Can genetic data confirm or refute historical records? The island invasion of the small Indian mongoose (*Herpestes auropunctatus*)

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Abstract Many studies aimed at reconstructing the invasion history of a species rely, in part, on inferences based on patterns of genetic variation. These inferences warrant careful interpretation, however. In particular, given the time scale of most invasions, the typical demography of invasive species in their invaded range, and the available molecular tools, the underlying assumptions of population genetic models will often be violated. Given this fact, we examined the potential of population genetic data for reconstructing the history of serial introductions of the small Indian mongoose, *Herpestes auropunctatus*. We used simulations to test the power of existing microsatellite data for testing the credibility of historical introduction records. Although our results are generally consistent with most historical records for *H. auropunctatus*, the existing data have low power to reject alternative historical hypotheses. Simulations of a wide range of founder population sizes show broadly overlapping results, making rather different historical scenarios of introductions difficult to rule out with typical datasets. We advocate caution in the use of molecular population genetics to infer the history of invasive species, and we suggest extensive simulations as a tool to evaluate, in advance, this approach for addressing important research questions.

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Introduction

The evolutionary history of introduced populations typically involves complex differences in propagule size and number and, occasionally, genetic admixture between populations from different native regions (Kolbe et al. 2004; Dlugosch and Parker 2008; Simberloff 2009). Coalescent theory and population genetic data (e.g., microsatellites and AFLPs) have aided in elucidating these historical population processes [reviewed by Beaumont (1999) and Stephens and Donnelly (2000)]. The chronological order of introductions across sites leads to theoretical predictions pertaining to variation in genetic diversity among populations within an introduced species' range (Estoup et al. 2001; but see Estoup et al. 2010 and Fitzpatrick et al. 2012). After an initial founding event and genetic bottleneck, subsequent serial introductions (e.g., from site A to B, from site B to C, etc.) should result in a decline in genetic diversity with each

successive introduction (Clegg et al. 2002). From this expected pattern of reduced genetic diversity, one might expect to infer the order of colonization (Estoup et al. 2001; Hufbauer et al. 2004; Kawamura et al. 2006).

Such a pattern requires careful interpretation (Fitzpatrick et al. 2012). Genetic variation can also reflect differences in the number of founders (Nei et al. 1975; Chakraborty and Nei 1977; Lande 1988; Spencer et al. 2000; Simberloff 2009), random variation in genetic diversity between groups of founders, or natural variation among founder sources (Kolbe et al. 2004). Furthermore, the initial population dynamics of introduced species play a significant role in determining how much genetic diversity is retained within and among populations. For example, a population that increases in size rapidly after a founder event will lose relatively little variation, whereas substantial variation can be lost when a founder population remains small for several generations (Nei et al. 1975).

Here, we use the small Indian mongoose, *Herpestes auropunctatus*, as a test case for the applicability of genetic data for inferring invasion history. The serial introductions of the small Indian mongoose to islands exemplify a well-documented, yet complex historical process in which the credibility of historical records might be tested. The native distribution of *H. auropunctatus* ranges from Iraq in the Middle East eastward to Myanmar, and from northern Pakistan southward through the center but not the south of the Indian subcontinent (Veron et al. 2007). In the late nineteenth and early twentieth centuries, *H. auropunctatus* was widely introduced to at least 64 islands in the Pacific and Indian Oceans, Caribbean and Adriatic Seas, and to two continental areas, the northeast coast of South America and Adriatic coast, for control of rats and snakes (Barun et al. 2011).

The veracity of introduction records is critical to sound management recommendations for conservation purposes. For instance, identifying the sources, routes, and order of introductions allows authorities to plan effective methods of interdiction (Rollins et al. 2009) and to determine whether eradication, if achieved, would simply be redressed by recurrent invasion (Abdelkrim et al. 2007). At least superficially, *H. auropunctatus* would appear to meet these criteria. In the late nineteenth and early twentieth centuries, rats caused significant losses in sugar cane production, and any attempt to control these pests was

widely publicized. Consequently, the introduction history of *H. auropunctatus* is often well-documented with the dates and numbers of individuals, including the sex of individuals, available for many introductions (Simberloff et al. 2000; Thulin et al. 2006). *H. auropunctatus* was first introduced to Jamaica in 1872 (Espeut 1882) followed by several subsequent introductions from Jamaica to islands in the West Indies (Hoagland et al. 1989) and to the Hawaiian Islands (Bryan 1938), and separately from Asia or from sites of previous introductions to Mauritius (Cheke 1987), the Fijian Islands (Gorman 1975; Morley 2004), Japanese islands (Abe et al. 1991; Ishii 1998; Kishida 1931; Yamada 2002; Yamada and Sugimura 2004), Ngazidja in the Comoro islands (Louette 1987), and Adriatic islands (Tvrtkovic and Kryštufek 1990; Barun et al. 2008). This species successfully reproduced and quickly spread throughout these islands, and it is thought that subsequent undocumented introductions are unlikely. *H. auropunctatus* is a poor swimmer, and all known colonizations were deliberately performed by humans, except for possibly a single introduction to a small island in Fiji where *H. auropunctatus* is believed to have rafted from a nearby, larger island after a hurricane (Craig Morley, pers. comm.).

Thulin et al. (2006) investigated the extent of genetic differentiation within and between introduced and native populations of *H. auropunctatus* and compared the inferred history based on results of genetic data analysis with the documented history of introductions. In at least one case, their data conflicted with a documented introduction scenario. The population on Fiji had more than four alleles per locus, but the documented introduction of only one male and one female predicts a maximum of four alleles per locus (barring an extraordinary mutation rate). This discrepancy could be explained if the single female was already pregnant with progeny of other males. However, analysis of mitochondrial DNA identified three unique haplotypes from Fiji, implying a minimum of three founding females (Barun et al. unpublished data).

Thulin et al. (2006) did not test the credibility of other introduction hypotheses. An examination of their data shows no apparent relationship between estimates of gene diversity (expected heterozygosity) and the accepted story of founder population size for these mongoose introductions (Fig. 1). One might

expect gene diversity to remain higher with larger founder size, but this is not the case for any introduction of *H. auropunctatus* for which the number of founders has been reported.

Given the conflict between the data and the introduction history on Fiji, and lack of relationship between gene diversity and reported founder population size for several other mongoose introductions, we advocate use of custom simulations to evaluate the ability of molecular population genetics to test recent historical dynamics in invasive species. Here, we have developed a simple simulation model to evaluate more broadly the potential for population genetic data to confirm or refute the completeness of other historical introduction records of *H. auropunctatus*. We use the published microsatellite data of Thulin et al. (2006) to parameterize simulations and to test the credibility of historical introduction records for five islands.

Materials and methods

Population sampling and microsatellite scoring

Collection of samples and PCR procedures are described by Thulin et al. (2006). They used eight microsatellite loci, but we found that three loci could not be scored reliably by independent observers. Therefore, we retained only five previously reported microsatellite loci (Hj34, Hj40, Hj45, Hj51 and Hj56) to score allelic differences. These data are now provided in Online Resource 1.
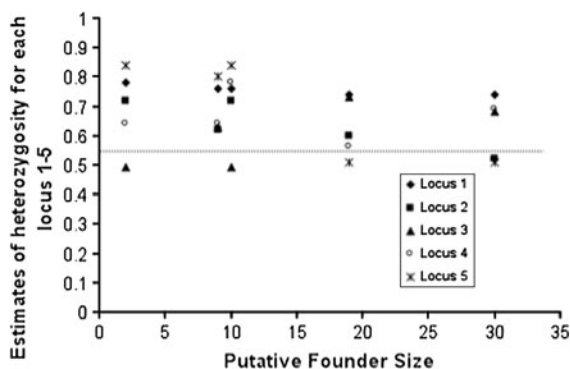

Fig. 1 Reported founder size for each population does not predict estimates of gene diversity (expected heterozygosity) from microsatellite data. *Dashed line* is the estimated gene diversity from the observed data from Bangladesh, representing the putative source population
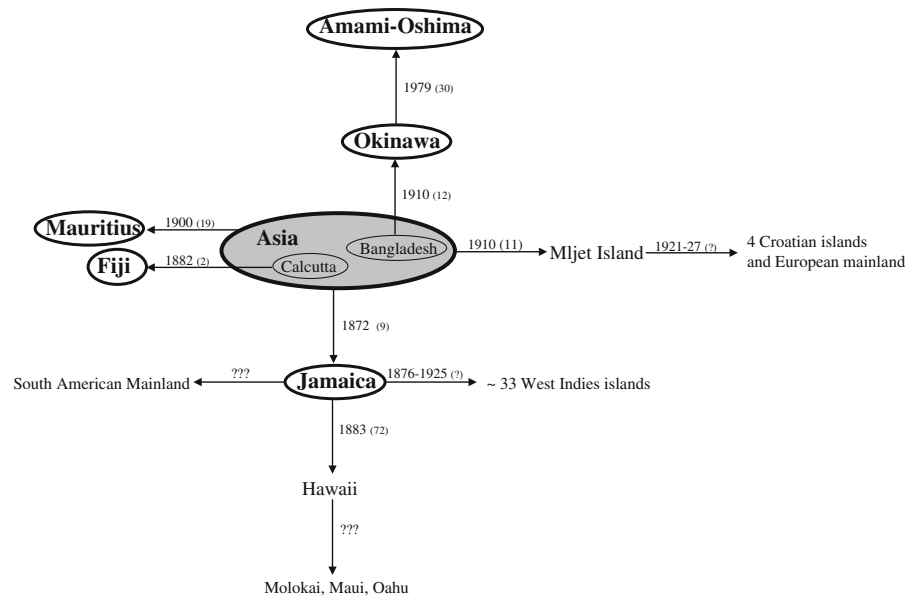
Simulations

We conducted simulations using the R 2.2 environment (http://www.r-project.org) to follow the stochastic loss versus persistence of alleles for each microsatellite locus during the demographic growth of populations after introduction to determine whether reported data on an introduction were statistically consistent with the estimated genetic variation. We opted to use our own forward-time simulations instead of a coalescent simulator, such as SIMCOAL (Laval and Excoffier 2004), because we wished to use logistic rather than exponential population growth, the coalescent approximation might not be accurate for small effective population sizes, and our scenarios are simple enough to be efficiently analyzed with this more direct approach.

We assumed introduced populations were derived from a parental population in Bangladesh and possessed the same initial frequency of alleles. Bangladesh is a source population for the Okinawa population and is less then 100 km from Calcutta, where all five populations are said to have originated (except Mauritius, for which this origin is uncertain but suspected). Indian laws that disallow export of DNA materials prevented us from obtaining samples from the Calcutta region. Alleles sampled in the introduced populations but not in the Bangladesh source populations were assumed to have a source allele frequency of 1 divided by the total number of source population alleles observed plus 1 (1/ $(2n + 1)$). In comparing simulations to data, we use only summary statistics, not allele identities. Therefore, our results do not depend on an assumption that the composition of alleles in the true source is identical to that in Bangladesh, only that the distribution of allele frequencies in Bangladesh is representative of the distribution of source allele frequencies. Simulations were conducted for Amami-Oshima, Fiji, Jamaica, Mauritius, and Okinawa, because these were the only populations with apparently clear documentation of both the numbers and sexes of the founders (see Fig. 2). The only stepping stone introduction with adequate documentation is from Bangladesh to Okinawa to Amami-Oshima (in 1910, six male and six female *H. auropunctatus* were reported to have been introduced to Okinawa, and then in 1979, 30 individuals were introduced to Amami-Oshima).

Each simulation consisted of a founder event of N_F diploid individuals followed by logistic population

Fig. 2 Schematic drawing of sequential founder events of the small Indian mongoose. In *bold* and *circled* are populations we simulated (modified from Thulin et al. 2006). The *numbers* given are year of introduction and in *parentheses* is the number of documented individuals introduced

growth for T generations. For each locus, $2N_F$ alleles were initially drawn, with replacement, from the source population. N_F was calculated as the effective population size accounting for sex ratio (Wright 1931; Hartl and Clark 1997) based on historical records. Each generation t, genetic drift was simulated by sampling $2N_t$ alleles from the previous distribution of allele frequencies. Population size N_t was calculated from the Beverton–Holt population growth model with a growth rate (r) of 3 and carrying capacity (K) of 1,000, 10,000, or 100,000. These numbers are based on the demography of *H. auropunctatus* (Nellis and Everard 1983).

We performed two sets of simulations using generation times of 6 and 12 months, respectively (Nellis and Everard 1983). At the end of each simulation, we recorded the number of remaining alleles in the introduced population and gene diversity (H_e; Nei 1973) based on final allele frequencies in simulated samples according to the real sample sizes (Thulin et al. 2006). We also conducted a two-step introduction simulation for Amami-Oshima in which an initial introduction to Okinawa in 1910 was simulated followed by an introduction in 1979 to Amami-Oshima as described above. We conducted 10,000 simulations for each locus of the introduced populations for each generation time. Values for demographic parameters used in simulations are found in Table 1. We then compared the distributions from simulation runs with the numbers of alleles and H_e

estimated from the real populations. If an empirical estimate was greater than 97.5 % or less than 2.5 % of the simulation values, we infer that the data are inconsistent with the historical record, given the assumptions of the model. The R code implemented for conducting simulations can be found in Supplemental Materials.

To evaluate more generally the sensitivity of the model to different founder sizes and carrying capacities, we simulated founder sizes of 5, 10, 25, 50, and 100 for each carrying capacity of 1,000, 10,000, and 10,000. We simulated 10,000 replicates of each parameter combination for 100 generations and sampled 35 diploid individuals. To evaluate how well allelic richness and gene diversity can help distinguish these alternative scenarios, we fitted linear discriminant functions to the simulated data and reported how often datasets were correctly classified. R code for these simulations is available in Online Resource 2.

Results

Five microsatellite loci exhibited between three and nine alleles among the five islands investigated (Table 2). Based on the number of alleles detected alone, the purported introduction history for the island of Fiji is inaccurate. As reported previously (Thulin et al. 2006), we detected more alleles at loci 1 and 5 than are theoretically possible based on a founding

Table 1 Genetic data for the simulated populations

Parameters							
Island	Founder N_e	Generations[a]	n of locus 1	n of locus 2	n of locus 3	n of locus 4	n of locus 5
Bangladesh (native range)	–	–	35	35	35	35	31
Pakistan (native range)	–	–	19	20	16	20	20
Jamaica[a]	9	130	44	47	46	42	46
Fiji[a]	2	119	35	35	35	35	35
Mauritius[a]	19	101	35	35	35	35	35
Okinawa[a]	12	92	93	93	85	91	90
Amami-Oshima[b]	30	18	43	32	39	42	39

Founder N_e is the initial number of introduced mongooses, generations is the number of generations from initial introduction to the time of tissue collection (assuming a 12 month generation time), and n of loci 1–5 is number of samples for each locus

[a] Assuming a 12 month generation time

[b] Two-step model: Calcutta to Okinawa and Okinawa to Amami-Oshima

Table 2 Number of observed alleles for each population for loci 1–5

Number of alleles					
Island	Locus 1	Locus 2	Locus 3	Locus 4	Locus 5
Bangladesh	6	6	7	7	8
Pakistan	2	2	3	7	3
Jamaica[a]	**7 (98.4)**	4 (23.9)	7 (94.4)	5 (55.3)	7 (84.5)
Fiji[a]	**9 (100.0)**	**5 (100.0)**	3 (39.2)	4 (89.1)	**8 (100.0)**
Mauritius[a]	5 (55.9)	5 (51.7)	**3 (0.6)**	6 (75.3)	8 (92.6)
Okinawa[a]	5 (83.3)	4 (45.9)	5 (71.5)	4 (41.5)	**3 (2.1)**
Amami-Oshima[b]	**6 (98.5)**	3 (15.0)	4 (38.0)	4 (47.1)	**3 (3.1)**

In parenthesis is the percentile of the observed number relative to the simulations (assuming a 12-month generation time). A two-step model was simulated for Amami-Oshima: Bangladesh to Okinawa and Okinawa to Amami-Oshima

Bold results are statistically inconsistent with the historical record

[a] Assuming a 12 month generation time

[b] Two-step model: Calcutta to Okinawa and Okinawa to Amami-Oshima

size of two individuals. No other single locus sample was inconsistent with its respective introduction history after correcting for multiple tests (Tables 2, 3). However, multilocus analysis provided more power to detect overall inconsistencies.

Comparison of average allelic richness and diversity per locus indicated that the reported scenarios are credible for Jamaica (if K is between 1,000 and 10,000) and Mauritius (if K is on the order of 1,000) but predict significantly more genetic variation than observed for both Okinawa and Amami-Oshima (Fig. 3).

Comparison among scenarios revealed limited ability to distinguish alternative introduction histories. Expected genetic variation after serial introduction to Amami-Oshima is indistinguishable from that expected

on Okinawa (Fig. 3i, j). More general scenarios with different founder sizes also generated broadly overlapping patterns of allelic richness and diversity (Table 4; Fig. 4). If a large carrying capacity could be assumed, correct classification was as high as 88 % for small founder sizes (Table 4d), but with small or unknown K, correct classification was under 70 % and as low as 12 % for larger founder sizes (Table 4a).

Discussion

Many recent studies have used molecular data to examine the influence of propagule pressure on the establishment and subsequent spread of successful

Table 3 Expected heterozygosity for each population for loci 1–5

He					
Island	Locus 1	Locus 2	Locus 3	Locus 4	Locus 5
Jamaica[a]	0.76 (93.9)	0.62 (46.9)	0.63 (35.7)	0.64 (49.0)	0.8 (93.6)
Fiji[a]	**0.78 (100.0)**	**0.72 (99.2)**	0.49 (47.8)	0.64 (88.3)	**0.84 (100.0)**
Mauritius[a]	0.76 (91.6)	0.72 (77.7)	0.49 (6.4)	0.78 (93.9)	0.84 (98.8)
Okinawa[a]	0.74 (94.5)	0.6 (52.5)	0.73 (86.6)	0.56 (37.7)	0.51 (12.8)
Amami-Oshima[b]	**0.74 (96.1)**	0.52 (36.3)	0.68 (73.6)	0.69 (81.0)	0.51 (15.2)

In parentheses is the percentile of the observed number relative to the simulations (assuming a 12-month generation time). A two-step model was simulated for Amami-Oshima: Bangladesh to Okinawa and Okinawa to Amami-Oshima

Bold results are statistically inconsistent with the historical record

[a] Assuming a 12 month generation time

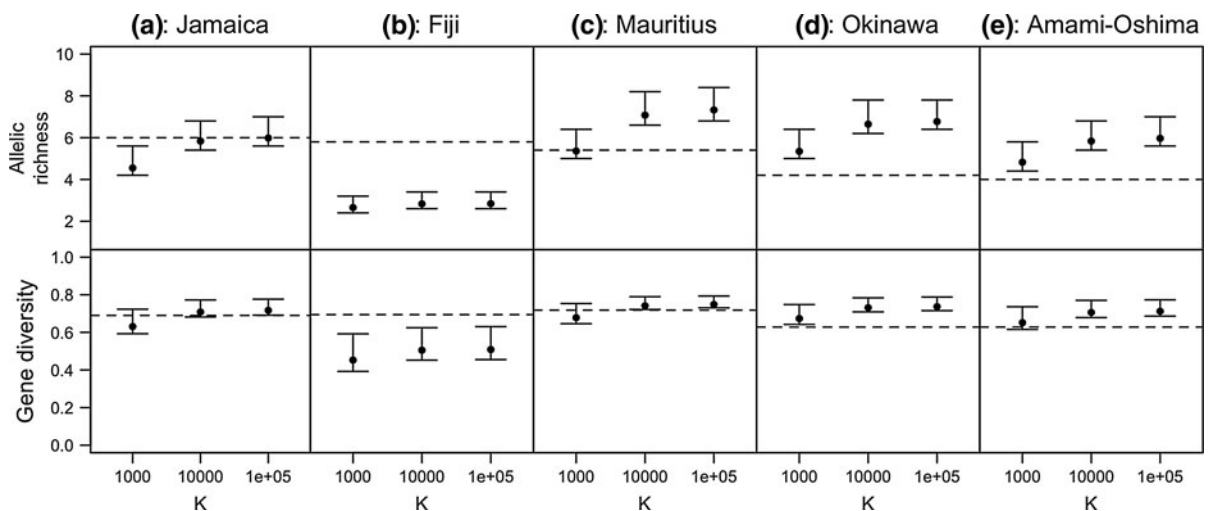[b] Two-step model: Calcutta to Okinawa and Okinawa to Amami-Oshima

Fig. 3 Multilocus analysis of genetic variation in five introduced populations of the small Indian mongoose. *Each graph* shows the mean and 95 % central range of allelic richness or diversity estimated from simulations assuming carrying capacity $K = 1,000$, 10,000, or 100,000. *Dashed horizontal lines* illustrate the estimates from observed data for each island

invasions (e.g., Genton et al. 2005; Kolbe et al. 2004; Lavergne and Molofsky 2007; Roman and Darling 2007; Saltonstall 2002). Specifically, several studies used genetic diversity and simulations to address whether single or multiple introductions (i.e., propagule number) occurred, and the qualitative sizes of these introductions (i.e., propagule size) (Ficetola et al. 2008; Ross and Shoemaker 2008; Arntzen et al. 2010). In the above studies, the authors did not address whether there was a contradiction between the historical records of an introduction and molecular evidence, nor did they explicitly evaluate whether alternative scenarios could be discriminated.

Genetic variation of introduced populations depends strongly on the past history of the invasive species within its native range (Taylor and Keller 2007), as mutation has minimal influence given the age of most biological invasions (less than 500 years old, and often much younger). How this variation is represented in introduced populations depends on propagule pressure, drift (population size), and sometimes natural selection. Therefore, understanding the historical pattern of genetic diversity within the native range is necessary to elucidate and understand factors affecting genetic diversity during invasions (Taylor and Keller 2007; Dlugosch and Parker 2008).

In our study, we observed some discrepancies between observed data and simulations. For the Japanese islands, this might be explained if Bangladesh is not a valid proxy for Calcutta. As noted

Table 4 Frequencies with which simulated data with a given founder size were classified as having the correct or incorrect founder size according to fitted linear discriminant functions. (a) LDF fitted to all simulated data. (b–d) LDFs fitted to the data subsets where the carrying capacity was $K = 1,000$, 10,000, and 100,000, respectively

Founder	Predicted				
Size	5 (%)	10 (%)	25 (%)	50 (%)	100 (%)
(a): All simulations					
5	68.18	31.78	0.04	0.00	0.00
10	15.59	60.82	22.75	0.77	0.06
25	3.25	27.08	23.88	25.14	20.65
50	1.32	24.95	9.76	12.40	51.58
100	0.81	22.57	10.25	4.40	61.97
(b): K = 1,000					
5	69.47	29.72	0.76	0.05	0.00
10	14.82	58.54	21.04	3.58	2.02
25	1.21	25.50	36.27	13.81	23.21
50	0.48	14.38	30.64	15.59	38.91
100	0.10	9.27	26.26	14.61	49.76
(c): K = 10,000					
5	83.61	16.39	0.00	0.00	0.00
10	6.09	85.03	8.82	0.06	0.00
25	0.01	10.01	64.73	19.87	5.38
50	0.00	0.81	29.37	35.26	34.56
100	0.00	0.05	10.48	26.17	63.30
(d): K = 100,000					
5	84.83	15.16	0.01	0.00	0.00
10	5.07	88.07	6.84	0.02	0.00
25	0.00	7.59	69.98	19.86	2.57
50	0.00	0.14	24.65	43.25	31.96
100	0.00	0.00	5.58	28.60	65.82

Fig. 4 Average allelic richness and diversity of five loci for each of 10,000 simulations with $K = 1,000$. **a** Each estimate using samples of 35 individuals. **b** 95 % density ellipses fitted assuming bivariate normal distributions. *Colors* represent different founder sizes: *black* = 5, *red* = 10, *blue* = 25, *yellow* = 50, *purple* = 100. (Color figure online)

a maximum of four alleles per locus), we are often unable able to reject alternative introduction scenarios encompassing a wide range of founder population sizes.

A number of authors have debated whether a particular population was initiated by a small or large number of founders and how much genetic variation the introduced population would retain. For example, in a review of aquatic invasions, Roman and Darling (2007) provided evidence that reduced genetic diversity in invasive populations is not as common as one would expect in spite of small founder size. Despite the common belief that insect invasions must have arisen through large and even multiple invasions, Zayed et al. (2007) showed that the solitary bee *Lasioglossum leucozonium* invaded North America most likely through the introduction of a singly-mated female. However, Estoup et al. (2010) concluded that accurate historical demographic information was much more important than genetic data for accurate

previously, most original founders are documented from the Calcutta region but Indian laws disallowing export of DNA materials forced us to use Bangladesh as the "native" population. Although Bangladesh is less then 100 km from Calcutta, our simulation results hint that Bangladesh may not be an adequate surrogate source. Low variation on the Japanese islands, despite large reported population sizes, suggests a more severe bottleneck or a source with lower variation. A more severe bottleneck might indicate that the reported introduction history is incorrect or that demographic stochasticity reduced the effective number of founders. Although it can be easy to refute very simple demographic scenarios, such as the origination of Fiji's mongoose population from a single pair (setting
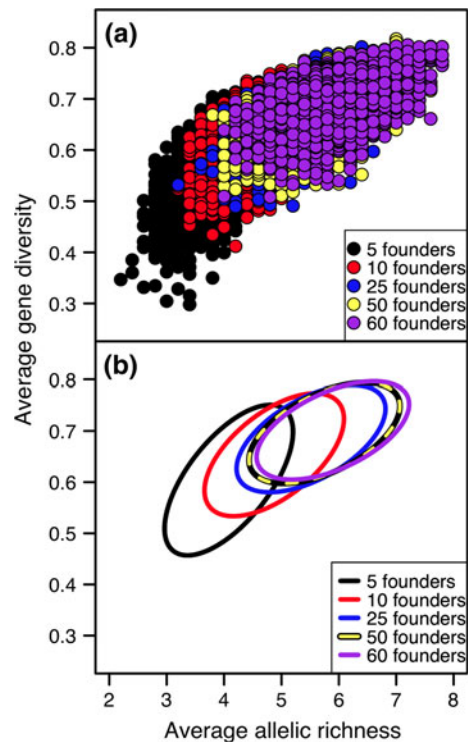
description of the cane toad (*Rhinella marina*) invasions in Australia. Our results lead to similar conclusions—genetic variation in small Indian mongoose populations is inconsistent with some assumed histories, but we cannot distinguish disparate alternatives, including serial introductions and widely different founder sizes.

Although there has been much optimism regarding the utility of genetic data to reconstruct the recent history of invasive species, this enthusiasm has largely not been tempered by acknowledgment of limitations in widely used methods (Fitzpatrick et al. 2012). We advocate that, before investigators draw inferences based upon the analysis of genetic information from invasive species, simulations of alternative/various hypotheses of invasion be conducted to assess the power of the methods and type of data acquired to make biological interpretations with confidence. When historical data suggest several founders, simulations can be used to test the plausibility of this proposed number of founders.

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