



## Conservation implications of invasion by plant hybridization

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### Abstract

The increasing number of invasive exotic plant species in many regions and the continuing alteration of natural ecosystems by humans promote hybridization between previously allopatric species; among both native as well as between native and introduced species. We review the ecological factors and mechanisms that promote such hybridization events and their negative consequences on biological diversity. Plant invasions through hybridization may occur in four different ways: hybridization between native species, hybridization between an exotic species and a native congener, hybridization between two exotics and by the introduction and subsequent spread of hybrids. The main harmful genetic effect of such hybrids on native species is the loss of both genetic diversity and of locally adapted populations, such as rare and threatened species. The spread of aggressive hybrid taxa can reduce the growth of, or replace, native species. The main factor promoting the formation of hybrids is species dispersal promoted by humans. However, the success and spread of hybrids is increased by disturbance and fragmentation of habitats, thus overcoming natural crossing barriers, and range expansions due to human activity. There are differences in flowering, pollination and seed dispersal patterns between parental species and hybrids. Hybrid resistance to pathogens and herbivores may also enhance the success of hybrids. To predict the mechanisms and consequences of invasions mediated by hybridization, extensive data on hybrid ecology and biology are needed, as well as carefully designed field experiments focused on the comparative ecology of parental populations and hybrids.

### Introduction

In the last few centuries there has been a massive movement of species around the globe as a result of trade, and massive alterations of the landscape as a result of human activity. The resulting biological invasions by exotic species are a major threat to the conservation of biodiversity (Vitousek et al. 1997). Whereas ecological research and the management of invasive species primarily focus on the direct ecological effects of such species, e.g., changes in ecosystem function and crowding out of native species, indirect effects of invasive plant species have been somewhat neglected.

One major indirect effect of the increasing number of exotic plant species and the continuing alteration of ecosystems is hybridization of closely related species.

In the context of plant invasions and for the remainder of this paper, four pathways of hybridization with different causes and effects must be distinguished: hybridization between native species, hybridization between an exotic species and a native congener, hybridization between two exotics, and the introduction and subsequent spread of natural or artificial hybrids resulting from intentional breeding.

Hybridization involving exotic species is linked to the spread and establishment of exotic species

(Williamson 1996). Examples with dire consequences are well known for animal species (Rhymer and Simberloff 1996). Hybridization among native and exotic fish species, for example, has resulted in the loss of many native taxa due to repeated unidirectional backcrossings and increased aggressiveness of hybrid forms compared to the parental taxa (Edwards 1979; Siddiqui 1979; Dowling and Childs 1992).

For plants, only scattered examples of hybridizing taxa can be found in the literature (Abbott 1992) and to date there has been no systematic attempt to explore the extent of hybridization among previously allopatric species as a threat to native biological diversity. Whereas in the case of natural hybridization novel phenotypes may be formed, increasing genetic diversity at both the population and species level, hybridization due to human activity may have the reverse effects because it may threaten the genetic integrity and persistence of native species.

The harmful effects of interspecific gene flow have been discussed for conservation purposes. Conservation implications have focussed on hybridization between crop plants and wild relatives (Ellstrand 1992) and between rare and common species (Rieseberg 1991; Ellstrand and Elam 1993), with special reference to insular plants (Levin et al. 1996). Nevertheless, in plants, the conservation problems posed by hybridization are not restricted to species at risk, or to species that hybridize. Hybridization can indirectly threaten other species of the community if an aggressively spreading hybrid taxon is formed, colonizing new environments and competing with native species.

The purpose of this article is to discuss possible ecological and genetic effects of hybridization due to human activity. We also discuss the ecological factors that promote the success of such hybrids. The main questions of this review are (1) what is the extent of such hybridization events? (2) what are the potential genetic and ecological consequences of this hybridization? (3) what are the ecological factors that promote invasion by hybridization and the spread of hybrids? and (4) what are the future research needs to understand the role of hybridization for plant invasions?

### Extent of hybridization

Although hybridization seems to be more common in plant than animal species, and more attention has been

paid by botanists than zoologists to the evolutionary role of hybridization (Anderson and Stebbins 1954; Stace 1975; Harrison 1993; Rieseberg 1995; Ellstrand et al. 1996), only few comprehensive data sets are available to assess the extent of human-mediated hybridization. Carr (1995), Ellstrand and Elam (1993) and Levin et al. (1996) suggest that such anthropogenic hybridization may be fairly common, but difficult to detect because many taxa remain poorly studied. However, because hybridization is common among plants there are good reasons to believe that the high number of exotic species in many regions results in the formation of new hybrids. Stace (1991) for example listed 715 putative hybrids in the British flora, 70 of that are the result of hybridization between introduced and native species, 21 between 2 introduced species and 4 between an introduced hybrid and a native species. In Ontario, 148 hybrid taxa are known, 31 of which are either introduced hybrids or the result of hybridization among introduced species. Three are hybrid taxa that originated through crossings between native and introduced species (Morton and Venn 1990). Tutin et al. (1964–1993) lists 27 hybrid taxa for Europe that are either introduced or the result of hybridization between a native and an introduced species. Dean et al. (1986) list 7 hybrids out of 64 alien plant species present in South Africa and Namibia.

Abbott (1992) stated that interspecific hybridization following species introduction can lead to rapid evolution of new plant taxa. Range expansion of hybrids can be rapid and hybrids can become weeds. However, there is still little information on the factors which influence their stability and spread. The allotetraploid *Tragopogon miscellus* originated in North America from hybridization between *T. dubius* and *T. pratensis* which were both introduced from Europe at the beginning of the century (Ownbey 1950). In less than half a century *T. miscellus* has significantly increased its number of populations within Idaho and Washington (USA) (Novak et al. 1991). The weedy status of some *Helianthus* (Asteraceae) in North America are classic examples of introgressive hybridization followed by range expansion. Native Indians probably introduced *Helianthus annuus* into California from the Great Plains (Heiser 1949; Stebbins and Daly 1961). Its introgressive hybridization with the endemic *H. bolanderi* has created a swarm of *bolanderi* and *annuus*-like plants which are very successful weeds in California (Rieseberg 1991).

Artificial hybrids are frequently formed in crop breeding programs and in horticulture. Such hybrids may escape areas of cultivation and become invasive taxa themselves. Furthermore, naturally produced hybrids may also be introduced to a new region and become invasive. In the Pacific Northwest of USA, meadow knapweed is a hybrid between the exotic black meadow (*Centaurea nigra*) and the exotic brown knapweed (*C. jacea*). Meadow knapweed populations are more common than the putative parental populations. Herbarium collections indicate that hybrids were probably introduced from Europe and did not arise exclusively in the introduced range (Talbot-Roché and Roché 1991). There are other well-documented examples of human-mediated hybridization that cause genetic and ecological conservation problems such as genetic assimilation and aggressive growth (Table 1).

### Effects of hybridization

Possible negative consequences of hybridization could be broadly divided into indirect genetic and direct ecological effects. Genetic effects mainly affect the hybridizing species involved, whereas ecological effects can have consequences at the community level. Genetic effects include dilution of the native species' genepool due to introgression (Abbott 1992). In extreme cases, this can lead to extinction of the native species (Anttila et al. 1998). There are several possible mechanisms that could lead to these genetic effects and we discuss several of them. Ecological effects occur when the hybrids themselves threaten native species by limiting, or promoting, resources or other important components of a community (e.g., pollinators, herbivores, pathogens). Here, even sterile hybrids can have negative effects.

#### Genetic effects

The most harmful genetic consequences of interspecific hybridization are the loss of genetic diversity and the loss of locally adapted populations (Rieseberg 1991; Ellstrand and Elam 1993). Interspecific hybridization could also lead to outbreeding depression when maternal and hybrid genotypes have high rates of aborted seeds or reduced seed sets (Ellstrand and Elam 1993). If the crosses show hybrid vigor, however, hybrids could have a faster growth and higher fitness

than parental species, leading to a higher competitive ability (Arnold and Hodges 1995).

Hybridization among previously allopatric species could be stabilized by polyploidy and introgression (Abbott 1992). Both polyploidy and introgression have the potential to create morphotypes that are able to invade new habitats or expand the distribution range of the former parental morphotypes. Polyploidy increases heterozygosity (Thompson and Lumaret 1992). Polyploid plants usually have larger seeds, higher rates of net photosynthesis, vigorous vegetative growth, wider physiological and ecological tolerances and greater plasticity of the mating system than progenitors (Levin 1983; Mitton and Grant 1984). These characteristics may promote the ability of hybrid taxa to colonize new habitats (Baker 1974).

Introgressive hybridization may also increase genetic diversity. Introgression may result in the transfer of traits between species and may be the source of new adaptations. It may also originate new races or species or conversely, reduce reproductive isolating barriers (Rieseberg and Wendel 1993). Potts and Reid (1988) describe hybridization between the endemic *Eucalyptus risdonii* and the more widespread native species, *E. amygdalina* in Tasmania after habitat fragmentation. Populations of introgressive hybrids similar to *E. risdonii* are now found within the *E. amygdalina* distribution range.

The genetic integrity of a common native species can be threatened by introgressive hybridization with a rare introduced species. The Californian cordgrass *Spartina foliosa* is hybridizing with the introduced *S. alterniflora* in San Francisco salt marshes (Daehler and Strong 1997). Although the population of the introduced cordgrass is small, it has higher male fitness than the native cordgrass. Pollen of *S. alterniflora* increased the seed set of the native plants almost eightfold and thus causes genetic dilution of *S. foliosa* (Anttila et al. 1998).

Garden plants are often the source of non-native genes that can be transferred into natural populations. At one site near Melbourne, Australia, the rare indigenous *Grevillea glabella* has hybridized with three garden-grown congeners: *G. baueri*, *G. rosmarinifolia*, and *G. juniperina*, because of pollen transfer by native birds. The result is a hybrid swarm that occupies a range of habitats including that of *G. glabella* (Carr 1995).

Hybridization between crop plants and weeds in disturbed habitats is a widespread phenomenon (Baker 1974, 1986). The European radish, *Raphanus sativus*

Table 1. Examples of human-mediated plant hybridizations and their conservation concerns.

| Hybrid taxon                                      | Parental species  | Region         | Conservation concern of hybrid taxon | Source <sup>a</sup> |
|---|---|----------------|--------------------------------------|---------------------|
| <i>Adenocarpus</i>                                | <i>A. foliosa</i> × <i>A. viscosus</i>  | Canary Islands | Range expansion                      | [1]                 |
| <i>Agrostis</i>                                   | <i>A. stolonifera</i> × <i>A. capillaris</i>  | Netherlands    | —                                    | [2]                 |
| <i>Arbutus xandrosterilis</i>                     | <i>A. unedo</i> <sup>b</sup> × <i>A. canariensis</i>  | Canary Islands | —                                    | [3]                 |
| <i>Argyranthemum</i>                              | <i>A. frutescens</i> × <i>A. coronopifolium</i>   | Canary Islands | Genetic assimilation                 | [4]                 |
| <i>Cardamine insueta</i>                          | <i>C. rivularis</i> × <i>C. amara</i>   | Switzerland    | Weed                                 | [5]                 |
| <i>Carex</i>                                      | <i>C. nigra</i> × <i>C. elata</i> ,<br><i>C. aquatilis</i> , <i>C. acuta</i>  | Netherlands    | —                                    | [2]                 |
| <i>Carpobrotus</i>                                | <i>C. edulis</i> <sup>b</sup> × <i>C. chilensis</i>   | California     | Aggressive growth                    | [6]                 |
| <i>Carpobrotus</i>                                | <i>C. edulis</i> <sup>b</sup> × <i>C. acinaciformis</i> <sup>b</sup>  | France         | Aggressive growth                    | [7]                 |
| <i>Centaurea</i>                                  | <i>C. nigra</i> <sup>b</sup> × <i>C. jacea</i> <sup>b</sup>   | USA            | Weed                                 | [8]                 |
| <i>Crataegus</i>                                  | <i>C. monogyna</i> <sup>b</sup> × <i>C. douglasii</i> var.<br><i>suksdorfii</i>   | Oregon         | —                                    | [9]                 |
| <i>Cypripedium</i>                                | <i>C. candidum</i> × <i>C. pubescens</i>  | Iowa           | Range expansion                      | [10]                |
| <i>Equisetum</i>                                  | <i>E. fluviatile</i> × <i>E. arvense</i>  | Netherlands    | —                                    | [2]                 |
| <i>Eucalyptus</i>                                 | <i>E. risdonii</i> × <i>E. amygdalina</i>   | Tasmania       | Range expansion                      | [11]                |
| <i>Fallopia</i> × <i>bohemica</i>                 | <i>F. japonica</i> var. <i>japonica</i> <sup>b</sup> ×<br><i>F. sachalinensis</i> , <i>F. japonica</i> var.<br><i>compacta</i> <sup>b</sup> | UK             | Aggressive growth                    | [12]                |
| <i>Grevillea</i>                                  | <i>G. glabella</i> × <i>G. baueri</i> <sup>b</sup> ,<br><i>G. rosmarinifolia</i> <sup>b</sup> , <i>G. juniperina</i> <sup>b</sup>           | Australia      | Range expansion                      | [13]                |
| <i>Helianthus annuus</i> subsp.<br><i>texanus</i> | <i>H. annuus</i> <sup>b</sup> × <i>H. debilis</i>   | Texas          | Weed                                 | [14,15]             |
| <i>Heracleum</i>                                  | <i>H. mantegazzianum</i> <sup>b</sup> ×<br><i>H. sphondylium</i>  | UK             | Aggressive growth                    | [16]                |
| <i>Juncus</i>                                     | <i>J. acutiflorus</i> × <i>J. articulatus</i>   | Netherlands    | —                                    | [2]                 |
| <i>Lantana</i>                                    | <i>L. depressa</i> × <i>L. camara</i>   | Florida        | Aggressive growth                    | [17]                |
| <i>Lavandula</i>                                  | <i>L. canariensis</i> × <i>L. pinnata</i>   | Canary Islands | Genetic assimilation                 | [3]                 |
| <i>Lonicera</i> × <i>bella</i>                    | <i>L. tatarica</i> <sup>b</sup> × <i>L. morrowi</i> <sup>b</sup>  | Eastern USA    | Aggressive growth                    | [18]                |
| <i>Lythrum</i>                                    | <i>L. salicaria</i> <sup>b</sup> × <i>L. alatum</i>   | Minnesota      | Genetic assimilation                 | [19]                |
| <i>Menta</i>                                      | <i>M. aquatica</i> × <i>M. arvensis</i>   | Netherlands    | —                                    | [2]                 |
| <i>Onopordum</i>                                  | <i>O. acanthium</i> <sup>b</sup> × <i>O. llyricum</i> <sup>b</sup>  | Australia      | Weed                                 | [20]                |
| <i>Opuntia occidentalis</i>                       | <i>O. ficus-indica</i> <sup>b</sup> × <i>O. littoralis</i>  | California     | Weed                                 | [21]                |
| <i>Raphanus</i>                                   | <i>R. angustifolius</i> × <i>R. minor</i>   | California     | Genetic assimilation                 | [22]                |
| <i>Senecio cambrensis</i>                         | <i>S. squalidus</i> <sup>b</sup> × <i>S. vulgaris</i>   | UK             | Aggressive growth                    | [23]                |
| <i>Spartina anglica</i>                           | <i>S. alterniflora</i> <sup>b</sup> × <i>S. maritima</i>  | UK, Washington | Aggressive growth                    | [24]                |
| <i>Spartina</i>                                   | <i>S. alterniflora</i> <sup>b</sup> × <i>S. foliosa</i>   | California     | Range expansion                      | [25]                |
| <i>Taraxacum</i>                                  | <i>T. platycarpum</i> × <i>T. officinale</i> <sup>b</sup>   | Yokai (Japan)  | —                                    | [26]                |
| <i>Tragopogon miscellus</i>                       | <i>T. dubius</i> <sup>b</sup> × <i>T. pratensis</i> <sup>b</sup>  | Idaho          | Range expansion                      | [27]                |
| <i>Vaccinium</i>                                  | <i>V. angustifolium</i> <sup>b</sup> × <i>V. corymbosum</i>   | Germany        | Range expansion                      | [28]                |
| <i>Viola</i>                                      | <i>V. tricolor</i> × <i>V. sudetica</i>   | Czech Republic | Range expansion                      | [29]                |

<sup>a</sup>[1] Humphries 1979, [2] Grootjans et al. 1987, [3] Salas Pascual et al. 1993, [4] Humphries 1976, [5] Urbanska 1987, [6] Albert 1995, [7] Suechs et al. 1999, [8] Talbott-Roché and Roché 1991, [9] Love and Feigen 1978, [10] Klier et al. 1991, [11] Potts and Reid 1988, [12] Bayley et al. 1995, [13] Carr 1995, [14] Stebbins and Daly 1961, [15] Rieseberg 1991, [16] Ochsman 1996, [17] Sanders 1987, [18] Barnes and Cottam 1974, [19] Anderson and Asler 1996, [20] O'Hanlon et al. 1999, [21] Benson 1969, [22] Panetsos and Baker 1968, [23] Ashton and Abbott 1992, [24] Thompson 1991, [25] Daehler and Strong 1997, [26] Watanabe et al. 1997, [27] Ownbey 1950, [28] Schepker and Kowarik 1998, [29] Krahulcová et al. 1996.

<sup>b</sup>Introduced species.

has hybridized with the already weedy *R. raphanistrum* and hybrids have become abundant in California and other areas of North America (Panetsos and Baker 1968). Escape of genes from engineered crops into wild populations could have adverse economic and ecological consequences if these genes confer fitness advantages to the wild plants. These issues have been extensively described elsewhere (Ellstrand and Hoffman 1990; Raybould and Gray 1994; Schmitt and Linder 1994).

#### *Ecological effects*

Major changes to the native community due to hybridization may result when hybrid genotypes are able to spread within a short time and, in various ways, impact the other native species (Table 1). In most of these cases the spread of hybrids is coupled with extensive vegetative proliferation (e.g., clonal growth). Thus, even sterile hybrids are able to invade new habitats and replace native species. The spread of the hybrids between the North American *Spartina alterniflora* and the native *S. maritima* in Great Britain is a recent and well-known case of plant invasion by hybridization (Thompson 1991). The allopolyploid *S. anglica*, produced as a result of chromosome doubling of F1 hybrids is characterized both by great reproductive success and aggressive rhizomatous growth. The fast colonization of marshes and estuaries by *S. anglica* and its rigid root system produce tidal sediment build-up. Sediment accretion increases the fertility of the ground and enhances colonization by other native plant species but may reduce diversity of birds that feed on invertebrates living in mud flats (Goss-Custard and Moser 1988). *Spartina anglica* has been introduced worldwide to protect foreshores from tidal erosion and to transform bare marshes to 'terrestrial' habitats. For instance, it was introduced in China in 1963 and 19 years later occupied an area greater than 33,000 ha (Chung 1983). The recently formed hybrids between *S. alterniflora* and *S. foliosa* in the San Francisco bay (California) could also accelerate habitat loss for shore birds and native life (Anttila et al. 1998).

Introgressive hybridization between the South African *Carpobrotus edulis* and the putative native *C. chilensis* is occurring in coastal California (Albert et al. 1997; Gallagher et al. 1997). The mat-forming clones of putative hybrids and backcrosses occupy large areas of dune and shrubland habitats that otherwise might be colonized by a variety of native species.

The hybrids are very similar in their growth and salt tolerance to the introduced taxon (Weber et al. 1998; Weber and D'Antonio 1999). Hybridization between the introduced *C. edulis* and *C. acinaciformis* is also taking place in some Mediterranean islands (Suechs et al. 1999). The hybrids are very invasive and are threatening some native species such as *Limonium* spp. (PANDION 1997).

Hybridization between two introduced species can lead to the production of new invasive taxa. In Europe pollen flow within Asian Japanese knotweeds, from *Fallopia sachaliensis* and *F. japonica* var. *compacta* to the male-sterile *F. japonica* var. *Japonica*, produced infertile allopolyploid hybrids ( $\times$  *bohemia*) with vigorous rhizomatous growth (Bailey et al. 1995) which reduce the establishment and growth of native species (Child et al. 1992) and makes its mechanical and chemical control difficult (Bimová et al. 1999). Differences between parental populations and hybrids may explain the resistance to control practices, and hence, different control strategies should take into account the variability of characters among morphotypes (O'Hanlon et al. 1999).

#### **Factors promoting the success of hybrids**

##### *Disturbance*

The primary cause of hybridization, especially between an introduced and a native species, is species dispersal. Natural hybridization is normally prevented by a number of biotic and abiotic mechanisms such as mating incompatibility, differences in phenology, dioecy, or geographical isolation (Stace 1975; Grant 1981). The stronger the isolating barrier, the stronger the intervention must be in order to break this barrier (Urbanska 1987). The break-down of former biogeographical and ecological mechanisms by disturbance and habitat fragmentation is a major force promoting hybridization, especially among native species (Baker 1986; Urbanska 1987; Grootjans et al. 1987). A well-studied example is hay meadows in the Netherlands affected by drainage and polluted subsurface flows (Grootjans et al. 1987). These habitats provide new environmental conditions that can be colonized by hybrids. Similarly, *Cardamine insueta* is a hybrid that originated from *C. rivularis* and *C. amara* in disturbed Swiss hay meadows and has become very invasive due to its asexual propagation (Urbanska 1987).

In southern California, the cactus *Opuntia occidentalis* is an hybrid between the native cactus *O. littoralis* and the introduced *O. ficus-indica*. Hybrids seem to be favored because they occupy a less inflammable habitat than parental species (Benson 1969). Annual Mediterranean grasses (*Bromus rigidus* and *Avena barbata*), promoting hot fires, to which cacti are not resistant invade the habitats of the native species. The introduced species seem to be restricted to deeper and moist soils. Clonal growth of the hybrids leads to dense stands that are to some extent less flammable (Benson 1969). In the Canary Islands disturbance has promoted hybridization between *Lavandula canariensis* and *L. pinnata* which is reducing genetic diversity through genetic assimilation of *L. pinnata* by *L. canariensis* (Humphries 1979).

Habitat alteration and fragmentation can also put in contact species which were ecologically isolated and be an indirect cause of genetic swamping between native species. In the Canary Islands, the rare endemic *Argyranthemum coronopifolium* is in danger of extinction due to introgressive hybridization with the more common congener *A. frutescens* (Humphries 1976). Range expansion by *A. frutescens* in the range of *A. coronopifolium* has been favored by extensive road construction and disturbance related to tourism (Brochmann 1984). As discussed by Levin et al. (1996), the swamping of *A. coronopifolium* has occurred in only 30 years. In these islands, deforestation has also been the cause of *Adenocarpus foliosus* expansion due to hybridization with *A. viscosus* (Humphries 1979).

Prairie remnants within the midwest of the United States of America are the exclusive habitat of the rare orchid *Cypripedium candidum*. Its congener, *C. pubescens*, is commonly found in woodlands and has a larger range than *C. candidum* (Niemann 1986). Land-use changes dating from European settlement has resulted in small isolated patches of prairie intermingled with woodland. The secondary contact between the two *Cypripedium* species has allowed introgressive hybridization. Genetic analyses have shown that hybrid populations are composed of later-generation backcrosses or recombinants. In Iowa, morphotypes similar to *C. pubescens* have acquired genetic traits from *C. candidum* that now allow them to occupy prairie habitats. The remaining scattered populations of *C. candidum* have low isozyme variability within each one (Klier et al. 1991). This loss of genetic variation has negative consequences for the conservation

of small populations because it reduces evolutionary flexibility, decreases individual fitness and increases the probability of population extinction (Ellstrand and Elam 1993).

#### *Flowering and pollination patterns underlying successful hybridization*

Partial overlap of the parental species flowering periods is necessary for hybridization to occur. A long flowering season and the presence of generalist pollinators or wind pollination rather than specialist pollination facilitate interspecific cross-pollination (Carlquist 1974). Classical theory predicts that for self-incompatible plants visited by the same insect pollinators the least frequent plant species would be at a disadvantage. This disadvantage will lead to a decrease of the standing crop in successive generations and ultimately to local extinction (Levin and Anderson 1970). However, for wind pollinated species and when hybridization occurs, even a rare species can persist despite an advantage in numbers held by the native species. The rare introduced *Spartina alterniflora* hybridizes with the common, native *S. foliosa*. Hybridization is diluting the gene pool of the native species and hybrids are spreading (Anttila et al. 1998).

In introgressive hybridization, backcrossing is usually biased towards a single parental population suggesting either that pollen flows mainly between hybrids and one parental species or that there is interspecific gamete competition. Differences in pollinator preference and constancy to certain species and morphotypes can produce variability in fruiting and seed set. There are several examples of the effects of variability in floral display and flower traits on insect attraction within a species complex (Kwak 1978; Whitten 1981; Ashton and Abbott 1992; Hazeldon et al. 1991). However, we are not aware of any study showing significant differences in pollinator preference between hybridizing native and introduced plants. The non-native *Carpobrotus edulis* and hybrid morphotypes resulting from crossing and introgression between *C. edulis* and the putative native congener *C. chilensis* are known to be successful invaders of coastal plant communities (Albert et al. 1997). *Carpobrotus edulis* and *C. chilensis* flowers are yellow and magenta, respectively. Hybrid flowers are intermediate in corolla diameter and can be either yellow or magenta. Vilà et al. (1998) found that both *Carpobrotus* species have large overlapping flowering periods (from March to

July) and flowers of both species are visited by the same Thysanoptera and Coleoptera taxa, suggesting a high potential for natural hybridization. Similarly, in hybridizing Louisiana irises, flowers of all taxa are visited by the same insects. Nevertheless, while *Iris brevicaulis* seeds result from interspecific mating, *I. fulva* produced seeds with similar genotypes to the maternal species due to interspecific gamete competition (Arnold 1994).

As already noted in the Genetic effects section, differences in pollen viability may also be responsible for differences in the direction of hybridization. In the Czech Republic, the introduced submontane *Viola tricolor* has hybridized with *V. sudetica* in foothill areas due to the introduction of limestone gravel (Krahulcovà et al. 1996). Higher pollen viability of some hybrid morphotypes than parental species leads to higher seed set.

#### *Other plant–animal interactions leading to hybrid invasion*

For some introduced species, successful reproduction and spread depends on seed dispersal by animals. Hybridization can modify the relative frequency of plant species where frugivores forage, increase the variability of fruit displays, as well as the quality of the food items which are cues for fruit consumers (Epling 1947; Stebbins and Ferlan 1956). Thus, hybridization may change frugivore choice and consequently, seed dispersal within the plant community.

Hybridization between the introduced *Crataegus monogyna* from Europe and the native *C. douglasii* var. *suksdorfii* takes place in western Oregon and possibly in Ontario, Canada with *C. punctata*. Hybrids have a higher population density than parental species which might be related to higher hybrid seed dispersal by birds. In western Oregon, fruits of the hybrid morphotypes share characters with both parental populations (Love and Feigen 1978). *Crataegus monogyna* is successfully dispersed by robins (Sallabanks 1993a) and produces a larger display of fruits than the native *C. douglasii* (Sallabanks 1993b).

Fruit preference trials have shown that hybrid morphotypes can be consumed as often as the introduced species to the detriment of the native species. In coastal California, the invasive *Carpobrotus edulis* and hybrid morphotypes produce more fruit per clone than the putative native *C. chilensis* primarily as a consequence of having larger clones. Vilà and D'Antonio

(1998a) have shown that marked fruits of *C. edulis* were removed faster than those of the other morphotypes and were preferred over *C. chilensis* fruit in a fruit transplant experiment. Scats from black-tailed jackrabbit (*Lepus californicus*) and black-tailed deer (*Odocoileus hemionus columbianus*) contained more seeds from *C. edulis* and hybrid morphotypes than from *C. chilensis*. Proportion of *C. chilensis* seeds in scats was very low compared to its seed set in that area. The germination rate of seeds from *C. edulis* and hybrid morphotypes was enhanced after gut passage, while the germination rate of *C. chilensis* decreased compared to seed germination rate of intact fruit. These results suggest that fruit selection by native frugivores may promote higher fitness of introduced and hybrid morphotypes than a putative native congener, and may therefore help to explain their successful spread.

Escape from pathogens and herbivores is assumed to be a cause of the success of introduced species (Crawley 1986; Blossey and Nötzold 1995). Some studies have found that hybrids can be more resistant to herbivores than parental species in natural hybrid zones (Boecklen and Spellenberg 1990; Strauss 1994), which may result in an increase in plant fitness. By contrast, other studies have found that hybrids have higher (e.g., Whitham et al. 1994), the same or intermediate (Fritz et al. 1994) susceptibility to herbivory than parental populations. Resistance to herbivory can mediate the spread of hybrids between the introduced *C. edulis* and the putative native *C. chilensis*. *Carpobrotus* hybrids have higher survival in response to native mammalian herbivores than *C. chilensis*. Survival to herbivory is also greater in hybrids than in *C. edulis* in certain habitats. The low attack rate on hybrid morphotypes may partially explain the invasive success of hybrids (Vilà and D'Antonio 1998b).

In biological control programs exotic species are treated as a single group. However, the full range of genotypic variation resulting from hybridization may influence the resistance and tolerance to biocontrol agents (O'Hanlon et al. 1999). We do not know of any biocontrol program which has taken into account this variability among genotypes.

#### **Concluding remarks and future directions**

Natural hybrid zones have to be protected because they may represent centers of plant evolution (Stebbins 1959). Hybrid swarms can also serve as founding

populations of new species, driving reticulate evolution in some plant taxa (Rieseberg 1995). Furthermore, plant hybrid zones may be refuges for rare phytophagous insect communities (Whitham et al. 1991). However, hybrid zones resulting directly or indirectly from human activity may be a threat to the maintenance of indigenous species and communities. Hybridization between introduced and native species is not rare, restricted to crop and wild plants (Ellstrand 1992) or between rare and common relatives (Rieseberg 1991; Ellstrand and Elam 1993). There is potential for hybridization between any introduced species and a native relative (Abbott 1992).

Since Abbott (1992) emphasized the great potential of studying the processes leading to interspecific hybridization our understanding on the ecology of human driven hybridization has progressed little. Few 'rules' exist that predict the potential of hybridization between introduced and native species. Our review suggests that hybridization should be analyzed in the context of the recipient community, because there are tight interconnections among the hybridizing plants, the native (or introduced) animals and the entire environment. The following avenues for research seem most promising to increase our understanding of the biological factors that promote the spread of hybrids and the ecological consequences of invasion by hybridization:

1. Although most research on hybridization has focused on biosystematic rather than on the ecology of hybrids, the extent of plant hybridization, both in terms of frequency and phylogenetic breadth, is not known. More detailed summaries of the number of hybrid taxa at the regional scale are needed. Documenting the extent of hybridization over a variety of spatial scales is critical. Central questions include whether the frequency of natural hybridization is different from the frequency of unintentional human-mediated hybridization (as the examples described in this paper), and whether there are phyletic patterns within this dichotomy.
2. Only a few studies have compared flowering and mutualism patterns between introduced and native species, between introduced species, or between native species after secondary contact. The outcome of further research in this field could provide the first step in understanding the biological causes promoting hybridization.
3. Most studies focusing on the fitness of hybrids only describe their reproductive output. However, seed set and seed viability are only the first stages of progeny recruitment. Studies should include research on the establishment of seedlings and their interaction with the environment by means of well designed field studies.
4. The ecological effects of hybridization are not well explored. Some well-known examples include invasion by *Spartina* and *Carpobrotus* hybrids due to their fast spread and clonal growth. Additional research should focus on the impact of hybridization at various levels of ecological complexity. Furthermore, the impact of artificial hybrids, created in breeding programs, has scarcely been explored and requires further attention.
5. From the management point of view interspecific gene flow can be achieved by removal of exotic species and increasing the size of the native population at risk (Rieseberg 1991). However, managers often treat exotic species as a single group. The full range of genotypic variation may influence the success of particular control strategies. Studies on the response of mechanical, chemical and biotic control of hybrids and parental populations will be helpful in both managing invasions and understanding the ecological and evolutionary aspects of host-choice by control insects and resistance to herbicides (O'Hanlon et al. 1999).
6. Most research on hybridization has been conducted on natural hybrids. We do not know whether the factors promoting the formation and success of the hybridization described in this paper differ from natural plant hybridization. We hypothesize that the factors may be the same, with the exception that in human-mediated hybridization the speed of hybrid recruitment could be faster because the allopatric parental species may not have genetic isolating barriers to overcome after secondary contact.
7. Similarly, we do not know if the factors leading to invasion are different for non-hybrid species than for hybrids. We suspect that the ecological factors are the same. However, propagule pressure of hybrids may be higher than for non-hybrids because mating between parental species and introgression increases the number of hybrid propagules.
8. In this review we have only considered hybridization between species. Mating between different ecotypes resulting from human activity is also occurring (e.g., the cultivated *Dactylis glomerata* in Spain). Such



intraspecific hybridization can result in the genetic dilution of some ecotypes and increase colonization by others (Lumaret 1990). If we take into account interspecific hybridization, examples of invasion by hybrids would increase several orders of magnitude. Unintentional man-mediated hybridization between ecotypes is also involved in biological invasion and needs further exploration.

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