High Genetic Diversity Despite the Potential for Stepping-Stone Colonizations in an Invasive Species of Gecko on Moorea, French Polynesia

Maria A. Tonione1*, Natalie Reeder2, Craig C. Moritz1

1 Museum of Vertebrate Zoology, University of California, Berkeley, California, United States of America, 2 Department of Biology, San Francisco State University, San Francisco, California, United States of America

Abstract

Invasive species often have reduced genetic diversity, but the opposite can be true if there have been multiple introductions and genetic admixture. Reduced diversity is most likely soon after establishment, in remote locations, when there is lower propagule pressure and with stepping-stone colonizations. The common house gecko (Hemidactylus frenatus) was introduced to Moorea, French Polynesia in the remote eastern Pacific within the last two decades and accordingly is expected to exhibit low diversity. In contrast, we show that H. frenatus on Moorea has exceptionally high genetic diversity, similar to that near the native range in Asia and much higher than reported for other Pacific island reptiles. The high diversity in this recently founded population likely reflects extensive genetic admixture in source population(s) and a life history that promotes retention of diversity. These observations point to the importance of understanding range-wide dynamics of genetic admixture in highly invasive species.

Introduction

Among the most important causes of native-species extinctions is interaction with invasive species [1]. Considerable effort has been expended on genetic analyses of invasive species to infer invasion history, the dynamics of genetic diversity, and how this might contribute to potential to adapt to and thrive within non-native habitats [2]–[4]. On one hand, recently introduced populations might have reduced diversity due to founder events [5]–[7], in which case their evident ability to adapt and spread represents something of a paradox [8]. Alternatively, multiple introductions involving divergent source populations can increase genetic diversity in invasive populations and promote evolutionary flexibility and the rate of spread [9]–[13]. The latter outcome depends on high propagule pressure (i.e. geographic proximity to diverse source populations and/or location on transport routes; [14]) and often takes time to develop [3], [9]. The former outcome, reduced diversity, is more probable in recently colonized and geographically remote locations, especially if there have been sequential founder events associated with a stepping-stone colonization process (e.g. [15]–[18]).

The islands of French Polynesia are among the most remote in the world and have a disharmonic biota derived by a mix of natural stepping-stone colonization from the western Pacific, natural colonizations from the east, and subsequent radiations, all overlain by recent human introductions [19]. The depauperate reptile fauna is dominated by species of geckos (including parthenogenetic species) and skinks, which colonized naturally (e.g. possibly Gehyra oceania, [20]) or as commensals in association with Polynesian migration [21]. A characteristic feature of these lizards, associated with evolutionarily recent and presumably stepping-stone colonizations, is genetic uniformity from the islands of the western Pacific to French Polynesia [20], [22]–[24]. Human-mediated introductions continue, the most recent invader, the Gold Dust Day Gecko (Phelsuma laticauda), being recorded on the island for the first time in 2006 [25].

The focus of the present study, the Common House Gecko Hemidactylus frenatus, is a prime example of an invasive species with demonstrated effects on native reptile faunas [26]–[28]. The native range of H. frenatus is uncertain. Recent studies have suggested a south Asian origin, although it may be that Indian and Sri Lankan lineages represent a different species from that in Myanmar and eastwards, as well as the invasive range of H. frenatus [29], [30]. Wherever in south Asia it originated, H. frenatus is now circumtropical, mostly as a human commensal, on both continents and islands. Invasion of the western tropical Pacific was assumed to have commenced some 4000 years ago with the early Polynesian and Melanesian migration, and continued with H. frenatus spreading as a stowaway on shipping and cargo boats [26], [28]. Since the mid 20th century, H. frenatus has spread through the eastern Pacific beginning in Hawaii in 1951, then Fiji in 1960 and Vanuatu in the 1970s–1980s [26]. Across the tropical Pacific, H. frenatus is largely restricted to human structures [26], [28], but has also been found in low numbers invading natural habitat as well (e.g. [27], [28], [31]). H. frenatus was first reported in French Polynesia in 1989 [21] and was not present on the adjacent island
Successful Invasion and Establishment

of Moorea in late 1980’s (C. Moritz, pers. obs., R. Fisher pers. comm.; [32]). From this we can conclude H. frenatus has been on Moorea for at most 22 years (∼20 generations).

Given the evident recent colonization, geographic remoteness, the likelihood of stepping-stone introductions, and also the low diversity observed in other species of lizards from the region, we expected H. frenatus on Moorea to have low genetic diversity, which would restrict their capacity to adapt to non-commensal environments. Alternatively, as preliminary analyses of this species on western Pacific islands revealed unexpectedly high mtDNA diversity [24], it is possible that the recently established Moorea population could have substantial diversity as a consequence of originating from an already admixed invasive population, although even here we would expect somewhat lower diversity due to sequential founder events. We test these alternative hypotheses by comparing genetic diversity on Moorea to that in south-east Asia (Myanmar and Indonesia), in or near the presumed native range. We also document the spread of H. frenatus on Moorea.

Results

Distribution on Moorea

Since its arrival no more than 22 years ago, H. frenatus has dispersed to occupy dwellings and other man-made structures in high numbers around the entire perimeter of the island; in contrast, no individuals of this highly conspicuous species were detected in repeated surveys of the interior forest (Fig. 1A). Lepidodactylus lugubris, previously common on buildings [32], and Gehyra oceanica common in interior forest but also found on buildings, are now rare relative to H. frenatus (Table S1).

Mitochondrial DNA

H. frenatus from Moorea (n = 21 samples) has highly diverse mtDNA, comparable to the variation observed across south-east Asia. There are 2 major groups (group 1 and group 2; Fig. 2A) and can be further divided into 4 subgroups (group 2a, 2b, 2c, 2d; Fig. 2A). The recently invaded Moorea population has three highly divergent haplotypes (group 1, 2a, 2d; Fig. 2A), each of which is closely related to those from Myanmar (Fig. 2A, mean Dxy among groups (%) = 7.3). Samples from the Indonesian islands, closer to the presumed native mainland range, are represented in each of the two major mtDNA groups, and again are closely related to haplotypes from Myanmar (Fig. 2A). The diversity within Moorea (θe = 0.043±0.022) is similar to that across all of Myanmar (θe = 0.035±0.019) and greater than found in our geographically dispersed samples in Indonesia (θe = 0.019±0.010; Table 1). Though not significant, estimates of Tajima’s D for both Myanmar and Moorea were positive (1.14 and 1.86 respectively), i.e. in the direction expected with recent admixture. Curiously, despite high overall diversity within Myanmar, there is little obvious phylogeographic structure within this region, with the two major mtDNA groups having broad and overlapping distributions (Fig. S1). Net sequence divergences (Dxy) between regions were relatively low, ranging from 0.39–1.24% (Table 1). Samples from Moorea and Myanmar showed no significant genetic divergence, whereas those from the Indonesian sample were significantly divergent from both Myanmar and Moorea (Fst = 0.27 and 0.25 respectively, p<0.001; Table 1).

To enable comparison with published data from India and elsewhere, we sequenced representatives of each major lineage for the 12S rDNA gene. The major groups observed across Myanmar, Indonesia, and Moorea cluster with those from elsewhere in the introduced range (Columbia, Hawai, Papua New Guinea, and China; [33]–[35]), and are highly divergent from the Indian haplotypes ([29], [30]; Fig. S2).

Nuclear DNA

We obtained sequence data for three nuclear loci from nearly all individuals and, again, the Moorea population had high diversity (Figs. 2B, S3; Table 1). As for mtDNA, multi-locus nDNA sequence diversity within Moorea (θe = 0.016±0.008) is on par with that across Myanmar (θe = 0.022±0.01) and higher than that in Indonesia (0.014±0.007). Population differentiation at the nuclear level was significant (p<0.001) for every pair of populations by country (Table 1; for information on individual nuclear loci see Table S2 and Fig. S3). However, assignment of

Figure 1. Sampled localities in Southeast Asia and on Moorea. (A) Map of Moorea showing H. frenatus localities sampled (open circles). localities H. frenatus was seen but not sampled (asterisks) and localities no H. frenatus was found (triangles). (B) Sampled localities in Southeast Asia. Black circles represent individuals from Myanmar; gray circles represent individuals from Indonesia. Inset: Map of the world; arrow pointing to approximate locality of Moorea.
doi:10.1371/journal.pone.0026874.g001
individuals to genetic groups using STRUCTURE did not reveal any coherent population structure at either K = 2 or K = 3 (Fig. S4). As a preliminary test for cyto-nuclear disequilibrium, we also tested for nDNA divergence between the two major mtDNA groups in a preliminary test for cyto-nuclear disequilibrium, we also tested for coherent population structure at either K = 2 or K = 3 (Fig. S4). As a preliminary test for cyto-nuclear disequilibrium, we also tested for nDNA divergence between the two major mtDNA groups in both Myanmar and Moorea; neither test was significant (nDNA FST = 0.0628, −0.0918 respectively, p > 0.05).

**Discussion**

Despite being geographically remote and having the potential for stepping-stone introductions, the *H. frenatus* population on Moorea has high genetic diversity, similar to that across widely separated samples from in or near to the native range (Myanmar) and higher than that across Indonesia, a colonized area much closer to the mainland. The high mtDNA diversity of *H. frenatus* on Moorea contrasts strongly with low diversity observed in other lizards that have colonized the eastern Pacific islands [20], [22–24].

It has been hypothesized that geckos experience faster mitochondrial evolution [36]–[38] in particular when comparisons to nuclear diversity can be made [39], [40]. Multilocus analyses of intraspecific gekkonid lineages in their native range typically reveal several-fold lower diversity at nuclear loci than for mtDNA (e.g. *Heteronotia binoei*; average nDNA/mtDNA π = 0.11; [41]) as expected given the higher mutation rate for mtDNA. However, in other studies of geckos following human-mediated introductions, there is unexpected high nuclear diversity compared to mitochondrial diversity perhaps as a result of a selective sweep reducing the latter (average nDNA/mtDNA π = 0.04; [42], [43]). A higher than usual ratio of nDNA/mtDNA diversity in each of the three regional samples of *H. frenatus* (nDNA/mtDNA π; Moorea = 0.30, Myanmar = 0.46, Indonesia = 0.73) was also found in this study but more sampling of non-admixed populations within the native range are needed to understand this pattern.

The genetic admixture in the Moorea population of *H. frenatus* can be explained by multiple introductions from geographically/ genetically distinct native-range sources (in situ admixture, e.g. [9]) or by one or more introductions from already genetically admixed populations(s), most likely from elsewhere in the Pacific (ancestral admixture). Multiple secondary introductions from already admixed populations could also cause this increase in diversity and appear to be the case here. These introductions likely represent an ongoing chain of admixture starting in or near the native range, as divergent groups within Myanmar are neither genetically structured (Fig. S1) nor distinct at nuclear loci. Overall, the evidence points to recent admixture among genetically divergent populations as the source of the high genetic diversity of the Moorea population of *H. frenatus*.

Based on limited geographic and genetic sampling, the Pacific Ocean populations are genetically more similar to those from Myanmar and other introduced populations (e.g. China, Hawaii; [34], [35]) than those in the presumed South-Asian native range (India, see Figure S2). Coordinated genetic analyses across the mainland Asian range of *H. frenatus* and related species are necessary to clarify species borders and relationships [37], [44] and to identify source populations (e.g. [9]), assuming these are not already obscured by secondary introductions. It is clear that the large and genetically diverse introduced population on Moorea avoided a genetic bottleneck, and the presence of high genetic diversity could have contributed to invasion success (e.g. [3]). But high diversity at neutral markers is not a prerequisite for invasive success; there have been many successful invasions with reduced genetic diversity (e.g. [3], [6], [45], [46]). In addition, the range of *H. frenatus* has recently expanded to include the western coast of Madagascar even though this population appears to have low genetic diversity for mtDNA relative to those studied here [47]. Life history characteristics can play an important role in promoting high retention of genetic diversity. For example, *H. frenatus* females are able to store enough sperm to form six clutches across the span of a year [48]; thus, even a small number of inseminated females can co-found a new population with high genetic diversity. In addition, *H. frenatus* eggs are often found under palm shingles of native houses or bark and when washed out to sea avoid desiccation [49].

Reptile extinctions on islands are causing significant decline in biodiversity [27], [50], [51]. The spread of invasive reptiles such as

---

**Table 1. Population diversity**

|        | mtDNA          |                  | nDNA           |                  |
|--------|----------------|-----------------|----------------|-----------------|
|        | n              | Moorea          | Indonesia      | Myanmar         | n              | Moorea          | Indonesia      | Myanmar         |
| Moorea | 22             | 0.04            | 1.13           | 0.39            | 18             | 0.02            | 0.0019         | 0.0049          |
| Indonesia | 18             | **0.25**        | 0.02           | 1.24            | 18             | **0.11**        | 0.01           | **0.0034**      |
| Myanmar | 17             | 0.08            | **0.27**       | 0.05            | 17             | **0.20**        | **0.16**       | 0.02            |

*Based on Tamura-Nei corrected average pairwise divergence (D0; above diagonal); within-population θ, (diagonal); population pairwise FST based on Tamura & Nei genetic differences (below diagonal). Bold numbers indicate statistically significant (p < 0.05).*
Successful Invasion and Establishment

H. frenatus will only exacerbate the problem as many studies on H. frenatus have shown that this gecko is a strong competitor and often displaces native geckos [26], [27], [32], [53]. So far, no H. frenatus have been found in the interior forest of Moorea (Fig. 1A) though expansion from commensal into natural habitats has been observed elsewhere [29]. Climatic niche modeling of H. frenatus predicts an even further expansion of suitable habitat particularly in South America and Africa [54].

Both genetic and natural history traits appear to be important factors leading to H. frenatus' successful colonization of the Pacific Islands. It is unclear which factors weigh most heavily in allowing introduced species to establish and spread, but it seems necessary to consider that founder populations may, through several mechanisms, maintain more genetic diversity than previously thought. Future work with H. frenatus would be to investigate the native range and the routes of introductions to test alternative invasion scenarios and estimate demographic parameters relevant to introductions and ultimately test other ecological or evolutionary hypotheses underlying invasions [55].

Materials and Methods

Surveys and Sampling

General sampling for H. frenatus and other geckos on Moorea was done for approximately one week in March 2006, one week in August 2008, and one week in April 2010. These included repeated surveys of human dwellings around the perimeter of the island, and primarily forest habitats in the interior. During the first trip in March 2006, we conducted a survey March 29th, from approximately 2100 h to 2300 h. During this informal survey, we drove around the perimeter of the island and stopped at seven different buildings and counted the gecko species we found (Table S1). All research was conducted under UC Berkeley Animal Care and Use Committee approval #R278-0509 (permit information: Protocol D’accueil D’un Chercheur ou Enseignant-Chercheur etrangere, Delegation a la Recherche (De la Polynesie Francaise)).

Molecular

We extracted DNA from vouchered specimens at the Museum of Vertebrate Zoology, University of California, Berkeley, and the California Academy of Science (Table S3). Twenty one sequences were from specimens sampled on Moorea while thirty-six samples were from within or adjacent to the native range including Myanmar and Indonesia (Figs. 1A, 1B). Total genomic DNA was isolated from liver using a standard high salt extraction [56]. We amplified approximately 650 basepairs of the mitochondrial cytochrome c oxidase subunit I (CO1). To compare our major mtDNA lineages with those published previously, we chose a representative from each group and sequenced 12S rDNA ([29], [33]–[35]; Fig. S2). We also PCR amplified three nuclear autosomal loci for a total of 762 bases (Table 2). Nuclear autosomal marker rpl14 was previously published in Fujita et al. [41]. The two other nuclear markers (LFABP and rpl10) were developed with the same methods as Fujita et al. [41] by random sequencing from a cDNA library for Heteronotia binoei, another closely related gekkonid lizard. Primers and conditions for both mitochondrial and nuclear markers can be found in Table 2. We amplified genomic DNA in 12.5 μL reactions with an initial denaturation at 94°C for 3 min, followed by 35 cycles of denaturation at 94°C for 30 s, 30 s annealing at specific temperatures for each locus as outlined in Table 2, and extension at 72°C for 60 s. Each reaction had ~20 ng genomic DNA, 0.5 μM of each primer, 1× PCR Buffer, 1.2 mM MgCl2, 0.6 mM dNTPs, and 0.5 U of Taq. We then purified the product using ExoSAP-IT (USB) and sequenced using BigDye v3.1 (Applied Biosystems). The purified sequence product was sequenced on an ABI 3730 automated DNA sequencer. Sequences were aligned using Geneious Pro (Biomatters, Auckland, New Zealand).

Mitochondrial DNA

Phylogenetic analyses for CO1 using maximum likelihood (ML) were conducted in RaxML [57] and partitioned by codon position. ML nodal support was calculated by analyzing 100 bootstrap replicates. To estimate the extent and distribution of sequence diversity, populations were grouped by collection country and compared using Arlequin v3.1 [58]. For each population pair we estimated divergence among populations (Dxy and Dst using the Tamura-Nei model; [59]) and pairwise Fst based on Tamura & Nei’s model of sequence evolution [60]. Additionally, we estimated within-population diversity (θu; [61]) and Tajima’s D [62] for each population.

For the 12 s phylogeny, we conducted a Bayesian phylogenetic analysis using MrBayes v 3.1.2 [63]. We first implemented MrModelTest v2.3 [64] to establish the HKY+I+G model best representative of the substitution process for the dataset. We allowed four incrementally heated Markov chains to proceed for 20 million generations, sampling every 1000 generations. Bayesian posterior probabilities were estimated after 2000 samples were discarded for burn-in. The tree was rooted with H. brookii from Carrazan and Arnold (Fig. S2; [33]).

Nuclear DNA

We inferred haplotypes computationally using the program PHASE v.2.1. [65], [66]. We then used these phased genotypes

Table 2. Marker conditions used in this study.

| Gene | Size (bp) | TA (°C) | Primers (5’-3’) | Source |
|------|-----------|---------|----------------|--------|
| CO1  | 650       | 48      | dgLCO-1490: GGTCAACAAATCATAAAGAYTGYG | Meyer [73] |
|      |           |         | dgHCO-2198: TAAACTTCCAGGTTGACCAAARAYCA |         |
| rpl14| 271       | 62      | exon 1: ACTGTATGACATTGTTAGATTCGC | Fujita et al. [41] |
|      |           |         | exon 2: GAACATGAGAAGACAGCAGCAGTCCG |         |
| rpl18| 226       | 60      | n108: GTTGTCCCTGAACGAGAAATCAACTTC | This paper |
|      |           |         | n109: ATTCAAAAATCTCCGCGGTCCTTTC |         |
| LFABP| 265       | 65      | n32: AGGGTATGTCCGAGGAGATTAGAAG | This paper |
|      |           |         | n33: GAGTTTCAATGTCGCGCTTAATAC |         |

doi:10.1371/journal.pone.0026874.t002
coded as allelic states to infer population structure in our nuclear loci using the Bayesian assignment STRUCTURE v2.3.1 [67]. We ran 10 iterations for K = 2 and K = 3 (Fig. S4). We used a burn-in of 100,000 steps, MCMC length of 500,000 steps and the correlated allele frequencies and the admixture ancestry model.

A multilocus genetic network was used in this study to visualize individual relationships. Using this approach, we are able to show a more realistic visual representation of ambiguous or incompatible phylogenetic signals, such as one that might be seen with recombination, using a net-like scheme [68]. In order to construct this genetic network, we first calculated the genetic distances among individuals at each nuclear locus. We used the uncorrected ‘p’ genetic distance matrices of the three nuclear loci. We visualized this network using Neighbor Net algorithm [72] in SplitsTree v4.6 [68]. In order to construct this genetic network, we first calculated the genetic distances among individuals at each nuclear locus. We used the uncorrected ‘p’ genetic distance matrices of the three nuclear loci. We visualized this network using Neighbor Net algorithm [72] in SplitsTree v4.6 [68]. Individual nuclear neighbor-joining trees can be found in Figure S3 and diversity at each locus in Table S2. As for mitochondrial DNA, we used Arlequin to estimate θ0, θA, and FST across nuclear loci.

Supporting Information

Figure S1 Map of Myanmar showing location of major CO1 lineages. (TIF)

Figure S2 Bayesian phylogeny of 12S sequences. Neighbor-joining tree includes 12S sequences from this study, Bansal and Karanth [29], Carranza and Arnold [33], Feng et al. [35], and Whiting et al. [34]. Numbers to the right of the names represent major CO1 groups found in this study. Posterior probabilities for the major groups are included on the branches. (TIF)

Figure S3 Unrooted Neighbor-joining network of (A) rpl18, (B) rpl14, and (C) LFABP. (TIF)

References

1. Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution 20: 110–110.
2. Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. Trends in Ecology & Evolution 22: 454–464.
3. Drögeusch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Molecular Ecology 17: 431–449.
4. Estoup A, Guillemaud T (2010) Reconstructing routes of invasion using genetic data: why, how and so what? Molecular Ecology 19: 4113–4130.
5. Nri M, Maruyama T, Chakraborty R (1975) Bottleneck effect and genetic variability in populations. Evolution 29: 1–10.
6. Tsutsui ND, Suarez AV, Holway DA, Case TJ (2006) Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences of the United States of America 97: 5946–5953.
7. Peacock MM, Beard KH, O’Neill EM, Kirchoff VS, Peters MB (2009) Strong founder effects and low genetic diversity in introduced populations of Coqui frogs. Molecular Ecology 18: 3603–3615.
8. Allendorf FW, Landquist LL (2003) Introduction: Population biology, evolution, and control of invasive species. Conservation Biology 17: 24–30.
9. Kolbe JJ, Glor RE, Schettino LRG, Lara AC, Larson A, et al. (2004) Genetic variation increases during biological invasion by a Cuban lizard. Nature 431: 177–181.
10. Loope K, Roy D, Bezaei E, Sivasundar A, Searshouse O (2018) Hybridization between distant lineages increases adaptive variation during a biological invasion: stickleback in Switzerland. Molecular Ecology 19: 3995–4011.
11. Zalewski A, Michalik-Pardziak A, Bartoszevicz M, Kozakiewicz M, Brzezinski M (2010) Multiple introductions determine the genetic structure of an invasive species population: American mink Neovison vison in Poland. Biological Conservation 143: 1355–1363.
12. Verhoeven KJF, Mace M, Wolfe LM, Briere A (2011) Population admixture, biological invasions and the balance between local adaptation and introgression depression. Proceedings of the Royal Society B-Biological Sciences 278: 2–8.
13. Vosin M, Engel CR, Viard F (2005) Differential shuffling of native genetic diversity across introduced regions in a brown alga: Aquaculture vs. maritime traffic effects. Proceedings of the National Academy of Sciences of the United States of America 102: 5432–5437.
14. Simberloff D (2009) The Role of Propagule Pressure in Biological Invasions. Annual Review of Ecology Evolution and Systematics 40.
15. Motro U, Thomson G (1982) On heterozygosity and the effective size of populations subject to size changes. Evolution 36: 1059–1066.
16. Clegg SM, Dogman SM, Kikkawa J, Moritz C, Estoup A, et al. (2002) Genetic consequences of sequential founder events by an island-colonizing bird. Proceedings of the National Academy of Sciences of the United States of America 99: 8127–8132.
17. Tholm CG, Simberloff D, Barun A, McCracken G, Pascal M, et al. (2006) Genetic divergence in the small Indian mongoose (Herpestes auropunctatus), a widely distributed invasive species. Molecular Ecology 15: 3947–3956.
18. Tinghultella RM, Zik M, Beveridge M, Simmons LW (2011) Island hopping introduces Polynesian field crickets to novel environments, genetic bottlenecks and rapid evolution. Journal of Evolutionary Biology 24: 1199–1211.
19. Gillespie RG, Clarke EM, Goodeacre SL (2008) Biogeography of the fauna of French Polynesia: diversification within and between a series of hot spot archipelagos. Philosophical Transactions of the Royal Society of London B Biological Sciences 363: 3335–3346.
20. Fisher RN (1997) Dispersal and evolution of the Pacific Basin gekkonid lizards Gehyra oxymorpha and Gehyra mutilata. Evolution 51: 906–921.
21. Case TJ, Bolger DT (1991) The role of introduced species in shaping the distribution and abundance of inland reptiles. Evolutionary Ecology 5: 272–290.
22. Austin CC (1999) Lizards took express train to Polynesia. Nature 397: 113–114.
23. Bruna EM, Fisher RN, Case TJ (1996) Morphological and genetic evolution appear decoupled in Pacific skinks (Scincidae: Eumeces). Proceedings of the Royal Society of London B-Biological Sciences 263: 681–688.
24. Moritz C, Case TJ, Bolger DT, Donnellan S (1993) Genetic diversity and the history of Pacific island house geckos (Hemidactylus and Lepidodactylus). Biological Journal of the Linnean Society 48: 113–133.
25. Ota H, Ineich I (2006) Colonization of the Gold Dust Day Gecko, Phelsuma laticeps (Reptilia: Gekkonidae), in Moorea of the Society Archipelago, French Polynesia. Current Herpetology 25: 97–99.

Figure S4 STRUCTURE plots for (A) K = 2 and (B) K = 3. (TIF)

Table S1 Individual counts of Hemidactylus frenatus, Lepidodactylus lugubris, and Gehyra oceanica in 7 buildings in Moorea. Localities: 1) Gump Station; 2) Magasin Ami René; 3) Herman Perles in Hauru; 4) Magasin Lai-Assan in Haaputi; 5) Chez Teima in Maatea; 6) Electricite de Tahiti in Vaiare; 7) Magasin Lee Hen in Pao Pao. (DOC)

Table S2 Diversity at each of the nuclear loci. Based on Tamura-Nei corrected average pairwise divergence (Dd, above diagonal); within-population θ0 (diagonal); population pairwise FST based on Tamura & Nei genetic differences (below diagonal). Bold numbers indicate statistically significant (p<0.05). (DOC)

Table S3 Sequences sampled with associated Genbank accession numbers. (DOC)

Acknowledgments

We would like to thank Jenner Branbury for help with the analysis, Tammy Lim, Eric Routman, and Jason Colby for critical comments. We are grateful to Winifred Tonioni for assistance in the field, Jim McGuire and Jens Vindum for samples, and Catherine Zhu and Charles Moritz for assistance with sequencing. We also thank members of the Moritz lab and members of the Gump Station, especially Neil Davies and Chris Meyer for assistance in Moorea.

Author Contributions

Conceived and designed the experiments: MT CM. Performed the experiments: MT NR CM. Analyzed the data: MT. Contributed reagents/materials/analysis tools: NR CM. Wrote the paper: MT CM.
26. Case TJ, Bolger DT, Petren K (1994) Invasions and competitive displacement among house geckos in the tropical Pacific. Ecology 75: 464–477.
27. Cole NC, Jones CG, Harris S (2005) The need for enemy-free space: The impact of an invasive gecko on island endemics. Biological Conservation 125: 467–474.
28. Hoskin C (2010) The invasion and potential impact of the Asian House Gecko (Hemidactylus frenatus) in Australia. Austral Ecology.
29. Ransel R, Karanth KP (2010) Molecular phylogeny of Hemidactylus geckos (Squamata: Gekkonidae) of the Indian subcontinent reveals a unique Indian radiation and an Indian origin of Asian house geckos. Molecular Phylogenetics and Evolution 57: 459–465.
30. Bauer AM, Jackman TR, Greenbaum E, Giri VB, de Silva A (2010) South Asia supports a major endemic radiation of Hemidactylus geckos. Molecular Phylogenetics and Evolution 57: 345–352.
31. McKown S (1996) A field guide to reptiles and amphibians in the Hawaiian Islands. Los Osos, California: Diamond Head Pub.
32. Ineich I, Blanc CP (1988) Distribution des reptiles terrestres en Polynésie Orientale. Anoll Research Bulletin 318: 1–75.
33. Carranza S, Arnold EN (2006) Systematics, biogeography, and evolution of mtDNA in Hemidactylus geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 38: 531–545.
34. Whiting AS, Bauer AM, Sites JW, Jr. (2003) Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). Molecular Phylogenetics and Evolution 29: 582–598.
35. Feng J, Han D, Bauer AM, Zhou K (2007) Interrelationships among gekkonid species inferred from mitochondrial and nuclear gene sequences. Zoological Science 24: 656–665.
36. Harris DJ, Batista V, Carretero MA, Ferrand N (2004) Genetic variation in Tarentola mauritanica (Reptilia: Gekkonidae) across the Strait of Gibraltar derived from mitochondrial and nuclear DNA sequences. Amphibia-Reptilia 25: 41–49.
37. Jesus J, Brehm A, Harris DJ (2006) Phylogenetic relationships of Hemidactylus geckos from the Gulf of Guinea islands: patterns of natural colonizations and anthropogenic introductions estimated from mitochondrial and nuclear DNA sequences. Molecular Phylogenetics and Evolution 34: 489–495.
38. Jesus J, Brehm A, Harris DJ (2006) Phylogenetic relationships of Lycodactylus geckos from the Gulf of Guinea islands: Rapid rates of mitochondrial DNA sequence evolution? Herpetological Journal 16: 291–295.
39. Arscott RJ, Lindeque P, Harris DJ, Mateo JA, Carranza S (2008) Systematics, biogeography and evolution of the endemic Hemidactylus geckos (Reptilia, Squamata, Gekkonidae) of the Cape Verde Islands: based on morphology and mitochondrial and nuclear DNA sequences. Zoologica Scripta 37: 619–636.
40. Austin JJ, Arnold EN, Jones CG (2004) Reconstructing an island radiation using mtDNA polymorphism. Genetics 125: 585–596.
41. Huelberrchen JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics (Oxford) 17: 734–735.
42. Nylander JA (2004) MrModeltest v. 2.0: Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
43. Stephens M, Donnelly P (2003) A comparison of Bayesian methods for haplotype reconstruction from population genotype data. American Journal of Human Genetics 73: 1162–1169.
44. Stephens M, Scheet P (2005) Accounting for decay of linkage disequilibrium in haplotype inference and missing-data imputation. American Journal of Human Genetics 76: 449–462.
45. Princard JK, Stephens M, Donnelly P (2000) Inference of population structure using multidisc genotype data. Genetics 155: 943–959.
46. Huson DH, Bryant D (2006) Application of phylogenetic networks in evolutionary studies. Molecular Biology and Evolution 23: 254–267.
47. Hasgawa M, Kishino H, Yano TA (1985) Dating of the human ape splitting by a molecular clock of mitochondrial-DNA. Journal of Molecular Evolution 22: 160–174.
48. Meyer CP (2004) Toward comprehensiveness: Increased molecular sampling within Cypriacidae and its phylogenetic implications. Malacologia 46: 127–136.