emphasis from isolation at the level of whole genomes to differential adaptation at the genic level and minimizes the importance of genetic coadaptation except at a few loci (Rieseberg & Burke, 2001; Wu, 2001). Under this framework, considerations of past and ongoing gene flow become essential.

GENE FLOW DURING INVASION

Pollen flow during invasions

Quite understandably, studies of plant invasions have focused on dispersal by seeds or other propagules capable of establishing new populations (reviewed in Petit & Vendramin, 2004). However, the role of pollen flow in promoting invasions should not be underestimated. Dispersal of genes occurs at two distinct phases of the plant life cycle: with the male gametophyte (the pollen) and with the juvenile sporophyte (the seed), the rest of the life cycle being represented by a sessile organism. The whole process is intrinsically asymmetrical, since the female gametophyte does not move. Furthermore, the seed and pollen components of gene flow are generally very unequal: pollen flow among established populations is estimated to be, on average, an order of magnitude greater than seed flow (Petit & Vendramin, 2004). This means that in 90% of the cases distant gene flow will result in an individual whose male gametic contribution originates from a migration event but whose female gametic contribution is of local origin. The non-local paternal alleles are tested first in the style for their compatibility with the maternal tissues, and then in the new embryo. This young embryo is subjected to diverse maternal influences, either genetic (including from its chloroplasts and mitochondria, of maternal origin in the majority of angiosperms), epigenetic or environmental. These maternal effects allow testing exotic genes in the prevailing local ecological and genetic context. Such a filtering process considerably facilitates the import of foreign genes, compared to a situation where the vehicle of invasion is a seed with 100% exotic constitution, thereby accelerating the naturalization process. Subsequent crosses with local genotypes may lead to segregation and recombination, allowing locally adapted alleles at some genes to be combined with advantageous alien alleles at other genes.

Interspecific gene flow as a route for plant invasions

This peculiar life cycle of plants (shared in part by some aquatic invertebrates where male gametes are disseminated by water) predisposes them to high levels of hybridization and introgression during invasions. Although, as a rule, only seeds can prospect new environments (Harper, 1977; p. 775), an exception occurs when a species colonizes a site already occupied by related interfertile species through pollen swamping, rather than by seeds. This would result in hybrids and possibly in backcrosses and other hybrid derivatives characterized by the maternal chloroplast and mitochondrial DNA genetic structure of the already established species and an increasing proportion of the nuclear genome of the invading species, as is thought to have happened during natural invasions of eucalypts and oaks following the last ice age (Potts & Reid, 1988; Petit *et al*., 1997, 2001, 2004b; Belahbib *et al*., 2001). A similar process has recently been reported in a salt marsh species (*Sarcocornia*), as part of a natural succession: In south-western Spain, pollen flow takes place from high-marsh *S. fruticosa*, some 1 km distant, to the stigmas of the established dominant *S. perennis* (Figueroa *et al*., 2003). The use of genetic markers indicates that each hybrid results from an independent pollination event. Succession might therefore be facilitated genetically (*S. perennis* stigmas facilitating the formation of hybrids) rather than simply ecologically (*S. perennis* enhancing sediment accretion). However, it is not clear if the process is restricted to the production of first generation hybrids or proceeds all the way to the 'resurrection' of the invading species, as in the case of the oaks and the eucalypts.

Displacement of native by invasive species by similar processes has gained widespread recognition in the field of invasion biology, where it has been called 'genetic assimilation' (e.g. Ellstrand & Elam, 1993; Mooney & Cleland, 2001; Sakai *et al*., 2001; Woodruff, 2001). The expression is suggestive since it implies that the invasive taxon is integrated into the gene pool of the native species (possibly with differential introgression of genes) and may not eliminate it completely, even if extinction of the native taxon (as a genetically 'pure' entity) ensues. Such contamination of native gene pools would generally involve mostly pollen flow (Potts *et al*., 2003). Unfortunately, the expression 'genetic assimilation' has been used since a long time with a completely different meaning (to indicate that environmentally induced phenotypes can become genetically fixed; Pigliucci & Murren, 2003). In any case, genetic assimilation (in the sense used in invasion biology) often predominates over demographic effects during interspecific encounters between compatible species (Huxel, 1999), although other outcomes are possible, such as the formation of fixed hybrid forms (Abbott, 1992).

Spartina anglica: when a textbook example turns out to be atypical

The cordgrass *Spartina anglica* represents an example of such a fixed hybrid form; it is in fact the classic textbook example of hybridization leading to a new invasive species (reviewed in Ainouche *et al*., 2004). However, it now appears to represent a relatively isolated case. *S. alterniflora* from eastern America has been introduced accidentally by shipping ballast during the end of the 19th century in southern England, where hybridization with the local *S. maritima* resulted in a sterile hybrid, *S. alterniflora* being the seed parent in the cross. Chromosome doubling in this hybrid gave rise to a new fertile allopolyploid species, *S. anglica*, a vigorous and aggressive perennial plant that has been actively colonizing British and then western European salt marshes since its formation (Raybould *et al*., 1991a). *S. anglica* has been subsequently introduced into China, Australia and New Zealand for land reclamation, given its ability to increase sediment accumulation, and has become invasive there as well. This new species is genetically isolated from its parents and is extremely genetically depauperate (Raybould *et al*., 1991a,b; Ayres & Strong, 2001; Ainouche *et al*., 2004), pointing to a genetic bottleneck at the time of its formation.

Large diversity due to multiple origins of allopolyploids through recurrent hybridization has since been found to be the rule rather than the exception (Soltis & Soltis, 1999), so the *Spartina* case is unusual, as is the fact that the introduced genotype acted only as mother in the cross. Interestingly, the introduction of *S. alterniflora* in the American Pacific coast has had rather different consequences: hybridization and recurrent backcrosses involving weakly divergent sister taxa resulted in successful hybrid swarms and new genotype combinations (Ainouche *et al*., 2004). In fact, cases where hybridization between an introduced and a native species has resulted in the spread of a novel invasive hybrid species are numerous and seldom involve a unique origin. For example, introgressive hybridization between the invasive *Rorippa austriaca* and the native *R. sylvestris* in Germany was bidirectional, and some of the invasive populations showed high within-population variation (Bleeker, 2003). Similarly, in European hawkweeds (*Hieracium*) introduced in New Zealand, multiple lineages were introduced and multiple cases of hybridization were identified (Trewick *et al*., 2004).

Invasion's menu: the hybrid soup

The term 'hybrid soup' has been used to stress that hybridization can infuse diversity and generate novel genotypes, masking deleterious genes and transferring favourable ones (Abbott, 1992). Such a merging of genotypes is further facilitated by the fact that, contrary to expectations of reduced diversity due to bottlenecks at the time of foundation, multiple introductions seem to be frequent (e.g. Kolar & Lodge, 2001). In fact, at least in human-induced tree invasions, they seem to represent the rule (Petit *et al*., 2004a). Altogether, this can provide considerable diversity for adaptive evolution to occur. For instance, the spectacular expansions of *Lythrum salicaria* in North America and *Echium plantagineum* in Australia seem to have been fostered by amalgamation of populations originating from different parts of Europe (Barrett, 2000). Similarly, in the USA, the most abundant genotype of the introduced *Tamarix* (which has invaded over 600,000 ha of riparian and wetland habitats) is a novel hybrid between two introduced Eurasian species (Gaskin & Schaal, 2002). Another case of the synergy between the invasion of a novel environment and hybridization is found in *Onopordum* thistles introduced from Europe into Australia (O'Hanlon *et al*., 1999). There is strong evidence for prior hybridization in Europe but opportunities for hybridization in Australia seem to be even greater. Multiple introductions of seed (including hybrid seed) and continuous dispersal have increased the contact among hybridizing taxa.

In England, studies based on molecular markers have demonstrated that *Rhododendron ponticum* has been introduced from several distinct populations from the Iberian Peninsula. In the northern part of its British range, introgression with another exotic *Rhododendron* species has resulted in improved resistance to low temperatures (Milne & Abbott, 2000). In weeds, there have been suggestions that extensive merging of populations and species and the subsequent hybridization may facilitate the spread of herbicide resistance (Jasieniuk *et al*., 1996). Similar transfers of genes probably take place during natural invasions between closely related species. In oaks, possession of new advantageous alleles by the later invading species (e.g. alleles involved in drought tolerance or competitive ability at high density), and simultaneous transfer of locally adapted alleles from the pre-existing species into the invading one (for instance, alleles involved in latitudinal adaptation) could have accelerated the process of postglacial recolonization (Petit *et al*., 2004b). These examples indicate that multiple introductions and subsequent interspecific gene flow may promote rapid evolution and further invasion (Ellstrand & Schierenbeck, 2000) and that a small number of genes could be preferentially transferred as a consequence of their impacts on adaptation and colonizing ability (Lee *et al*., 2003).

Intraspecific invasions

Saltonstall (2002) used the term 'cryptic invasions' to indicate the spread of non-native genotypes within the range of members of their own species, following unintentional (and largely unrecognized) introductions. The adjective 'cryptic' emphasizes the difficulties involved in detecting intraspecific invasions, which may require the use of molecular methods. Initial introduction will nearly always involve seeds or vegetative plant parts, since it is hard to envisage how humans could unintentionally foster long distance pollen flow. However, as in cases of interspecific gene flow, subsequent steps of intraspecific invasions will generally take advantage of pollen flow, given the presence of receptive congeners, at least in allogamous taxa. An exception is provided by the invasion of European populations of the common reed, *Phragmites australis*, into North America (Saltonstall, 2003). A combination of chloroplast and nuclear markers showed that native individuals had not hybridized with individuals belonging to the introduced lineage. The native North American *Phragmites* stock has therefore remained genetically pure after 150 years of coexistence with the European populations, probably because this species reproduces mostly vegetatively. As in the case of *Spartina anglica* discussed above, this example is particularly appealing because the story is so clear, but once again the model may not be very general. In general, extensive gene flow between introduced and native individuals will lead to some level of introgression, making subsequent assignments of geographical origin more difficult. A typical case is provided by studies of gene flow between natural and cultivated populations, as in alfalfa (*Medicago sativa*) in Spain (Muller *et al*., 2003). The difficulty to identify autochthonous material in many European forest trees after intensive plantations further illustrates this point (e.g. König *et al*., 2002).

Gene-specific invasions

Direct studies of gene-specific invasions, whether within species or within complexes of hybridizing species, are still in their infancy. An excellent example, however, is provided by the work of Morrell *et al*. (2003) on DNA sequence variation in wild barley *Hordeum vulgare* ssp. *spontaneum* across its native range, which spans the Mediterranean portion of the Middle East and adjacent south-west Asia. Nucleotide diversity and differentiation at the nine sampled nuclear loci were more heterogeneous than in expectations based on replicates of the same neutral process. It was therefore concluded that the genome of wild barley is a mosaic of different histories generated by different evolutionary processes. Despite inbreeding and a sessile growth habit, dispersal was sufficient for migration to occur across the 3500-km range of the species. At one locus a single haplotype has spread rapidly enough to occur, unmodified by mutation, across the entire range of the species whereas other genes indicate the presence of highly diverged region-specific mutations, representing locally adapted types. It would be important to carry out studies such as that by Morrell *et al*. (2003) in situations where native and introduced invasive plants have hybridized. This would allow testing the hypothesis of gene-specific spread due to directional selection for invasiveness, as suggested for *Rhododendron* or for European oaks.

CONCLUSION: A GENE VIEW OF THE HOMOGENIZATION OF BIOTAS

Despite a couple of decades of intensive research on biological invasions, unexpected results obtained during recent molecular systematic and phylogeographical analyses indicate that the magnitude and number of invasions are still largely underestimated. For instance, Palmé & Vendramin (2002) sampled presumably wild populations of hazelnut (*Corylus avellana*) across Europe in the frame of a comparative phylogeographical study (Petit *et al*., 2003). No sign of introgression was apparent at the morphological level when sampling, but subsequent molecular typing indicated the presence of widely divergent chloroplast DNA from other *Corylus* species and cultivars, a clear case of contamination of a wild gene pool. Intraspecific invasions might be particularly difficult to detect but could become commonplace. At a global scale, widespread dissemination by man of individuals from the same or from different but compatible species is expected to increase both inter- and intraspecific gene flow. The increasing abundance and distribution of generalist pollinators (Richardson *et al*., 2000b) and the modified reproductive phenologies induced by climatic change (Williams *et al*., 2000) may also lead to elevated hybridization rates, as should more direct perturbations of ecosystems. This latter suggestion is supported by a number of studies involving both introduced and native species. For instance, Choler *et al*. (2004) demonstrated that in alpine *Carex* species genotype integrity is better maintained in optimal habitats, whereas introgressed individuals are favoured in ecologically marginal habitats. Increased hybridization rates during periods of rapid environmental changes seem therefore to represent the normal adjustment of plants' genetic system to perturbations and are not restricted to human-induced environmental changes (Petit *et al*., 2004a). Drawing such parallels between natural and human-induced invasions should help fulfilling Vermeij's (1996) agenda by integrating invasion biology further into current ecological and evolutionary thinking. Despite the similarity with natural processes, the merging of distant floras brought together by humans, combined with extended edge effects due to fragmentation of the landscapes and to other environmental changes, may lead to unprecedented levels of interspecific exchanges and hence to an increased invasibility of plant communities (Ellstrand & Schierenbeck, 2000).

As shown throughout, these exchanges are not limited to cases of abrupt speciation and to first generation hybrids, which seem to have been over-emphasized. Instead, they generally imply introgression, resulting in highly gene-specific patterns of invasion. This illustrates the limits of the use of higher categories such as species or hybrid taxa as appropriate entities to report and discuss all forms of invasions.

Clearly, the process of homogenization of the floras worldwide is taking place at all levels of the biological hierarchy, down to the individual and genic level, where it is hardest to recognize and hence to mitigate. So far, while ecologists have been well aware of the negative consequences of invasion, population geneticists have often failed to acknowledge the potentially negative consequences of increased rates of gene flow (e.g. on local adaptation), given their (often uncritical) emphasis on the maintenance of diversity (Petit *et al*., 2002). Due to its peculiar position at the junction between different fields of investigation, the study of the relationships between hybridization and invasion may help attenuate the barriers between invasion biology and conservation genetics caused by different traditions and a deficit of interdisciplinary dialogue.

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