

# 7 Genetics of Invasive Species in New Zealand

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## 7.1 Introduction

The genetic architecture of invasive species is now considered to be an important factor governing the long-term success of colonization in a new environment, as this is critical for the subsequent ability of invasives to respond to natural selection (Lee 2002). A clearer understanding of the genetics of invasive species has the potential to provide insights into the mechanisms of invasions as well as determining the genetic changes associated with the process of invasions. Genetic information may also be used to determine factors such as the origin and relative success of invasive species, and provide potential for investigating novel methods of control.

New Zealand offers opportunities to investigate the genetic processes underlying invasive species. Mainly this is due to a significant number of invasive species in New Zealand being deliberately introduced and, as a consequence, having well-documented introduction histories that enable post-colonization genetic investigations to be carried out. In addition, New Zealand is a heterogeneous landscape that possesses many natural barriers along with varying climatic conditions, facilitating multiple founder events, as well as providing colonizers with a range of selection pressures. Given these factors, relatively few studies have taken advantage of the opportunities presented by such introductions. This chapter reviews the research that has attempted to address the genetics of alien species in New Zealand, and suggests potential future research directions that can take advantage of these systems.

## 7.2 Genetics of Colonization

The principles of colonization genetics have been well documented through a range of publications that have investigated these in relation to classical models of founder events and allopatric speciation (Mayr 1963; Baker and Steb-

bins 1965; Carson 1971; Barton and Charlesworth 1984). Generally, invasive alien species experience the same effects as do natural colonizers, in that there is an initial establishment phase followed by rapid growth and subsequent invasion. The genetic consequence of such founder events has been one of the central tenets of allopatric speciation (Barton and Charlesworth 1984). The predicted genetic outcomes following a dramatic reduction in population size associated with founder events are a reduction in genetic variability, and, if species experience several independent founder events, this can result in genetic divergence among founding populations. Random genetic drift (Wright 1931) is the chance process most often advocated as the cause of the observed genetic change.

The extent of genetic change following founder events is predicted to be highly contingent on the size of the initial founding population. If the founding population is large, then there may be no substantial loss of genetic variability (i.e., allelic diversity) in the newly established range, as there is a high probability of all the genetic variants in the parental population being represented in the founder population (Kambhampati et al. 1990). Alternatively, if the initial founding population is small and subsequent establishment in the new range results in even smaller isolated subpopulations, then random genetic drift will play an increasingly important role in the loss or restructuring of variation. Thus, the effects of founding events and subsequent genetic drift are often difficult to distinguish (Barton and Charlesworth 1984).

The most recognized genetic consequence of colonization is the loss of genetic variability, due to founding individuals representing only a subset of the species' variability. Recessive alleles have a higher probability of becoming homozygous and being exposed to the effects of selection, with many alleles potentially becoming disadvantageous due to the new imbalance in the epigenotype or change in selective value (Mayr 1963). From the perspective of colonizing ability, genetic changes can either facilitate this or have a negative effect. An extreme example of where a reduction in genetic diversity post-colonization has resulted in significant changes in behavior in an invasive species is the Argentine ant, *Linepithema humile* (Tsutsui et al. 2000, 2001; Tsutsui and Case 2001). This species becomes a successful invader due to the loss of both self-recognition and aggressive territoriality, enabling the formation of "supercolonies" extending up to thousands of kilometers. However, there have been few studies that have addressed the importance of genetics in the establishment and early success of invasive species (Roderick and Howarth 1999). Rather, most studies have used genetic markers to investigate the origins and population genetic structure of invasive species.

## 7.3 New Zealand Examples

The most studied systems within New Zealand in regard to genetics of species arriving after European colonization have been a result of either the deliberate introductions of a desired species (e.g., birds, biocontrol agents) or the accidental arrival of an economically important pest species (insects, weeds). These studies have primarily investigated the genetic changes that have occurred after colonization, or used genetic data to retrace the history of an invasion to determine the source population.

### 7.3.1 Bird Species

The many passerine birds that were introduced to New Zealand from England in the 19th century provide opportunity for evolutionary biologists to investigate population differentiation within a microevolutionary time frame. Chapter 9 addresses the ecological factors that have enabled some species of introduced birds to successfully establish in New Zealand where others have not. We will review what is known regarding the levels of genetic differentiation and founder effect following their introduction.

Genetic studies that have investigated genetic differentiation and rates of evolution in introduced bird species include those of the house sparrow, *Passer domesticus* (Parkin and Cole 1985), the common myna, *Acridotheres tristis* (Baker and Moeed 1987), the starling, *Sturnus vulgaris* (Ross 1983), and the chaffinch, *Fringilla coelebs* (Baker 1992). All of these employed isozyme electrophoresis to compare population genetic structure and levels of genetic variability between introduced populations and those from the source of introduction. Bird introductions into New Zealand are relatively well documented, with historical records of dates, numbers and origins of those individuals involved in the founding process, enabling clear comparisons to be made. Each of these species showed high rates of genetic differentiation in the introduced populations, which can be attributed to genetic shifts promoted by bottlenecks and random drift. This has occurred to such a degree in mynas, for example, that after a relatively short evolutionary period of 100–130 years, these genetic shifts are equivalent to differences observed between subspecies of birds (Baker and Moeed 1987). Some losses of genetic variability were observed in terms of reduction of alleles per locus, but mostly these alleles were rare in the native population initially. Heterozygosity levels and proportion of polymorphic loci remained stable between introduced and native source populations.

Each of these studied bird species has been successful at establishing in New Zealand, and has not been compromised by the reduction in genetic variation relative to the source population. As a factor that may limit the potential for suc-

cess in a new habitat, genetics is difficult to quantify, as data are unavailable from unsuccessful introduction attempts. However, Duncan et al. (1999; and see Chap. 9) have shown that successful introductions and subsequent range size of birds in New Zealand are positively related to the number of individuals introduced. This could be partly attributed to the likelihood of larger introductions providing the required genetic architecture for adaptation to the new environment, rather than resulting in a dramatic loss of genetic variability.

### 7.3.2 Biocontrol Agents

Biological control practitioners have long been concerned with how best to select and release biocontrol agents. Maximizing both the establishment of biocontrol agents and the suppression of target species are critical factors in using biological control as a tool for pest management. Genetic information can help in improving the probability of selecting appropriate biotypes with desirable attributes that are able to adapt to introduction into a new environment. Retrospective analysis of two biocontrol agents in New Zealand has attempted to determine genetic factors that may have contributed to their success of establishment.

#### Argentine Stem Weevil Parasitoid

One concern of biological control practitioners is whether some ecotypes of an agent will establish more readily or be more effective in suppressing the target species. In New Zealand, the strategic use of an existing program for the biological control of Argentine stem weevil, *Listronotus bonariensis* (Kuschel), has allowed scientists to investigate the relative success in establishment of various ecotypes of the Argentine stem weevil parasitoid, *Microctonus hyperodae* (Winder et al. 1997; Iline et al. 2002).

Parasitoids were collected from different locations in South America across a diverse range of geographic and climatic zones. Collections of eight “ecotypes” were then established, and over 240 lines generated (Goldson et al. 1990). Equal numbers of each ecotype were reared and released in order to maximize the genetic diversity of *M. hyperodae*, and thus facilitate establishment and success in New Zealand. It was hypothesized that the populations most suited to the conditions prevailing at each release site would out-compete those that were less “pre-adapted”, and eventually become dominant. The use of genetic data subsequent to the release could provide insight into the importance of biocontrol agent “pre-adaptation” and the nature of any inter-ecotypic competition.

Studies in the laboratory have shown that the ecotypes varied significantly in aspects such as fecundity, photoperiodic response, and morphometrics. A

morphometric method showed that parasitoids from east of the Andes had out-competed those from west of the Andes throughout New Zealand during 1992–1995 (Phillips et al. 1994). Efforts to develop more precise methods of discriminating between the populations using genetic data have been unable to differentiate between *M. hyperodae* ecotypes (Winder et al. 1997). Recent developments of tandem repeat primers, and use of the polymerase chain reaction (PCR) to amplify anonymous DNA regions have now enabled differentiation of the populations into two genetically distinct types that can be classified as originating from either east or west of the Andes. A preliminary survey of allozyme variation has also shown the same trans-Andes pattern of subdivision between east and western populations, although this is not reflected by inter-population variations in diapause behavior or egg load (Iline et al. 2002).

### Broom Twig Miner

Broom twig miner, *Leucoptera spartifoliella* Hübner (Lepidoptera: Lyonetiidae), an accidentally introduced species, shows considerable potential as a biocontrol agent for broom, *Cytisus scoparius* (L.) Link (Syrett and Harman 1995). Since its arrival, this species has successfully colonized and dispersed throughout the country. Harman (2003) has compared the genetic variability of the broom twig miner from populations in New Zealand with that of populations from the native range in Western Europe. The aim was to determine the geographic origin of the broom twig miner in New Zealand, and to investigate post-colonization genetic changes using mitochondrial DNA (mtDNA) and amplified fragment length polymorphisms (AFLPs).

The genetic variability, measured by AFLP analysis, indicated that populations from the native range of broom twig miner showed little differentiation, which implies widespread gene flow. Although no matches for the New Zealand mtDNA were found in any of the other populations surveyed, the information does not support the hypothesis of Syrett (1990) that broom twig miner arrived in New Zealand on ornamental cultivars of broom imported from North America. A single founder event of small propagule size is suggested by the mtDNA data. Although both AFLP and mtDNA data show some loss of genetic diversity in New Zealand populations, compared with those from the native range, the AFLP data show that this could largely be attributed to the loss of less frequent alleles. In general, the New Zealand populations still show considerable genetic diversity. This is probably a result of broom twig miner populations having the capacity to grow steadily, as indicated by estimates of per capita rate of increase ( $r$ ) in New Zealand conditions (Harman 2003). Therefore, any bottlenecks that might occur through colonization events are likely to be short, with little impact on genetic variation.

### 7.3.3 Pest Species

Determining the genetic variation of an introduced pest species can enable post-colonization population genetic structure to be characterized, and the origin of the source population to be identified. This information can be used to design realistic and effective integrated control programs, e.g., ability to source appropriate biocontrol agents, and to identify the presence of insecticide resistance genes.

#### Australian Sheep Blowfly

One of the most comprehensive studies investigating the post-colonization genetics of a pest species in New Zealand has been carried out on *Lucilia cuprina* (Wiedemann), the Australian sheep blowfly. This species is the principal fly involved in flystrike of sheep in Australia and South Africa (Mackerras and Fuller 1937). In Australia, the first record of strike on the mainland was from Queensland in 1883, and by 1915 flystrike had become a major problem of the sheep industry. Collection material in Australia contains no *L. cuprina* specimens dated earlier than 1912, other than one specimen assumed to have been collected in southwestern Australia between 1864 and 1867 (Norris 1990). The origin of *L. cuprina* in Australia is hypothesized to be South Africa by Norris (1990), with the subspecies *L. cuprina cuprina* likely to have been introduced repeatedly into eastern Australia from a variety of Pacific regions. Therefore, the origin of *L. cuprina* in Australia is speculative, with only the estimated time of introduction relatively accurate, being based on museum collection material.

Flystrike in New Zealand had been apparent since the 1870s, but only became serious enough to warrant attention in the 1920s when the actual species were characterized and control measures put into place. From 1982 onward, there was a change in prevalence and severity of flystrike, one contributing factor being the arrival of *L. cuprina*, first detected in 1988. Subsequent investigation of preserved material found *L. cuprina* present since the early 1980s, when collections were first made. Hence, it is possible that the presence of *L. cuprina* in New Zealand could have gone unnoticed for at least a decade. Following the arrival of *L. cuprina*, the prevalence of this species in flystrike samples progressed from 20 to over 60% representation in a period of 2 years (Heath et al. 1991). It is likely then that this species was initially present in relatively low numbers, the first surveys showing that only 1.8% of flies trapped were this species (Dymock and Forgie 1993).

Initial interest in the genetics of *L. cuprina* was whether this arrival in New Zealand also introduced resistance to organophosphates (OPs). The genetic basis of OP resistance in Australian populations of *L. cuprina* has been well

documented and attributed to mutations in the esterase gene *aE7* (Parker et al. 1991; Newcomb et al. 1997). One mutation encodes a phosphatase with enhanced ability to hydrolyse diethyl OPs over dimethyl OPs, whereas another mutation has the opposite ability. Dose-mortality data together with biochemical assays were carried out on New Zealand populations, and showed that resistance to the diethyl OP diazinon was present at a very high frequency (Gleeson et al. 1994). Subsequent molecular data have been collected that revealed two diethyl-resistance mutations associated with haplotypes present in extant flies from New Zealand (Newcomb et al. 2005), along with a haplotype possessing the amino acid substitution conferring resistance to dimethyl OPs, found in a pinned museum specimen collected from Wellsford, New Zealand in 1989 (C. Yong, D. Gleeson, R. Newcomb, unpublished data).

Further genetic studies of *L. cuprina* in New Zealand were carried out using allozyme electrophoresis and mtDNA data. The aims were to determine the genetic effects of colonization in terms of genetic variability and differentiation, and to attempt to identify the geographic origin of *L. cuprina* in New Zealand. The allozyme study revealed high levels of genetic variability (allelic diversity and differentiation) in some New Zealand and Australian populations (Gleeson 1995). This was attributed to an initially large founding population, seasonal fluctuations in population size further facilitating the effects of genetic drift. Although the isozyme results were able to determine population structure, the results were unable to accurately assess the level of relatedness between geographic populations in order to investigate potential origin or to estimate the time of colonization. Source was investigated using mtDNA sequence divergence through restriction fragment length polymorphisms (RFLPs) and cytochrome oxidase subunit I (COI) sequence data (Gleeson and Sarre 1997). Potential colonization time of *L. cuprina* in New Zealand was estimated by screening populations for evidence of the fitness modifier gene, which enables flies that are resistant to diazinon to be equal in fitness to those that are susceptible, in the absence of the insecticide (McKenzie and Clarke 1988). This gene was found to be predominant in Australian populations in the late 1970s, and is closely linked to the white-eye (*w*) locus on chromosome III (McKenzie and Game 1987; McKenzie and Clarke 1988). Evidence for multiple introductions was apparent from the RFLP and DNA sequence data (Gleeson and Sarre 1997), with several haplotypes existing in New Zealand. Measures of fluctuating asymmetry gave evidence for a fitness modifier present in New Zealand populations, and a crossing experiment showed the New Zealand fitness modifier locus is closely linked with *w* (D. Gleeson, unpublished data).

This *L. cuprina* study showed the importance of multiple datasets in understanding the genetics of colonization. It is clear from the syntheses of insecticide resistance, allelic diversity, mtDNA, and fitness modifier genetic data that, rather than a single introduction with limited numbers of colonizers, either large or multiple introductions from a predominantly Australian source occurred.



## Rose-Grain and Green Spruce Aphids

The rose-grain aphid (*Metopolophium dirhodum*) and the green spruce aphid (*Elatobium abietum*) were both accidentally introduced into New Zealand. The former colonizes barley predominantly, whereas the latter feeds on spruce (*Picea* spp.). Investigation of the levels of genetic diversity in both species in New Zealand has been carried out and comparisons made with populations from the UK (Nicol et al. 1997, 1998). The rose-grain aphid is native to the UK, whereas the green spruce aphid is an introduced pest that probably arrived in the UK before 1500 A.D., along with Norway spruce (*P. abies*).

The rose-grain aphid is a recent introduction into New Zealand, having been first recorded in the North Island in 1981 and in Canterbury (South Island) in 1982. In Europe, this species causes direct damage to cereal crops, and damage through virus transmission. In Europe, *M. dirhodum* overwinters as eggs on Rosaceae or as parthenogenic females on Graminae. In New Zealand, however, only nonsexual forms have been recorded and the aphid overwinters parthenogenetically on cereals. Genetic variation was investigated at both a microgeographic (<1 km) and a macrogeographic scale, comparing *M. dirhodum* in New Zealand with that in a country where they are native (Scotland), using randomly amplified polymorphic DNA (RAPD)-PCR analysis. There was a significant temporal effect on the ratio of genotypes in populations collected in the field, with no significant spatial aggregation of genotypes. All populations from New Zealand and Scotland showed significant genetic diversity, with Scottish populations showing more diversity than there is in New Zealand. Given the relatively high levels of genetic diversity in New Zealand, despite the populations being entirely parthenogenic, it is likely that there have been multiple introductions from other locations within the native range of the rose-grain aphid (Nicol et al. 1997).

Genetic diversity of the green spruce aphid was assessed using RAPD-PCR analysis to evaluate this method for determining the origin and number of introductions of this aphid into New Zealand (Nicol et al. 1998). It also provided an opportunity to investigate an invading species in two countries with contrasting population dynamics. Samples were collected from four locations in the UK that were up to 240 km apart, and from up to six locations in New Zealand that were up to 1,200 km apart. A high degree of genotypic diversity was found in the UK populations, in comparison with New Zealand. This is presumed to be due to a very limited founder population, a short period of establishment, continued isolation, and lack of sexual reproduction in New Zealand, in contrast to the UK.



## Argentine Stem Weevil

Native to South America, the introduced pasture pest Argentine stem weevil (*Listronotus bonariensis*) is thought to have been accidentally introduced into New Zealand and Australia through grasses or hay used as stockfeed on trading ships. This species was first reported in New Zealand in 1927, with a maximum of 200–250 generations elapsing since its establishment.

Geographic populations of *L. bonariensis* were analyzed using RAPD-PCR in an attempt to determine the geographic origin of the pest (Lenney-Williams et al. 1994). Morphologically indistinguishable individuals were collected from nine South American, five New Zealand, and one Australian population. The results indicated that the sampled New Zealand populations originated from the east coast of South America. This initial screen of the genetic makeup of these populations has provided useful information to assist in identifying appropriate source populations of biocontrol agents.

## White-Fringed Weevil

White-fringed weevil, *Naupactus leucoloma* Boheman, was first found in New Zealand in 1945 (Todd 1968), with the origin being hypothesized as North America. Although this species arrived in New Zealand 50–60 years ago, the fact that it is parthenogenic outside of its native range (Lanteri and Normack 1995), coupled with a long generation time, would result in limited opportunities for natural genetic variation to arise outside of major mutation or recombination events. Hardwick et al. (1997) investigated the level of RAPD-PCR variation in New Zealand populations, compared with that in Victoria, Australia. In this relatively small study, three different genetic profiles were revealed from two New Zealand populations, with two profiles being revealed in a single paddock. It is possible that this variation has arisen after colonization, or that there had been multiple introductions of this pest species, although there is currently no knowledge of the extent of genetic variation occurring in other native or introduced populations of *N. leucoloma*.

### 7.3.4 Invasive Plants

Few studies have sought to determine the genetic characteristics of successful invasive plants, although they are likely to be subject to genetic constraints similar to those of other colonizing species (Barrett 1992). It is generally accepted that the founder effect and subsequent genetic drift in small, isolated populations result in lower genetic diversity and increased spatial genetic differentiation in adventive populations, compared with native populations

(Schierenbeck et al. 1995). The impacts of these processes on plant fitness and invasive potential are unclear, although population genetics theory predicts that founding populations may be at a disadvantage relative to native taxa. This conclusion is based on expectations of decreased fitness resulting from (1) inbreeding depression in small founding populations, and (2) genetic drift resulting in the loss of adaptive genetic diversity (Young et al. 1996).

Paradoxically, despite these potential genetic constraints, a large number of plant species have become extremely successful invaders, out-competing locally adapted native species over wide areas and across diverse ecosystems. In New Zealand, the ratio of naturalized alien plant species to native species is approximately 1:1, which is reported as one of the highest ratios of any country or region (Williams and Lee 2001). Evidently, a narrow population genetic focus alone is inadequate to explain the contribution of genetic factors to the apparent success of invasive plants.

Recent studies point to the importance of plant reproductive strategies and genomic factors in enabling species to overcome the genetic constraints associated with founder processes, and in facilitating the successful colonization of new habitats. Many plant species exhibit variable levels of sexual and vegetative reproduction, possess polyploid genomes, and are able to hybridize with close relatives. These attributes can potentially increase levels of heterozygosity in colonizing populations, guard against the negative consequences of inbreeding depression, and facilitate rapid adaptation to new conditions through hybridization and genomic reorganization (Barrett 1992; Arnold 1997; Levin 2000).

## Hawkweed

*Pilosella officinarum* F.W. Schultz & Sch. Bip. (usually known in New Zealand as *Hieracium pilosella* L.), mouse-ear hawkweed, is native to Britain and Europe and has successfully colonized New Zealand after being accidentally introduced in the late 19th century as a contaminant of grass seed. Since its introduction, the species has spread over a wide geographic area and forms a dominant component of the vegetation across a diverse range of habitats. *P. officinarum* reproduces both vegetatively through ramet fragmentation and also through the production of sexual and apomictic (maternally derived) seed (Chapman et al. 2000).

Despite the expectation of reduced genetic diversity arising from bottleneck events associated with its introduction, Chapman et al. (2000) found that levels and patterns of genetic diversity in New Zealand populations of *P. officinarum* were similar to those reported for closely related facultatively apomictic species in their native ranges (Widén et al. 1994). New Zealand populations of *P. officinarum* differed only in that they exhibited slightly increased genetic differentiation, possibly reflecting the effect of local genetic

drift in founder populations at the periphery of an expanding range. *P. officinarum* is known to have a flexible and complex breeding system, involving predominant apomixis and low levels of sexual reproduction among clones possessing various levels of polyploidy (Jenkins and Jong 1997). It has been suggested that the levels of clonal diversity present in the species reflect latent variation that arose through sexual reproduction and hybridization in ancestral populations, and that has since become fixed through polyploidy and apomixis (Chapman et al. 2000). Occasional events of sexual reproduction between polyploid clones are capable of generating a range of new recombinant genotypes, exposing this latent genetic variation to natural selection in new environmental contexts. Such a strategy may result in the species having an increased potential to colonize new habitats, evolve rapidly and persist. The patterns of genetic variation present in New Zealand populations of *P. officinarum* suggest that such processes may be at least partially responsible for its success in colonizing a wide range of new habitats.

### 7.3.5 Hybridization and Invasive Potential

Genetic studies (Warwick et al. 1989; Rieseberg et al. 1995; O'Hanlon et al. 1999) have increasingly highlighted the importance of hybridization and subsequent genomic reorganization to the success of plant invasions worldwide. The potential for hybridization between different species or races of invasive plants that may have been geographically or ecologically isolated in their native ranges is greatly increased when such taxa are brought together under disturbed or novel ecological contexts (Warwick et al. 1989; Arnold 1997). Hybridization can generate a new gene pool with greatly increased genetic diversity and heterozygosity relative to levels present in the parental taxa. This process can facilitate rapid adaptation by exposing a wide range of novel recombinant genotypes to natural selection, many of which may be better adapted to the new conditions than are the parental species, and may therefore have increased invasive ability. There is great potential for this phenomenon to be examined in New Zealand, with so many invasive genera present comprising a number of potentially interfertile entities (e.g., in the genera *Carduus*, *Hieracium*, *Brassica*, *Festuca*, *Passiflora*). The importance of understanding hybridization within the context of invasive potential is highlighted by the development of genetically manipulated crops, some of which may be capable of interbreeding with invasive species already established in the environment. Genetically engineered traits such as *Bt* expression may confer considerable selective advantages to weedy relatives.

## 7.4 Potential Genetic Impacts on Indigenous Biota

The “invasion” of alien genes into indigenous species represents a potentially serious and intractable problem that has so far received little scientific attention in New Zealand. In plant species, one particular genetic consequence of plant invasion is genetic assimilation through the introgression and permanent incorporation of genes from adventives into the gene pools of native species through hybridization. The possibility of hybridization between indigenous and naturalized species has been studied infrequently in New Zealand, the only examples being in *Acaena* (Rosaceae; Webb et al. 1988), *Carpobrotus* (Aizoaceae; Chinnock 1972), and *Epilobium* (Onagraceae; Raven and Raven 1976). Spontaneous natural hybrids have been reported between the naturalized *Epilobium ciliatum* and two indigenous species, *E. brunnescens* subsp. *brunnescens* and *E. melanocaulon* (Raven and Raven 1976). In *Epilobium*, a number of fertile hybrids between indigenous and naturalized species have been generated experimentally (Brockie 1966), highlighting the potential for hybridization to occur between indigenous and naturalized species in the wild. Experimental studies also suggest that hybridization may occur naturally between the invasive *Calystegia silvatica* and the indigenous *C. sepium* (Convolvulaceae; Ogden 1978), and also between naturalized *Polygonum persicaria* and the indigenous *P. salicifolium* (Polygonaceae; Webb et al. 1988). Despite these experimental findings, and the fact that some of the most aggressive naturalized species have closely related indigenous congeners, including *Myosotis* (Boraginaceae), *Ranunculus* (Ranunculaceae), and *Senecio* (Asteraceae), there are few documented accounts of natural hybridization between indigenous and naturalized species in New Zealand. However, hybridization might be difficult to detect without the use of molecular markers, as hybridizing species commonly possess characters that are morphologically similar, difficult to interpret, and could be masked by environmental factors that influence growth habit. For example, observations that cultivated Tasmanian *Myoporum insulare* R. Br. is hybridizing extensively with the New Zealand native *Myoporum laetum* Forster. (ngiao) in the Auckland region (NZ Department of Conservation, unpublished data) require genetic analysis to verify the identity of putative hybrids and the local extent of introgression. There is clearly a wider need to investigate the possibility of hybridization using molecular approaches to better understand and predict the genetic consequences of plant invasions for the New Zealand biota.

## 7.5 Conclusions

Genetic effects following the colonization and invasion of New Zealand have been studied in relatively few cases for a variety of reasons. The outcomes of these studies have shown that there are ranges of genetic effects that do occur after colonization, although it is often difficult to attribute genetics as a factor in the success or failure of invasive species. However, specific genotypes can facilitate success in some cases, e.g., sheep blowfly and insecticide resistance gene. It is clear that further invasions are likely, and that many risks are posed to the indigenous biota, in particular through hybridization with exotics. The extent to which this is currently occurring is little known and presents opportunities for future research, particularly when considering potential impacts of releasing genetically modified plants into the environment.

Another area where genetic research can assist in the study of biological invasions is in a better understanding of the invasive process and adaptive genetic variance that underlies the success of invasive species. Recent research suggests that only a small number of genes along with epistatic genetic variance can have a major impact on colonizing ability. Advancements in the field of genomics are now providing the tools necessary to investigate the genomic characteristics of successful invaders.

It has also been suggested that genetics should have a larger role in the development of policy to manage and control invasive species through a better understanding of the risks that particular genotypes pose (Allendorf and Lundquist 2003). At present, focus on invasive species in New Zealand is at the taxon level, whereas in the future, genetic risk associated with invasives is likely to have greater emphasis.

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