Molecular Ecology (2005) **14**, 2915–2922 doi: 10.1111/j.1365-294X.2005.02586.x

SHORT COMMUNICATION

Detecting past population bottlenecks using temporal genetic data

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Abstract

Population bottlenecks wield a powerful influence on the evolution of species and populations by reducing the repertoire of responses available for stochastic environmental events. Although modern contractions of wild populations due to human-related impacts have been documented globally, discerning historic bottlenecks for all but the most recent and severe events remains a serious challenge. Genetic samples dating to different points in time may provide a solution in some cases. We conducted serial coalescent simulations to assess the extent to which temporal genetic data are informative regarding population bottlenecks. These simulations demonstrated that the power to reject a constant population size hypothesis using both ancient and modern genetic data is almost always higher than that based solely on modern data. The difference in power between the modern and temporal DNA approaches depends significantly on effective population size and bottleneck intensity and less significantly on sample size. The temporal approach provides more power in cases of genetic recovery (via migration) from a bottleneck than in cases of demographic recovery (via population growth). Choice of genetic region is critical, as mutation rate heavily influences the extent to which temporal sampling yields novel information regarding the demographic history of populations.

Keywords: ancient DNA, population bottlenecks, population history, serial coalescent, SIMCOAL, temporal data

Received 27 July 2004; revision received 15 December 2004; accepted 14 March 2005

Introduction

Information regarding population size change contributes significantly to our understanding of the evolutionary history of a species. Many population bottlenecks directly reflect influential events in the behavioural, physical or ecological environment of species. Bottlenecks increase the rate of random genetic drift (Wright 1931) and increase inbreeding (e.g. Saccheri *et al*. 1999) leading to the loss of genetic variation (e.g. as documented in Hoelzel *et al*. 1993; Taylor *et al*. 1994) which may lead to lower levels of individual fitness (Woodworth *et al*. 2002), reduced resistance to parasites and diseases, and reduced ability to respond to environmental change (Lacy 1997; Reed *et al*. 2002). Bottlenecks are also important given their potential role in speciation (Mayr 1963; Slatkin 1996) and founding events (Barton & Charlesworth 1984).

Persistent challenges in the context of detecting past population bottlenecks from genetic variation of extant populations include ascertaining (i) the timing (and/or cause) of the event, (ii) the magnitude of the bottleneck, and (iii) the extent of recovery of the population size. Patterns of neutral multilocus genetic variation in extant populations have successfully revealed recent, often anthropogenic, bottlenecks in small populations (e.g. Cornuet & Luikart 1996; Luikart *et al*. 1998; Garza & Williamson 2001). Temporal genetic data on the scale of a few generations have also been used to infer recent demographic history (e.g. Keller *et al*. 2001; Miller & Waits 2003) through estimation of the harmonic mean of effective population size during the time interval between the sampling events (Waples 1989; Williamson & Slatkin 1999; Anderson *et al*. 2000; Wang 2001; Berthier *et al*. 2002). Hierarchical

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coalescent models (Storz & Beaumont 2002; Beaumont 2003) allow for more complicated changes in population size, including bottlenecks, but are most powerful in the context of multilocus data and relatively recent bottlenecks. Ancient bottlenecks (hundreds to thousands of generations in the past) are more difficult to detect because populations have had more time to accumulate mutations. Summary statistics such as Tajima's *D* (Tajima 1989), mismatch distributions (Rogers & Harpending 1992; Schneider & Excoffier 1999), and coalescent-based maximum-likelihood approaches (e.g. Kuhner *et al*. 1995, 1998) have been used to estimate the long-term effective size of a single population and rates of long-term exponential growth but are less successful at identifying sharp declines in population size.

Historical genetic samples from populations of the past are a promising source of additional information regarding demographic history. Certain fossil assemblages (e.g. stratified deposits) allow sampling at several time points over the course of millennia from a single location (Hadly *et al*. 1998, 2003; Leonard *et al*. 2000; Lambert *et al*. 2002). Given that DNA can be extracted from fossil bones and teeth (Hofreiter *et al*. 2001), the extent of change in genetic variation through time may provide additional power to investigate historical changes in population size. Temporal genetic data can be modelled using the serial coalescent, allowing both modern and ancient samples to be considered as part of the same evolutionary process (Rodrigo & Felsenstein 1999). A Bayesian approach based on the serial coalescent can generate posterior distributions for estimates of mutation rate, effective size and exponential growth rate based on temporal genetic data (i.e. Drummond *et al*. 2002; Lambert *et al*. 2002). However, this method does not explicitly consider models with population bottlenecks, nor does it allow investigation of the influence of sample size on inferential power.

Coalescent theory predicts rescaling of the branch lengths (proportional to the bottleneck intensity) in the section of the genealogy where the bottleneck occurred (Nordborg 2001). Prebottleneck branch lengths therefore are longer than postbottleneck branch lengths. Because the branch lengths are correlated with the number of mutations, we expect the degree of change in genetic variation between ancient and the modern genetic samples to yield insight into population history.

We investigated the extent to which temporal sampling increases the power to detect historical population bottlenecks of varying severity. We generated temporal samples of DNA sequences using serial coalescent simulations, and used two summary statistics (gene diversity and Tajima's *D*) within a Monte Carlo framework to investigate how often ancient data in combination with modern data (called the 'temporal' approach) allowed us to reject the null hypothesis of constant population size, and how this rate of rejection depends on effective population size, bottleneck size and sample size. By comparing modern and temporal approaches (inference based solely on modern samples) we revealed conditions under which temporal sampling is more informative. We also investigated the sensitivity of our results to demographic (population growth) or genetic (gene flow from a neighbouring population of constant size) recovery following the bottleneck, mutation rate and the timing of the population bottleneck.

Materials and methods

Serial coalescent simulations and demographic scenarios

Using serial coalescent simulations (Anderson *et al*. 2004; Hadly *et al*. 2004), we modelled genetic data both for modern samples and for ancient samples dating to 2001 generations in the past (unless otherwise stated). A bottleneck (instantaneous reduction in population size) occurred 2000 generations ago, immediately following the temporal sampling. Population size reductions (bottleneck intensity) included 99%, 95%, 90%, 50% and 20%, where 90% refers to the reduction in size (e.g. a population of size 100 000 is reduced to 10 000). In models including demographic recovery, populations grew exponentially to historical prebottleneck size between ancient and modern sampling. Genetic recovery included emigration from a second population (which did not undergo a bottleneck) for 500 generations ($N_em = 5$) following the bottleneck. Five effective population sizes were modelled: 10 000, 25 000, 50 000, 100 000 and 250 000, corresponding to θ ($2N_e\mu$) values of 0.2, 0.5, 1, 2 and 5, respectively. In order to mimic data commonly used in ancient DNA studies, we modelled a single haploid locus. We assumed a finite-site mutation model for a sequence length of 300 bp (as a standard sequence length available for ancient DNA data) and a mutation rate of 3%/million years (Myr)/bp (average substitution rate for mitochondrial cytochrome *b* for small mammals based on Conroy & Cook (1999) and Jaarola & Searle (2002). We modelled four different sample sizes: 10, 20, 50 and 100 samples each for ancient and modern sampling.

Summary statistics and statistical power

Estimates of gene diversity (Takahata & Nei 1985) and Tajima's *D* (Tajima 1989) were calculated for both the modern and ancient genetic data for all models. For each model, we generated summary statistic distributions for modern sampling, for ancient sampling and for the difference between the statistic values at modern and ancient for all combinations of sample size and effective size. We generated similar summary statistic distributions for the null hypothesis of constant size. Statistical power for the temporal (P_t) and

modern approach (P_m) was calculated using these sets of distributions. Here power is the probability of correctly rejecting the null hypothesis of constant population size. For a given bottleneck intensity hypothesis, power corresponds to the inverse of the overlap (1-overlap) between statistic values for the null, constant population-size hypothesis and the bottleneck hypothesis (excluding overlap due to the specified significance level $\alpha = 0.05$). As simulations are used to generate statistic values for both alternate and null hypothesis distributions, our power estimates correspond to the probability of rejecting the null hypothesis based on a Monte-Carlo significance test.

For gene diversity, P_m was calculated as the proportion of modern statistic values (for a given bottleneck hypothesis) lower than the 5th percentile of the null hypothesis distribution for gene diversity (since the bottleneck results in decreased gene diversity in the modern). For Tajima's D, P_m was calculated as the proportion of modern statistic values higher than the 95th percentile of the null hypothesis distribution for Tajima's D (since the bottleneck results in increased value of Tajima's D in the modern sample).

P_t was calculated based on information from both ancient and modern sampling. For every model, we calculated the change in summary statistic value between the modern and the ancient sample. The change in gene diversity (ΔGD) is given by

$$\Delta GD = GD_m - GD_a$$

where GD_m is the gene diversity of the modern sample and GD_a is the gene diversity of the ancient sample. The change in Tajima's D is defined similarly. P_t for gene diversity was calculated as the proportion of the ΔGD distribution for the bottleneck hypothesis with values lower than the 5th percentile of the ΔGD distribution for the null hypothesis distribution. Similarly, P_t for Tajima's D was calculated as the proportion of the ΔTD distribution for the bottleneck hypothesis with values higher than the 95th percentile of the ΔTD distribution for the null hypothesis distribution.

Sensitivity analyses

Mutation rates of 2%, 4%, 6%, 10%, 20% and 50%/Myr/bp were modelled for a 95% bottleneck and $N_e = 25\,000$ and 100 000 ($n = 20$). This range of mutation rates corresponds with estimates for mammals, including typical mitochondrial markers (Brown *et al*. 1979; Meyer *et al*. 1999; Pesole *et al*. 1999). Additionally, sampling time points 5000, 2000, 1000, 500 and 100 generations before the modern were modelled for a 95% bottleneck, gene diversity (N_e = 25 000) and Tajima's D ($N_e = 100\,000$) for $n = 20$. In all cases, the ancient sampling was modelled just prior to the population bottleneck.

Results

Bottleneck models

Average gene diversity and Tajima's D estimates for simulated samples were concordant with theoretical expectations. Average gene diversity estimates for simulated ancient samples were consistent with mutation–drift equilibrium. For bottleneck models without recovery, gene diversity based on simulated modern samples was lower than gene diversity for simulated ancient samples. Additionally, the average change in gene diversity between ancient and modern samples decreased with intensity of the bottleneck. Average estimates of Tajima's D for simulated ancient samples were approximately zero, as expected. The average Tajima's D estimates for simulated modern samples were positive, as expected for populations that have undergone a bottleneck. The more intense the bottleneck, the greater were deviations from population equilibrium and hence the larger were Tajima's D values.

Both bottleneck intensity and effective population size influence P_m and P_t (Table 1) when gene diversity is considered. For $\theta = 0.2$ and 0.5 (which corresponds to $N_e = 10\,000$ and 25 000, e.g. as estimated in humans and common chimpanzees, Jensen-Seaman *et al*. 2001) the discrepancy between the modern and temporal approaches is relatively high, with the modern approach having no power at any bottleneck intensity. At $\theta = 1.0$ and higher [which corresponds to $N_e \geq 50\,000$ and higher, e.g. as estimated for leopards (Spong *et al*. 2000), Southern elephant seals (Slade *et al*. 1998) and in small mammals (Hadly *et al*. 2004)] the two approaches provide similar power. Additionally, the power to detect intense bottlenecks is higher for large θ ($\theta = 5.0$, $n = 20$, $P_m = 0.874$, $P_t = 0.928$) than for smaller effective sizes ($\theta = 0.5$, $n = 20$, $P_m = 0$, $P_t = 0.621$). For lower $\theta \leq 0.5$, Tajima's D provides no power with either the modern or temporal approach. For $\theta \geq 1.0$, both modern and temporal approaches provide power, but the difference between P_t and P_m is not significant. In general, gene diversity provides more power to detect population bottlenecks than does Tajima's D. P_m and P_t increase with sample size for gene diversity and Tajima's D. Power increases significantly with sample size for Tajima's D. For gene diversity, increase in P_t is only marginal for $n > 20$.

Recovery from the bottleneck

When populations have recovered from a bottleneck via population growth [e.g. as in many species of seals and sea lions (Weber *et al*. 2004)], P_t is greater than P_m (Fig. 1) for both gene diversity and Tajima's D. However, models with population growth result in lower power for both summary statistics than do models without growth. When populations have recovered from a bottleneck via immigration, e.g.

Table 1 Power based on the modern and temporal approach for gene diversity and Tajima's D (P_{mgd} and P_{tgd} and P_{mtd} and P_{ytd}, respectively) for different parameter values [θ and sample size (n)] and models (nr: no recovery after population bottleneck, bottleneck intensity)

θ	Model	n	P_{mgd}	P_{tgd}	P_{mtd}	P_{ttd}
0.2	nr, 0.99	10	0	0.229	0	0.02
0.2		20	0	0.320	0.001	0.016
0.2		50	0	0.345	0.001	0.01
0.2		100	0	0.305	0.001	0.022
0.2	nr, 0.95	10	0	0.271	0.14	0.026
0.2		20	0	0.299	0.011	0.026
0.2		50	0	0.299	0.006	0.024
0.2		100	0	0.336	0.014	0.054
0.2	nr, 0.90	10	0	0.235	0.019	0.051
0.2		20	0	0.272	0.035	0.041
0.2		50	0	0.320	0.023	0.048
0.2		100	0	0.334	0.036	0.059
0.2	nr, 0.50	10	0	0.103	0.82	0.077
0.2		20	0	0.12	0.064	0.065
0.2		50	0	0.135	0.056	0.070
0.2		100	0	0.101	0.074	0.097
0.5	nr, 0.99	10	0	0.412	0	0.001
0.5		20	0	0.621	0.004	0.042
0.5		50	0	0.657	0.001	0.06
0.5		100	0	0.692	0.004	0.083
0.5	nr, 0.95	10	0	0.323	0.037	0.036
0.5		20	0	0.481	0.034	0.099
0.5		50	0	0.525	0.049	0.096
0.5		100	0	0.603	0.069	0.148
0.5	nr, 0.90	10	0	0.219	0.049	0.046
0.5		20	0	0.352	0.124	0.143
0.5		50	0	0.376	0.117	0.166
0.5		100	0	0.429	0.139	0.223
0.5	nr, 0.50	10	0	0.065	0.059	0.05
0.5		20	0	0.113	0.128	0.105
0.5		50	0	0.13	0.143	0.114
0.5		100	0	0.187	0.145	0.145
1.0	nr, 0.99	10	0	0.638	0.014	0.005
1.0		20	0.89	0.827	0.007	0.037
1.0		50	0.91	0.857	0.014	0.116
1.0		100	0.93	0.889	0.017	0.187
1.0	nr, 0.95	10	0	0.305	0.125	0.1
1.0		20	0.391	0.467	0.13	0.154
1.0		50	0.39	0.573	0.185	0.314
1.0		100	0.392	0.645	0.231	0.414
1.0	nr, 0.90	10	0	0.171	0.121	0.103
1.0		20	0.218	0.286	0.152	0.276
1.0		50	0.195	0.361	0.168	0.436
1.0		100	0.209	0.444	0.223	0.565
1.0	nr, 0.50	10	0	0.064	0.093	0.304
1.0		20	0.073	0.067	0.061	0.072
1.0		50	0.062	0.088	0.099	0.045
1.0		100	0.055	0.126	0.108	0.05
2.0	nr, 0.99	10	0.817	0.823	0.068	0.066
2.0		20	0.834	0.906	0.091	0.154
2.0		50	0.841	0.956	0.09	0.255
2.0		100	0.869	0.967	0.125	0.331
2.0	nr, 0.95	10	0.124	0.307	0.183	0.198
2.0		20	0.255	0.442	0.21	0.294
2.0		50	0.261	0.559	0.328	0.513
2.0		100	0.306	0.694	0.353	0.644
2.0	nr, 0.90	10	0.269	0.259	0.092	0.157
2.0		20	0.157	0.261	0.152	0.153
2.0		50	0.134	0.336	0.276	0.169
2.0		100	0.169	0.376	0.266	0.223
2.0	nr, 0.50	10	0.021	0.073	0.091	0.078
2.0		20	0.067	0.089	0.083	0.074
2.0		50	0.055	0.094	0.082	0.058
2.0		100	0.076	0.136	0.064	0.079
5.0	nr, 0.99	10	0.837	0.632	0.251	0.184
5.0		20	0.874	0.928	0.331	0.386
5.0		50	0.959	0.974	0.431	0.564
5.0		100	0.967	0.993	0.515	0.653
5.0	nr, 0.95	10	0.21	0.15	0.16	0.17
5.0		20	0.25	0.32	0.214	0.31
5.0		50	0.303	0.5	0.319	0.528
5.0		100	0.37	0.752	0.434	0.663
5.0	nr, 0.90	10	0.065	0	0.095	0.125
5.0		20	0.107	0.162	0.151	0.276
5.0		50	0.151	0.232	0.195	0.386
5.0		100	0.171	0.496	0.215	0.463
5.0	nr, 0.50	10	0.034	0.014	0.06	0.29
5.0		20	0.043	0.06	0.076	0.136
5.0		50	0.063	0.06	0.075	0.07
5.0		100	0.069	0.133	0.079	0.099

possible effects of glacial cycles (Hofreiter *et al*. 2004) or impact of climate change on a particular population (Hadly *et al*. 2004), the discrepancy between approaches is correlated with bottleneck intensity. For intense bottlenecks (> 0.75), P_t is lower for models with gene flow than for those without gene flow. For less intense bottlenecks (< 0.75), P_t is higher for models with gene flow than for models without gene flow. Similar trends are observed for both summary statistics.

Sensitivity analyses

Simulations at different mutation rates reveal that for both statistics, P_t and P_m increase with mutation rate (see Supplementary material). For high mutation rates (50%/Myr/bp), the modern and temporal approaches provide very similar power. The timing of the bottleneck has a significant impact on power. For gene diversity, the difference between P_t and P_m is highest for older bottlenecks, while for Tajima's D, the difference between P_t and P_m is highest for intermediate bottleneck ages (Fig. 2).

Discussion

Our goal was to evaluate the statistical power to detect population bottlenecks using genetic data. Using serial

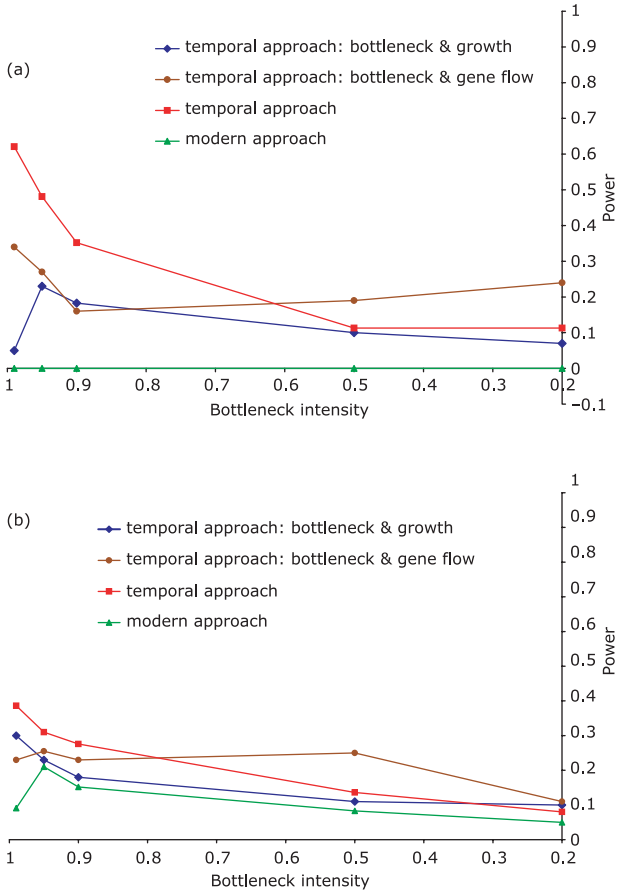

Fig. 1 Power ($n = 20$) to reject a null hypothesis of constant population size for an intense (0.95) bottleneck. Figure reveals power for bottleneck followed by demographic recovery (exponential growth to prebottleneck size) and genetic recovery (immigration into the bottlenecked population for 500 generations). Power based on both the modern (based on only modern data) and temporal (based on modern and ancient data) DNA approaches using (a) gene diversity [simulations are for $\theta = 0.5$ ($N_e = 25\,000$)] and (b) Tajima's D [simulations are for $\theta = 2.0$ ($N_e = 100\,000$)] are shown. Power for models with no demographic recovery is also shown. Simulations assume mutation rate = 3.3%/million years/bp and sequence length = 300 bp.

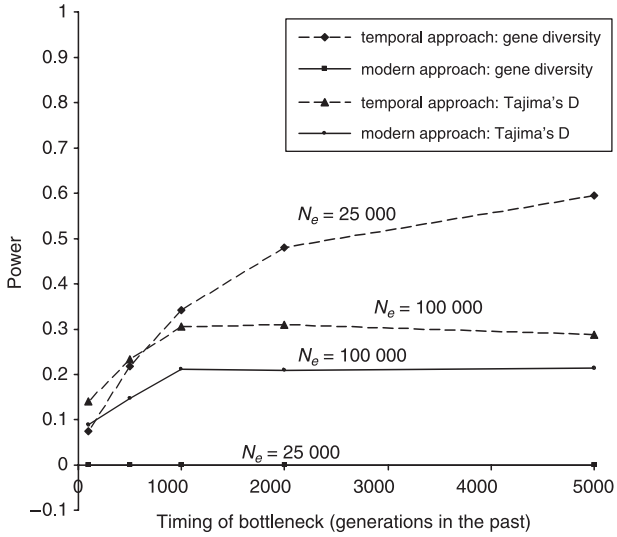

Fig. 2 Power to reject the null hypothesis of constant population size for different bottleneck times in the past (5000, 2000, 500, 200 and 100 generations before present) using the modern and temporal approach for gene diversity ($\theta = 0.5$, $N_e = 25\,000$) and Tajima's D ($\theta = 2.0$, $N_e = 100\,000$). All models assume a bottleneck intensity of 0.95 and a sample size of 20.

coalescent simulations of a broad range of demographic models we inferred the population histories that correspond to an increase in power with the addition of ancient DNA. We present plausible situations where modern data alone provide no power to detect prior history of population size change, and outline the increase in statistical power that ancient data provide.

Simulations demonstrated the difficulty of detecting past population size reductions of ≤ 50%, using either the modern or temporal approach. In the case of more intense events (> 50% reduction in population size), however, the temporal approach can be used to reject a constant population size. Our results corroborate other studies by demonstrating that with severe bottlenecks (> 90% reduction in population size) and for large effective sizes, the modern approach can be effective in rejecting the null hypothesis of constant size.

For gene diversity in 60% of the cases where modern data fail to reject the null hypothesis, the temporal approach is successful given certain models. Simulations revealed that analysis based on 20 ancient and 20 modern samples almost always provides more power than analysis based on 100 modern samples. For Tajima's D, the temporal approach provides up to twice as much power as the modern approach. In general, gene diversity provides more power than does Tajima's D for both the modern and temporal approaches; Tajima's D rarely provides a power higher than 0.2. Differences between results for Tajima's D and gene diversity suggest that these two statistics might provide complementary information. For example, under the temporal approach, rejection of the null hypothesis of constant size based on gene diversity, without rejection of the null hypothesis based on Tajima's D, is consistent with a small population having undergone a relatively recent bottleneck.

Sample size has little impact on the power of both the modern and temporal approaches. Sample sizes on the order of 20 should be adequate to investigate past population processes involving bottlenecks and efforts to increase modern sample size are much less valuable than using fewer but ancient samples (as long as they are prior to the bottleneck event). This is very encouraging for ancient DNA studies and for studies using museum specimens where collecting large numbers of samples is often difficult.

For lower θ (≤ 0.5), the complete failure of the modern DNA approach to detect a population bottleneck reflects two factors. First, the modern sample for the bottleneck scenarios often has a gene diversity of zero for the sequence lengths we investigated. The postbottleneck size is very small and the lineages coalesce relatively quickly. These short branch lengths in combination with a low mutation rate result in few haplotypes and very low diversity. Second, due to sampling effects, the 5th percentile of the null distribution (constant population size) of gene diversity for the modern sample is zero. For θ ≤ 0.5 it is therefore not possible to reject the null hypothesis. As a result, for these effective sizes the temporal approach provides much more power.

The advantages of the temporal DNA approach are highlighted in the models of genetic recovery (gene flow) following a bottleneck. Gene flow increases power because the hypothesis-testing approach allows rejection of a closed population. With gene flow, gene diversity remains high particularly when the bottleneck is not very intense. Thus, even for moderately intense bottlenecks followed by gene flow, the temporal approach provides far more power than the modern approach for detecting evolutionary history. The increased value of P_t is dependent on levels of pre- and postbottleneck gene flow. We modelled a change from $N_em = 0$ (prebottleneck) to $N_em = 5$ (postbottleneck). Larger changes in N_em will result in further increased P_t and smaller changes in N_em will decrease P_t.

Sensitivity analyses revealed that temporal DNA approaches are particularly valuable in the context of intermediate mutation rates (e.g. a mutation rate of 10–15 times that of cytochrome *b*, as has estimated for the mtDNA control region, Pesole *et al*. 1999). Additionally, gene diversity is more sensitive to higher mutation rate than is Tajima's *D*. For more slowly evolving genetic regions such as cytochrome *b* (2–6%), temporal DNA data can be informative regarding population history when samples are separated by thousands of generations. Few published single population temporal DNA studies span such a timescale (e.g. Hadly *et al*. 1998, 2004). Our study indicates that for sampling intervals on the order of a few hundred generations, rapidly mutating regions in the mitochondrial genome (e.g. control region) would provide more power, and for these situations, Tajima's *D* will provide more power than will gene diversity.

Our analyses are also instructive in the context of detecting population bottlenecks using only modern genetic samples. For example, consider a true population history including a 95% bottleneck for a study population with low θ = 0.5. If the data include sequence from 300 bp of a mitochondrial coding gene (i.e. lower mutation rate) for 20 modern samples, power to reject the null hypothesis will be zero. If ancient sampling is not possible, should the researcher (i) increase sample size, (ii) add a marker from a genetic region with higher mutation rate, or (iii) increase sequence length? Our simulations demonstrate that adding 30 samples (total sample size = 50) will not increase the power. Adding 300 additional base pairs of sequence (600 bp of a coding mitochondrial gene for 20 samples) will increase power to 0.39. But the highest gain in power (0.61) will be if an additional marker with higher mutation rate (10%/Myr/bp) is sequenced (for 300 bp and 20 samples).

Serial coalescent simulations revealed that under many conditions, ancient DNA sequence data significantly improve the power to infer past population processes. Using a hypothesis-testing framework, we demonstrated that the advantage conferred by ancient sampling depends on the summary statistic, effective population size, mutation rate and bottleneck intensity, and less so on the sample size. Demographic recovery (modelled as exponential population growth) after a population bottleneck is consistent with less power to reject the null hypothesis of constant size. However, genetic recovery (via immigration) after a population bottleneck is consistent with greater power to reject the null hypothesis. These results demonstrate the value of ancient DNA in the investigation of past population processes.

Acknowledgements

We thank M. van Tuinen, Y. Chan, K. O'Keefe, S. Cohen and three anonymous reviewers for comments on an earlier version of this manuscript. We thank A. Horsburg and C. Roseman for helpful discussions and S. Reddy for programming assistance. This work was partially supported by an NSF grant DEB #0108541 to E. Hadly and J. Mountain.

Supplementary material

The supplementary material is available from http://www.blackwellpublishing.com/products/journals/suppmat/MEC/MEC2586/MEC2586sm.htm

Table S2. Power based on the modern and temporal approach for gene diversity (P_{mgd} and P_{tgd} and P_{mtd} and P_{ytd} respectively) and its sensitivity to mutation rate (m) for two effective sizes (25 000 for gene diversity and 100 000 for Tajima's *D*)

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Uma Ramakrishnan investigates patterns of genetic variations in human and animal populations, and the clues they provide into past history. Elizabeth Hadly examines how population biology, ecological process, history of lineage and climate interact to influence past, present and future biodiversity in terrestial vertebrates, particularly mammals. Joanna Mountain's research focuses on the origins and implications of human genetic diversity. Dr Mountain combines genetic and non-genetic data to infer population history, emphasizing the relatively understudied continent of Africa.
