

The Neutral Zone

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Abstract

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Things to do

1. perhaps contact Masden to discuss power
2. Ben to give time series model estimates on simulations
3. Ben to write section on time series estimates
4. add a figure of networks to Box 2 a la Perc

Why are there so many different kinds of things?

The experience of entering a tropical rain forest is very much like that of walking into a great museum. In both, it is easy to be overwhelmed by the sheer abundance, variety and beauty of the things they contain. But the resemblance between living and human-made things runs deeper than our aesthetic responses to them. Plants and paintings are not only immensely diverse, they also appear both to be designed. Contemplate a strangler fig or a painting by Vermeer, and it seems possible to deduce what purposes both their features serve.

Which is why Darwin explained organic diversity as the product of natural selection [29]. His argument, restated, is familiar. A complex world has many niches, ways to make a living. Competition among genetically variable individuals engenders natural selection which fills niches with species adapted to each. The steady state level of diversity, then, depends on the complexity of the environment: how many niches it contains or, to put it another way, how finely species can subdivide resources. As Darwin himself put it, selection's incessant blows drive "ten thousand sharp wedges" into Nature's face.

The argument is familiar because it is one of the mainsprings of ecological and evolutionary theory. Many ecologists have invoked it to explain the diversity of particular taxa or communities, while others have developed theoretical models to show how, in detail, it might work [73, 57, 43, 21, 97]. Population geneticists have developed their own versions of it to explain some of the genetic variation observed within populations [31, 69, 23, 30], and so have cancer biologists to explain the diversity of tumour cell types [82, 92]. But it is also familiar because economists and sociologists, some of them inspired by Darwin and his successors, but replacing natural selection's invisible hand with the market's, have explained the diversity of firms and their products in much the same way [20, 54, 65, 105, 49, 18, 109, 41]. They are the reason that talk of "niches", "resource partitioning", "generalists" and "specialists" can be so often heard in business schools.

There is, however, another kind of explanation of diversity that does not rely on competition, selection or niches at all. This second idea, again common to both ecologists and evolutionary biologists, supposes that much, if not all, diversity is not adaptive, but is merely the result of a process in which new entities are continually generated — species by speciation and genetic variants by mutation — and whose fates are dictated by stochastic processes so that while some go extinct others multiply [63, 28, 56, 9]. In such neutral theories, the steady state level of diversity does not depend on the world's complexity, but only on the rate at which new variants appear in the population and its effective size.

Returning to the museum, cultural evolutionists have applied neutral theory to the explanation of cultural diversity as well. There are neutral models of Neolithic pot decor, baby names, languages, and even cryptocurrencies too [87, 107, 48, 12, 15, 72, 106, 13, 1, 32, 88]. Moreover, social physics and network science offer many similar models to explain various cultural and social phenomena such as the citation habits of scientists [108, 112, 8, 83, 89, 101]. These models are not couched in the language of mutation and selection and so their connection to biology is obscure, but, as stochastic, population-based, generative models they are very much the same. And, when they assume that individuals have an equal probability of reproduction, they are neutral models by another name.

The appeal of neutral models lies in their simplicity. Built from only a few parameters, and assuming almost nothing about the structure of the world, they can generate all the diversity you please. Their weakness is that they do not explain the seemingly ubiquitous signatures of design. The result has been controversy. Among population geneticists¹, after a decades-long truce [64, 53, 98], a dispute between those who believe that neutral theory is worthless and those who regard it as fundamental, has broken out again [61, 59]. Among ecologists, arguments over its use have rumbled for years [103, 67, 122, 104]. Its recent application to cancer genomics [124] resulted a similar spat [115, 51, 78, 123, 7, 126].

At heart, these are all disputes about the evidence required to favour adaptive over neutral explanations. And, since the evidence for neutrality has often been the same in different fields, the same disputes have often been unwittingly replayed. For this reason, here we take a look at neutral models of many sorts, unify them in a common framework, and take a critical look at the methods that have been used to test them.

¹Here something about the origin, Kimura, and early controversy

Varieties of neutrality

Neutral models assume a population of reproducing entities with variable, heritable, attributes and in which new heritable variants — mutations — periodically appear. These are generic features of evolutionary models. But the essence of neutrality is that the survival and reproductive success of the entities do not depend upon those attributes. In population genetics this means that an individual’s reproductive success does not depend on its genotype; in macroevolution that the probability that a species speciates or goes extinct does not depend its genus; in ecology that the probability that an individual reproduces or dies does not depend on its ecological niche; in cultural evolution that the probability that an individual transmits its knowledge or habits by social learning to the next generation does not depend on what it knows or does.

But this diversity of terminology is cumbersome. And, since we want to emphasize the deep similarities of the various neutral models, we will speak generically of “populations”, “variants” and “individuals”, but also show how these terms correspond to those used in different fields (Box 1.). The sampling process that affects variant frequencies is known as genetic, ecological or cultural drift.

In this review we will consider “infinite variants” (or alleles) processes, which have been applied to many phenomena, but not “infinite sites” models suitable only for DNA sequences. But both come in several different flavours that differ in their generative processes: what they assume about how individuals are born, reproduce and die. The three most popular, each named for its originator, are the Wright-Fisher, Moran and Yule processes (Box 1). Figure 1 shows, by simulation, that all of them produce rich evolutionary dynamics in which new variants arise, sometimes become very common, and sometimes go extinct. They are also very simple. Neutral models may also incorporate population structure and its attendant forces of dispersal and immigration as well much else besides. But, regardless of such elaborations, it is the absence of selection that makes a model neutral.

The problem illustrated

The detection of any kind of selection in a population is, then, evidence against a purely neutral model. But some kinds of selection challenge their domain more directly than others. That purifying selection sweeps many new, deleterious, variants from populations, or even that positive selection fixes rare, advantageous, variants is conceded by all (e.g., [59]). Arguments about neutrality really hinge on whether it is sufficient to account for all the variety that fills our world.

Population geneticists have identified several different kinds of diversity-promoting (or “balancing”) selection. But, in most fields, the clear favourite is negative frequency dependent selection. In this kind of selection, rare variants have a fitness advantage over common ones, and so increase in frequency until they have the same relative fitness as others. The result is a population in which multiple variants are actively maintained at intermediate frequency.

In population genetics, negative frequency dependent selection is responsible for spectacular genetic polymorphisms such as those of the HLA complex in humans, self-incompatibility loci in plants and shell colours in snails [6, 90]. In ecology, it underpins niche-based explanations for the diversity of ecological communities [118, 2]. In cultural evolution, where selection is typically spoken of as a “transmission bias”, [16, 102] it is known as “anti-conformity bias” [85]. The idea is that humans sometimes run against the conformist grain, preferentially copy rare behaviours and ideas, and so cause them to become more common.

To illustrate this, we also simulated populations that were identical to our neutral populations, but subject to negative-frequency dependent selection (Figure 1).² The variants in these populations, like those in their neutral counterparts, also experience drift, but the addition of selection causes them to be more diverse. The gain is subtle: all our populations, selected or neutral, contain many variants whose frequencies change from generation to generation. But the difference can be shown by its effect on the fundamental diversity number, θ .

²Give details: strength of selection

The fundamental diversity number

Theta describes the flux of variants through a population. It has its origins in Kimura’s neutral theory [63] where it appears in many analytical results about the behaviour of neutral Wright-Fisher and Moran populations [28, 36], but was made famous by Hubbell [56] who called it “the fundamental biodiversity number”. For Wright-Fisher and Moran processes, θ has a very simple relationship to population size, N , and mutation rate, μ : For Wright-Fisher processes:

$$\theta = 2N\mu; \tag{1}$$

and for Moran processes:

$$\theta = \frac{N\mu}{1-\mu}. \tag{2}$$

Since all our simulations were based on $\mu = 0.001$ and $N = 1000$, it follows from equations 1 and 2 that our neutral Wright-Fisher population has $\theta = 2$ and neutral Moran population $\theta \approx 1$. For such neutral populations, its value reveals the relative importance of the processes involved. If $\theta < 1$, then evolution is dominated by drift, but if > 1 by mutation.

Theta can be estimated from a population sample. Ewens, who derived a sampling theory for neutral Wright-Fisher and Moran populations, showed that all the information concerning θ resides in the number of variants observed in a sample [35, 36]. Applying his estimator, $\hat{\theta}$, to our neutral populations gives values of 2.3 and 1.1 (Wright-Fisher and Moran respectively), close to their theoretical values. Applying it to our selected populations gives $\hat{\theta} = 20$ (Wright-Fisher) and 10 (Moran), which implies mutation rates or population sizes about ten-fold larger than their neutral counterparts. But, as noted above, these parameters were the same in all our simulations. The difference in $\hat{\theta}$ is selection’s effect.

This exercise shows the power of negative frequency dependent selection to maintain more diversity than neutral forces alone. It also shows that it would be easy to distinguish between neutral and selective explanations for diversity from variant frequencies (rather than direct measurements of fitness or experimental manipulations) if we knew N and μ . Unfortunately, we usually don’t — but only that the first is a large number and the second a very small one. So most tests of neutrality are based on variant frequencies alone. In the following sections, we illustrate how they work, discuss how they have been used, and what they reveal.

Variant abundance distributions

When we classify individuals by the variants to which they belong, and count them, we often find that a few variants are very common, but that many are very rare. Variant abundance distributions are, in other words, right-skewed. Such distributions have fascinated scientists in many fields for almost a century. That is because they can be generated by very simple neutral models. But does that mean that they are evidence against selection?

The early-twentieth century botanist J. C. Willis thought so [127, 128]. He found that the distribution of plant genus sizes plotted on an arithmetic scale, formed a “hollow curve” but, plotted on a double logarithmic scale, a linear one. Counting the surnames of Swiss farmers and the hotels in British towns produced the same result [128, pp. 35–39]. Such distributions could not, he therefore argued, be the product of natural selection; they must be explained by some other general law. He was vague about what that might be, but his results inspired Yule to produce the first neutral model, one that generated a power law distribution, just what Willis had found.

Where Willis and Yule led, many have followed. When Hubbell sought to demonstrate the explanatory power of his Unified Neutral Theory of Biodiversity, it was to species abundance distributions that he turned [56]. His theory, which was based on Wright-Fisher and Moran processes, predicted either a log-series or else new kind of distribution, the zero-sum multinomial. Just such distributions seem to exist in nature [56, 119]. In cultural evolution, neutral theories have been used to explain the power law distributions shown by artefacts of many kinds [14, 48, 12, 52, 11, 106, 116, 75, 96, 95, 93, 32].³ Regardless of the particulars,

³add material about power law in network science[89]

the argument is always the same: here are some things (species, pots, baby names, citations) that show a particular kind of abundance distribution (log series, zero-sum multinomial, power law); here is a simple neutral process (Wright-Fisher, Moran, Yule) that can produce such a distribution; therefore neutrality reigns.

This reasoning, although widespread, is an example of “the fallacy of the converse”[78]. We may agree that a model of neutral evolution produces a particular abundance distribution, but the existence of such distributions in nature does not prove that the world is neutral. This is for two, related, reasons.

The first is statistical. Tests of neutrality based on abundance distributions depend on our ability to accurately classify them; to distinguish, say, a log-series from a log normal or a power law. But nature is rarely so neat. Real distributions are often blends of the idealized distributions of statisticians’ dreams, and, in reality, statistical tests struggle to tell them apart [24].

The history of citation research illustrates the problem. More than fifty years ago, de Solla Price [112] claimed that the distribution of citations in scientific articles followed a power law, a pattern that neutral network models seemingly explained [8]. But now that we have vastly more data, and much more rigorous model-fitting methods, it appears that citation data often fit a variety of distributions equally well [101, 24, 17].

The second reason, which depends on the first, is that the general shapes of abundance distributions are in fact insensitive to selection ⁴. As predicted by theory, (Box 2), our neutral Wright-Fisher and Moran simulations generate log-series variant abundance distributions at steady state, and the Yule generates a power law (Figure 2, A–C). But so do our negative-frequency dependent selected populations — and they were under strong selection (Figure 2, E–F).⁵

That abundance distribution are hard to tell apart, and that any given kind of distribution can be produced by a variety of processes, explains why tests of neutral theory that depend on them so often become mired in quarrels about statistical techniques (e.g., [119, 79, 34, 80, 25]). It also explains why many scientists, particularly evolutionary geneticists and ecologists, have concluded that they’re not up to the job [44, 10, 118, 80, 81, 67, 100, 81, 89, 77, 3]. Yet neutral models continue to be proposed as explanations of abundance distributions in new phenomena ranging from tumour variants to cryptocurrencies [124, 32]. It seems that the lessons, so hard-won in ecology and evolutionary biology, always need to be taught anew [114, 78, 7].

Probing abundance distributions

Neutral theory does not just predict what kinds of abundance distributions we should see in nature, but also their shapes. For Wright-Fisher and Moran neutral processes, the shape of the abundance distribution is, in fact, given by fundamental diversity number, θ (equivalent to Fisher’s α for a log series). For reasons discussed above, θ has not often been used directly to test neutrality. Ewens’ sampling theory, however, has, for it is the basis of the Slatkin exact and Watterson–Ewens tests.

The idea behind them is this. Suppose that, in a given sample of size n , we observe k variants. The individuals in our sample might be distributed or “configured” across the variants in many possible ways. For example, if $k = 5$ and $n = 30$, the variants could be configured as a very right-skewed distribution (23, 3, 2, 1, 1) or a more even one (8, 7, 6, 5, 4). Ewens’ sampling theory allows us to simulate the distribution of variant configurations produced by an neutral infinite variants process. To test the neutrality of a population, we compare the observed configuration to this neutral distribution, rejecting neutrality if the observed configuration is sufficiently improbable.

This comparison is the basis of Slatkin’s exact test of neutrality [111, 110]. It is general and favours no particular alternative hypothesis. That is a virtue, but not an unalloyed one, when we do have a clear selective alternative in mind. When we do, a comparison of some summary statistic of the variant configurations may provide a more sensitive test than the configurations themselves [111]. The Watterson-Ewens test is based on the observation that the homozygosity of a population, $\hat{F} = \sum_i p_i^2$, is particularly good at discriminating between right-skewed neutral distributions and the more even ones produced by balancing selection [120, 121]. The term “homozygosity” may suggest that the test is irrelevant to ecology and cultural evolution whose

⁴Put some of the refs below in here

⁵This has to be justified using the final simulations

entities are equivalent to haploid organisms, but here homozygosity is not an attribute of an individual, but the probability that any two variants drawn at random from a population are identical by descent.

Versions of both tests have been applied to genetic variants [42, 66], ecological communities [33, 58], and assemblages of archaeological artefacts [107, 113, 95, 96, 75, 93]. But Ewens warned that all tests based on his sampling theory were weak. This weakness is due to the association among variants in samples that arises from their common evolutionary history. They could, he said, fail to reject neutrality, even “appreciable” selection was present [36, p. 352]. Indeed, we cannot reject the neutrality of our selected populations by means of either test⁶. Just as tests based on classifying abundance distributions are insensitive to selection so too, it seems, are variant configuration tests that describe their shapes.

The importance of dynamics

Although all of the tests used above have their origin in population genetics, they’re not much used there now. That is because population genetics tests take advantage of the fact that genomes provide an in-built picture of the results of neutral evolution — putative neutral variants such as synonymous substitutions — against which the putative effects of selection can be tested. This makes them much more powerful than any of the tests we’ve considered above. It seems clear that we need more information than abundance distributions can provide. The most obvious source of additional information comes from the dynamics of variants, how they change over time.

(information that they contain is so much greater than static abundance distributions.

1. [74] used limited time series data to show that the fish species of an English estuary could be divided into common, persistent, residents and rare, sporadic, immigrants, and that only the latter showed a log-series species abundance distribution consistent with neutral theory.
2. Neutral theory supposes the strict fitness equivalence of individuals. From this it follows that the abundance of any given variant is an unbiased random walk or martingale [71]. By contrast, mechanisms such as niches or anti-conformity bias that give rise to negative frequency dependence result in variant abundances that are mean-reverting; mechanisms such as competitive dominance and conformity bias that give rise to positive selection of some variants, and hence negative selection of others, result in abundances that show directionality. Finance economists have developed tests to distinguish these behaviours in stock market prices [38, 37, 94]. Inspired by these, [71] applied panel unit-root tests to BCI abundance data and showed....

But given that neutral theory often assumes zero-sum dynamics — that is, the number of individuals in the population is fixed — we do not want to test the relative abundances of variants, but rather their frequencies. Here, in the absence of mutation, the neutral dynamics are governed by a binomial process for the case of two variants, or a multinomial for many. Thus, a suitable test would search for deviations from binomial or multinomial dynamics in frequency space. Given this we devise five models and apply them to our simulations: (i) neutral; (ii) homogenous constant selection; (iii) heterogenous constant selection; (iv) homogenous frequency dependent selection; (v) heterogenous frequency dependent selection. By “homogenous” we mean that all variants are constrained to have the same relative fitnesses, by “heterogenous” that they are not⁷. By “constant” we mean that selection is frequency independent. We estimate the posterior distribution of [relative fitness?] for each variant. Thus, we can obtain not merely a statement of the global neutrality of the population, but identify variants that are non-neutral.

3. One approach, taken by Crema and collaborators [27, 26, 60], rests on comparing the abundance distributions of variants among time-steps in a population. Neutral and selection models give different predictions as to how distributions should change, and they test among these models using an Approximate Bayesian Comparison framework. Their approach is as follows. First, they estimate the distance between the observed abundance distributions at adjacent time-steps. Then they simulate many populations which vary in population size, N , mutation rate, μ , transmission rate and a selection parameter

⁶put P values in Figure 2

⁷do we really want homogenous treatments at all? Why not just focus on the heterogenous treatments?

that dictates whether a population has conformist, anti-conformist, or unbiased transmission, and estimate the distances between the simulated timesteps. They then pull out 1000 simulations with the closest distance to the observed distances. These are the models that best explain the data. They hope to find that this subset is enriched for a particular set of parameter values, that is, that they can favour one set of models over another. To some degree they can. What's nice about this is that since it does not depend necessarily on analytical results based on a standard Wright-Fisher or Moran models, its generative structure can be made unique to a particular case and it need not assume equilibrium.

ABC approaches have also been used to test abundance distributions in cancers [125].

4. <http://www.genetics.org/content/genetics/192/2/599.full.pdf> <http://www.genetics.org/content/genetics/early/2016/03/01/genetics.115.260001>
<https://arxiv.org/pdf/1409.8529.pdf>
5. [39, 88] for another test, one that is applied to language. Their test does not allow for mutation.
6. Good et al. 2017 do something similar for the LTEE but it appears to be binomial (major and minor clades) and bolted onto a hidden Markov model to account for transitions among mutational states? (Deeply opaque) [46].
7. Levy et al. 2015 on tracking yeast lineages Also deeply fucking opaque. But should be able to explain how they distinguish neutral from selected lineages [70].
8. Network/citation literature. I think that there are a variety of papers that show that cumulative advantage is not the whole deal — and show super-linear attachment rates by looking at longitudinal data and modelling them [45] and other references therein.
9. Our test is currently limited in two important ways. First, it cannot deal with variants that are new or go extinct, so we restrict our sample to those that are present throughout. To the degree that extinction is caused by purifying selection, then, we will underestimate its presence. Second, our model does not have a sampling theory: it assumes that we know abundances without error. Our test is closely related to one devised by [76, 62] for the two-variant haploid case and they have provided a sampling theory, but we leave extending this to the multinomial case for the future.

Conclusion

1. These aren't all the tests, but they're some of the most important ones. Mention a few others (e.g., comparison of communities; Harpole 2010).
 - (a) turnover test
 - (b) Ricklefs's speciation time test?
 - (c) Using phylogenetics to test neutral theory
 - (d) Coalescent models? I agree we can talk about this, they are more a methodological advance IMO in terms of providing a better framework for analysis / simulation rather than an entirely new model.
 - (e) Using replicate populations to test neutral theory
2. A summary of the strengths and weaknesses of tests of NT.
3. The philosophy of using NT as a null, vs. alternate model fitting. (See Crema for a philosophical discourse on this; also Rosindell). At least what is plain is that we can't just look for conformity to NT predictions.
 - (a) This problem applies with even greater force to more elaborate neutral models such as Hubbell's UNTB which introduces another parameter, dispersal, to explain species abundance distributions in local communities. Unsurprisingly, this model can fit a much wider range of empirical distributions than one that contains only mutation as a source of diversity; it has even been said to

be “robust” in the face of density dependent selection [118, 47]. We, however, see this as a vice rather than a virtue, for that is merely to say that the UNTB is even harder to falsify than the basic model we considered.

- (b) Some workers, acknowledging the weakness of abundance distribution tests, defend a preference for neutral models on the grounds that they contain fewer parameters than models that incorporate selection [14, 5]. But, when choosing among competing models, parsimony should be viewed as a criterion of last resort. After all, we do not merely seek a neat mathematical description of the world, but an understanding of the processes that have shaped it. And, given the weakness of abundance distribution tests, any fit of empirical data to neutral predictions cannot be regarded — as it often is — as evidence that the world really is neutral.
- 4. Up till now we have discussed tests of neutrality that consider the properties of populations as a whole. Such tests simply rule out the possibility that the abundance of some variants are determined by neutral forces while others are not, or that the effects of different kinds of selection cancel out in the aggregate. Any test capable of unravelling the forces regulating the abundance of individual variants requires information beyond static distributions or even single-generation changes in frequency.
- 5. The key point is that we should not suppose that populations are neutral *as a whole*. Rather, it is that certain variants may be neutral with respect to each other. But it is generally very unlikely that all variants are selectively neutral. The key thing is to develop tests that allow us to distinguish neutral from non-neutral variants. That is what the infinite-sites class-tests do in genomics. Given that, we need an additional source of information beyond static SADs. That is mostly likely to come from time series. But it might also come from replication.
- 6. The utility of Neutral Theory. Its many possible extentions. Perhaps Ecological theory is the most sophisticated since it incorporates dispersal explicitly.
- 7. There is no NT in the business world/firms etc. Why not?

Boxes & Figures

Box 1: The varieties of neutral models

There are deep similarities between neutral theories in population genetics, ecology, macroevolution, cultural evolution and network science. Some of these similarities have been often noted [68, 22, 55, 5, 67]; others are less familiar. Some are due to descent from a common ancestral theory; others seem to be the result of convergent evolution. Whatever their origin, or the phenomena they attempt to explain, neutral theories all consider a population of individual entities partitioned into variant classes. The following table shows how. For each we also give one classical reference.

field	population	variant	individual	reference
population genetics	population	allele	organism	[63]
macroecology	community	species	organism	[56]
cultural evolution	assemblage	idea or behaviour	artefact	[87]
macroevolution	clade	subclade or genus	species	[130]
network science	network	degree class	node	[8]

Most neutral models are based on one of three generative processes. The best known, due to Sewall Wright and R. A. Fisher, assumes that all individuals are born and die in a single generation [129, 40]. But some individuals, chosen at random, reproduce: their offspring are the next generation. Since the birth and death rates are equal the population size, N , is constant. Moran’s process assumes that at each time step one individual, chosen at random, reproduces and one individual, chosen at random, dies^a. Here, too, population size is constant but, unlike Wright-Fisher, individuals may be young or old. The models are very similar a Wright-Fisher generation being comparable to Moran $\frac{N}{2}$ time steps. The factor of 2 in this formula comes about because a generation refers to the time interval between birth and reproduction not between birth and death, which would tend to be twice as long. Yule’s process is like Moran’s except that no-one dies and so the population size increases exponentially [130]. For a mathematical sketch of these models see Box 2.

Each of these processes has found favour in different fields. The Wright-Fisher and Moran processes are the basis of neutral models in population genetics [63, 28, 36]. Hubbell used both in his *Unified Neutral Theory of Biodiversity* [56], as have other ecologists since. The Wright-Fisher process has been widely used in cultural evolution [87, 12]. The Yule process, in contrast, has not generally been used as neutral model in the above sense. However, stripped of heritable variation, the Yule process appears in macroevolutionary theory as the equal-rates Markov branching model used in the analysis of phylogenetic trees [19, 50, 84, 86] and as the “cumulative advantage” or “preferential attachment” mechanism that underpins much of network science [108, 112, 8, 83, 89, 101]. Contrary what the term “cumulative advantage” suggests, these network models are in fact neutral (Box 3).

^acite Moran1958

Box 2: Neutral theory: basic analytical results

Neutral theories have been the basis of many analytical results — some exact, others approximate — that make many predictions. Here we focus on one: the abundance distribution, that is, $V(n)$, the number of variants (alleles, species, artefact variants) expected in precisely n individuals. To derive $V(n)$ we begin with a master equation giving the probabilities of an increase, b_n , or decrease, d_n , in the number of individuals belonging to a variant with abundance n . For the Moran generative process, the master equation is given by:

$$b_n = (1 - \mu) \frac{n(N - n)}{N(N - 1)} + \mu \frac{n}{N}$$

$$d_n = (1 - \mu) \frac{n(N - n)}{N(N - 1)} + \mu \frac{n}{N}$$

where N is the number of individuals in the population and μ is the probability of mutation per birth event. This has a stationary solution given by

$$S(n) = \frac{\theta}{n} \frac{\Gamma(N + 1)}{\Gamma(N + 1 - n)} \frac{\Gamma(N + \theta - n)}{\Gamma(N + \theta)}$$

where $\theta = N\mu/(1 - \mu)$ and $\Gamma(z)$ is the gamma function given by $(z - 1)!$ for integer z and $\Gamma(z) = \int_0^\infty x^{z-1} e^{-x} dx$ otherwise [117, 4]. When the population is large compared to the most abundant variant so that $\frac{N-n}{N-1} \approx 1$, the abundance distribution can be approximated as a log-series [Not $\phi(x)$ on the left – $V(n)$?]:

$$V(n) = \theta \frac{(1 - \mu)^n}{n}$$

Another approximate solution assumes an infinite population but does not require the most abundant species to be comparatively rare, hence it applies to both variant-poor and rich communities. In this case we characterise $V(n)$ as a continuous function $\phi(x)$ so that $\phi(x)dx$ gives the number of variants with a relative abundance $\frac{V(n)}{N}$ between x and $x + dx$.^a

$$\phi(x) = \theta x^{-1} (1 - x)^{\theta-1}$$

In these models θ is a compound parameter that more naturally describes the behaviour of the model than its individual components. First discovered by population geneticists [63], it is variously known as the “population mutation rate”, “population innovation rate” or, in ecology, as the “fundamental biodiversity number” [56].

The infinite haploid variants neutral Wright-Fisher process, has an abundance distribution identical to the Moran process. But here $\theta = 2N\mu$.^b

The master equation for a neutral Yule process is

$$b_n = pn, \quad d_n = 0$$

which yields a power-law abundance distribution given by [what is on the left?]:

$$V(n) = e^{-pt} (1 - e^{-pt})^{n-1}$$

^aWhat is this distribution in English? Looks like a power law. If so, isn't this what [5] finds in the diatom dataset? cf. [99] and his powerbend?

^bMore has to be said about WF — that's where all the confusion lies! a log-series?!

Box 2: The network connection

A remarkable array of phenomena — wealth, city sizes, word use in texts, the magnitude of earthquakes, scientific citations, and node degrees of many different kinds of networks, to name but a few — are said to show power law abundance distributions [131, 108, 89]. Many, in fact, probably do not [24, 91]. Even so, versions of the Yule process, which generates a power law distribution, have often been invoked to explain them [108, 83, 89]. Applied to the degree distributions of networks, one of these versions, subtly different from Yule’s original, is known as the “cumulative attachment” [112] or “preferential attachment” [8] mechanism. Since this network version is so much more prominent than its ancestor, here we outline the relationship between the two.

In both versions of Yule’s model new individuals are linked to individuals already present in the population; but where the original model focuses on the production of variation, the network version focuses on the production of the links themselves. Despite this difference, the generative rules have a similar structure. In the original the probability that a newly born individual will inherit some variant is nearly proportional to the frequency of that variant in the population. In the network version the probability that a newly born individual — a node — will link to an existing individual — its attachment rate — is nearly proportional to the number of links that the older individual already has, its degree: the preferential attachment rule. *Nearly* since both models allow for novelty. In the original model, there is a small probability that a new individual will ignore its inheritance and mutate into a new variant; in the network version, there is a small probability that a new individual will ignore the preferential attachment rule and link to some randomly chosen individual.^a Finally, in the network version, there is an analog of selection too. Just as negative frequency dependent selection generates diversity, so too, when the relationship between attachment rate and degree is less than proportional, the result is a network in which links are evenly distributed across nodes. Conversely, just as positive frequency dependent selection results in a population dominated by just a few variants, if the relationship between attachment rate and degree is greater than proportional, the result is a network in which links are concentrated into a few hubs [101, 91].

In ecological terms the network model captures the reproductive structure of the population. Since it says nothing about inherited variation it is not an evolutionary model. Even so, preferential attachment can have evolutionary consequences in the real world. That is because, in biology and culture alike, reproducing entities are invariably vehicles for inherited variants, and preferential attachment will alter their frequencies. To see this consider the citation habits of scientists. We all view the literature with Olympian omniscience and detachment, citing our predecessors’ papers, and so perpetuating their ideas, solely according to their merits — except when we cite a paper just because it’s cited in lots of other papers we’ve read. To the degree that we fail to live up to the scholarly ideal, then, the evolution of science is shaped by the arbitrary consequences of preferential attachment — Yule’s process [112, 8, 130].^{b,c}

^aor could it create a new node to attach to - I thought this was the more common scenario, but perhaps I was wrong.

^bTO BE ADDED: the “advantage” being in ecology, a species with more individuals having an advantage over a species with few, whilst the individuals themselves feel no effects of their species identity

^cNeeds a network figure I think, rather like Perc’s, showing the effect of cumulative advantage.

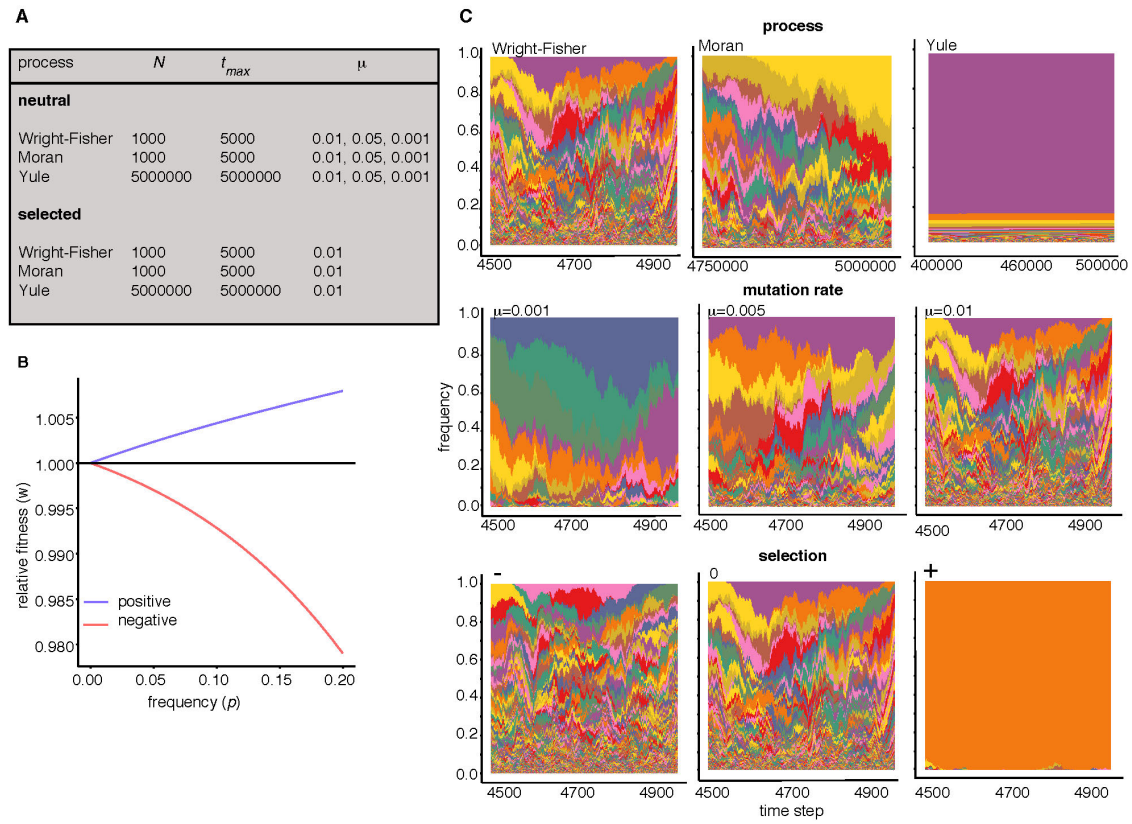


Figure 1

Figure 1: **Simulating evolution.** **A** Simulation scheme. We simulated neutral Wright-Fisher, Moran and Yule processes for three mutation levels ($\mu = 0.01, 0.005$ and 0.0001) and, for one mutation level ($\mu = 0.01$), imposed either negative frequency dependent, positive frequency dependent, or no selection, with ten replicate populations of each. We ran each simulation until steady state: $t_{max} = 5000$, XXX and XXXXX time steps for the Wright-Fisher, Moran and Yule processes respectively. **B** Selection. For the selected treatments we imposed positive and negative frequency dependent selection (conformist and anti-conformist transmission biases) on our simulated populations. The curves show the probability that a variant will reproduce, or be copied, as a function of its frequency, p , in each selection regime relative to the neutral probability. **C** How generative process, mutation rate and selection affect variant diversity. Each colour represents the frequency of a particular variant **Top row.** Generative process. From left to right, neutral Wright-Fisher, Moran and Yule processes; all with $\mu = 0.01$. The Wright-Fisher and Moran-Hubbell processes have the same rate of evolution if we allow that $N/2$ Moran time steps equals one Wright-Fisher time step. **Middle row.** Mutation rate. From left to right, increasing mutation levels increase variant diversity; all neutral Wright-Fisher processes with $N = 1000$. **Bottom row.** Selection. From left to right, negative frequency dependent selection ($-$) maintains higher levels of diversity than neutrality (0) which, in turn, maintains higher levels of diversity than positive frequency dependent selection ($+$); all Wright-Fisher processes with $\mu = 0.01$ and $N = 1000$. Our simulations aren't very extensive, but our purpose is illustrative; in most cases others have delineated their properties by either analytical results or much more extensive simulations.

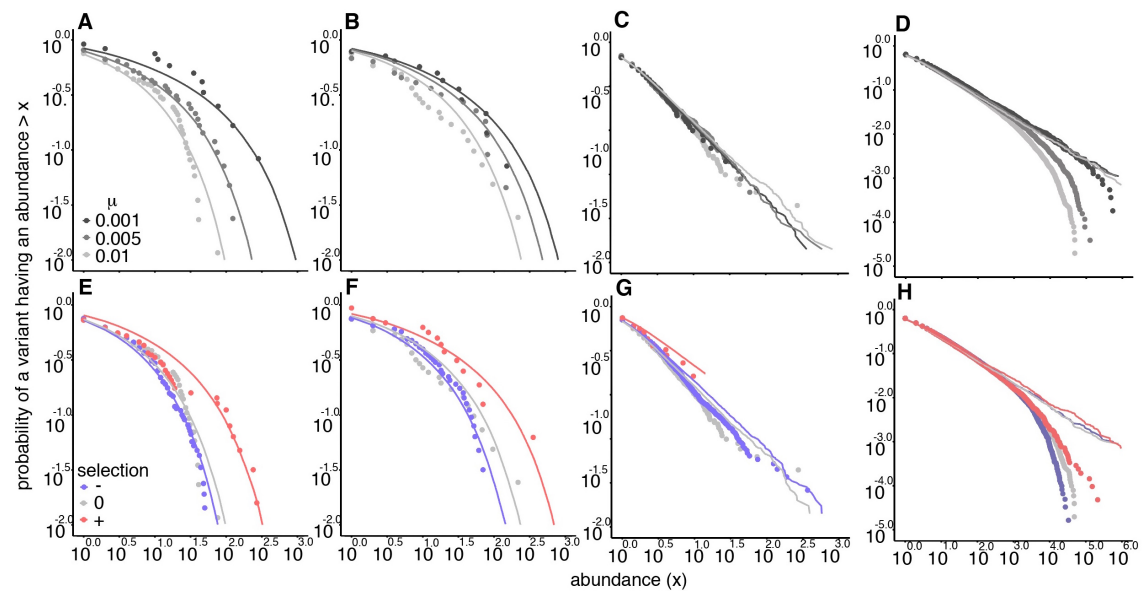


Figure 2

Figure 2: **Abundance distributions do not distinguish neutrality from selection.** Complementary cumulative distribution functions of stationary for simulated populations evolving under Wright-Fisher, Moran or Yule processes and the Bentley-Shennan corpse-accumulation version of the Wright-Fisher process **A-D**: the effect of mutation rate under neutrality. Three mutation levels: $\mu = 0.001, 0.005$ and 0.01 ; **E-H**: the effect of three selection regimes: positive frequency dependent selection (+), negative frequency dependent selection (-) and neutral (0); all for $\mu = 0.01$. Analytical results predict, at steady state, a log-series distribution for neutral Wright-Fisher and Moran-Hubbell populations and a power law for neutral Yule populations. There is no analytical prediction for the Bentley corpse-accumulation population but previous simulations show that it should be a power law with a bend in the upper tail. We fitted three theoretical distributions, log-series, Poisson log normal and power law to each observed distribution by maximum likelihood, determined the best fit by AIC, and found in each case that the best fit was consistent with these predictions. For any given process, the form of the distribution is unaffected by varying mutation levels or selection. For the Wright-Fisher and Bentley populations the simulation was run for 5000 time steps; for Yule populations, 500,000 time steps and for the Moran populations 5000,000 time steps. The Wright-Fisher, Bentley and Moran-Hubbell populations had 1000 individuals; for Yule the population began with one individual and ended with 500,000.

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