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LETTER

A mean field model for competition: From neutral ecology to the Red Queen

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Abstract

Individual species are distributed inhomogeneously over space and time, yet, within large communities of species, aggregated patterns of biodiversity seem to display nearly universal behaviour. Neutral models assume that an individual's demographic prospects are independent of its species identity. They have successfully predicted certain static, time-independent patterns. But they have generally failed to predict temporal patterns, such as species ages or population dynamics. We construct a new, multispecies framework incorporating competitive differences between species, and assess the impact of this competition on static and dynamic patterns of biodiversity. We solve this model exactly for the special case of a Red Queen hypothesis, where fitter species are continually arising. The model predicts more realistic species ages than neutral models, without greatly changing predictions for static species abundance distributions. Our modelling approach may allow users to incorporate a broad range of ecological mechanisms.

Keywords

Macroecology, neutral ecology, Red Queen hypothesis.

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INTRODUCTION

Understanding the mechanisms governing spatial and temporal patterns of biodiversity on the Earth has proven a formidable challenge. A step forward came with the development of the neutral theory of biodiversity (Hubbell, 1979 2001; Chave, 2004; Rosindell *et al*., 2011; O'Dwyer & Chisholm 2013), which showed that many static patterns of biodiversity can be explained by the mechanisms of random drift, dispersal and speciation, without including the effects of species differences (Hubbell, 2001; Volkov *et al*., 2003; Etienne, 2005; Etienne & Alonso 2005; Volkov *et al*., 2007; Etienne *et al*. 2007; Chisholm & Lichstein 2009; Condit *et al*., 2002; Chave & Leigh 2002; Rosindell & Cornell 2007, 2009; O'Dwyer & Green 2010; Vellend, 2010). Neutral theory has had considerably less success in predicting dynamic patterns of diversity, from decadal-scale species abundance fluctuations to geological ages of species (Leigh, 2007; Wang *et al*., 2013; Chisholm & O'Dwyer 2014). For example, in the case of rainforest trees, species ages predicted by neutral theory are sometimes older than the age of the Earth (Nee, 2005). This suggests that even an approximate understanding of temporal patterns of biodiversity requires a consideration of what neutral theory leaves out: species differences. Incorporating these differences into biodiversity modelling is therefore a priority.

We focus on deterministic, selective differences between species, mediated by competitive interactions. Competition is a core ecological process, in which interactions between organisms affect their relative reproductive success. Competitive differences between species can be driven both by 'niche' differences, where species' abundances are stabilised by specialisation, and by 'fitness' differences, where some species competitively replace others. Both are potentially relevant mechanisms for determining patterns of diversity (Chesson, 2000; Ricklefs, 2003); both are represented mathematically by *asymmetries* in the strengths of competitive interactions between species. But introducing species asymmetries into mathematical biodiversity models leads to two critical problems. First, introducing these interactions tends to lead to models that are analytically intractable. Second, without a systematic principle underlying the strength of competitive interactions, this approach introduces potentially hundreds of new parameters (Haegeman & Loreau 2011). With so many parameters to vary, and the vast majority difficult to determine empirically, any improved fit for ecological patterns lacks clear interpretation.

While we clearly need to go beyond neutral models, it seems that introducing even the simplest species differences through competition will leave us with models that are both hard to solve and hard to interpret. And yet there is reason to think that biodiversity dynamics could be understood with simple models, if we could only discover how to introduce additional ecological mechanisms in a parsimonious way. When aggregated across large numbers of organisms, many biodiversity patterns appear to be robust emergent properties of ecosystems, in that their qualitative form does not depend on the underlying complexities and idiosyncrasies of each system (Blythe & McKane 2007; Chave *et al*. 2002). But we lack a principled way to distinguish relevant from irrelevant parameters, and the analytical intractability introduced by any kind of species asymmetry only makes this problem harder.

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Here, we provide tractable, general, mathematical methods that incorporate destabilising species fitness differences, and we apply the resulting framework to solve a specific example based on species fitness differences and the Red Queen hypothesis. This classic scenario was originally introduced to explain extinction rates of both species and higher level taxa (Van Valen, 1973; McCune, 1982), and represents the idea that under some circumstances organisms must keep increasing in fitness just to stand still, in evolutionary terms. In our Red Queen model, speciation continually produces fitter species, which have a net competitive advantage over older, extant species, unlike neutral models. We solve this asymmetric, multispecies model and make predictions for three large-scale patterns of biodiversity: total species richness, the species abundance distribution and species ages. The species abundance distribution is one of the most successful predictions of neutral theory, and we find that it is largely robust to introducing the Red Queen asymmetry. On the other hand, we show that species asymmetry introduces significant differences in community dynamics, and we obtain more realistic, shorter species ages than neutral models. These results provide evidence for the hypothesis that species differences are more important for dynamic than static patterns of biodiversity, and our framework provides the tools for a much more comprehensive exploration of asymmetries in ecology (Levin, 2002; Blythe & McKane 2007).

COMMUNITY DYNAMICS, SPECIES AGES AND RED QUEEN HYPOTHESIS

To infer the mechanisms driving ecological community dynamics, ecologists build mechanistic models and compare their assumptions and predictions to empirical data. These data are often in the form of statistical patterns such as species abundance distributions and species area curves. A more complete understanding of biodiversity and biogeography will require models that predict not just these static patterns, but also dynamic patterns on various timescales. The introduction of neutral theory into ecology lead to a new interest in these kinds of tests, but, as noted above, neutral theory itself was ultimately shown to give inadequate descriptions of time-dependent patterns. The failure of neutral models to predict realistic species ages, in particular, provides a natural starting point for an improved model of biodiversity.

Several possible resolutions of these issues with long-term dynamics and species ages have been proposed, but so far none has been entirely satisfactory. First, there is the introduction of selective differences between species due to a fluctuating environment, considered by Allen & Savage (2007). In their model, environmental stochasticity led to more realistic species ages, but at the cost of introducing demographic rates that are large relative to observed generation times. Second, it is possible that neutral theory's predictions of species ages fail not because of the neutrality assumption, but because of the assumption that the system has reached a steady state. There is evidence that species abundances equilibrate much faster under neutral dynamics than do species ages, so it may be possible to resolve the species age problem by relaxing the assumption that the system is at the steady state. A problem with this approach is that if initial conditions are important, then these initial conditions must be parameterised. This destroys the original theory's parsimony, for doing this makes nearly any distribution of species ages possible by choosing the right initial conditions. Nor would assuming disequilibrium reduces neural theory predictions of excessively long extinction times.

Here, we consider a third possible mechanism driving short species ages: deterministic directional evolution. Deterministic evolution can be broadly separated into biotically driven and abiotically driven evolution. In the Red Queen model of biotic evolution, competitive forces drive a never-ending succession of species, with absolute fitness increasing over time. Under the abiotic model, evolution is driven mainly by factors such as climate and geological events. Directional biotically driven evolution has been observed in long-term bacterial experiments (Elena & Lenski 1997; Wiser *et al.*, 2013), in viruses (Clarke *et al.*, 1994) and in evolutionary arms races (Vermeij, 1986). On macroevolutionary timescales, paleobiological studies suggest that abiotic factors dominate directional evolution (Benton, 2009). Regardless of the exact mixture of biotic and abiotic factors, directional evolutionary processes have in common the continual appearance of new, fitter species and the disappearance of old, less-fit species.

Intuitively, models of directional evolution should predict steady-state species ages that are more realistic (i.e. shorter) than those predicted by neutral theory, but a quantitative treatment of community dynamics under directional evolution requires specification of the fitness landscape, i.e. we must specify what the possible fitnesses of new species are relative to extant species. A typical framework in evolutionary biology (Desai *et al.*, 2007) is a fitness landscape where a new species has an incremental change in fitness relative to its 'parent' species, providing a ladder of relative species fitnesses. This type of fitness landscape has been investigated in molecular evolution (Neher & Hallatschek 2013), where it leads to radically different allele- and site-frequency spectra than predicted by neutral models. In ecology, this could be problematic because the neutral species abundance distribution (the ecological equivalent of an allele-frequency spectrum) already provides a good fit to data and so radical changes may lead to a worse description of the static patterns that neutral theory largely gets right.

We therefore consider a different kind of fitness landscape, where a new species has a competitive advantage over all extant species due to its novelty alone, irrespective of its parent species. For example, species population growth rates may be limited by host-specific predators or pathogens (Comita *et al.*, 2010; Mangan *et al.*, 2010), leading to a competitive advantage for new species (who have a lower pathogen or predator load) over extant species, but such that this advantage diminishes over time as the species acquires enemies. This new species advantage could also approximate circumstances where only species with a fitness advantage over extant species are likely to

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reach appreciable abundances (it might be imagined that some species with submaximal fitness arise too, but go extinct relatively quickly and can be ignored in a first approximation).

Regardless of the specific driver of this kind of directional evolution, the resulting fitness landscape can be modelled in a similar way. For this reason, we group these different biological scenarios together under the umbrella of the Red Queen hypothesis. Again, we consider a ladder of species interactions, but where new species always appear at the top of the ladder. This assumption alone does not specify the relative fitnesses of different species, and one way to calculate species relative fitnesses in the model would be to make the competitive advantage of species A over B proportional to the difference in age of the two species. We make a simpler choice (and we provide evidence in the Supporting Information that this does not make a big difference to the evolutionary dynamics), which is to assume that new species have the same competitive advantage over all extant species. Each species then sees three distinct groups: newer, fitter species; conspecifics; and older, less-fit species. We represent competition between species by interaction coefficients, α_{ij} which encode the competitive effect of species j on species i, and depend on speciation times τ_j and τ_i:

$$\begin{aligned} &\alpha_{ij} = \alpha(1-\epsilon_0) \text{ for } \tau_j < \tau_i \\ &\alpha_{ii} = \alpha \\ &\alpha_{ij} = \alpha(1+\epsilon_0) \text{ for } \tau_i < \tau_j. \end{aligned} \tag{1}$$

Here, α is a coefficient characterising the strength of competition, and ε_0 is a constant between 0 and 1 that introduces species asymmetry. In summary, we address the issue of problems with neutral dynamics by introducing deterministic, selective differences between species. While the mathematical methods we will introduce could be applied to quite general fitness landscapes, we focus on the species interactions defined by eqn (1), which we also argue may capture much of the general behaviour of a broader class of landscapes.

MODEL AND MEAN FIELD THEORY

Our model community contains many competing species. Each species i has the same intrinsic net birth and mortality rates, b and d, and competitive interactions characterised by the Lotka–Volterra-like interaction rates α_{ij}, introduced above. In contrast to neutral ecology, the degree of competition between different species may vary for different i and j, and selective forces may influence the community through these differences. We also incorporate speciation at a per capita rate v, whereby a new species may arise with a single individual. This speciation process in effect slightly reduces the effective birth rate for each extant species, as extant species very slowly "shed" individuals into new species, as in neutral theory (Hubbell, 2001; Volkov *et al.*, 2003). Putting these features together, the community is described by the following master equation for the conditional probability $\mathcal{P}_\tau(\{n_i\}|\{\tau_i\})$ for species abundances n_i:

$$\begin{aligned} \frac{d\mathcal{P}_\tau(\{n_i\}|\{\tau_i\})}{d\tau} = (b-v)\sum_k &[(n_k-1)\mathcal{P}_\tau(n_1,\ldots,n_k-1,\ldots|\{\tau_i\}) \\ &- n_k\mathcal{P}_\tau(n_1,\ldots,n_k,\ldots|\{\tau_i\})] \\ &+ d\sum_k[(n_k+1)\mathcal{P}_\tau(n_1,\ldots,n_k+1,\ldots|\{\tau_i\}) \\ &- n_k\mathcal{P}_\tau(n_1,\ldots,n_k,\ldots|\{\tau_i\})] \\ &+ \sum_k \alpha_{kk}[(n_k+1)n_k\mathcal{P}_\tau(n_1,\ldots,n_k+1\ldots|\{\tau_i\}) \\ &- n_k(n_k-1)\mathcal{P}_\tau(n_1,\ldots,n_k,\ldots|\{\tau_i\})] \\ &+ \sum_{k\neq j}\alpha_{jk}[(n_j+1)n_k\mathcal{P}_\tau(n_1,\ldots,n_j+1,\ldots,n_k,|\{\tau_i\}) \\ &- n_jn_k\mathcal{P}_\tau(n_1,\ldots,n_j,\ldots,n_k,\ldots|\{\tau_i\})]. \end{aligned} \tag{2}$$

This probability distribution depends on the absolute time, τ, and is conditioned on the set of speciation times $\{\tau_k\}$ of all species that appeared in the community up until τ. The first bracketed summation on the right-hand side represent the birth process, at a per capita rate $b - v$, and the sum over species index k is due to the possibility of birth events for each species. The second summation corresponds to mortality for all extant species at a per capita rate d. We note that some of these terms appear with positive signs, representing the increase in $\mathcal{P}_\tau(\{n_i\}|\{\tau_i\})$ due to transitions into that configuration of species abundances, whereas others appear with negative signs, representing the opposite process. For example, the birth process from n_i to $n_i + 1$ acts to reduce the probability $\mathcal{P}_\tau(\{n_i\}|\{\tau_i\})$. The remaining terms are due to intra-specific and inter-specific competition, and contain interaction rates proportional to the parameters α_{ij}, chosen above to reflect the Red Queen–type fitness landscape. These terms are nonlinear in species abundances. For example, in the final term we have an interaction between species j and species k, resulting in a mortality event. The probability that any two individuals in species j and species k interact is proportional to the current number of individuals of each of the two species, leading to the product n_jn_k. For compactness we have not explicitly included the appearance of new species in this equation. The equations governing speciation can be written down by defining $\mathcal{P}$ to have an infinite number of entries which initially have zero abundance, and subsequently transition to non-zero abundance with a speciation rate v.

We now make a series of approximations, detailed in Supporting Information, beginning with a mean field theory approach which treats each species as interacting with the *average* background of other species. The mean field approximation states that in the limit of a large number of species, we expect the correlations between the abundances of any two species to be small. This assumption means that the dynamics of a focal species is determined only by the mean dynamics of all the other species, rather than being coupled individually to the fluctuations in every other species. We can then factor the probability distribution $\mathcal{P}_\tau(\{n_k\},\{\tau_k\})$,

$$\mathcal{P}_\tau(\{n_k\},\{\tau_k\}) \simeq \prod_i P_\tau^{\{i\}}(n_i,\{\tau_k\}). \tag{3}$$

This is necessarily an approximation to the full community dynamics, which we expect to be a good approximation when the

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number of species is large. This mean field theory leads to a tractable model of our community, and we now focus on steady-state solutions for the marginal probability $P_{\tau}^{\{i\}}(n_i|\{\tau_k\})$, averaged over all other speciation times $\tau_{k\neq i}$. We also drop the explicit species indices i in this marginal probability because all species enter the same (averaged) background of competitors, and we rewrite this marginal probability as $P(n|t)$, the probability that a given species has an abundance n, conditioned on its age t.

Applying our approximation step by step, we show in Appendix S2 that the probability that a species has abundance n a time t after it enters the community, $P(n|t)$, solves the following mean field master equation,

$$\frac{dP(n|t)}{dt} = (b-v)[(n-1)P(n-1|t) - nP(n|t)] + (b-R(t))[(n+1)P(n+1|t) - nP(n|t)]. \tag{4}$$

The first pair of terms in eqn (4) represents the birth of individuals at per capita rate $b - v$, whereas the second pair of terms approximates the effects of intra-specific and inter-specific competition, represented by a time-dependent mortality process with a per capita rate $b - R(t)$. $R(t)$ is fully determined by the mathematical model that we have already introduced, and depends on this focal species' age, t, therefore acting to change a species' net fitness through time. This time-dependent fitness is the only part of eqn (4) that differs from the standard, neutral theory master equation (Volkov *et al.*, 2003), but we will show below that it significantly changes neutral theory predictions.

We have formulated this model so that each species experiences the average effect of all other species in the community, and so the natural expectation is that the effect of $R(t)$ should be to decrease species fitness with age, reflecting the competitive advantage for newer species over older species in our Red Queen hypothesis. We now show that this expectation is accurate, and derive an analytical solution for $R(t)$. In Appendix S2 we first show that $R(t)$ can be explicitly written as:

$$R(t) = rv\left(\int_t^{\infty}\langle n(t')\rangle dt' - \int_0^t \langle n(t')\rangle dt'\right), \tag{5}$$

where the parameter $r = (b-d)\varepsilon_0$ translates the asymmetry ε_0 into a demographic rate, and $\langle n(t)\rangle$ is the expected species abundance as a function of its age. This equation has an intuitive interpretation. The first term is a sum over abundances of all species that appeared in the community before the focal species, which contribute a net positive term to the focal species fitness. Similarly, the second term sums over abundances of species that appeared after the focal species, contributing a net negative term to species fitness. In Appendix S2, we then derive the following explicit solution:

$$R(t) = r\left[\frac{2(r+v)}{r+ve^{(r+v)t}} - 1\right]. \tag{6}$$

This solution for $R(t)$ initially takes value r at $t = 0$, and decreases over time, asymptoting to $-r$: This is the backwards conveyer belt arising from the Red Queen hypothesis, and is shown in Fig. 1 for various parameter values.

We can now derive a solution for $P(n|t)$, by plugging $R(t)$ given by eqn (6) into our mean field master eqn (4). We solve this master equation for a point speciation process (Hubbell, 2001), where abundance $n = 1$ when species age $t = 0$:

$$P(n|t) = \frac{\langle n(t)\rangle[\langle n(t)\rangle F(t)]^{n-1}}{[1+\langle n(t)\rangle F(t)]^{n+1}}, \tag{7}$$

for $n > 0$. For large new-species advantage, we will see that growth in abundance will initially be almost deterministic, whereas in the neutral case drift dominates. The functions $\langle n(t)\rangle$ and $F(t)$ depend on speciation rate v and new species advantage, r, and are given by

$$\langle n(t)\rangle = \frac{(r+v)^2 e^{(r+v)t}}{(r+ve^{(r+v)t})^2}$$
$$F(t) = \frac{vr(b-v)}{(v+r)^3}\left[2(v+r)t + \frac{v}{r}(e^{(v+r)t}-1) + \frac{r}{v}(1-e^{-(v+r)t})\right]. \tag{8}$$

$\langle n(t)\rangle$ is also the expected species abundance through time, whereas $F(t)$ is related to an integral of $\langle n(t)\rangle$, and given in more detail in Appendix S3. We note that for any alternative landscape and different $R(t)$, $P(n|t)$ always takes the same exponential form in n, but with different functions $\langle n(t)\rangle$ and $F(t)$.

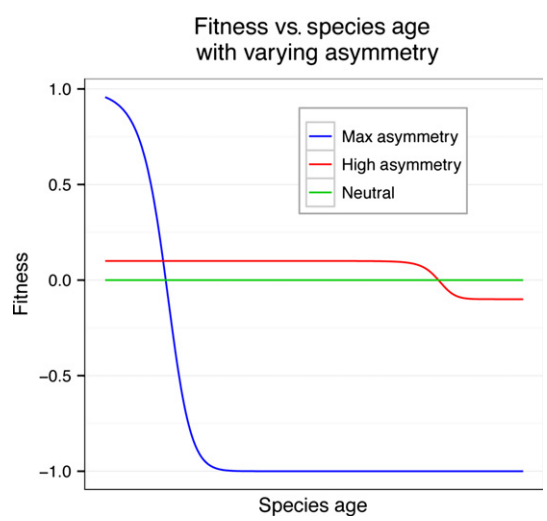

Figure 1. The fitness of a single species through time, with per capita speciation rate $v = 10^{-4}$ in all three cases, and initial species fitness defined in terms of the asymmetry parameter ε_0 by $r = (b-d)\varepsilon_0$. The three cases shown are $r = 1$ (maximal, red), $r = 10^{-2}$ (high, blue) and 0 (neutral, green).

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RESULTS

We began with a community with birth, death, competition and speciation. Through our approximations and choice of landscape, we have taken an intractable, interacting multispecies community in eqn (2), and by considering species asymmetries but ignoring niche differentiation we have transformed it into a linear, single-species master equation, (4), involving explicitly just birth, death and speciation. This equation *implicitly* summarises the entire effect of the competitive interactions through the time dependence of these birth and mortality rates. We now present results for expected species richness, the species abundance distribution and the expected age of a species as a function of its abundance. In general, the results for each of these three quantities must be obtained by numerical integration. However, in the neutral limit, when the asymmetry r between species is small, or in a highly asymmetric community, where r is much larger than the speciation rate ν, we can obtain analytical results, derived in Appendix S3 and presented below.

Expected Species Richness and Species Abundance Distribution

The expected Species Abundance Distribution (SAD) is given by the following integral of our analytical solution for $P(n|t)$:

$$S(n) = \nu J \int_0^\infty dt P(n|t). \tag{9}$$

This should be thought of as a sum over the possible contributions from species of all ages, which has then been averaged over speciation times. We can compute this integral numerically for any given choice of parameters ν and r, and to support the validity of our mean field and other approximations, we compared this mean field expected SAD to the SAD arising from simulations of our full community dynamics, as defined by eqn (2). The details of the simulations are given in Appendix S4 and our results are shown in Fig. 2, where we compare the mean field and simulated SAD. We examine a range of parameter values for ν and J, each designed such that the expected number of species is always relatively large, but allowing us to test our results for different speciation rates. The mean field approximation for expected species abundances performs well in comparison with the average abundance across all simulation runs, suggesting that our mean field approximation works as an approximation of the steady-state distribution of species abundances. We note that the speciation rate and community size in our simulations are too small to be realistic; the prohibitive computational power needed to simulate a full interacting community with realistic parameters is one reason that our mean field formalism is useful.

In the neutral limit, $r = 0$, species richness is given by the usual analytical result arising from neutral models (Hubbell, 2001; Volkov *et al.*, 2003):

$$S_{\text{neut}} = \frac{\nu J}{b-\nu} \log\left(\frac{b}{\nu}\right). \tag{10}$$

In contrast, in the highly asymmetric limit we have a new result, detailed in Appendix S3: $S_{\max}=2S_{\text{neut}}$, exactly twice the neutral species richness.

We can also derive exact results for the SAD in neutral and extreme Red Queen limits. In the neutral limit, the SAD reduces to the usual neutral log series (Hubbell, 2001; Volkov *et al.*, 2003). In the opposite limit of $r \gg \nu$, we have another new result. We still observe an exponential drop-off for large abundances, but for abundances $n \ll 1/\nu$ the behaviour is captured by

$$S_{\text{asym}}(n) = \frac{\nu J}{bn}\left(2 - \left(\frac{b}{b+r}\right)^n\right). \tag{11}$$

In the most extreme non-neutral limit, when $r = b$, this reduces to $\frac{2\nu J}{bn}$ for $n \gg 1$. We note that this mathematical result is strictly true in the limit of $\nu \to 0$. Our numerical results show that in this limit of $r \gg \nu$, and ν still finite, there is approximately $1/n$ scaling behaviour with an exponential cut-off for $n > 1/\nu$. This echoes results from early studies introducing asymmetry into neutral theory (Pueyo *et al.*, 2007): In the extreme non-neutral limit, we recover a SAD which has the same scaling behaviour as the log series.

How can we understand the origin of this log series–like behaviour? In the limit $r = b$, the dynamics of individual species are increasingly well approximated by deterministic trajectories with small fluctuations around them. This is quite unlike the neutral case, when the expected trajectory $\langle n(t)\rangle = e^{-\nu t}$ is almost always a poor approximation to any given species' actual abundance through time. We now consider what would happen if we assume that the fluctuations around the expected trajectory were *actually* zero. If this were the case, we could write a 'deterministic' probability distribution $P_{\text{det}}(n|t) = \delta(n - \langle n(t)\rangle)$, where δ is the Dirac delta function, which is zero unless n equals $\langle n(t)\rangle$. This in turn results in a deterministic species abundance distribution, as shown in Appendix S3:

$$S_{\text{det}}(n) \sim \frac{2\nu J}{bn}, \tag{12}$$

for n less than the maximum value of $\langle n(t)\rangle$, which is $\frac{(\nu+r)^2}{4\nu r}$. In this expression, the $\frac{1}{n}$, log series–like factor arises due to our mean field approximation, whereas the factor of 2 is because the expected trajectory $\langle n(t)\rangle$ passes through each value of n twice; once as the species is increasing in abundance, and once as it is decreasing.

While heuristic, this gives us some insight into why the combination of large numbers of species (mean field) and very strong asymmetry (deterministic trajectories) leads to the same scaling behaviour as the neutral log series, but with an overall factor of 2. This analysis does not identify the neutral-like exponential cut-off that we see numerically, as the deterministic approximation inevitably breaks down when n is near its maximum, and therefore does not agree with our earlier exact analytical results for species richness. Finally, we note that this result clarifies the importance of both stochastic and deterministic forces at any intermediate asymmetry, where the SAD interpolates between the stochastic, neutral result and the deterministic result above, as demonstrated by our simulation and analytical results in Fig. 2.

Species Ages

So far, we have identified analytical results for species richness and the SAD in both neutral and extreme Red Queen limits. But the results show that this species asymmetry has a relatively minor effect. Even in the most asymmetric limit,

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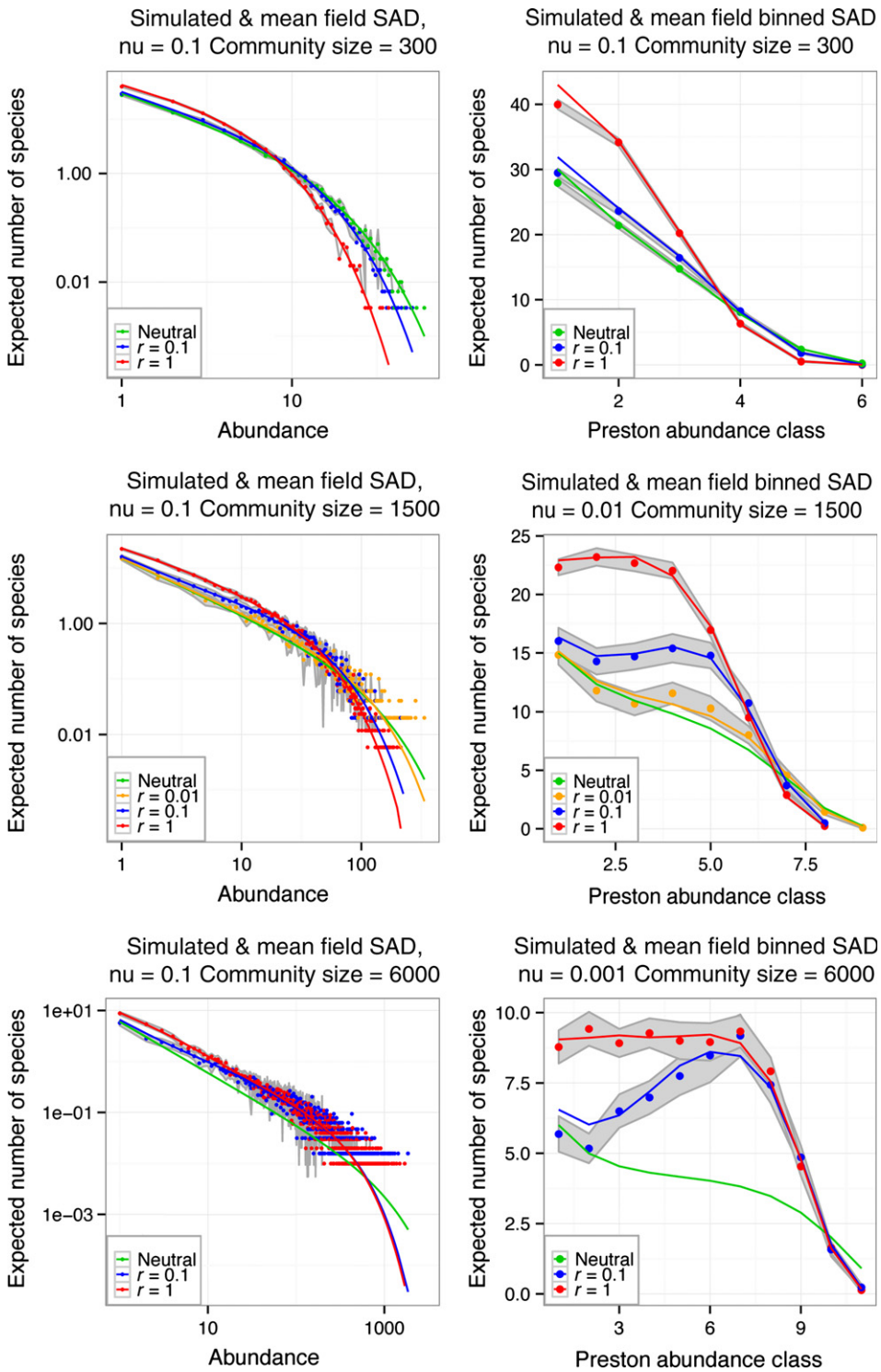

Figure 2. Species asymmetry leaves the shape of the Species Abundance Distribution (SAD) largely unchanged. Left panels show the raw SAD and right panels are binned into Preston abundance classes. Simulation results are plotted as dots, with a grey 95% confidence interval, while mean field results are plotted as solid lines. Each pair of panels plots SADs for communities with a given speciation rate, represented by differing values of ν, and within each plot are multiple values of r in units of birth rate, b, from the extreme, asymmetric case of $r = 1$ to the neutral case of $r = 0$. For the lower two speciation rates, only the mean field result for neutral case is shown, for comparison with the more general values of r. We note that the intermediate case of high asymmetry has a "hump-shaped" SAD, interpolating between two bounding log series.

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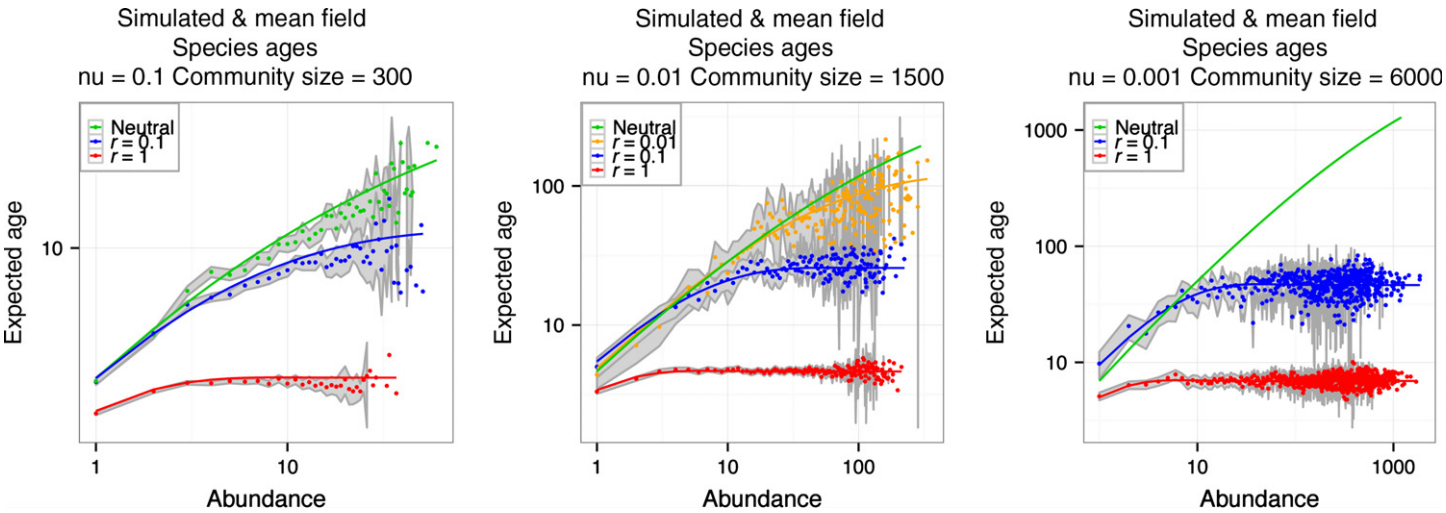

Figure 3. In Red Queen models, the expected species age reaches an asymptotic limit as a function of abundance. The three plots show simulated and mean field results for three different speciation rates and community sizes. We compare our mean field expected age (solid lines) to simulations (dots and grey 95% confidence interval) of our full community, and plot the neutral result (green line) for comparison.

we only see an overall factor of 2 relative to the neutral results – the shape of the SAD is largely unchanged. We now turn to the distribution of species ages, defined as the expected age of a species as a function of its current abundance. Neutral theory has drawn criticism for overestimating the age of abundant species, with this overestimate largely arising due to the long time it takes a population to reach a high abundance solely through drift (Leigh, 1981; Nee, 2005; Leigh, 2007). Mathematically, this expectation value is given by:

$$T(n) = \frac{\int_0^\infty dt\ tP(n|t)}{\int_0^\infty dt P(n|t)}.$$

In Fig. 3, we show that expected species ages increase initially with abundance, before reaching an asymptotic limit. The result indicates that by introducing species asymmetry we can potentially avoid the neutral theory's prediction of overlong lifetimes for large populations.

Again, we can compute this integral numerically for any given choice of parameters v and r, and to support the validity of our model we compared the mean field expected species age as a function of abundance to the equivalent distribution arising from simulations of our full community dynamics, as defined by eqn (2). The details of the simulations are given in Appendix S4, and our results are shown in Fig. 3. In the neutral limit, the solution for $T(n)$ reduces to a closed-form, analytical expression,

$$T_{\text{neut}}(n) = \frac{1}{v}\left(\left(\frac{b-v}{b}\right)^{-n} B[1-v/b, 1+n, 0] + H_n + \log[v/b]\right), \tag{13}$$

where B is the incomplete beta function, and H_n are harmonic numbers (Abramowitz & Stegun 1972). For large n, this increases logarithmically with abundance, leading to the issues previously identified with neutral theory: For very abundant species, neutral species ages are larger than consistency with the geological record would require (Chisholm & O'Dwyer 2014). In the opposite, asymmetric limit of $r \gg v$, we have a more complicated analytical result for the expected species age as a function of abundance, given in Appendix S3. However, despite its apparent complexity, for large n this result asymptotes to

$$T_{\text{asym}}(n) = \frac{1}{r}\log[r/v]. \tag{14}$$

This asymptotic behaviour is also apparent from our simulations, shown in Fig. 3. Instead of increasing indefinitely with abundance as in neutral theory, Red Queen species can have realistic ages even for abundant species.

DISCUSSION

Neutral ecology introduced a framework for understanding and predicting macroecological patterns (Hubbell, 2001; Rosindell *et al.*, 2011), making the radical assumption that species differences do not significantly affect these patterns. Its early successes in matching species abundance distributions suggested that this assumption might be reasonable. On the other hand, neutral predictions often fail to match dynamical patterns of biodiversity in nature (Nee, 2005; Leigh, 2007; Wang *et al.*, 2013). An example is the distribution of species ages as a function of current species abundance, where it has been argued that neutral species would be much older than those observed in real communities – even in the cases where the species abundance distribution matches well. One possibility was that by introducing species differences, the biology underlying those differences will incrementally improve predictions that work well (like species abundances) and salvage those that do not (species ages). Comparing these time-dependent patterns against theoretical predictions could also help identify what mechanisms associated with species differences are most important.

We have addressed this by introducing a tractable model for competing species. This framework incorporates demographic stochasticity, speciation and the competitive interactions and

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selective forces arising from adaptation. We introduced approximations to make this model solvable, outlining their domains of applicability, and reinforced these results with numerical simulations. This approach allowed us to reduce our general framework to a linear stochastic master equation with time-varying demographic rates. It is in these rates that the impact of competition and adaptation is encoded, and this formulation is the central new mathematical result arising from our approach. The neutral theory has been compared to the ideal gas in physics: A first approximation to be built on (Volkov *et al.*, 2003; Zillio & Condit 2007; Rosindell *et al.*, 2011). But it may be that ecology without selective differences is an inadequate starting point. Including such differences between species is analogous to adding interactions to the ideal gas.

We find that in the neutral limit our master equation reduces to the standard, neutral theory master equation. Moving beyond neutrality, we solved exactly for a type of Red Queen hypothesis, where every new species has a fitness advantage over extant species, and this new species advantage declines over time due to the introduction of yet newer, fitter species. This kind of landscape may be relevant in ecological systems that undergo directional evolution, or where diversity is maintained in part through predation or interactions like plant–soil feedbacks (Comita *et al.*, 2010; Mangan *et al.*, 2010). These feedbacks affect plant dynamics in numerous ways, but one effect may be that new species have fewer predators or pathogens by virtue of their novelty. It could also reflect a quasi-cyclical scenario, where new species have an advantage over extant species, but phenotypes are cycling over the long term (Dieckmann *et al.*, 1995; McGlone, 1996). Our results for this Red Queen model are best described as a function of the asymmetry between species. As this asymmetry becomes larger, we find that species ages become much shorter, whereas the species abundance distribution at first becomes more 'humped', but is otherwise largely unchanged. In the maximally asymmetric community, the species abundance distribution approaches a log series, providing a mathematical underpinning to previous expectations that neutral-like patterns may be found in highly asymmetric ('idiosyncratic') communities (Pueyo *et al.*, 2007).

Our formulation in terms of competitive interactions allows for the possibility of stabilising mechanisms (Chesson, 2000; Wright, 2002). If we were to remove speciation in our current model, one species would eventually drive the others extinct, with no long-term coexistence, reflecting our choice to focus on fitness differences rather than niche differences. Instead, we could introduce multiple niches through an appropriate, more complex fitness landscape, which could be compared to previous combinations of niche structure and neutrality (Purves & Pacala 2005; Zillio & Condit 2007; Chisholm & Pacala 2010). In contrast to fitness differences, the stabilising mechanisms of niche differentiation may increase species ages, particularly in the absence of environmental fluctuations, but are likely to be an important part of a more general framework. In summary, our model takes a step from neutral theory towards this more general 'statistical mechanics of heterogeneous populations, in which new types are continuously appearing' (Levin, 2002; Blythe & McKane 2007). In particular, we note the role of high diversity in simplifying apparently complex communities, much like sheer large numbers are enough to simplify interacting systems in physics and chemistry. This mirrors the macroecological intuition that high diversity leads to emerging regularities, but we now have a mathematical approach on which to support and guide this intuition.

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STATEMENT OF AUTHORSHIP

JOD and RAC designed the study, performed the research, provided new methods and wrote the manuscript.

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