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Abstract Understanding the introduction history and the impact of founder events on invasive species is crucial to understanding the evolutionary mechanisms driving successful invasions. Recently, there has been increased discussion of the "paradox" of invasions, the high success of introduced populations that presumably have limited genetic diversity associated with founder events. The western mosquitofish *Gambusia affinis* is an ideal species for evaluating this paradox, because it has been widely introduced from its native range in central Texas, USA. This species was introduced to the North Island of New Zealand, circa 1930, and has since invaded aquatic habitats across the North Island. We conducted a microsatellite assay of populations from both the native and introduced range to verify the documented history of invasion and to assess the impact of serial introduction events on the genetic diversity of recently established New Zealand populations. The molecular data were consistent with the documented introduction history. In addition, we found sharp reductions in the allelic richness and the heterozygosity of the introduced populations relative to the original native populations, indicating the presence of founder effects. We also observed the development of strong genetic structure within the introduced range, which is absent within the native range. Finally, we applied approximate Bayesian computation to the introduction scenario to estimate the long-term effective population sizes for the sampled populations.

Keywords Invasive · *Gambusia affinis* · Founder effects · Introduction history · Serial introduction

Introduction

The reconstruction and verification of introduction history for invasive species is an important task for understanding the evolutionary ecology of invasive species (Dlugosch and Parker 2008; Estoup and Guillemaud 2010; Sax et al. 2007). Historically, the ability to reconstruct the introduction history for an invasive species depended on written records, which are often sparse or non-existent. Fortunately, the advent of molecular ecology has provided important tools for reconstructing invasion histories (anole lizard; Kolbe et al. 2004; Ctenophora; Reusch et al. 2010; fire ant; Tsutsui et al. 2001). This information is important as the reconstruction of introduction routes

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can provide vital information for the prevention and management of invasions, as well as for the study of the ecological and evolutionary forces involved with successful invasions (Estoup and Guillemaud 2010).

The evolutionary mechanisms underlying successful invasions are not well understood (Lee 2002). Introduced populations often experience reductions in population size, which in turn increase vulnerability to inbreeding, drift and ultimately extinction (Frankham 1998, 2005; Hedrick and Kalinowski 2000). Further, population genetics theory predicts that such founding events will result in reduced genetic variation relative to the original source population (Allendorf and Lundquist 2003; Nei et al. 1975) and thus constrain evolutionary potential. In fact, heterozygosity and/or allelic richness are often reduced for introduced populations compared to source populations (Dlugosch and Parker 2008; Leberg 1992; Stockwell et al. 1996). However, the high success of many invasive species has called into question whether these presumed genetic bottlenecks are a true constraint on population establishment (Allendorf and Lundquist 2003; Sax and Brown 2000).

A number of recent studies have sought to examine the apparent "paradoxical" success of invasive populations that start from small, theoretically, genetically impoverished populations (Fridley et al. 2007; Roman and Darling 2007; Sax and Brown 2000). A recent study examined how populations of brown anole lizards (Kolbe et al. 2004), which should have been genetically diminished due to founder effects, have been able to persist and adapt to new environments. A critical factor in the success of these introduced populations was the occurrence of multiple introductions from divergent sites within the native range (Kolbe et al. 2004). These multiple introduction events appeared to contribute to within-population genetic diversity, due to the admixture between the genetically divergent founder populations. By contrast, limited neutral diversity in invasive species (Lindholm et al. 2005; Stockwell et al. 1996) has not always constrained evolutionary potential (Brooks and Endler 2001; Stockwell and Weeks 1999).

These findings underscore the importance of understanding the introduction routes of invasive populations and the genetic impacts that species introductions can have on newly founded populations. These questions are well suited to invasive species such as mosquitofish, which have been extensively introduced world-wide. The western mosquitofish (*Gambusia affinis*), and its congener, the eastern mosquitofish (*Gambusia holbrooki*), are native in south central and southeastern US, but collectively have become one of the most abundant and widespread freshwater fishes in the world due to their presumed ability to control mosquitoes (Krumholz 1948; Pyke 2005). Mosquitofish have general attributes that are expected to facilitate the retention of genetic diversity for introduced populations including rapid population growth rates (Leberg 1990, 1993), as well as multiply-sired broods and sperm retention (Chesser et al. 1984; Robbins et al. 1987). These latter two traits can increase the effective population size (Sugg and Chesser 1994), because genes from males can be introduced even if these sires are not part of the colonizing population.

The first reported transfer of *G. affinis* outside of the contiguous United States was in 1905 by Albert Seale (Krumholz 1948; Seale 1905; Van Dine 1907). Seale transferred 150 *G. affinis* from south central Texas to the island of Oahu in the Hawaiian archipelago. From this Oahu introduction, mosquitofish were subsequently introduced to a number of other islands including Hawaii, Molokai, Kaui, Maui (Van Dine 1907), the Philippines (Juliano et al. 1989; Seale 1917) and New Zealand (McDowall 1990).

Previous studies verified the documented introduction of *G. affinis* into the Hawaiian Islands and evaluated the evolutionary and genetic impacts of these introductions on the founder populations (Scribner et al. 1992; Stearns 1983). A genetic survey revealed no significant loss of alleles for the introduced Hawaiian populations as compared to the ancestral Texas populations (Scribner et al. 1992), and Hawaiian populations actually showed increased levels of heterozygosity. Both findings supported the hypothesis that Hawaiian *G. affinis* populations experienced little or no founder effects as a result of their introduction. This high genetic diversity is of particular interest because Stearns (1983) reported evolutionary divergence among the introduced Hawaiian mosquitofish populations for a number of life history traits.

The introduction of *Gambusia* spp. to New Zealand has limited documentation. There were three attempts to introduce *Gambusia* spp. to New Zealand starting in 1928 and culminating in the successful establishment of a population in 1930 (McDowall 1990). The first two attempts, which involved fish from the Hawaiian Islands in 1928, and fish from Sydney, Australia in 1930, both reportedly failed due to mortality. Information for both attempts is limited with little detail on the number of transferred individuals or exact source locations (McDowall 1990). The third, and successful, attempt established a population of *G. affinis* in New Zealand in 1930. These fish arrived in New Zealand from the Hawaiian Islands on board a ship named the *Aorangi*. The fish were released in a pond on the grounds of the Auckland Botanical Gardens (now known as the Auckland Domain, Auckland's oldest park), but the number of founders was not documented. Within one year (1931) the populations were said to be thriving (McDowall 1990).

The first "wild" introduction of *G. affinis* individuals in New Zealand was to Lake Ngatu in 1933 (King 1997; Krumholz 1948; McDowall 1990). While no explicit documentation exists on the number of founders or the source population, presumably they came from the robust population at Auckland Botanical Gardens. Following introduction to Lake Ngatu, there have been numerous un-documented introductions throughout the North Island.

The objective of this study was to use a new set of molecular markers (Purcell et al. 2011) to evaluate the documented history of introduction for *G. affinis* into New Zealand. In addition, we aimed to evaluate the impact of serial introductions on the genetic diversity of the two introduced populations in relation to the native populations. Finally, we apply an emerging Bayesian approach to estimate demographic characteristics for both the founder and introduced populations.

Methods

To evaluate the introduction history of *G. affinis* on the North Island of New Zealand we sampled locations from two regions, the native range in central Texas, USA, and the introduced range in the region of the North Island in New Zealand (Fig. 1), to compare the genetic characteristics and relationships among populations (Table 1). In 2009, individual *G. affinis* were sampled from three native range populations in south central Texas. Samples were also collected, in 1999, from Auckland Domain, NZ, the putative founder population (Krumholz 1948; McDowall 1984) and from Lake Ngatu, the site of the first "wild" release of *G. affinis* in New Zealand (Fig. 1). All fish were collected via dip net and euthanized using a lethal dose of MS-222 (IACUC # A0902), and then preserved in 75 % ethanol.

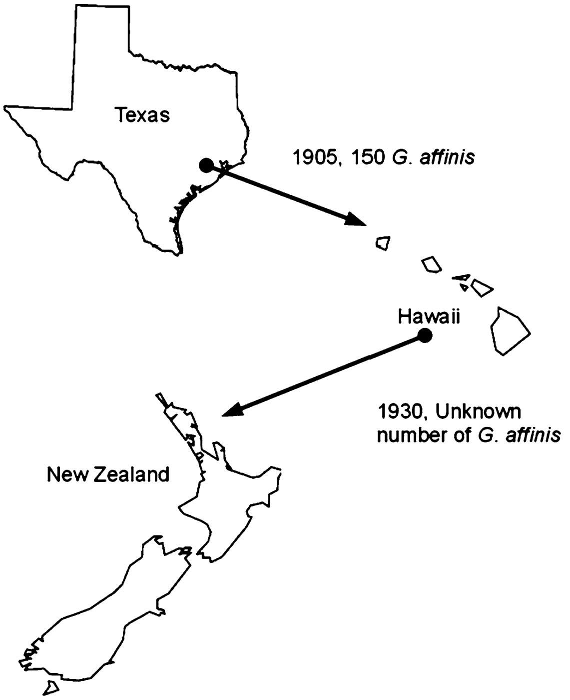

Fig. 1 Map of introduction history for *G. affinis* with *lines* representing direction of fish transfer and introduction. The *line* annotations represent the year of transfer, number of transferred individuals

We extracted genomic DNA from 30 individuals from each sampling site using the Puregene tissue extraction protocol (Gentra Systems). We assayed all samples for 10 microsatellite loci, which were amplified following conditions of Purcell et al. (2011). Amplification products were analyzed on a 3730 DNA Analyzer (Applied Biosystems), and electropherograms were scored using GeneMarker v1.85 (SoftGenetics), and visually verified for accuracy. We analyzed the entire data set using MICROCHECKER 2.2.3 (Oosterhout et al. 2004) and found no evidence for the presence of null alleles.

We evaluated our dataset for deviations from Hardy-Weinberg Equilibrium (*HWE*) and for evidence of linkage disequilibrium (*LD*) using the GENEPOP 4.0 web interface (Raymond and Rousset 1995; Rousset 2008). We calculated a number of genetic

Table 1 Genetic characteristics summary table for all sampled population, symbols indicate: (N) the number of samples, (A_R) the allelic richness, (H_E) the expected heterozygosity, (H_O) is the observed heterozygosity and (P_A) is the number of private alleles in that population

Sample	Spatial coordinates						
	Lat.	Lon.	N	A_R	H_E	H_O	P_A
Native populations							
Brazos River, TX	28.94	95.379	30	12.33	0.76	0.72	2.44
Clear Lake, TX	29.56	96.067	30	11.88	0.75	0.73	1.66
Lake Houston, TX	29.91	95.147	30	11.44	0.75	0.69	1.66
Non-native populations							
Lake Ngatu, NZ	−31.01	174.90	30	7.77	0.69	0.68	0.66
Auckland domain, NZ	−35.03	173.19	30	4.55	0.52	0.48	0.33

diversity measures for all sampling locations. Allelic richness was calculated using FSTAT 2.9.3 (Goudet 1995), and the effective number of alleles (A_E), the observed (H_O) and expected (H_E) heterozygosity and the mean number of private alleles (P_A) for each population were calculated using GENALEX 6.4 (Peakall and Smouse 2006). We evaluated patterns of genetic diversity between native and introduced regions with descriptive statistics due to the limited number of populations sampled.

We calculated the genetic relationship between sampling locations with pairwise F_{ST} using FSTAT 2.9.3 (Goudet 1995) and tests of genic and genotypic differentiation using GENEPOP 4.0 (Raymond and Rousset 1995; Rousset 2008). We used chord distance (Cavalli-Sforza 1967) as calculated by the program GENEDIST, to visualize the relative genetic relationship between populations, and generated an UPGMA tree using the DRAWTREE program; both programs are components of the PHYLIP 3.69 package (Felsenstein 2004).

To evaluate the genetic structure between sampled locations as well as between regions, we used a Bayesian assignment test to sort sampled genomes into putative groups. We used BAPS 5.2 (Corander et al. 2008) to investigate the genetic structure of the sampled populations due to its assignment accuracy at low F_{ST} values (Latch et al. 2006). In BAPS, we examined our dataset for clusters, consisting of >3 individuals (Corander et al. 2003), using the admixture model. We ran simulations for $K_{\max}$ ranging from 1 to 6, with 10 replications for each possible $K_{\max}$ value.

Finally, we used Approximate Bayesian Computation (ABC) methods (Beaumont et al. 2009; Bertorelle et al. 2010; Csilléry et al. 2010), to estimate the long-term effective population size of our sampled populations, as well as the un-sampled Hawaiian populations. We used DIYABC 1.0.4.38, an implementation of ABC developed by Cornuet et al. (2008). Our reference table, which forms the basis of the parameter estimation, consists of 3,000,000 simulated data sets. Each record in the reference table is based on 18 summary statistics: including one sample statistics for the mean number of alleles, genic diversity, allele size variance, and Garza-Williamson's M (2001). The remaining summary statistics were two-sample statistics for the mean number of alleles and pairwise F_{ST} estimates. We used DIYABC to estimate effective population size for both our sampled and the un-sampled populations under the published introduction scenario (Fig. 3).

Results

Of the 10 microsatellite loci examined we found a single locus (Gaaf 14) to routinely deviate from *HWE* and therefore it was removed from further analyses. We found no significant deviations from *LD* within our data set. Heterozygosity values were notably consistent within each region, and we observed larger values for source populations ($H_E = 0.75$–0.76; $H_O = 0.69$–0.73) when compared to introduced populations ($H_E = 0.52$–0.69; $H_O = 0.48$–0.68). Likewise, we observed relatively high allelic richness in the native populations ($A_R = 11.4$–12.3) in comparison to introduced populations ($A_R = 4.5$–7.7). We also found that native populations have a higher number of private alleles ($P_A = 1.6$–2.4) relative to introduced populations ($P_A = 0.3$–0.6).

The divergence between the native and introduced populations can also be seen more clearly in the UPGMA tree based on chord distance (Fig. 2). Again, the greatest divergence between our sample locations is between the introduced and native range (Fig. 2). However, within region divergence is similar for the introduced range (chord distance value = 0.034) compared to the native range (chord distance range 0.031 to 0.036). We also evaluated divergence within and among regions with other estimators (F_{ST} and BAPS) because Chord Distance (D_A) has limited sensitivity to changes effective population size (Kalinowski 2002).

The overall F_{ST} estimate for all sampled locations was $F_{ST} = 0.096$, with pairwise estimates ranging from 0.002 to 0.214 (Table 2). The greatest pairwise F_{ST} estimates were found between populations that occurred in different regions, with a range of 0.078–0.214 (Table 2). Divergence estimates among the three Texas populations ranged from 0.002 to 0.009, while divergence between the two populations in New Zealand was higher, with a value of 0.088. Strikingly, the divergence between Lake Ngatu (LN) and its presumed founding stock, Auckland Domain (AD), was similar to the divergence estimates between LN and the native Texas populations (Table 2). This same pattern of differentiation was found in our examination of genotypic and genic allele frequency differentiation, with a low number of significant locus differences among the three native (Texas) populations but a high number between native (Texas) and introduced populations (New Zealand) and between the two New Zealand populations (Table 2).

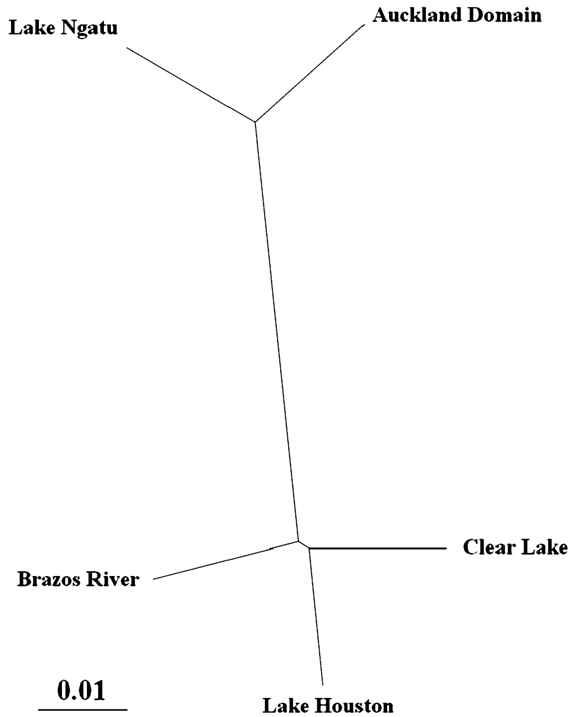

Fig. 2 UPGMA tree of population divergence based on chord distance

Our Bayesian clustering analysis conducted with BAPS 5.2 was consistent with the analyses using F_{ST} in giving the highest support he presence of 3 distinct clusters within our six sampling locations ($K_{\max} = 3$). There was strong support for genetic structure between the native and introduced regions. We found additional support for genetic sub-structure within the introduced sampling sites, with Auckland Domain and Lake Ngatu both representing distinct clusters.

Finally, our ABC analysis estimated the effective population size for each population lineage using the published introduction history as our scenario (Fig. 3). We found only small differences in the genetic diversity among the Texas samples, and the genetic structure analysis indicated the presence of a single panmictic population. Therefore, we treated the Texas samples as a single population for our ABC analysis. This simplified the model scenario procedure and maximized our sampling of the "native" genetic variation. Our analysis estimated that the largest population (approximately = 9,260; 95 % CI = 7,930–9,950; Table 3) was the Texas population. The introduced sites were found to have lower estimated sizes with Lake Ngatu being the largest (approximately = 6,550; 95 % CI = 3,250–9,780) and Auckland Domain more than an order of magnitude smaller (approximately = 593; 95 % CI = 179–5,630).

Discussion

The documented history indicates *G. affinis* was introduced to New Zealand from the Hawaiian archipelago approximately 80 years ago (McDowall 1990). In turn, Hawaiian populations were originally derived from *G. affinis* populations within the species native range in central Texas (Krumholz 1948; Seale 1905; Van Dine 1907). We found no evidence to contradict

Table 2 Pairwise F_{ST} values among sampled sites are above the diagonal

	Brazos River, TX	Clear Lake, TX	Lake Houston, TX	Lake Ngatu, NZ	Auckland Domain, NZ
Brazo River, TX	–	**0.009**	**0.009**	***0.091***	***0.209***
Clear Lake, TX	1/2	–	0.002	***0.078***	***0.203***
Lake Houston, TX	0/1	1/2	–	***0.084***	***0.214***
Lake Ngatu, NZ	*9/9*	*8/8*	*8/8*	–	**0.088**
Auckland domain, NZ	*9/9*	*9/9*	*9/9*	8/9	–

Emboldened values are significant at an adjusted nominal level for multiple comparisons. Counts of significant ($P < 0.05$) genotypic and genic tests of allele frequency differentiation (genotypic/genic) are below the diagonal. Italicized values represent pairwise comparisons between native and introduced samples

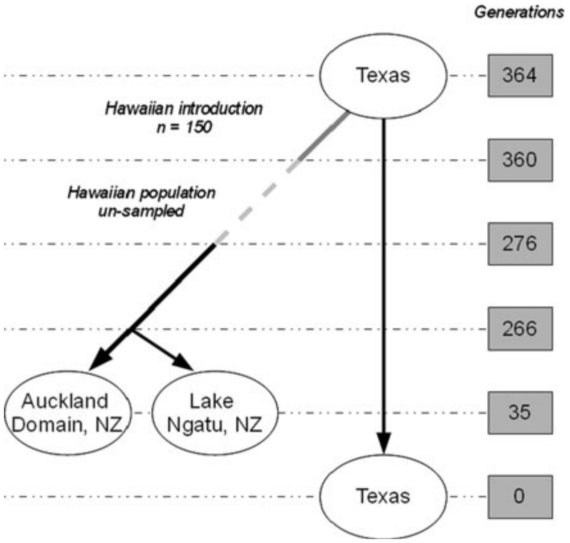

Fig. 3 DIY ABC scenario with sampled location at the terminal end of each lineage. Bottleneck size and un-sampled populations are *italicized*. *Dotted lines* are indicators of *G. affinis* generations relative to population sampling (lines not to scale)

Table 3 Effective population size (N_E) estimates for each lineage using approximate Bayesian computation (ABC) analysis, with 95 % CI

Population	Median	CI	
		0.05	0.95
Texas	9,360	7,930	9,950
Lake Ngatu, NZ	6,550	3,250	9,780
Auckland Domain, NZ	593	179	5,630

the published record of introduction. Approximately 97 % of the alleles found in our microsatellite assay of the New Zealand populations were also present in the native Texas populations. In contrast, a comparison between the native Texas populations and an out-group population from within the native range but in Louisiana (unpublished data) showed Louisiana and Texas populations shared only 14 % of the alleles.

Our examination of the impact of serial introduction events on the genetic diversity of *G. affinis* populations showed clear evidence for the presence of founder effects. We found a 52 % reduction in the allelic richness (A_R) of introduced populations relative to native populations (Table 1). This finding drastically differs from the high level of genetic variation for the Hawaiian populations. Scribner et al. (1992) reported increased heterozygosity and retention of allelic diversity for allozymes in the introduced Hawaiian *G. affinis* populations compared to the ancestral populations in Texas. By contrast, we found a substantial reduction in heterozygosity within New Zealand populations having an observed heterozygosity (H_O) of 0.48–0.68, compared to high heterozygosity for the native populations ($H_O = 0.69$–0.73). This loss of allelic richness and heterozygosity is comparable to another study of *G. affinis* which showed a reduction of heterozygosity and allelic diversity for *G. affinis* populations introduced to California from two populations in Texas circa 1922 (Stockwell et al. 1996), and mimics the general pattern of reduced diversity observed for introduced populations (Dlugosch and Parker 2008; Stockwell et al. 1996).

The loss of diversity and altered allele frequencies had a dramatic effect on genetic distance between the native and introduced ranges as reflected in the neighbor joining tree (Fig. 2). The overall F_{ST} value for our data set was 0.096, and we observed significant levels of divergence for all population comparisons with the exception of two of the Texas populations (Clear Lake (CL) vs. Lake Houston (LH)). These findings indicated the likelihood of genetic structure within both the introduced and native ranges. To evaluate this possibility we used Bayesian clustering analysis, the results of which indicated the presence of three clusters. This clustering analysis confirmed our results based on genetic distance metrics, and interestingly indicated the development of genetic sub-structure within the non-native New Zealand populations, which notably was not evident for the native Texas populations.

The oddity of the genetic divergence within the introduced population is that the founding population at Auckland Domain had lower diversity (both A_R and H_o) relative to the descendant populations at Lake Ngatu. This pattern deviates from expected decline of genetic diversity following sequential founder events (Clegg et al. 2002; Lambert et al. 2005; Leberg 1992). This would suggest that a driver other than founder events has molded the genetic diversity of the New Zealand populations (Nei et al. 1975; Maruyama and Fuerst 1985). In fact, for populations that are founded in a rapid sequence, one may expect that population specific differences in effective population size may alter genetic diversity. Our reduced diversity at Auckland Domain is consistent with the hypothesis that diversity in this site was further reduced subsequent to the founding of Lake Ngatu.

To examine long-term effective population size within our data we employed the emerging technique of approximate Bayesian analysis. A number of studies have effectively used this technique to model demographic parameters of populations (Bertorelle et al. 2010; Csilléry et al. 2010; Guillemaud et al. 2009). Our analysis model, based on the documented introduction history, indicated considerable difference in the effective populations size among the populations (Texas = 9,260; Auckland Domain = 593; Lake Ngatu = 6,550). This difference in the long-term N_e is thus a likely explanation for the depressed genetic variation in the initial founder population (AD). We suggest that this Ne reduction is most likely driven by differences in habitat availability (Alò and Turner 2005; Johnson et al. 2004) between these two sites. In fact, habitat availability at Auckland Domain is very limited (0.2 ha) relative to Lake Ngatu (57.1 ha).

Our findings run counter to a recent discussion of the “paradox” of successful invasions following introduction events (Fridley et al. 2007; Roman and Darling 2007; Sax and Brown 2000). Kolbe et al. (2004) hypothesized that admixture resulting from the introduction of divergent stock populations increased the within population diversity and facilitated successful introduction of non-natives to novel environments. While this hypothesis has been shown to be quite feasible for other systems (Gaither et al. 2010; Keller and Taylor 2010; Vidal et al. 2009), founder effects were still evident for the two New Zealand mosquitofish populations, which despite reduced genetic diversity persisted for 81 years (243–324 generations) after the 1930 introduction event. Further, mosquitofish are now widely distributed across the North Island indicating that reduced genetic variation has not constrained the spread of this species. We hypothesize that assisted colonization events are less likely to be repeated for species that are capable of rapid establishment as is the case with Poeciliid fishes.

Our results indicate the presence of considerable founder effects within the initial *G. affinis* introduced population and the initial ‘wild’ introduction site. We also found strong evidence of genetic structure within the introduced populations. While we report a decline in genetic diversity of the introduced populations, the wide dispersal of this species throughout the North Island seems to indicate that founder effects have not suppressed this species ability to adapt to novel habitats. This finding is not surprising given that bottlenecks often reduce neutral variation with little or no effect on quantitative trait variation (Dlugosch and Parker 2008; Lindholm et al. 2005) the true driving force behind adaptive potential. These findings suggest that assisted colonization is driving the spread of *G. affinis* within New Zealand. The manner of dispersal and the potential isolation of local populations are important factors for the management and control of this species on the North Island of New Zealand. Further analysis of the genetic structure and connectivity of this species is necessary before any clear management plan can be prescribed however, these findings could be increasingly important given the continued degradation of natural habitats and given the negative ecological implications of this species (Pyke 2005, 2008).

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