

Evolving weeds and biological control

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Summary

Founder events in colonization, hybridization, and interactions with native species and agents, as well as strong natural selection in their new environments, can result in a mix of genotypes in an invasive species very different from those of the propagules or the population of origin. Some populations of invasive *Spartina* spp. in Pacific estuaries have been separated from the specialist planthopper *Prokelisia marginata* for many generations, while virtually no native *Spartina* populations in Atlantic and Gulf coast estuaries of NA, have experienced this separation. We found lower resistance and tolerance among six *Spartina* populations that have been long-separated from the planthopper than in six *Spartina* populations that had been consistently exposed to it.

Spartina alterniflora genotypes varied more in their ability to resist and support planthoppers in a population that had been separated from the herbivore for many generations (in Willapa Bay, WA) than in one that had been consistently exposed to the planthopper (in San Francisco Bay, CA). In the former, some plant genotypes experienced >50% shoot mortality while others experienced none. In contrast, no genotype in the latter experienced >20% shoot mortality. Population growth rates of the herbivore paralleled this pattern among cordgrass genotypes from the two populations.

One Willapa Bay genotype of *S. alterniflora* lacked resistance to the planthopper while being quite tolerant of high herbivore densities that developed upon it. Plant genotypes with this combination of traits could result in self-defeating biological control. These tolerant genotypes could foster herbivores and increase in frequency at the expense of the vulnerable genotypes. The presence of tolerant genotypes suggests the need for complementary chemical and/or mechanical control. Attention to the frequency and nature of genetic variation in vulnerability to natural enemies on target species is germane to both the science and the practice of biological control.

Keywords: cordgrass, resistance, self-defeating biocontrol, *Spartina*, tolerance, weed evolution.

Introduction

Biological control is an applied discipline within the larger new science of invasive species. While genetic change during invasions has not been well studied, the underlying ecological processes of dispersal and isolation after colonization are just those that facilitate allopatric speciation and form the rationale of the modern synthesis of evolutionary theory (Mayr 1970). Paleontology also gives evidence of rapid change during invasions (Vermeij 1996).

Plant populations vary greatly in their resistance to and tolerance of natural enemies (Strauss and Agrawal 1999), and successive invasive species from different

parts of the native range can hybridize. These processes create a large array of unusual genotypes (Ayres *et al.* 1999); thus we should expect ample raw material for evolution in weeds as a matter of course. Furthermore, large selection gradients are generated by the lack of natural enemies and different competitive regimes in new environments. These factors make invasive plants prime candidates for rapid evolution (Thompson 1998). Understanding the evolution of weeds is pertinent to safe and effective biocontrol.

Our research has focused upon an idea suggested by the evolution of invasive *Spartina* species that we term “the potential for self-defeating biological control”. The rationale is that natural selection for herbivore resistance and tolerance (vulnerability) are relaxed during spread of an invasive plant before agents are released (see e.g. Blossey & Nötzold 1995). This could lead to evolution of increased genetic variance in vulnerability to herbivores as recombination generates

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new genotypes as the invasive population grows rapidly. The high genetic variance would yield a high variance in phenotypes in the weedy population, with a broad range of vulnerability to agents. In this situation, introduced agents would eliminate vulnerable genotypes and leave a target population upon which the natural enemy had little effect. Without complementary control of the less vulnerable genotypes by some other means, natural selection could lead to self-defeating biological control. The invulnerable population would then proliferate.

Spartina as invasive species

Spartina species are perennial, wind pollinated, obligately outcrossing grasses in their native ranges. As the largest and most productive saltmarsh plants at high latitudes, *Spartina* species (cordgrasses), have large ecological and economic effects in the estuaries where they invade (Garcia Rossi *et al.* (2004), Ayres *et al.* 1999).

Invasive populations of *S. alterniflora* (and *S. anglica*) that have not recently (or perhaps ever) been in contact with the specialist planthopper *Prokelisia marginata* appeared to have lower mean resistance and tolerance to herbivory by this planthopper than native populations that have been exposed to it continuously (Daehler & Strong 1997, Wu *et al.* 1999). Preliminary observation suggested that the variation in vulnerability was also higher in populations of cordgrass that lacked a recent history of association with this herbivore. The ideal experimental design was precluded when some strains of our cordgrass were destroyed. Nevertheless, we were able to compare a population of *S. alterniflora* that had been released from herbivory when introduced to Willapa Bay, Washington State, USA about 100 years ago with a population introduced to San Francisco Bay about 25 years ago that has never been separated from this planthopper. Both populations are outside *S. alterniflora*'s native range (Daehler & Strong 1996). The planthopper is a native of San Francisco Bay, with native Californian cordgrass, *S. foliosa* as its host (Denno *et al.* 1996).

Spartina anglica is a new species created in the 19th century in England by hybridization between *S. alterniflora*, introduced from North America, and *S. maritima*, native to Europe (Raybould *et al.* 1991). Specialist insect herbivores of *Spartina* are native to Atlantic and Gulf coast estuaries of North America. The most abundant herbivores are planthoppers in the genus *Prokelisia* spp. (Denno *et al.* 1996, Heady & Wilson 1990). Others include the stem-boring cecidomyid fly *Calamomyia alterniflorae* (Gagne 1981) and the scale insect *Haliaspis spartinae* (Strong *et al.* 1984, Liu & Howell 1994). Thus, *S. anglica* comprises the *S. maritima* genome, which has never experienced *P. marginata*, and that of *S. alterniflora*, which evolved with this planthopper. We have no knowledge of any population of *S. anglica* being subject to herbivory by

P. marginata, while the *S. alterniflora* part of its hybrid has an ancient, but recently interrupted interaction with the planthopper.

Spartina anglica was deliberately introduced to parts of Britain, Europe, China, New Zealand, Australia, Tasmania, and Puget Sound, Washington State, USA, and is now considered a serious weed in these countries. *P. marginata* has been introduced to Willapa Bay, WA for biological control of *S. alterniflora* (Grevstad *et al.* 2003).

Methods

Studying cordgrass vulnerability to *P. marginata* presents technical challenges common with sap-feeding insects, such as many species of Homoptera, upon long-lived plants. *P. marginata* is tiny, and the amount of vascular fluid removed by each insect is small and difficult to quantify (Walling 2000). Numbers of planthoppers upon the plant build through a series of generations over the growing season. Both oviposition wounds and sap removed by feeding planthoppers are potentially harmful to the plant, though we failed to find evidence that plant diseases are transmitted by these planthoppers (Davis *et al.* 2002).

We tested the effect of the planthopper upon cordgrasses in greenhouse assays. We measured effects of *P. marginata* upon vegetative growth and survival, but not on seed set. First, we asked how contact history between cordgrass populations and the planthopper affected the suitability of host plants for insects (resistance). Second, we asked how contact history affected the ability of cordgrass to withstand the herbivore (tolerance). Finally, we asked if a history of separation from the herbivore could affect within-population variance of vulnerability to it.

To understand resistance, we contrasted six populations of *Spartina alterniflora* and *S. anglica* that have been separated from *Prokelisia marginata* for many generations with six native populations of *S. alterniflora* that have never grown apart from this herbivore. We examined oviposition rate, nymphal emergence from eggs, rate of nymphal development to adults, and planthopper population growth rate of the insects and five plant traits – biomass, length of shoots, shoot number and mortality, leaf number, and plant mortality. To understand resistance independently of tolerance, we measured oviposition, nymphal emergence, and nymphal development to adults at planthopper densities so low that the herbivore did not degrade the plant. The most sensitive indicator of *P. marginata* damage to *Spartina* sp. is distinctive chlorosis of leaf tips, and the density of insects used in the resistance experiments was less than that causing chlorosis. Tolerance was measured as the plant trait value when grown with *P. marginata* divided by the trait value of replicate plants grown without it. In nature, planthopper colonies build up through several generations during the growing season, and we measured

increase in planthopper density for a test of the interaction of cordgrass and *P. marginata*. Planthoppers increased to densities that harmed the cordgrass, which means that population increase is a measure that combines resistance and tolerance. Planthopper density was divided by stem length, to adjust for different plant sizes among cordgrass populations. Details of the methods are in Daehler *et al.* (1996), Wu *et al.* (1999), and Garcia Rossi *et al.* (2004).

Results

Suitability of host plants for insects

Resistance to *Prokelisia marginata* was greater in cordgrass populations that have never been separated from it than in those populations that have evolved in separation from this herbivore. Development of second-instar nymphs to adults was higher on long-separated plants (72%) than on never-separated plants (50%, test of *a priori* hypothesis, $t = 8.0$, $df = 4$, $P = 0.0013$, Figure 1). Nymphal development on the seven native populations of *S. alterniflora* from the Atlantic coast was 53% and was 46% from San Francisco Bay (never separated from the planthopper). This was in contrast to plants with the opposite plant–insect contact history (development on Willapa Bay *S. alterniflora*, 71%; on *S. anglica* from Puget Sound, 69%; Tasmania, 74%; and Victoria, Australia 74%). Planthopper mortality did not differ by plant–insect contact history (22% on long-separated provenances, 22.4% on never-separated natives,

$t = 0.1$, $df = 4$, $P = 0.92$), therefore the distinction was due to developmental rate rather than survival.

The rate of nymphal emergence was twice as high on cordgrasses from populations separated from the planthopper for many generations than on the cordgrasses from populations with the opposite plant–insect contact history. An average of 9.7 nymphs emerged per each founding male–female pair on Willapa Bay *S. alterniflora*, significantly higher than the 4.6 nymphs emerging per male–female pair on cordgrasses from Virginia ($t = 3.7$, $df = 71$, $P < 0.001$, based on log-transformed data). Oviposition rates over 30 days did not differ as a function of contact history, and female planthoppers laid, on average, 31.2 eggs ($t = 1.9$, $df = 6$, $P = 0.11$) on plants from Willapa Bay and San Francisco Bay cordgrass.

Ability to withstand herbivory

The tolerance of *Prokelisia marginata* was greater in cordgrass populations of long-standing associations with the planthopper than in those that have been separated from it for many generations. Native *Spartina alterniflora* from Virginia grew better under herbivore pressure than did the Willapa population of *S. alterniflora* and populations of *S. anglica* (Figure 2). The advantage of the Virginia plants was greatest for biomass ($F_{4,20} = 4.4$; $P = 0.01$) and leaf number ($F_{4,20} = 4.9$; $P = 0.006$), but advantage over plants that have been long-separated from the insect was also substantial for shoot number ($F_{4,20} = 2.5$; $P = 0.07$) and shoot length ($F_{4,20} = 2.6$; $P = 0.07$). The mean effect on

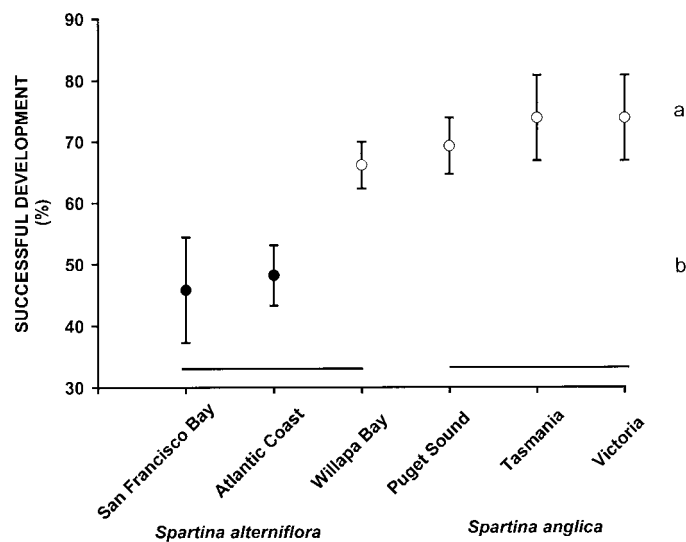


Figure 1. Development of *Prokelisia marginata* nymphs to adults during a 12-day experimental period, as a function of contact history. By *a priori* contrast, development on the cordgrass that has never grown apart from the planthopper (b) was lower than on cordgrasses that had grown apart from the herbivore for many generations (a). Redrawn from Garcia-Rossi *et al.* (2004).

biomass was statistically nil in the Virginia population. Herbivory reduced shoot length 1.2-fold, shoot number 1.6 fold and leaf number 1.7-fold in this native population of cordgrass (Figure 2). The reductions caused by the herbivore in all traits were much greater for plants that have evolved in the absence of the planthopper, ranging from reduction of 2.2-fold for shoot number in Willapa Bay *S. alterniflora* to a 7.7-fold reduction in shoot number and leaf number for *S. anglica* from Puget Sound.

Plant mortality paralleled the results for the other measures of tolerance to the planthopper. None died during growth without the planthopper. With planthoppers, plant mortality was zero for Virginia *S. alterniflora*; 25% for Willapa Bay *S. alterniflora*; 43% for Australia *S. anglica*, 50% for Puget Sound *S. anglica*, and 50% for Tasmania *S. anglica* (test of *a priori* hypothesis of lower mortality in the long standing cordgrass–planthopper associations, Kruskal-Wallis Test, $\chi^2 = 7.4$, $df = 1$, $P = 0.006$).

Planthopper population growth measures the combined effects of resistance and tolerance. In the experiments, just as in nature, planthoppers became dense and caused chlorosis, curled and dead leaves, and hopper burn. Planthopper populations grew faster on plants from cordgrasses long-separated from the planthopper than on plants with continuous contact with the insect. Densities grew from 0.5 to 1.9/cm of stem on the native Virginia *S. alterniflora* and to an average of 4.7 planthoppers/cm shoot on plants of the long-separated cordgrasses over one generation (10 weeks) of the planthopper ($t = 2.25$, $df = 38$, $P < 0.03$). For the long-separated plants, final density was 3.1 on *S. alterniflora*

from Willapa Bay, and on the *S. anglica*, 4.7 from Australia, 9.3 from Puget Sound, and 2.6 from Tasmania.

Intrapopulation variation

S. alterniflora from Willapa Bay has been separated from the planthopper for *ca.* 100 years. This cordgrass had much higher variation among genotypes in population growth rate of the planthopper, and in harm caused by it, than cordgrass from San Francisco Bay (never separated). The plant genotypes from Willapa Bay supported a wide range of densities, 1.3 to 12.8 planthoppers/cm stem (mean 11.5), *ca.* 10-fold the range for genotypes from San Francisco Bay (0.7 to 1.9 planthoppers/cm of stem, Figure 3). The poorest plant genotype for planthoppers from Willapa Bay was close to the average from San Francisco Bay. Most genotypes from Willapa Bay supported planthopper densities two to seven fold greater than any from San Francisco Bay. Seven of eight Willapa Bay genotypes had mean densities greater than the highest planthopper density of San Francisco Bay genotype.

The range of relative shoot survival (survival with the planthopper/survival without it) was higher among Willapa Bay genotypes (range = 0.72, from 0.3 to 1.1; overall mean survival = 0.6, $se = 0.09$) than among genotypes of cordgrass from San Francisco Bay (range = 0.6, from 0.8 to 1.5, overall mean survival = 1.0) of *S. alterniflora* (ordinate, Figure 3). Planthoppers killed more than half of the shoots of three of eight Willapa Bay genotypes, while they killed no shoots in one other from the same population. In contrast, they killed no

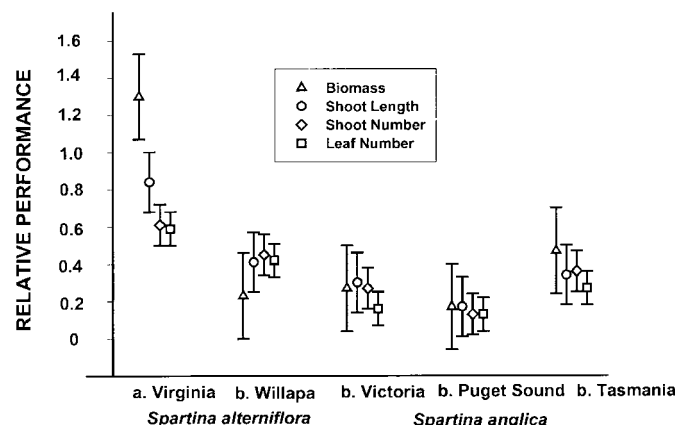


Figure 2. Relative performance of cordgrass measured as a ratio of the value of the trait for plants grown with *Prokelisia marginata* over that for plants growing without the planthopper, as a function of contact history. By *a priori* contrast, native cordgrass (a) from Virginia suffered less from herbivory in all four plant traits than did cordgrasses that had been separated from the planthopper for many generations (b). Redrawn from Garcia-Rossi *et al.* (2004).

more than a fifth of shoots of any San Francisco genotype. The coefficient of variation among genotypes was greater for Willapa Bay (44.9%) than for San Francisco Bay for relative shoot survival (20.8%, $P < 0.05$ by F test, Zar 1984). Plant mortality paralleled this pattern. The planthoppers killed *ca.* 35% of plants of a few Willapa Bay genotypes and none of the others ($\chi^2 = 14.6$, $df = 1$, $P < 0.0001$), while they killed very few plants of any genotype from San Francisco Bay ($\chi^2 = 4.1$, $df = 1$, $P < 0.5$).

Shoot survival decreased with increasing planthopper density (Figure 3). Genotypes from San Francisco Bay had highest survival and lowest planthopper density, with relatively little variation. Genotypes from Willapa Bay account for most of the relationship in Figure 3. The most interesting genotype in the study is the uppermost point in Figure 3. This genotype departs conspicuously from the rough negative correlation between tolerance and the densities of planthopper colonies that developed during this long experiment. While other genotypes from Willapa Bay were harmed by even quite low densities of the planthopper, this unusual genotype was virtually unaffected by the third-highest density (8.5 planthoppers/cm of stem) of the 17 genotypes in the experiment. Thus, this Willapa Bay genotype lacked resistance to the planthopper, while being quite tolerant of it. This genotype would promote biological control of other genotypes while resisting biological control itself.

Discussion

Cordgrasses *Spartina alterniflora* and *S. anglica* that have been separated from the specialist planthopper *Prokelisia marginata* for many generations are much more vulnerable to this herbivore than cordgrasses populations never separated from it. All comparisons of all traits investigated (three insect traits, five plant traits) showed the six invasive cordgrass populations, all estranged from *P. marginata*, were more vulnerable than the six populations that have never been separated from this insect.

Pertinent to enduring biological control, within-population variation in traits related to both tolerance and resistance was much greater among genotypes of *Spartina alterniflora* in a population that had long been separated from the planthopper than in a population that had never been separated from it. The relationship between cordgrass shoot survival and planthopper population growth epitomizes these results (Figure 3). Consistent with previous findings (Daehler and Strong 1995), San Francisco Bay genotypes varied little in this relationship, and none suffered greatly from the low densities of planthopper that built up over the 20-week experiment. In contrast, Willapa Bay genotypes varied greatly in both shoot survival and planthopper population growth. While the harm done to most genotypes of the estranged cordgrass population was substantial, a subset was different.

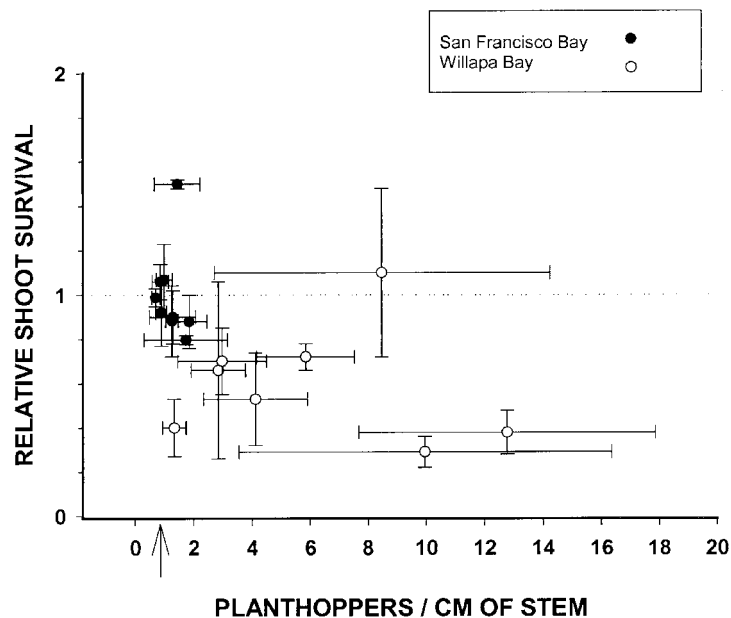


Figure 3. Variation among genotypes in population growth rate of *Prokelisia marginata* and in shoot death caused by this herbivore to *Spartina alterniflora* from Willapa Bay, which has been separated from the planthopper for *ca.* 100 years, and that from San Francisco Bay, which has never been separated from it. The arrow indicates the density of 0.66 planthoppers/cm of shoot at the beginning of this 20-week experiment.

One Willapa Bay genotype was virtually unaffected by the moderately high densities of the planthopper developing during the experiment. This genotype lacked resistance, but was tolerant of the planthoppers that grew upon it. Genotypes with this combination of traits could be self-defeating to biological control. Initially, such genotypes could accelerate control by producing many herbivores to harm the other, more vulnerable plant genotypes. In the longer-term, however, the effectiveness of the agent would decrease as the tolerant genotypes increased due to the selection pressure imposed by the biological control agent.

Genetic variation in vulnerability to natural enemies is important to biological control. Agents impose substantial natural selection (Gould *et al.* 1997), and the simplicity of foodwebs in biological control (Hawkins *et al.* 1999) can magnify selection differential due to enemies (Holt and Hochberg 1997). It is interesting that many plants have evolved resistance to chemical control (Georghiou 1990), while we have very few examples of evolved resistance to biological control; most concern insect pests (Muldrew 1953, Fenner 1983, Young 1986).

Our results provide an example of the potential for evolution of resistance to biological control, with an interesting twist of extra evolutionary dynamics caused by high variance in vulnerability of the weed. The enemy-free environment and relaxed selection in which invasive plants find themselves before biological control could lead to evolution of this increased variance (Colosi and Schaal 1992, Thompson 1998).

S. alterniflora has spread over approximately 6000 ha of previously open intertidal habitat during the 20th century in Willapa Bay, WA, amounting to about 30% of the 19,000 ha of intertidal lands suitable for this plant in the Bay. The invasion degrades habitat of shorebirds, waterfowl, fish, benthic invertebrates, and valuable clams and oysters (Anon. 1993, 1997). In summer of 2000, *P. marginata* from San Francisco Bay was introduced to Willapa Bay under permit of the Washington Department of Agriculture with unanimous approval of The Technical Advisory Group on Biocontrol of Weeds, of the US Department of Agriculture, APHIS. The introduction of this insect was made only after extensive host-specificity testing and disease screening (Davis *et al.* 2002, Grevstad *et al.* 2003).

In the event that planthopper densities grow sufficiently high (Grevstad *et al.* 2004), the result could be decreased spread rate or abundances of some *S. alterniflora* genotypes (those resembling the open points on the lower half of Figure 3). Initial success of biological control of this sort could drive natural selection favouring genotypes tolerant of the planthopper, which in the longer run could erode the effectiveness of biological control. In this scenario, other measures such as mechanical or chemical control (Patten 2002) would be necessary to prevent spread of cordgrass genotypes that are impervious to the planthopper. One could advo-

cate the choice of agents with impact so severe that no host genotypes survive (extremely high virulence), but such agents are unknown in the specific case under discussion and not very frequent in cases of weed control (Kennedy *et al.* 1987, Julien 1992). An understanding of the spatial distribution of tolerant/vulnerable genotypes could lead to strategies to minimize the evolution of tolerance. For instance, if there was clear spatial segregation between these categories of genotypes, one could release only in susceptible-dominated areas.

Cases at least reminiscent of ours include biological control of rush skeletonweed, *Chondrilla juncea* in Australia (Burdon *et al.* 1981). A fungus, *Puccinia chondrillina*, and an eriophyid mite, *Aceria chondrillae*, were introduced and attacked one of the three forms of the weed preferentially to the other forms. In less than a decade after introduction of the agents, the geographical distribution of the attacked form of rush skeletonweed had decreased greatly, while that of the other two forms, which compete with the attacked form, increased concomitantly. A second case is the contemplated biological control of *Lantana camara* by the leaf spot pathogen, *Mycovellosiella lantanae* var. *lantanae*, in South Africa. Some biotypes of *L. camara* are resistant to all of the fungal isolates (Den Breeyen 2004). This situation at least raises the possibility of replacement of *L. camara* biotypes that are vulnerable to this fungus with biotypes that are not.

Evolution of weeds is a pertinent topic for biological control. Invasive species can experience strong selection in their new environments. The processes of founder effect during colonization, spread, and possible hybridization with native or subsequent introduction of other strains, interaction with native species and with introduced agents can result in a mix of genotypes very different from those of the propagules or the population of origin.

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