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Cultural specialization and genetic diversity: Killer whales and beyond

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ABSTRACT

Culturally-transmitted ecological specialization can reduce niche breadths with demographic and ecological consequences. I use agent-based models, grounded in killer whale biology, to investigate the potential consequences of cultural specialization for genetic diversity. In these models, cultural specialization typically reduces the number of mitochondrial haplotypes, mitochondrial haplotype diversity, mitochondrial nucleotide diversity, and heterozygosity at nuclear loci. The causal route of this decline is mostly indirect, being ascribed to a reduction in absolute population size resulting from cultural specialization. However, small group size exacerbates the decline in genetic diversity, presumably because of increased founder effects at the initiation of each cultural ecotype. These results are concordant with measures of low genetic diversity in the killer whale, although culturally-transmitted ecological specialization alone might not be sufficient to fully account for the species' very low mitochondrial diversity. The process may also operate in other species.

1. Introduction

Culture (i.e., behavior transmitted by social learning) can affect genetic diversity (Creanza and Feldman, 2016; Premo, 2012; Whitehead et al., 2019). One potential method is culturally-mediated migration in which the population is subdivided culturally (Premo and Hublin, 2009). For instance the cultures held by individuals or groups may determine migrations or acceptable mates, leading to a subpopulation structure, which in turn can lower overall genetic diversity through processes such as bottlenecks (Premo and Hublin, 2009). Genetic diversity can also be reduced if selection on cultural traits reduces the diversity of neutral genes that are transmitted in parallel with the cultural traits, a process known as cultural hitchhiking (Whitehead, 1998). Conversely, the diversity of functional genes, and neutral genes that hitchhike on them, can be increased through novel selection pressures introduced by cultural practices that affect different population segments (Creanza and Feldman, 2016). These processes have been suggested as drivers of unusual patterns of genetic diversity in patrilineal humans (Creanza and Feldman, 2016; Whitehead et al., 2002) and whales with matrilineal social systems (i.e., in which daughters typically spend their lives with mothers and share cultural practices with their matrilineal relatives) (Whitehead et al., 2017).

An important form of cultural evolution is cultural specialization in which groups of animals narrow their niche breadths as they learn specialized diets or foraging methods from other group members. This can lead to individuals or groups possessing particularly constrained diets, and may have important ecological and evolutionary implications (Ford et al., 2010; Riesch et al., 2012; Tinker et al., 2009; Whitehead and Ford, 2018).

Here, I use agent-based models to consider whether the process of cultural specialization can affect genetic diversity. The models are constructed from the perspective of the killer whale (*Orcinus orca*), a species for which cultural specialization has been particularly important. Killer whales are divided into ecotypes that differ fundamentally in diet. Many ecotypes have extreme specializations, sometimes concentrating on just one species of prey even though closely-related and often more abundant species are available (Riesch et al., 2012). The diet of the species as a whole, however, is extremely diverse and ranges from small fish to large whales (Riesch et al., 2012). There is strong evidence that the segregation of killer whale ecotypes was initiated by the cultural specialization of matrilineal groups (Riesch et al., 2012), although the evolutionary history of killer whale ecotypes seems a complex pattern of admixture and vicariance (Foote et al., 2019).

Agent-based models suggest that cultural specialization in killer whales might be expected to reduce overall population size and resource abundance but increase group extirpation rates, trends which seem consistent with understanding of the species (Whitehead and Ford, 2018). Compared with non-matrilineal cetacean species of similar geographical ranges, killer whales possess remarkably low mitochondrial DNA diversity (Whitehead et al., 2017). However, the numbers of alleles at nuclear microsatellite loci are not much reduced com-

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pared with species of similar population sizes (Whitehead et al., 2017).

The formation of ecotypes through cultural specialization could have had an influence on genetic diversity through several processes. These include: genetic bottlenecks resulting from few ecotype originators (Foote et al., 2016); competition between protoecotypes, either among those with similar ecological niches or more generally (i.e., "classical" cultural hitchhiking (Whitehead et al., 2017)); population segregation as a consequence of ecotype formation (i.e. "culturally-mediated migration" (Premo and Hublin, 2009)); or the reduction in population size that seems to be a general outcome of cultural specialization (Whitehead and Ford, 2018).

This paper uses a modification of an agent-based killer whale-based cultural specialization model (Whitehead and Ford, 2018) to examine whether such processes are likely to influence species-wide genetic diversity in either the mitochondrial or nuclear genomes. Natural selection for niche breadth, in which the position and breadth of the resource consumption function of an offspring is heritable but slightly different from that of its parent(s), is another potential route to specialization (e.g., Doebeli et al., 2007; Taper and Chase, 1985). A modification of the model investigates whether natural selection for niche breadth has similar effects on genetic diversity to cultural specialization.

2. Methods

I use agent-based models to investigate the relationship between cultural specialization and genetic diversity. While the agents represent individuals, they are aggregated into kin-based groups. All members of a group share resource use parameters and dynamics. Therefore, ecological aspects of the modelling are carried out at the group level. Some elements of the modelling are taken directly from the equations of Whitehead and Ford (2018) who investigated demographic and ecological effects of cultural specialization. These elements are summarized here with reference to the relevant equations in Whitehead and Ford (2018). Changes and additions are described completely, including the genetic modelling. Table 1 lists the model parameters.

2.1. Dynamics of killer whale demography and resources

Each of M resource types, j, is normally distributed on a [0,1] unidimensional resource axis, with mean p_j, SD w_j, and overall abundance $a_j(t)$ at timestep t. The overall distribution of resources, $R(t,x)$ is illustrated by the lower panels of Fig. 1 of Whitehead and Ford (2018). The dynamics of resource distribution are a result of consumption by the agents (see below) and logistic resource renewal at rate π (see Eq. (4) of Whitehead and Ford (2018)). Stochasticity in resource dynamics is explored in Appendix A.

The sex-structured agent population is composed of $G(t)$ groups at time t. Group i has group size $n_i(t)$ and its members all have an identical normally-distributed resource use function (mean $c_i(t)$; standard deviation $d_i(t)$) on the resource axis at time t. $d_i(t)$ represents the niche breadth, indicating the degree of specialization (Egas et al., 2005).

The consumption potential of group i on resource j in time step t, $CP(i,j,t)$, is the product of the abundance of the resource ($a_j(t)$), group size ($n_i(t)$) and the probability distribution of the resource multiplied by the resource use function, as in Eq. (2) of Whitehead and Ford (2018). The actual consumption is adjusted so that the amount of resource consumed by an individual is less than 1, and the total amount of resource j consumed is less than $a_j(t)$ (see Eq. (3), and two subsequent unnumbered equations of Whitehead and Ford (2018); these adjustments occur very rarely in practice).

Each time step, individuals die with probability 1-$r_{\min}$ and, if they are female, reproduce one offspring with probability

$$\Pr(reproduce\ if\ female) = \frac{2\cdot(r_{\max}-r_{\min})\cdot\sum_j CP(i,j,t)/n_i(t)}{\left(\sum_j CP(i,j,t)/n_i(t)+q\right)} \quad (1)$$

This gives a population increasing by a factor of $r_{\max}$ per time step with unlimited resources and decreasing by $r_{\min}$ per time step with almost no resources. The parameter q indicates the dependency of population change on per capita resource capture.

Groups become extirpated when $n_i(t+1)=0$, resulting in $G(t+1)=G(t)-1$. Groups that grow sufficiently large such that $n_i(t+1)>N$, where N is the maximum group size, divide to produce two daughter groups with slightly separated mean resource consumptions, but the same SD's (see two unnumbered equations between equations 5 and 6 of Whitehead and Ford (2018)).

2.2. Genetic profiles and mating

Each new offspring has a sex, male or female, randomly chosen with equal probability. They retain this sex throughout their life. They also have a mitochondrial haplotype on a sequence of length b base pairs. They inherit this mitochondrial haplotype as well as group membership from their mother. With probability μ_{mit} there is a mutation, leading to a novel 1 base pair change from their mother's haplotype.

Each individual also has a nuclear genotype represented by z binary single-nucleotide-polymorphism (SNP) unlinked loci. At each locus, each new individual receives randomly one allele from its mother and one from its father. There is a mutation rate of μ_{SNP} for each inherited allele.

I consider two mate-selection mechanisms:

a) Fathers are selected randomly from living males (i.e., random mating mechanism).
b) For any offspring, the probability that a living male is its father is proportional to the products of the resource use functions of the mother and that male, but zero if the male and mother are in the same group (i.e., assortative mating mechanism). This represents a situation in which mating does not occur between close relatives, but is usually between animals with similar use of resources, as seems to occur in at least the "resident" ecotype of killer whales (Barrett-Lennard, 2000).

2.3. Cultural specialization

At each time step, each group may change its resource consumption function with probability α. In this case, first the mean of the resource consumption function in the next time period, $c_i(t+1)$, is chosen to optimize the consumption potential (equation 6 of Whitehead and Ford (2018)). Then, the consumption potential in the next time period is calculated for three values of the niche breadth $d_i(t+1)$: unchanged ($d_i(t+1)=d_i(t)$); specialization by a factor $1/s$ ($d_i(t+1)=d_i(t)/s$); and generalization by a factor s ($d_i(t+1)=d_i(t)\cdot s$). Whichever of these produces the highest consumption potential is selected.

Although this process includes the possibility of specialization (narrowing of niche breadth) and generalization (broadening of niche breadth), from now on it will be referred to as "specialization". In runs of the model, specialization predominated while the founder generalist niche breadths narrowed to approximate the width of individual resources on the resource axis (w_j) (Whitehead and Ford, 2018). After this, specialization and generalization had similar and low rates of occurrence.

Table 1
Parameter values chosen for model, as well as the range of values for varied parameters (modified from Whitehead and Ford (2018); changes noted in footnotes).

Parameter		Comments	Standard value	Range
	Varied parameters:			
M	No. resource types	Increases potential population size and no. of ecotypes	32	[16 64]
w	Width of each resource: $w_j = Uniform([w, 2{\cdot}w])$	How far can specialization go?	0.008	[0.004 0.016]
N	Size of groups at splitting	Affects mean group size and other outputs	30	[15 60]
π	Rate of resource renewal (/time step)	Higher resource renewal allows larger population size	0.3	[0.15 0.6]
f	Assimilation rate of resources	Low assimilation rate allows larger population size, more resource depletion; chosen to give a population size in the thousands, as with killer whales (Riesch et al., 2012)	0.00005[a]	[0.000035 0.00007]
q	Dependency of population change on per capita resource capture	Low q allows larger population size	0.00015	[0.00011 0.00021]
α	Rate of innovation (potential specialization) per group per time step		0.002	[0.001 0.004]
s	Reduction in width of resource consumption curve with specialization (increase in width on generalization)	High values decrease specialization rate, but provide large changes	2	[1.4 2.8]
σ_c	Variation of mean value of resource use function from parent to offspring	Reflects inverse of heritability of mean value of resource use function (only natural selection model)	0.005	[0.0025 0.01]
σ_d	Variation of SD of resource use function from parent to offspring	Reflects inverse of heritability of niche breadth (only natural selection model)	0.02	[0.014 0.028]
	Fixed parameters:			
T	Number of time steps		40,000[b]	
p_j	Mean value of resources		*Uniform*([0,1])	
$a_j(0)$	Initial abundance of resources		*Uniform*([0,1])	
$G(0)$	Initial no. groups	Has almost no effect as density dependence, together with group extirpation/splitting process, quickly reaches a fairly stable number of groups and individuals	10	
$d_i(0)$	Initial SD resource consumption potential (niche breadth)	Model assumes initial broad resource breadth	0.3	
$c_i(0)$	Initial mean resource consumption potential	Groups are initially somewhat more efficient near centre of resource distribution, although differences between groups	*Normal*(0.5,0.2)	
r_{min}	Minimal rate of increase in adverse circumstances	Based on decline rate of "Southern Resident" killer whales in poor conditions of 1996–2001	0.9	
r_{max}	Maximal rate of increase in favorable circumstances		1.05[c]	
$h(0)$	Initial number of haplotypes	Chosen to give a reasonable number of haplotypes, but has almost no effect on results, as burn-in runs adjust number of haplotypes towards approximate equilibrium	10	
b	Number of base pairs in mitochondrial sequence	Chosen to give a reasonable number of haplotypes	8000	
μ_{mit}	Mitochondrial mutation rate per base pair during reproduction	From Ho and Lanfear's (2010) estimate for cetaceans, adjusted for a mean reproductive rate of 0.1 per time step.	2.10^{-7}	
z	Number of SNPs sequenced	Chosen to give reasonably stable genetic diversity	50	
μ_{SNP}	SNP mutation rate per base pair during reproduction	Chosen to maintain reasonable genetic diversity	3.10^{-5}	

[a] This is reduced by half from $f = 0.0001$ used by Whitehead and Ford (2018) increasing the population size. The revised model used in this paper is sex specific while the original was asexual, so this change gives similarly-sized breeding populations for the two models.
[b] This is increased from $T = 4000$ used by Whitehead and Ford (2018) to allow genetic diversities to stabilize.
[c] This is increased from $r_{max} = 1.035$ used by Whitehead and Ford (2018) as explained in the main text.

I consider two variants of the model, one with specialization ($\alpha > 0$) and one without ($\alpha = 0$).

2.4. Summary of model

The process in each time step, t, is:

1. Calculate $CP(i,j,t)$, the consumption potential of group i on resource j.
2. Calculate abundance of each resource, j, at next time step $\{a_j(t + 1)\}$.
3. Females reproduce one offspring with probability given by Eq. (1).
4. Offspring have a randomly chosen sex, their mother's mitochondrial haplotype (unless there is a mutation) and are members of their mother's group.
5. Fathers are chosen randomly (random mating) or by ecological overlap with the mother (assortative mating). At each SNP locus they receive one randomly chosen allele from each parent (unless there is a mutation).
6. Individuals die with probability 1-r_{min}.
7. Extirpated groups are removed.
8. Large groups are split.
9. Groups have the option to innovate with probability α. Each of these groups first optimizes the position of the mean of its resource use function, $c_i(t + 1)$, and then they specialize or generalize if the expected CP is increased.
10. The following measures of genetic diversity are calculated at the end of each time step: number of mitochondrial haplotypes; mitochondrial haplotype diversity (the probability that two individuals have different mitochondrial DNA sequences); mitochondrial nucleotide diversity (the mean number of nu-

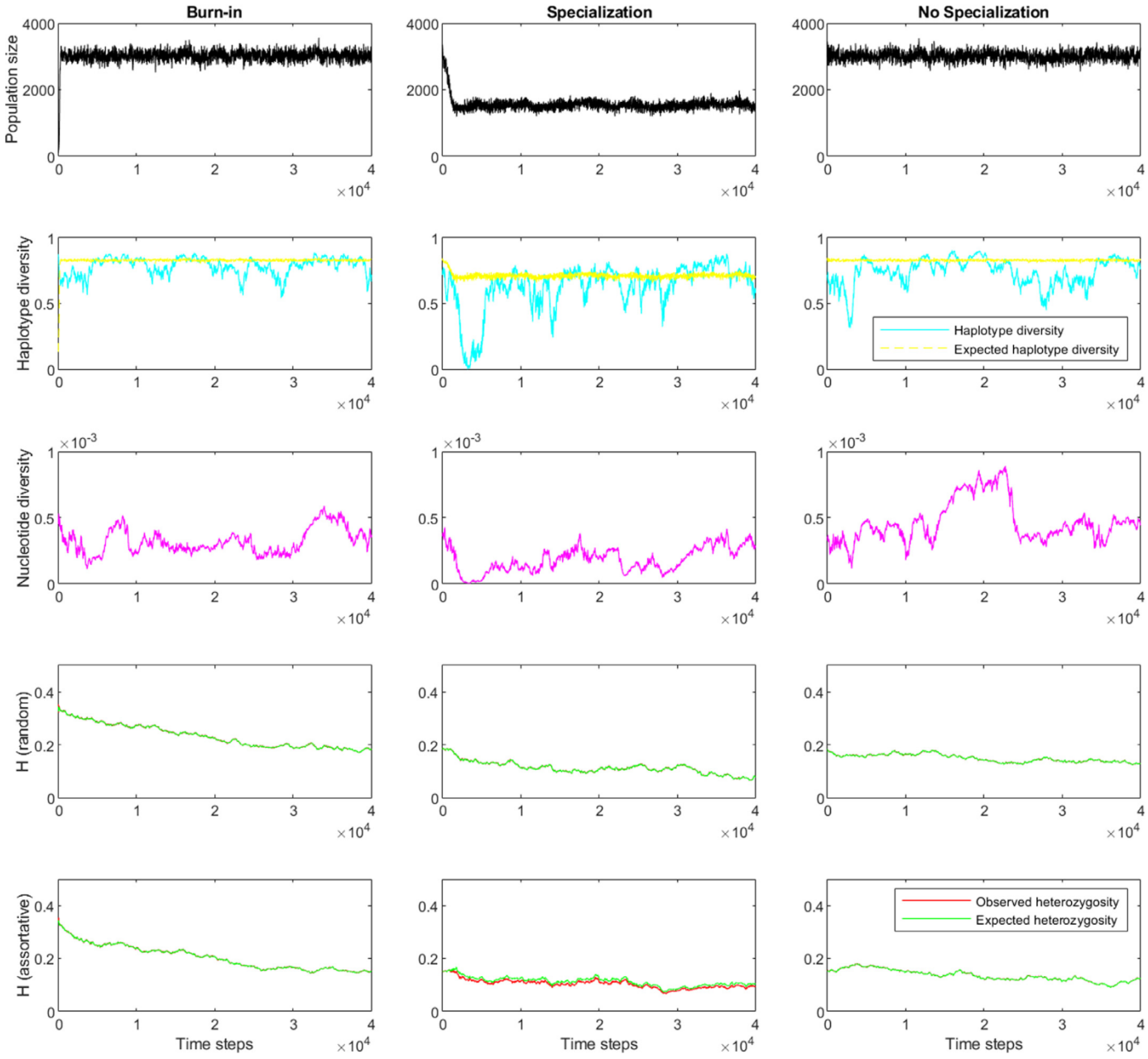

Fig. 1. Temporal trajectories of output measures from a replicate of the model using the standard parameters. The three columns are the burn-in run (without specialization) and then two test runs (each starting from the end of the burn-in run), with and without specialization. The rows give the population size (row 1), mitochondrial haplotype diversity (with expected diversity given population size and mutation rate) (row 2), mitochondrial nucleotide diversity (row 3), and observed and expected heterozygosity of SNPs for random mating (row 4) and assortative mating (row 5). With the exception of the case with assortative mating and specialization, the expected and observed heterozygosities are sufficiently similar that they are plotted on top of one another.

cleotide differences per site in pairwise comparisons between individuals); SNP heterozygosity (the proportion of loci that are heterozygous across individuals and loci); expected SNP heterozygosity (the probability that, at a randomly chosen locus, any two alleles, chosen at random from the population, are different to each other; closely related to nucleotide diversity).

2.5. Parameters of model and running model

The model parameters are listed in Table 1, together with their standard values and the range of variation that was explored. The non-genetic parameters largely follow those in the models of Whitehead and Ford (2018), and approximate what might be expected for killer whale populations if time steps are years. However, r_{max} is increased from 1.035 as used by Whitehead and Ford (2018) to $r_{max} = 1.05$, as the earlier model used a group-based binomial model of reproduction, necessitating some rounding (see equation 5 of Whitehead and Ford (2018)) and led to a small bias in reproductive rate at the group sizes typical of the model runs. Reproduction in the current model (Eq. (1)) does not have this rounding or this bias, and the change in r_{max} approximately aligns the reproductive rates of the two models. There are two other changes in parameters from Whitehead and Ford (2018) for reasons explained in Table 1 footnotes.

Genetic parameters (b, μ_{mit}, z, μ_{SNP}) were chosen to be realistic, as well as to give reasonable baseline genetic diversity and run

times for the models. The most arbitrary choice was in the mutation rate at the SNP loci, μ_{SNP}. However, trial runs with the rate increased by a factor of 10, or reduced by a factor of 10, compared with the standard value ($\mu_{SNP} = 3.10^{-5}$; Table 1), gave similar results.

Each replication of the model begins with the random derivation of the resource spectrum. For each of M resource types, the mean value is chosen randomly from the uniform [0 1] interval, the SD from the uniform [w 2 w] interval, and the overall abundance from the uniform [0 1] interval. Each of the $G(0)$ initial groups has an initial mean resource consumption potential ($c_i(0)$) from a normal random distribution (mean = 0.5, SD = 0.2) and initial SD resource consumption potential of $d_i(0) = 0.3$. Each group initially has $N/3$ members, with individuals equally likely to be of either sex. Initially all members of a group have the same haplotype, selected randomly from $h(0)$ ordered haplotypes, successively 1 base pair different from the previous and subsequent haplotypes in the ordering. Each of the z SNP alleles has an initial minor allele frequency randomly chosen between 0.05 and 0.5. Given these allele frequencies, each initial individual is randomly allocated two alleles at each locus.

The model is then run for T (T = 40,000) time steps without cultural innovation ($\alpha = 0$) to stabilize the demography and genetic variation. Following this burn-in section, the demographic, genetic, and resource data are saved, and used as the starting point for each of two test runs of T time steps, one with cultural specialization ($\alpha > 0$) and one without ($\alpha = 0$). The model generates two SNP datasets for each individual, using random mating and assortative mating respectively. This is feasible as the mating mechanism has no effect on demography, resource dynamics, or mitochondrial genetics of the cultural specialization model. For each test run the following output measures are calculated, all of which are means over the second half of the test run ($T/2$, $T/2 + 1$, ..., T time steps from start of run):

- population size, $\sum_{n_i}(t)$;
- number of mitochondrial haplotypes;
- mitochondrial haplotype diversity;
- expected haplotype diversity (Birky et al., 1983):

$$Ex.\ haplotype\ diversity = \frac{\sum_i n_i(t) \cdot \mu_{mit}}{1 + \sum_i n_i(t) \cdot \mu_{mit}} \quad (2)$$

- mitochondrial nucleotide diversity: the mean, over the mitochondrial sequence, of the proportion of pairs of individuals with different nucleotides;
- heterozygosity of SNPs (calculated separately for random mating and assortative mating mechanisms);
- expected heterozygosity of SNPs given population-wide allele frequencies and Hardy-Weinberg equilibrium (calculated separately for random mating and assortative mating mechanisms).

If the burn-in run or either of the test runs ends in population extirpation, a replication is excluded from subsequent analysis. This left 300 replications of the model (78% of those replications attempted). For each replication, demographic, ecological, and cultural parameters are chosen by multiplying the standard value of the parameter (given in column 4 of Table 1) by 2^u, where u is a uniform random number on the interval [−1 1], except [−0.5 0.5] for parameters f, q, and s, and σ_d (see 2.7), as higher variation in these parameters produces extinctions and/or other unrealistic results (Whitehead and Ford, 2018). Some parameters, including the genetic parameters, are not varied because they are either less relevant to the research questions at hand or there is no expectation that reasonable variation would affect the general trend of the results (Table 1).

2.6. Analysis

Genetic diversity is typically highly related to population size (Birky et al., 1983) and, in the bottleneck scenario proposed for killer whales by Foote et al. (2016), it might be expected to be inversely related to group size, with this perhaps being exacerbated by cultural specialization. I fitted nonlinear models (based upon Eq. (2)) to the measures of genetic diversity for each test run using as predictors total population size at the end of the test run (n), group size at the end of the test run (g) and whether ($X = 1$; $\alpha > 0$) or not ($X = 0$; $\alpha = 0$) there was specialization:

$$Diversity = \frac{\beta_1 n + \beta_2 g + \beta_3 X + \beta_4 g \cdot X}{1 + \beta_1 n + \beta_2 g + \beta_3 X + \beta_4 g \cdot X} \quad (3)$$

For the number of haplotypes, I used a simpler linear model:

$$Number\ of\ haplotypes = \beta_1 n + \beta_2 g + \beta_3 X + \beta_4 g \cdot X \quad (4)$$

2.7. Preliminary investigation of natural selection for niche breadth

In this version of the model, the distribution and dynamics of resources, agents, and genes are as described in 2.1 and 2.2, with the exception that resource use functions are individual-specific rather than group-specific. Then, each newborn, i, possesses a resource use function perturbed slightly from that of its parent(s) ($m(i)$), c_i: Normal($c_{m(i)}$,σ_c), d_i: $d_{m(i)} \cdot e^{\text{Normal}(0,\sigma_d)}$. Here, σ_c and σ_d reflect the inverse of the heritability of the mean values of the resource use functions and logarithmic niche breadths, respectively. Specialization is specified by selection for smaller d_i and generalization by selection for larger d_i. Three inheritance mechanisms are investigated, relating to the mating systems described above:

- "random": random mating, with $c_{m(i)} = (c_{mother} + c_{father})/2$; $d_{m(i)} = (d_{mother} + d_{father})/2$
- "assortative": assortative mating, with $c_{m(i)} = (c_{mother} + c_{father})/2$; $d_{m(i)} = (d_{mother} + d_{father})/2$
- "female inheritance": random mating, with $c_{m(i)} = c_{mother}$; $d_{m(i)} = d_{mother}$

In these models there is no cultural inheritance of niche breadth. The models are run as described above for cultural evolution, except that only one type of mating (random or assortative) was considered for each run (as the mating type affects inheritance of the resource use function with the first two inheritance mechanisms, and thus demography). In the burn-in runs, $\sigma_d = 0$.

3. Results

The trajectories of the output measures are shown for a model replication with the standard parameters (see column 4 of Table 1) in Fig. 1. This instance illustrates the general results from the test runs of 300 model replications with randomly varied parameters (mean output measures in Table 2). The population size quickly stabilizes at the beginning of the burn-in, but when specialization is introduced and niche breadths narrow, population size is substantially reduced (a mean of 45% reduction over all replications; Table 2). Mitochondrial haplotype and nucleotide diversity both vary considerably over each trajectory, with haplotype diversity ranging from a little above to considerably below the theoretically expected level given population size and mutation rate (Eq. (2)). Nuclear SNP diversity is less variable than mitochondrial diversity but takes considerably longer to stabilize in the burn-in section and to decline with specialization. Comparing the specialization test runs with the controls without specialization (Table 2) shows clear reductions in mitochondrial haplotype and nucleotide diversity, as well as nuclear SNP heterozygosity with either random or assortative mating (Table 2). The reduction in heterozygosity is greatest with cultural specialization and assortative mating,

Table 2
Summary of population size and measures of genetic diversity for 300 pairs of test runs (mean over test runs of mean over second half of time steps in each run).

	Specialization	No Specialization	Ratio (Specialization/ No Specialization)
Population size	1901	3450	0.55
Number of haplotypes	14.1	24.4	0.58
Haplotype diversity	0.609	0.715	0.85
Haplotype diversity/Expected haplotype diversity	0.874	0.870	1.00
Nucleotide diversity	0.00022	0.00036	0.63
Expected SNP Heterozygosity (random mating)	0.108	0.158	0.68
Expected SNP Heterozygosity (assortative mating)	0.095	0.154	0.62
Observed / Expected SNP Heterozygosity (random mating)	1.001	1.001	1.00
Observed / Expected SNP Heterozygosity (assortative mating)	0.895	1.001	0.89

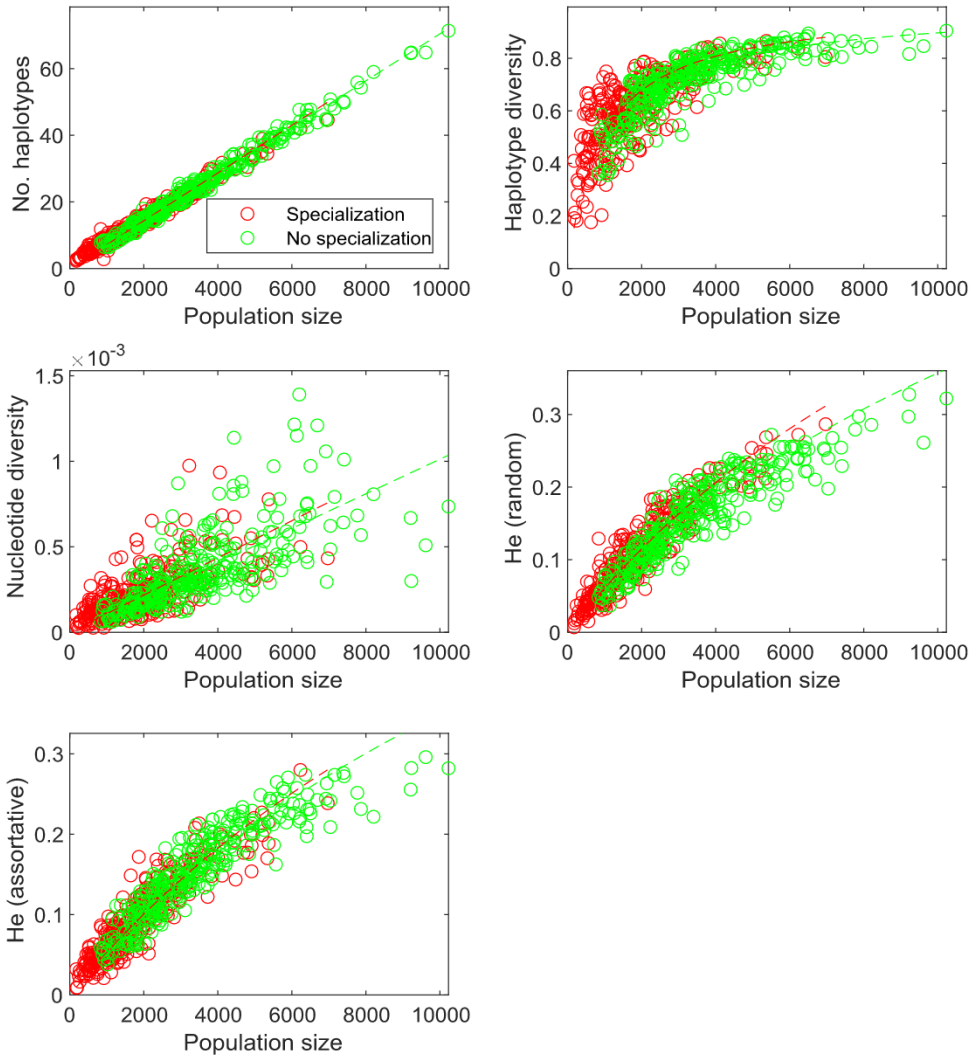

Fig. 2. Relationships between measures of genetic diversity and population size for test runs of model with (red) and without (green) cultural specialization. Fitted models are shown for each measure and treatment Eqs. (3) and ((4) with $\beta_2 = \beta_3 = \beta_4 = 0$). He is expected heterozygosity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and this, as might be expected, is the only scenario in which there are indications of departure from Hardy-Weinberg equilibrium (indicated by a reduction in observed heterozygosity below expected heterozygosity; Table 2; Fig. 1).

Thus, the process of cultural specialization generally reduces genetic diversity, but how? That the trajectories of mitochondrial haplotype diversity for both the specialization and control runs are similarly placed with respect to the predicted haplotype diversity given population size Fig. 1; 2nd row of plots) provides a hint. But when the measures of genetic diversity are plotted against population size (Fig. 2), it becomes clear that population size is a much better predictor of genetic diversity than whether cultural specialization has been operating. Due to the broad parameter space explored, there is a considerable range of population sizes where there are measures of genetic diversity from both specialization runs and control runs. Fitted nonlinear models (simplified versions of Eqs. (3) and ((4) run separately for the control and specialization test run data without considering group size; i.e. $\beta_2 = \beta_3 = \beta_4 = 0$)

Table 3
Results of nonlinear models of measures of genetic diversity: regression coefficients and *P*-values of *t*-tests for significance of factor in model.

Measure of genetic diversity	Regression coefficient (*P* value)			
	Population size	Group size	Specialization	(Group size) X (Specialization)
Number of haplotypes	0.006871 ($P = 0.000$)	0.046703 ($P = 0.000$)	0.082146 ($P = 0.728$)	0.026537 ($P = 0.158$)
Haplotype diversity	0.000820 ($P = 0.000$)	0.004579 ($P = 0.168$)	−0.283622 ($P = 0.000$)	0.041350 ($P = 0.000$)
Nucleotide diversity	0.000000 ($P = 0.000$)	0.000003 ($P = 0.000$)	−0.000013 ($P = 0.580$)	0.000002 ($P = 0.401$)
Expected heterozygosity (random mating)	0.000054 ($P = 0.000$)	0.000787 ($P = 0.000$)	0.027940 ($P = 0.000$)	−0.001258 ($P = 0.001$)
Expected heterozygosity (assortative mating)	0.000049 ($P = 0.000$)	0.001237 ($P = 0.000$)	0.005037 ($P = 0.259$)	−0.000522 ($P = 0.148$)

are shown for each diversity measure against population size in Fig. 2. There is no clear indication that the specialization runs had lower diversity than the control runs given population size (Fig. 2).

In the fully fitted non-linear models Eqs. (3) and (4), population size was the most important predictor of the measures of genetic diversity, but the coefficients for group size were also all positive and nearly all statistically significant (at $P < 0.05$; Table 3). Thus, genetic diversity increases with both population size and group size. The residual effects of specialization and its interactions with group size are less consistent in direction and mostly not statistically significant. However, with specialization operating, haplotype diversity is more greatly reduced than would be predicted by low population and group size, and this extra decrease is especially strong at small group sizes (Table 3). Therefore, there is particularly low haplotype diversity at small group sizes with specialization. For nuclear heterozygosities, especially with random mating, these effects are reversed (Table 3).

To examine the influence of variation in input parameters on output diversity measures, I correlated the input parameter values (M, w, N, π, f, q, α, s) with the residuals, after fitting the models in Eqs. (3) and (4), for the specialization test runs of each replication of the model. The absolute magnitudes of these correlations were all less than 0.23, suggesting that the input parameter values had little residual impact on genetic diversity.

Using the standard values of the parameters (column 3 of Table 1), an altered version of the model added stochasticity to the renewal rates of the different resources (π), or their carrying capacities $a_j(0)$, or both (as described in Appendix B of Whitehead and Ford (2018)). There is no indication that stochastic variation in resource abundance changes measures of genetic diversity, given population and group size and the presence or absence of specialization (Appendix A).

The preliminary investigations of the potential effects of natural selection of niche breadth on genetic diversity used the modification of the cultural evolution model described in 2.7. With either random or assortative mating and niche breadth being a quantitative multi-locus trait inherited equally from both parents, there was no evolutionary reduction in niche breadth and no demographic or genetic consequences in these simulations. With niche breadth inherited entirely from the mother and random mating, there was selection for specialization so that niche breadth and population size were reduced (as in Whitehead and Ford (2018)). In this scenario, the number of mitochondrial haplotypes and nuclear heterozygosity were reduced by natural selection for niche breadth, as might be expected given the lower population size (Fig. 3). However, mitochondrial haplotype and nucleotide diversity generally increased (Fig. 3), in this case presumably because of linkage to selected genes.

4. Discussion

4.1. Cultural specialization and genetic diversity

Heterogeneous environments may promote the evolution of specialization through either genetic (Van Tienderen, 1991) or cultural (Whitehead and Ford, 2018) inheritance. That specialization promotes functional genetic diversity is suggested by theory (Lewontin, 1974) and supported by empirical and theoretical evidence (Jasmin and Kassen, 2007; Kassen, 2002). The consequences of specialization in the face of environmental heterogeneity for the diversity of neutral genes have received much less attention, even though supposedly neutral genes (such as the mitochondrial D-loop and microsatellites) are frequently used as measures of genetic diversity and in analyses of its implications (such as effective population size) and consequences (such as ecological resilience (Whitlock, 2014)).

With cultural specialization, no genes are directly involved in the specialization, so that all are essentially neutral, although some could hitchhike on selective cultural variants that are being transmitted in parallel (i.e. cultural hitchhiking, Whitehead, 1998). The analyses in this paper suggest that cultural specialization generally reduces both mitochondrial and nuclear genetic diversity.

However, this reduction is very largely a consequence of the smaller size of specialized populations. Specialization typically leads to more intense use of some resources, reducing prey abundance well below maximum sustainable yield levels. Other resources are neglected by the specialist predators. These effects reduce overall population size for specialist predators compared with generalists (Whitehead and Ford, 2018). Theoretically, and in practice, population size is an important determinant of genetic diversity (Frankham, 1996), although, in the case of mitochondrial DNA, perhaps not as much as once thought (Bazin et al., 2006; Vachon et al., 2018).

After population size, the models suggest that the second most important predictor of genetic diversity is group size. As cultural specialization takes place at the group level, new resource use profiles are group-specific and held by the members of the group. Thus, if group size is small, the phenotype and the genes that relate to that phenotype are maintained in just a few individuals. This means that the importance of founder or bottleneck effects within ecotypes is inversely proportional to group size. Thus, genetic diversity within ecotypes will tend to negatively relate with group size, and, when aggregated over the population, so will overall genetic diversity. This fits with ideas suggested by Foote et al. (2016) for killer whales.

The results of the models indicate an additional effect: specialization may further reduce mitochondrial haplotype diversity below that predicted by low population and group size, with this reduction particularly important when group size is small. This may, at least partially, be the result of classical cultural hitchhiking whereby particular haplotypes are promoted or disfavored due to their linkage with selected cultural traits (Whitehead, 1998), in this case niche position and breadth.

4.2. Genetic diversity and the killer whale

The species for which we have best evidence that cultural specialization has operated in important ways is the killer whale (see Riesch et al., 2012). In Vachon et al.'s (2018) analysis of genetic diversity among cetacean species, latitudinal range (an index of

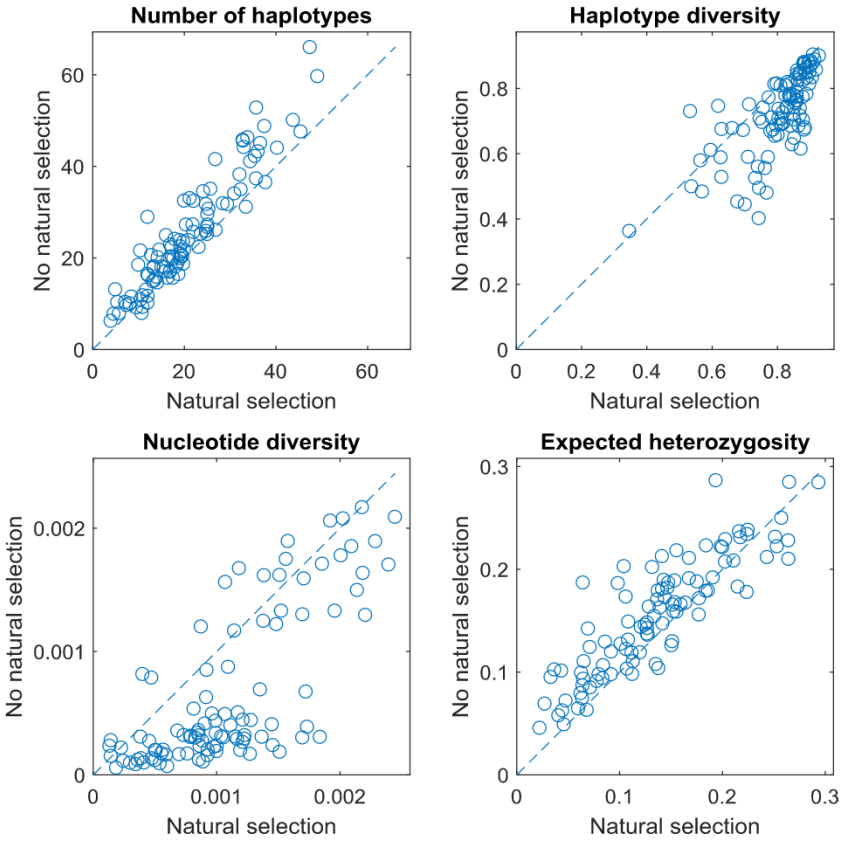

Fig. 3. Comparison of measures of genetic diversity from 100 model replications for runs with and without natural selection of niche breadth. The dashed line indicates the expected relationship if natural selection of niche breadth has no effect on genetic diversity.

habitat diversity) and the presence of a matrilineal social system together provided a better predictor of mitochondrial diversity than population size. Mitochondrial diversity increased with latitudinal range, but was particularly low for species with matrilineal social systems, including the killer whale. The cultural specialization process modeled here could explain some, but perhaps not all, of this discrepancy: the mitochondrial nucleotide diversity of the killer whale is reduced by approximately 90% from what might be expected for a cetacean species with its latitudinal range (Vachon et al., 2018), whereas the simulations in this paper suggest that cultural specialization reduces mitochondrial nucleotide diversity by a mean of about 37% (Table 2). Cultural hitchhiking on non-dietary socially-learned behavior, or non-cultural processes such as direct selection on the mitochondrial DNA (Mesnick et al., 1999) and/or purely demographic bottlenecks (Hoelzel et al., 2002), could explain the remainder of the diminution. Alternatively, in runs of the model, mitochondrial haplotype diversity varied considerably over time, especially with specialization (e.g., Fig. 1, row 2, column 2); the very low haplotype diversity of killer whales could be attributable to a trough in the time series with cultural specialization as the primary cause.

Killer whale nuclear diversity, as indicated by the number of alleles at microsatellite loci (corrected for sample size, ascertainment bias, and the general richness of the locus), is about as expected for a cetacean species given its population size, but it is low when the covariate is latitudinal range (Vachon et al., 2018; Whitehead et al., 2017). These results are concordant with the model explored in this paper. Cultural specialization may well have reduced killer whale population size but left it with a large latitudinal range (the largest of any non-human mammal) as groups specialized on different prey types and perhaps used cultural transmission to colonize new niches. Genetic diversity, both mitochondrial and nuclear, would have declined with population size, and therefore appear low relative to latitudinal range.

The reduction of genetic diversity through cultural specialization could have occurred in other species beyond the killer whale. Perhaps the most obvious candidates are the four other species of matrilineal cetacean with abnormally low mitochondrial diversity: the sperm whale (*Physeter macrocephalus*), the short-finned pilot whale (*Globicephala macrorhynchus*), the long-finned pilot whale (*G. melas*) and the false killer whale (*Pseudorca crassidens*) (Whitehead et al., 2017). The sperm whale's population is culturally divided into clans which differ in vocalizations and other behavioral traits (Rendell and Whitehead, 2003; Whitehead and Rendell, 2004). However, the clans seem to show only modest trophic specialization (Marcoux et al., 2007). We do not have candidate specialist groups for the other matrilineal species, and available information suggests that they are not particularly specialist (e.g., Gannon et al., 1997). Another possible candidate is the wolf (*Canis lupus*), a species for which there is evidence of social learning abilities (Range and Virányi, 2013), as well as that trophic specialization affects gene flow (Carmichael et al., 2001).

4.3. Natural selection for specialization: effects on genetic diversity

An alternative route to specialization is natural selection of genetically-heritable niche breadth. This can lead to some of the same demographic consequences of cultural specialization, but typically much more slowly (Whitehead and Ford, 2018). My attempts to model the genetic consequences of this route to specialization for a killer whale-like species were not particularly successful. With random mating or the modelled version of assor-

tative mating, natural selection for niche breadth failed to select for specialization. In theory and in experiments with other species, natural selection can induce specialization, although there is generally a requirement for either uniparental inheritance of niche breadth or assortative mating based upon ecological traits (e.g., Bolnick, 2006; Dieckmann and Doebeli, 1999; Doebeli et al., 2007; Jasmin and Kassen, 2007). However, these studies used simpler systems with fewer resource types. It could be that inducing specialization through selection of biparentally-inherited niche breadth among generalists with many resource types available is less feasible, even with assortative mating. By reducing the number of resource types from 32 to 2 (and increasing the parameter q to maintain population size) there was some reduction in niche breadth, and genetic diversity, with assortative mating and natural selection of niche breadth after 40,000 time steps in 2 runs of the model. However, this scenario is not compatible with the wide variety of potential resource types likely available to the archetype generalist killer whale.

Uniparental genetic inheritance of niche breadth did lead to specialization and changes in genetic diversity. As perhaps would be expected, mitochondrial nucleotide and haplotype diversity were increased, as the mitochondrial gene is transmitted in parallel with those for niche breadth, while nuclear diversity decreased. But uniparental genetic inheritance of niche breadth seems unlikely for the killer whale, or most other vertebrates. Although the evaluation of the genetic consequences of natural selection on niche breadth did not include a full, or even reasonable, range of model options and parameter values, it seems unlikely that natural selection of niche position and breadth can explain the low genetic diversity of the killer whale.

However, cultural specialization and natural selection are not mutually exclusive. Culturally-learned changes in behavior may be followed by genetic selection within the culturally-determined niche, a process known as “genetic assimilation” (West-Eberhard, 2003). This has likely occurred with killer whales. Foote et al. (2016) found genomic signatures of selection for niche-specific traits in killer whale ecotypes. Once niches have been narrowed culturally, and assortative mating maintains genetic variation within defined ecotypes, this is fertile ground for genetic selection and gene-culture coevolution (Whitehead et al., 2019).

5. Conclusion

Agent-based models grounded in the life history and ecology of the killer whale simulated cultural specialization, in which groups of related animals reduce their niche breadth through social learning. Cultural specialization typically reduced the diversity of nuclear and mitochondrial genes. Much of this reduction can be explained because cultural specialization reduces population size, and population size is an important predictor of genetic diversity. However, secondarily, small group sizes predict further reduction in genetic diversity, presumably because there are then fewer founders of specialized trophic ecotypes.

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Hal Whitehead: Conceptualization, Formal analysis, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jtbi.2020.110164.

Appendix A

Fig. A.1

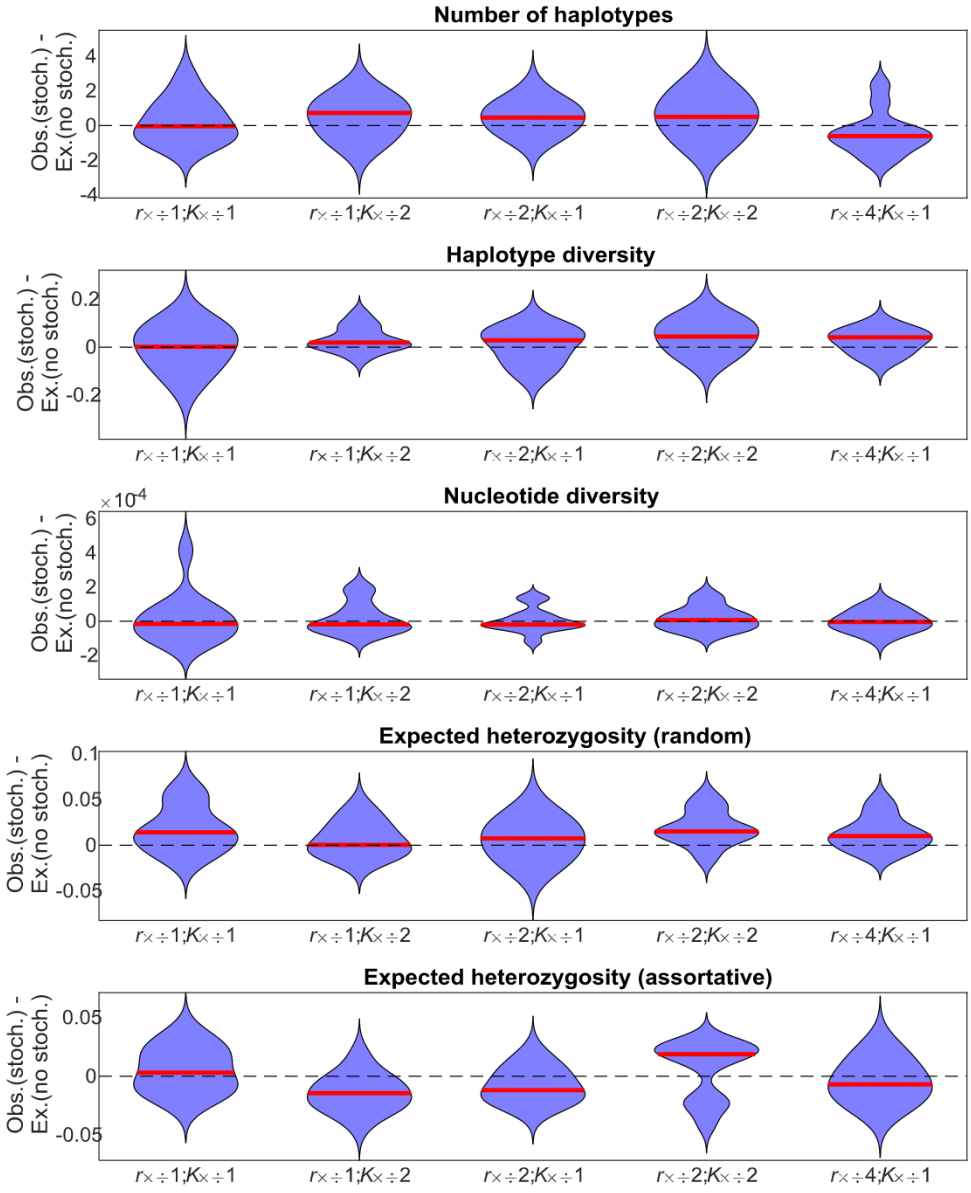

Fig. A.1. Distributions (violin plots) of observed minus expected (from fitted models to runs from replications without stochastic variation in resources as in Eqs. (3) and 4) measures of genetic diversity, for 12 runs each with different types of stochastic variation in renewal rate of resources (r) and carrying capacities of resources (K), with specialization. " × ÷2" indicates varying between half the original value and twice the original value (column 3 of Table 1); " × ÷1" indicates no variation; " × ÷4" indicates varying between 1/4 the original value and four times the original value (only possible for renewal rate; when variability of a factor of four was applied to carrying capacity, populations almost invariably crashed). For details of methods, see Whitehead and Ford (2018).

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