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Getting here from there: testing the genetic paradigm underpinning introduction histories and invasion success

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ABSTRACT

Aim To explore the potential of genetic processes and mating systems to influence successful plant invasions, we compared genetic diversity of the highly invasive tropical treelet, *Miconia calvescens,* in nine invasive populations and three native range populations. Specifically, we tested how genetic diversity is partitioned in native and invaded regions, which have different invasion histories (multiple vs. single introductions). Lastly, we infer how levels of inbreeding in different regions impact invasion success.

Location Invaded ranges in the Pacific (Hawaii, Tahiti, New Caledonia) and Australia and native range in Costa Rica.

Methods Genetic diversity was inferred by analysing variation at nine microsatellite loci in 273 individuals from 13 populations of *M. calvescens*. Genetic structure was assessed using AMOVA, isolation by distance (IBD) within regions, a Bayesian clustering approach, and principal coordinates analysis.

Results Microsatellite analysis revealed that invaded regions exhibit low levels of allelic richness and genetic diversity with few private alleles. To the contrary, in the native range, we observed high levels of allelic richness, high heterozygosity and 78% of all private alleles. Surprisingly, despite evident genetic bottlenecks in all invasive regions, similarly high levels of inbreeding were detected in both invasive and native ranges (F_{IS}: 0.345 and 0.399, respectively). Bayesian clustering analysis showed a lack of geographical structure in the Pacific and evidence of differing invasion histories between the Pacific and Australia. While Pacific populations are derived from a single introduction to the region, multiple introductions have taken place in Australia from different source regions.

Main conclusions Multiple introductions have not resulted in increased genetic diversity for *M. calvescens* invasions. Moreover, similar inbreeding levels between native and invaded ranges suggests that there is no correlation between levels of inbreeding and levels of standing genetic diversity for *M. calvescens.* Overall, our results show that neither inbreeding nor low genetic diversity is an impediment to invasion success.

Keywords

Genetic diversity, inbreeding, invasive species, *Miconia calvescens*, microsatellite.

INTRODUCTION

Biological invasions are one of the key factors that negatively impact global biodiversity (Ruesink *et al.*, 1995; Vitousek *et al.*, 1997), and invasion success is often believed to be the result of human-mediated dispersal (Drake *et al.*, 1989; Williamson, 1996; Vitousek *et al.*, 1997). Such dispersal often includes multiple introduction events (Durka *et al.*, 2005; Genton *et al.*, 2005; Marrs *et al.*, 2008) and provides a ready means for movement to take place between regions that have historically acted as barriers (Wilson *et al.*, 2009). These biogeographical shifts may include alterations to ecological and

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evolutionary processes and result in changes in species composition and dynamics at local, community and landscape scales (Lee, 2002; Prentis *et al.*, 2008).

Genetic diversity of invasive species in their new range is substantially altered through the introduction process, with new populations often demonstrating reduced genetic diversity compared with source populations (Barrett & Kohn, 1991). Nevertheless, similar levels of genetic diversity in the introduced range compared with the native range are often found (e.g. Durka *et al.*, 2005; Genton *et al.*, 2005; Marrs *et al.*, 2008; Ward *et al.*, 2008). Typically, higher genetic diversity in invasive populations is associated with multiple introductions, and it has been argued that such increased propagule pressure is a prerequisite for successful invasion (Barrett & Husband, 1990; Ellstrand & Schierenbeck, 2000; Pappert *et al.*, 2000; Sakai *et al.*, 2001; Gaskin & Schaal, 2002; Roman & Darling, 2007). Genetic variation might accumulate over the course of multiple introductions, especially when introductions occur from geographically isolated sources (Le Roux *et al.*, 2011), a phenomenon that is thought to play an important role in overcoming lag phases (Sakai *et al.*, 2001). Furthermore, subsequent admixture or intraspecific hybridization between previously allopatric genetic entities can significantly contribute to invasion success (Ellstrand & Schierenbeck, 2000).

In cases where inbreeding is present, its negative effects on fitness may be reduced in the face of range expansion (Pujol *et al.*, 2009). Overall, however, it appears that lower levels of inbreeding corresponds with increased genetic diversity, and that inbreeding depression may serve as one of the principal factors that regulate evolution of mating systems (Barrett, 2002; Lande & Schemske, 1985; Goodwille *et al.*, 2005). Self-incompatibility does not tend to pose a discernible problem for species persistence, although self-fertilization (Barrett, 2002) and asexual reproduction tend to increase at geographical limits (Peck *et al.*, 1998) or otherwise marginal habitats (Pujol *et al.*, 2009).

Comparing non-native populations with differing invasion histories over broad geographical ranges and making comparisons in both native and invaded ranges may provide insights to better understand genetic underpinnings of different introduction scenarios and subsequent invasion success, and while there is a growing literature addressing genetics around successful plant invasions, relatively few studies compare genetic diversity for tropical species in both the native and invasive regions (but see DeWalt & Hamrick, 2004). Furthermore, encountering a study system in which there is reasonable knowledge of the introduction history, as well as contrasting patterns of introduction can be challenging.

For the invasive small tree *Miconia calvescens*, we have good information regarding the time and pathways of such different introduction patterns across two invasion regions that span a broad geographical range (Australia and islands spanning *c.* 5000 km across the Pacific). Our objective was to better understand the patterns and processes involved in successful invasion and their consequences for genetic diversity and inbreeding. To do so, we apply population genetic approaches to compare differences in genetic diversity for this relatively long-lived tropical treelet that has become a pervasive invader and has exerted tremendous negative impacts on native biodiversity in tropical island forests (Meyer & Florence, 1996). We tested the paradigm of genetic diversity and introduction history while exploring the relationship between inbreeding and invasion success (sensu Fig. 1 in Le Roux *et al.*, 2011). We asked whether Pacific island populations of *M. calvescens* demonstrate similar levels of genetic diversity to Australian *M. calvescens* populations and compared introduction histories between these regions. We also include 'outgroup' native range populations to infer how genetic diversity has been affected during the colonization of *M. calvescens* in Australia and Pacific islands and to understand what influence this may have on invasion success. Overall, this work aims to provide insights into the processes shaping standing genetic diversity and the evolutionary potential of invasive species in general.

STUDY SPECIES AND INTRODUCTION HISTORY

Miconia calvescens (hereafter Miconia) is a fleshy fruited, small-seeded, treelet that ranges from 6 to 16 m tall and is native to Central and South America (Meyer, 1998) where it occurs in populations from 20 °N in Mexico, Panama and Costa Rica to 20 °S in Ecuador, Peru, Brazil and Argentina (Meyer, 1996). In the native range, it most frequently occurs in disturbed areas including secondary growth, pastures, along trails, rivers, and roads, or in light gaps in old growth forests, generally above 600 m in elevation (Meyer, 1996, 1998; Artavia-Mata, 2006). Miconia reaches sexual maturity and generally reproduces at 4–5 years of age. The fleshy berries (*c.* 6–7 mm in diameter) are purplish black at maturity and contain an average of 200 seeds (*c.* 0.65 mm diameter) (Meyer, 1998). Miconia attracts a large suite of vertebrate frugivores, mainly birds, who act as dispersal vectors (Westcott & Dennis, 2006; Spotswood, 2010). The distinct purple and green bi-coloured leaf morph for which Miconia is noted is restricted to populations in the northern part of the native range; invasive populations share this colour morphology. Self-fertilization has been shown to occur regularly in its introduced range in Tahiti, although trials to test whether apomixes occurs in Miconia were inconclusive (Meyer, 1998). Overall, the relative contribution of self-fertilization compared with out-crossing is not well understood.

Australia

Miconia was introduced in Queensland to the Townsville Botanic Gardens in 1963 and is thought to have originated from Sri Lanka via Miconia plants that originated from Mexico (Csurhes, 1998). Its spread in the Wet Tropics Region has been facilitated by plant nurseries and accidental escape. To date, more than 40 naturalized populations have been recorded in North Queensland (Brooks & Jeffery, 2010), and the earliest recorded plants at the largest infestation are believed to have

arrived *c.* 30 years ago. Known populations range in size from just a few individuals to several thousand plants and plants are separated by several to tens of kilometres from other known populations. All known populations are undergoing active removal as Miconia is a declared Class 1 weed under the Queensland Land Protection (Pest & Stock Route Management) Act 2002 and the species is the target of nationally cost-shared eradication programme.

Pacific Islands

Miconia was introduced to Tahiti in 1937, and since then, the species has spread to over 70% of the island's forested lands, forming dense monotypic stands in large areas (Meyer & Florence, 1996). From here, Miconia has spread to and has become established in many of the major French Polynesian high volcanic islands (Moorea, Raiatea, Tahaa, Nuku Hiva and Fatu Hiva). Miconia was introduced to the Northern Pacific *c.* 24 years later (1961) to the Hawaiian Islands of Hawaii and Oahu and secondarily to Maui in the early 1970s as a popular ornamental (Medeiros *et al.*, 1997; Le Roux *et al.*, 2008). Miconia was introduced to New Caledonia in the 1970s in a private botanic garden near Noumea (province Sud) and has since naturalized (Goarant & Meyer, 2010). In Hawaii, Miconia does not form stands of the same density as occur in Tahiti (Le Roux *et al.*, 2008), though it forms much higher density populations than in Australia (B.D. Hardesty, pers. obs.). Aggressive containment and eradication efforts against Miconia in Hawaii have presumably slowed or restricted the species from forming monotypic stands as it has been carried out in Tahiti. The potential role of lag phase and differences in introduction times in patterns of invasiveness between populations across Pacific islands has been documented (Le Roux *et al.*, 2008) but in Australia is not well understood.

MATERIALS AND METHODS

Population sampling and DNA extraction

Thirteen *M. calvescens* populations were sampled from invaded ranges in the northern Pacific Hawaiian Islands, southern Pacific Society Islands, New Caledonia, Australia and its native range in Costa Rica (Fig. 1, Table 1). For each population, leaf material from 10 to 30 individual plants was collected (total $N = 273$ individuals), although data are reported only for those samples where DNA extraction and subsequent fragment analyses were successful. Wherever possible, samples were collected from adult plants at least 25 m apart. Plant material was placed and dehydrated in sealed plastic pouches containing Drierite™ (W.A. Hammond Drierite Co. Ltd., Xenia Ohio, USA) or silica. Locality name, region, and latitude and longitude were recorded for populations sampled (Table 1).

Total genomic DNA was extracted according to the manufacturer's protocol with the mini or 96 DNeasy Plant Kit (Qiagen, Qiagen Pte Ltd., Germantown, MD, USA) from 40 to 50 mg leaf material that was frozen in liquid nitrogen. All extractions were stored at −80 °C.

Microsatellite analysis

We used the nine microsatellite loci MicB9, MicD101, MicC103, MicB109, MicD114, MicB102(a), MicB2, MicD118 and MicB117. Details concerning the isolation, characterization, and internal repeat structure of the loci can be found in Le Roux & Wieczorek (2008). Polymerase chain reaction (PCR) amplification of loci was performed in 10 μL volumes with the Multiplex PCR Kit (Qiagen) by combining primer pairs into multiplex reactions following Le Roux *et al.* (2008). Polymorphisms were screened using an ABI PRISM 377XL DNA sequencer (PE Applied Biosystems, Foster City, Califor-

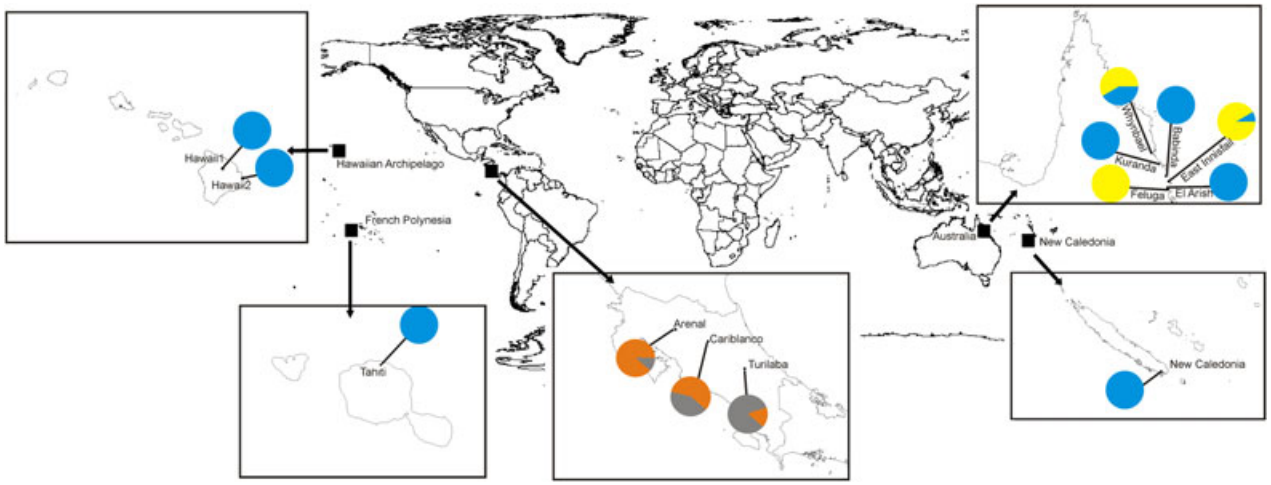

Figure 1 Map illustrating the global distributions of native and invasive populations of *Miconia calvescens* sampled in this study. Colour coded pie charts indicate the proportion of individuals within each population that corresponds to a particular STRUCTURE-identified genetic deme (see Fig. 4 for details). Deme membership was assigned when 80% or more of an individual's genome belonged to that particular deme.

Table 1 Location and population genetic parameters for each of the sampled native and invasive populations.

Region	Site	Lat	Long	N	N_A (avg)	N_{PA}	H_O	H_E	F_{IS}
Pacific	Hawaii1	19.81	−155.45	30	14 (1.6)	2	0.016	0.027	0.56
	Hawaii2	19.58	−154.52	27	18 (2.0)	3	0.067	0.102	0.36
	Tahiti	−17.52	−149.44	24	18 (2.0)	2	0.061	0.077	0.24
	New Caledonia	−22.30	166.79	23	22 (2.4)	2	0.079	0.101	0.25
Australia	Babinda	−17.33	145.92	21	26 (2.9)	0	0.048	0.012	0.63
	E. Innisfail	−17.54	146.03	11	15 (1.7)	0	0.062	0.101	0.43
	El Arish	−17.81	145.98	23	11 (1.2)	0	0.005	0.015	0.70
	Feluga	−17.89	146.01	8	11 (1.2)	0	0.083	0.076	−0.02
	Kuranda	−16.83	145.64	26	9 (1.0)	0	0.000	0.000	NA
	Whyanbeel	−16.37	145.32	24	21 (2.3)	2	0.082	0.144	0.45
Costa Rica	Cariblanco	10.27	−84.17	38	86 (9.6)	22	0.422	0.624	0.34
	Arenal	10.48	−84.74	9	28 (3.1)	3	0.198	0.325	0.46
	Turrialba	9.79	−83.53	9	50 (5.6)	10	0.650	0.767	0.24
Overall				273		46	0.136	0.182	0.39

N, number of individuals sampled; N_A (avg), average number of alleles; N_{PA}, number of private alleles; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient.

nia, USA), and PCR products were sized relative to a molecular size marker (LIZ500; PE Applied Biosystems). DNA fragments were analysed using the program GeneMarker version 1.4 (SoftGenetics, LLC, State College, PA, USA).

Statistical analysis

Within-and among-population genetic diversity

The number of alleles (N_A), private alleles (N_{PA}), pairwise F_{ST}, observed heterozygosities (H_O) and expected heterozygosities (H_E) were calculated for each population using GenAlEx6 (Peakall & Smouse, 2006). We calculated inbreeding coefficients (F_{IS}) for each population and region using FSTAT293 (Goudet, 1995).

A Mantel test with 1000 permutations was conducted to determine the relationship between geographical distance and genetic differentiation between populations $[F_{ST}/(1 - F_{ST})]$ as proposed by Rousset (1997) and implemented using the ISOLDE feature of Genepop (Rousset, 2008). The matrix of pairwise F_{ST} values was regressed against a matrix of geographical distances separately for the native region and each of the two invaded regions. Pairwise values of F_{ST} were calculated using GenAlEx6 (Peakall & Smouse, 2006).

All populations were used in an analysis of molecular variance (amova, Excoffier *et al.*, 1992) to examine the distribution of genetic variation at three hierarchical levels: within populations, among populations within invaded and native regions, and among invaded and native regions. The significance is determined by comparison with a null distribution derived from permuting haplotypes, individuals or populations at the appropriate hierarchical level (Excoffier *et al.*, 1992). Overall, statistical comparisons of several genetic diversity indices [observed heterozygosities (H_O), gene diversities (H_s) and inbreeding coefficients (F_{IS})] between native and introduced regions *and* different introduced regions (Australia vs. Pacific) were performed with FSTAT293 (Goudet, 1995). Finally, pairwise individual genetic distances and F_{ST} values were used separately in a Principle Coordinate Analysis (PCoA) to examine the genetic clustering of individuals and populations from native and introduced ranges respectively using GenAlEx6 (Peakall & Smouse, 2006).

Bayesian estimates of population structure

A Bayesian clustering assignment approach was used to assess the population structure among invasive populations throughout the Pacific and Australia and native populations from Costa Rica and to estimate the geographical scale of population differentiation, as implemented in structure version 2.2 (Falush *et al.*, 2007). When analysing these results, we applied the ΔK method (Evanno *et al.*, 2005) to infer the number of genetic clusters (K) contained in our sample. As this method only detects the uppermost level of genetic structure, we used a hierarchical approach to detect all layers of genetic substructure (sensu Coulon *et al.*, 2008). Using the options to ignore population affiliation when defining genetic clusters, assuming independence among loci, and allowing admixture, five independent runs of 100,000 iterations were run, following a burn-in period of 10,000, for each value of K (Pritchard *et al.*, 2000). We estimated whether the true value of K fell between 1 and 8 for each level of analysis.

RESULTS

Microsatellite genetic diversity

Within-population genetic diversity

In the nine microsatellite loci analysed, a total of 97 alleles were identified, an average of 10.8 alleles per locus. The number of alleles per locus ranged from 5 (locus D114) to 16 [locus

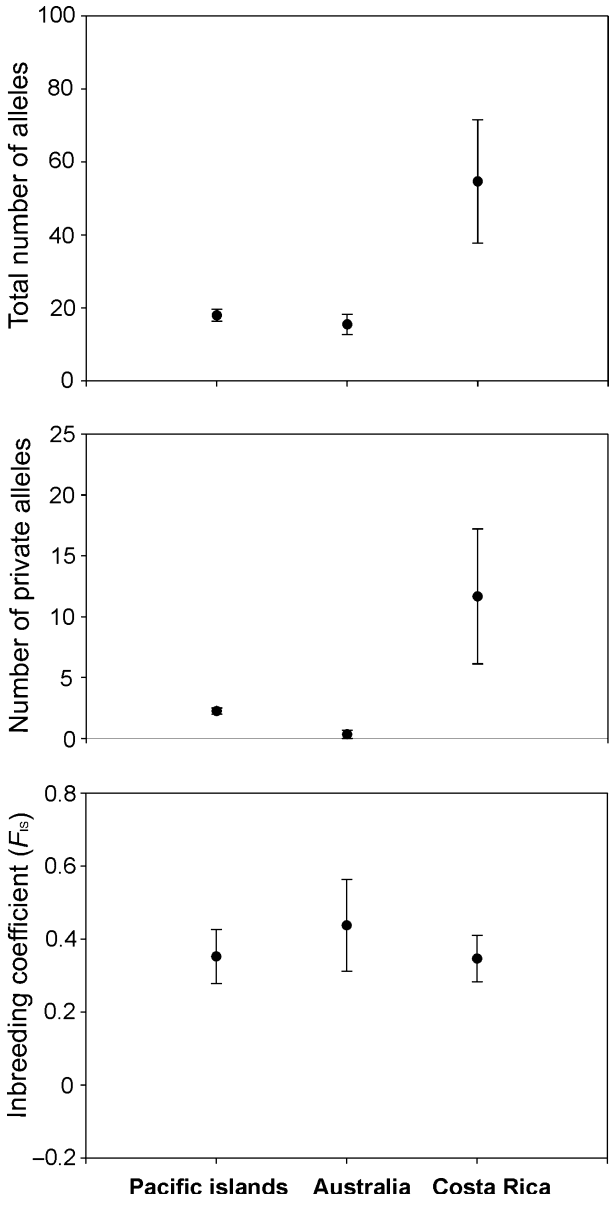

Figure 2 Graphs showing mean (±SE) of genetic diversity indexes [number of alleles (top), private alleles (middle), inbreeding coefficient (bottom)] for invasive Pacific island and Australian and native Costa Rican populations of *Miconia calvescens*.

B102(a)]; within populations, the mean number of alleles ranged from 9 to 86 (Table 1). The large differences in mean number of alleles observed here were mainly because of differences between invasive populations (Average N_A: 16.5) and native populations (Average N_A: 54.7) (Fig. 2). A total of 46 private alleles were observed ranging from 0 to 22 per population, again with the majority residing within native populations (Average N_{PA}: 11.7) rather than invasive populations (Average N_{PA}: 1.1) (Fig. 2).

Overall, expected heterozygosities ranged from 1.2% to 76.7%, with a mean of 18.2% across all loci. Observed heterozygosity ranged from 0.0% (Kuranda) to 65% (Turrialba), with a mean of 13.6% across all loci. All but three

Table 2 (a) Statistical comparison of allelic richness (R_S), unbiased gene diversity (H_S), observed heterozygosity (H_O), and inbreeding coefficient (F_{IS}) for (a) native and invasive regions and (b) Pacific vs. Australia populations of *Miconia calvescens*.

	R_S*	H_S**	H_O**	F_{IS}
(a)				
Native	2.477	0.627	0.418	0.333
Invasive	1.143	0.068	0.043	0.370
	R_S	H_S	H_O	F_{IS}
(b)				
Pacific	1.217	0.101	0.069	0.317
Australia	1.157	0.075	0.039	0.476

*$P < 0.001$, **$P < 0.05$.

Australian populations showed lower observed heterozygosity than expected: at Babinda observed heterozygosity was notably higher than expected; at Feluga, it was only slightly higher, and at Kuranda, the population was fixed across all loci. Inbreeding coefficients were generally high (Average F_{IS}: 0.39), ranging from −0.02 to 0.70. Excluding the Feluga population, (F_{IS} = −0.02), all other populations showed F_{IS} values higher than 0.24.

While we observed significant differences between allelic richness, unbiased gene diversity and observed heterozygosity between the native and invasive regions, there was no significant difference in inbreeding coefficient between them (Table 2a). When comparing Australia and Pacific populations, we found no significant differences between allelic richness, gene diversity, heterozygosity and inbreeding coefficient (Table 2b), which may be expected given there are similar times since introduction in the two regions (except in Tahiti where Miconia was introduced earlier).

Among-population genetic diversity

Pairwise F_{ST} ranged from extremely low, 0.012 between populations from New Caledonia and Australia (Babinda), to very high, 0.5 between different populations within Australia (Feluga and Kuranda) (Table 3). Overall, these values represent a wide range of differences for population genetic divergence. Furthermore, we detected no significant isolation by distance (IBD) between populations in either of the two invaded regions. In Costa Rica, however, a significant IBD effect was detected ($P < 0.02$).

Genetic distances were also used in a PCoA to investigate the relative position of individuals and populations in multidimensional space. The first two principle coordinate (PCoA) axes explained 63.7% and 18.0% of the genetic variation among individuals respectively, for a total of 81.7% (Fig. 3a). Two distinct genetic clusters were resolved corresponding to one cluster comprised of all native range individuals from Costa Rica and a few individuals from the Australian Feluga and East Innisfail populations: a second cluster was comprised

Table 3 Genetic structure in *Miconia calvescens* in its invasive and native ranges based on microsatellite data, given as pairwise F_{ST} values between populations (below the line).

	Hawaii1	Hawaii2	Tahiti	New Cal	Babinda	East Innis	El Arish	Feluga	Kuranda	Whyanbeel	Cariblanco	Arenal	Turrialba
Hawaii1	–	59	4203	6224	7616	7618	7637	7640	7615	7619	7678	7612	7761
Hawaii2	0.026	–	4168	6240	7649	7651	7670	7673	7648	7653	7628	7651	7711
Tahiti	0.017	0.023	–	4591	6820	6804	6806	6800	6861	6904	7805	7757	7849
New Cal	0.018	0.022	0.017	–	2249	2231	2228	2223	2296	2345	12,380	12,330	12,430
Babinda	0.020	0.024	0.014	0.012	–	26	53	62	64	125	14,560	14,510	14,620
East Innis	0.132	0.115	0.118	0.090	0.074	–	30	39	90	151	14,550	14,500	14,610
El Arish	0.014	0.034	0.020	0.022	0.021	0.178	–	10	115	174	14,560	14,500	14,650
Feluga	0.199	0.194	0.174	0.125	0.110	0.094	0.261	–	124	184	14,550	14,500	14,610
Kuranda	0.013	0.044	0.028	0.027	0.027	0.238	0.018	0.504	–	61	14,630	14,570	14,690
Whyanbeel	0.066	0.072	0.071	0.056	0.045	0.049	0.082	0.041	0.086	–	14,626	14,571	14,683
Cariblanco	0.239	0.211	0.220	0.208	0.195	0.171	0.245	0.179	0.252	0.167	–	66	88
Arenal	0.283	0.264	0.267	0.236	0.222	0.222	0.286	0.246	0.295	0.222	0.071	–	153
Turrialba	0.352	0.317	0.325	0.315	0.304	0.315	0.358	0.333	0.366	0.299	0.107	0.195	–

Pairwise geographical distance between sites (km) is shown above the line.

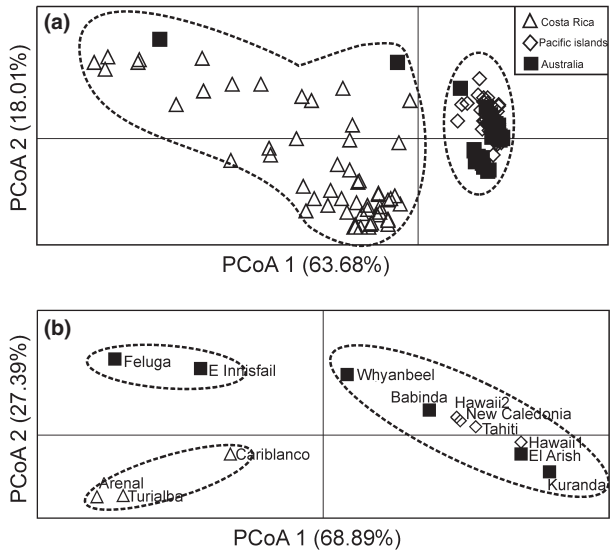

Figure 3 Biplots of the first two axes of a principle coordinate analysis of genetic variation for nine microsatellite loci showing (a) the first two axes for individuals and (b) the first two axes for populations. Hashed lines are drawn around apparent groupings.

of individuals from the remaining Australian and Pacific populations. When considering populations, the first two principle coordinate (PCoA) axes explained 68.9% and 27.4% of the genetic variation for a total of 96.3%. Biplots of these show high geographical structure between invasive and native populations (Fig. 3b) with three distinct clusters: Costa Rican populations, Australian populations (Feluga and East Innisfail) and the rest of the invasive populations from Australia and throughout the Pacific.

The hierarchical AMOVA based on sampled populations revealed that the majority of genetic variation (57.0%) resided among native and invasive regions, while 7.0% was distributed among populations within regions, and 36.0% of the variation resided within individual populations. While the fixation index among populations within the regions is much lower than at the two other levels, at each level differences were statistically significant.

Bayesian estimates of population structure

Following the method of Evanno *et al.* (2005), the model-based clustering method implemented in STRUCTURE (Falush *et al.*, 2007) identified two hierarchical levels of subdivision (summarized in Figs 4 & S1, Supporting Information). The first level of analysis delineated two genetic clusters ($K = 2$): the native Costa Rican range (Cariblanco, Arenal and Turrialba) and the invaded range (Pacific and Australian regions). The AMOVA results indicated that most of the variation (57.0%) could be explained by differences among these regions and is thus in support of the initial clustering by STRUCTURE. These clusters, native and invasive, were incorporated into subsequent separate sublevel assignment analysis. This second level of analysis of invasive populations identified two distinct genetic clusters within the invasive range. First, a single Pacific cluster (as identified in Le Roux *et al.*, 2008) harboured some individuals (from Whyanbeel) and some entire Australian populations (Babinda, El Arish and Kuranda). Second, an Australian-only cluster encompassed two populations (East Innisfail and Feluga) and the remainder of individuals from the Whyanbeel population. These results are supported by the population-level PCoA analysis that identified the same three clusters, with Whyanbeel in between the Pacific and Australian-only cluster (Fig. 3a,b). The second level of analysis of native populations identified two distinct genetic clusters within Costa Rica. Overall, the first cluster corresponded to Arenal, while the second corresponded to Turrialba. Cariblanco is geographically midway between Arenal and Turrialba and appeared to be mixed/admixed for these two clusters (Fig. 1). These findings suggest that IBD

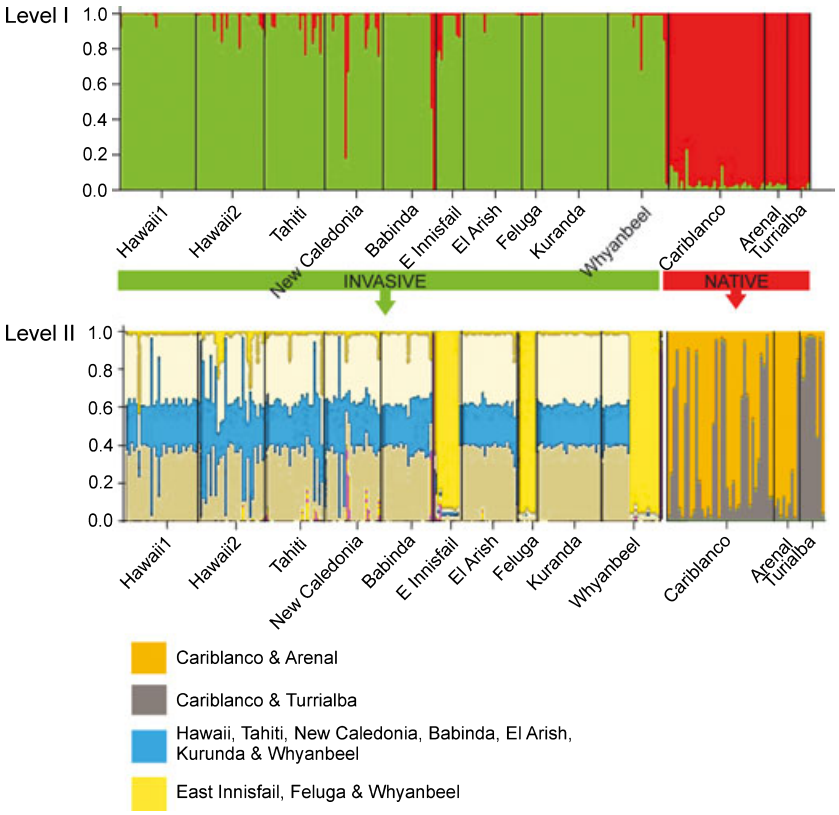

Figure 4 Structure Q plots representing hierarchical analysis to estimate the number of genetic clusters (K). The plot for each of the three analyses was generated using the value of K associated with ΔK_{max} (see Fig S1 for details). Each individual included in an analysis is represented by a vertical bar indicating its individual membership coefficients. Colour codes at bottom of figure are those used in Fig. 1 to illustrate the geographical distribution of the four distinct genetic demes.

may explain the genetic differentiation between Costa Rican populations.

DISCUSSION

The importance of the number of independent introductions or source populations in shaping levels of genetic variation of invasive species within their new range has been noted (Sakai *et al.*, 2001; Dlugosch & Parker, 2008; Wilson *et al.*, 2009; Le Roux *et al.*, 2011). In general, higher genetic diversity is associated with multiple introductions. However, few studies have compared the genetic diversity of tropical woody species in both native and introduced ranges (but see DeWalt & Hamrick, 2004).

Miconia calvescens is highly inbred and genetically depauperate throughout populations sampled across its invasive range. Our findings indicate that Costa Rican populations have, on average, over three times more alleles than populations in the invasive range. In addition, most invasive populations showed lower heterozygosity than expected and high levels of inbreeding, suggesting that Miconia may have experienced severe bottlenecks in its introduced range. Surprisingly though, similarly high levels of inbreeding were also observed among the genetically diverse Costa Rican populations.

Invasive Miconia populations in the Pacific Region (Hawaii, Tahiti, and New Caledonia) and Australia appear to represent independent colonization events. Low genetic diversity and differentiation among Pacific island populations suggest a single source of introduction, which is consistent with the known historical evidence of introduction to the Pacific region (discussed in Meyer, 1996; Le Roux *et al.*, 2008). Indeed, Hawaiian Islands and New Caledonian populations are thought to be of Tahitian origin according to historical (Goarant & Meyer, 2010) and molecular data (Le Roux *et al.*, 2008; Figs 1, 2 & 4). In contrast, we show genetic evidence for multiple introductions to Australia, with some populations demonstrating genotypes consistent with a Pacific islands source, while for other populations, the source of introduction is unclear. Interestingly, one Australian population (Whyanbeel) harboured individuals from both of these independent sources (Fig. 4) but without admixture occurring, indicative of restricted gene flow/outcrossing. Limited outcrossing is further supported by (1) consistent genetic variation between the sampled populations in the Pacific, regardless of the number of reproductive individuals and population size in the area (also see Le Roux *et al.*, 2008) and (2) the overall lack of congruence between geographical and genetic distance within invasive Australasian populations. For example, we observe high F_{ST} values between geographically close populations (Feluga and Kuranda, $F_{ST} = 0.54$), and low levels of genetic differentiation between the geographically distant populations from New Caledonia and Babinda ($F_{ST} = 0.012$).

Inbreeding is expected to occur during the invasion process, particularly for invasions typified by excessive selfing and/or few founding individuals such as for Miconia. In this scenario, the negative effects of inbreeding depression might be expected to retard population growth and range expansion. Our results

show that Miconia populations experience high levels of inbreeding not only in their invasive range (average $F_{IS} = 0.33$) but also in the native range ($F_{IS} = 0.37$), in spite of the fact that surveyed populations in Costa Rica are not particularly disturbed, do not occur in marginal habitats and have high levels of standing genetic diversity. Multiple aspects of the reproductive biology of Miconia in its native range make such high inbreeding unexpected. First, Miconia trees in Costa Rica flower in a synchronous manner within populations. Phenological observations indicate that Miconia trees flower once a year in a short episode that typically starts in November and ends in Mid December. Such synchronized flowering should promote xenogamy (A. Araya-Anchetta and O. Rocha, Kent State University, unpublished data). In contrast, Miconia may reproduce up to three times per year in Tahiti, and at least twice annually in both Australia and Hawaii. Second, Miconia are primarily pollinated by bees and some tropical bees are capable of foraging long distances (Dick *et al.*, 2003). Also, at least in Costa Rica, not many other species flower when Miconia is flowering, and many generalist bee pollinators are likely to be limited to visiting only flowering Miconia (A. Araya-Anchetta and O. Rocha, unpublished data). However, we are also aware that low Miconia density in the native range may limit inter-tree pollinator movement, thus reducing the likelihood of outcrossing.

Overall, the low population density and flowering behaviour observed in Miconia may also favour self-reproduction in the native range. Flowering phenology in this species can be characterized as mass flowering, where individual trees produce a large number of flowers over a relatively short period of time. This may prevent generalist pollinators from moving between distant Miconia trees and may result in high levels of geitonogamy. Moreover, Miconia trees in Costa Rica are also capable of producing fruits in the absence of pollinators, further support that self pollination may occur widely (A. Araya-Anchetta and O. Rocha, unpublished data). However, fruits produced in the absence of pollinators bear fewer seeds, produce seeds that are less likely to germinate, and require more time to germinate than seeds produced with open-pollination (A. Araya-Anchetta and O. Rocha, unpublished data). The observed levels of inbreeding and the ability to produce seeds even in the absence of pollinators suggest that highly deleterious alleles may be kept at low frequencies in their native range and that levels of inbreeding depression are in fact low.

Given that new populations are generally derived from one or few individuals, the relatively short time since introduction, and Miconia's ability to self pollinate, we expect reduced genetic diversity and associated high levels of inbreeding. In Australia, new populations are still regularly discovered in the Wet Tropics Region with single or a few seedling plants found in local gardens, to larger populations with a more widespread spatial distribution, despite an active eradication programme (Brooks & Jeffery 2010; Hardesty *et al.* 2010). Here, Miconia is likely to be widely consumed and dispersed long distances by frugivorous birds (Westcott & Dennis, 2006; Murphy *et al.*, 2008) and we find new plants long distances from any known reproductive adult. Taken together, this information and our current data suggest that outlying clusters and new populations may readily result from a single propagule (also see Le Roux *et al.*, 2008).

In addition to long distance dispersal by frugivores, large-scale disturbances such as cyclones can also affect invasion spread. In Tahiti, where cyclones occur frequently, we see Miconia occurring in much higher density than it does in the Hawaiian Islands where there are fewer such events. However, in Australia where cyclones also regularly occur, we do not see Miconia densities similar to those observed in Tahiti, which may be partially because of time since introduction. After a recent cyclone disturbance in Australia there may have been a temporary surge in Miconia recruitment; however, 35% of seedling recruits experienced mortality within 15 months (Murphy and Brooks 2009). Furthermore, dense monocultures of larger Miconia plants are not yet encountered in the Australian invaded range for *M. calvescens* (Brooks & Jeffery, 2010) or for the closely related *M. nervosa* and *M. racemosa* that have also invaded in Australia and co-occur with *M. calvescens* there (Hardesty *et al.* 2011).

In contrast to its density in invaded regions, Miconia does not form monocultures or dense stands in its native range (Meyer, 1996; B.D. Hardesty, pers. obs.). While genetic load can result in sterility or near sterility in some plant populations (Weins *et al.*, 1989), this is clearly not the case for Miconia, as populations are persistent and spread readily, particularly where eradication or containment efforts fail. It is difficult to measure or estimate the impact of inbreeding depression on growth or spread; however, it appears that high levels of inbreeding in Miconia throughout novel ranges result in no impediment to invasion success. The species can reach maturity in 4–7 years, it produces tremendous seed crops, it persists in both high and low light environments and the seeds are readily dispersed by a wide array of frugivores – all key factors that contribute to its success as an invader.

Because of the tremendous economic and biodiversity impact of Miconia, a biological control programme was initiated in the Pacific islands of Hawaii and French Polynesia nearly 15 years ago. Careful consideration of biocontrol agents is needed so that effective management decisions can be made with minimum impact to biodiversity. To date, this long-standing effort has failed to find suitable pest agents that control Miconia populations, although testing continues (R. Barreto, Universidade Federal de Vicosa, pers. comm.). Perhaps this is because control efforts have focused on native Miconia from Brazil and Costa Rica (Picanço *et al.*, 2005), which appears, for Costa Rican populations at least, not to be the geographical source for populations that have successfully invaded multiple regions. Moreover, discussion has recently opened as to the certainty of whether the Miconia used for biocontrol agent testing in Brazil is in fact the same species of Miconia that has been such a successful invader in the Pacific and Australia (R. Barreto, pers. comm.) and that occurs across Mexico and Central America. DNA barcoding and other genetic methods may be an important first step to ascertain

species and population level suitability for biological control purposes, as control agents may not be ubiquitous across a broad geographical range such as that across which Miconia occurs.

Our findings do not fit the generally accepted paradigm that multiple introductions from multiple, genetically diverse sources facilitate invasion success by increasing genetic diversity and genetic novelty, thereby reducing the effects of inbreeding (Bossdorf *et al.*, 2005; Lavergne & Molofsky, 2007). It is also generally assumed in the invasion literature that high genetic diversity always corresponds to low inbreeding and *vice versa* but, again, here we illustrate that this is not always true but may be very dependent on species life-history traits (Schoen & Brown, 1991). Logistical and monetary considerations often preclude the inclusion of native *and* invasive samples for comparative genetic studies. However, such comparisons are necessary in order to reliably disentangle the processes shaping genetic diversity and its distribution in invaded populations. Without data from the native range, one may have concluded that inbreeding levels were solely a consequence of existing low levels of genetic diversity in invaded regions. Studies such as ours demonstrate that other factors such as pollinator behaviour and phenology may better explain the observed patterns and point to the importance of including native range sampling to compare to invaded regions.

Ideally, future studies would have greater native range sampling and incorporate additional information about the population ecology in both native and invaded environments. Testing the potential survivorship of different genotypes in novel environments could also provide useful insights into invasiveness. Such further explorations will help to not only understand pathways to invasion and likelihood of success, but also identify potential impacts to local biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Mean rate of change in the model choice criterion, $L(K)$, and ΔK a predictor of the number of clusters K at each of the three scales of sampling; (a) across all sampled populations, (Level I, Fig. 4), (b) invasive range only (Level II, Fig. 4), and, (c) native range only, (Level II, Fig. 4).

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BIOSKETCHES

Britta Denise Hardesty is a research scientist at the Commonwealth Scientific and Industrial Research Organization in Australia and **Johannes J. Le Roux** is a lecturer at the Centre for Excellence in Invasion Biology at Stellenbosch University in South Africa. They are both molecular ecologists whose research interests include understanding underlying causes and consequences of plant invasion. Author contributions: B.D.H. and J.J.L.R. conceived the ideas, collected and analysed the data and led the writing. O.R. and J.-Y.M. supplied data and assisted with writing, A.W. and D.W. provided support and writing input. B.D.H. and J.J.L.R. are both molecular ecologists whose research interests include understanding underlying causes and consequences of plant invasion.

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