

Do fitness-equalizing tradeoffs lead to neutral communities?

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Received: 2 December 2010 / Accepted: 10 December 2010
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Abstract Neutral theory in ecology is aimed at describing communities where species coexist due to similarities rather than the classically posited niche differences. It assumes that all individuals, regardless of species identity, are demographically equivalent. However, Hubbell suggested that neutral theory may describe even niche communities because tradeoffs equalize fitness across species which differ in their traits. In fact, tradeoffs can involve stabilization as well as fitness equalization, and stabilization involves different dynamics and can lead to different community patterns than neutral theory. Yet the important question remains if neutral theory provides a robust picture of all fitness-equalized communities, of which communities with demographic equivalence are one special case. Here, I examine Hubbell's suggestion for a purely fitness-equalizing interspecific birth–death tradeoff, expanding neutral theory to a theory describing this broader class of fitness-equalized communities. In particular, I use a flexible framework allowing examination of the influence of speciation dynamics. I find that the scaling of speciation rates with birth and death rates, which is poorly known, has large impacts on community structure. In most cases, the departure from the predictions of current neutral models is substantial. This work

suggests that demographic and speciation complexities present a challenge to the future development and use of neutral theory in ecology as null model. The framework presented here will provide a starting point for meeting that challenge, and may also be useful in the development of stochastic niche models with speciation dynamics.

Keywords Life history tradeoff · Species abundance distribution · Macroecology · Competition · Coexistence · Stochastic community models

Introduction

Hubbell (2001) challenged a key assumption of community ecology, namely that the coexistence of species requires species niche differences. Hubbell proposed that species often coexist in communities instead due to their similarities. He proposed a “neutral theory” in which individuals of different species are ecologically identical, and hence speciation, dispersal limitation, and demographic stochasticity are the primary determinants of community composition and structure. Despite mixed empirical success (McGill 2006), this neutral theory works surprisingly well given its simplicity.

Hence, some have argued the community pattern predictions tested are insensitive to whether species coexist through similarities or differences (e.g. Bell 2001). Hubbell himself suggested that neutral theory may even describe many niche communities (Hubbell 2001; Levine 2002). He argued that when species differ, tradeoffs tend to equalize fitness across individuals of different species, and that this fitness equalization is essentially what neutral theory assumes. However,

Electronic supplementary material The online version of this article (doi:10.1007/s12080-010-0107-8) contains supplementary material, which is available to authorized users.

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Hubbell's original argument is not completely accurate. Tradeoffs can involve stabilizing mechanisms as well as fitness-equalizing mechanisms (Chesson 2001; Adler et al. 2007). Under stabilization, species invade from low abundance (i.e., there is a rare species advantage). To most, this is the hallmark of true niche differences between species. Under fitness equalization, species' abundances are just as likely to go up as down from any starting abundance. Stabilization leads to different community properties than the neutral case, just as frequency-dependent selection leads to different population genetic structure than the neutral case (Neuhauser 1999), although since the difference may be small at high diversity Chishom (2010) and stabilization may lead to the same range of patterns as neutrality Chave et al. (2002), whether the difference can be empirically distinguished is unclear. Thus, neutral theory does not in general describe communities with stabilizing tradeoffs, i.e., it does not describe niche communities, and may still be useful as a null model (or a "null theory" (Harte 2004)) for tests for niche assembly, although some novel approaches may be required.

However, it is an open question whether communities with purely fitness-equalizing tradeoffs are well described by current neutral theory (Chave 2004). Instead of equal fitness, Hubbell's original neutral theory takes the more stringent assumption that all individuals have equal birth and death rates (i.e. they are "demographically equivalent"). But species vary in birth and death rates, with "ecological equivalence" (if it exists) arising because those species with high birth rates also have high death rates, leading to equal fitness across species. Reproductive investment comes at the cost of adult survival. Growing evidence points to interspecific variation and tradeoffs in reproductive investment and adult survival (e.g. Resnick 1985; Gunderson 1997; Saether and Bakke 2000; Forbis and Doak 2004; Moles et al. 2004). Once one considers the entire age structure of populations, one realizes there is a great deal of demographic complexity to consider (Roff 1992; Metcalf and Pavaud 2006). So for neutral theory to describe any real communities, or at least provide a null model whose rejection is evidence of niche assembly rather than other complexities, it must accurately describe communities where species vary in demographic rates and achieve "similarity" through tradeoffs that lead to equal fitness.

Recently, ecologists have begun studying cases where species differ in birth and death rates but not in fitness (Ostling 2004; Etienne et al. 2007; Lin et al. 2009; Allouche and Kadmon 2009) (in contrast to models

where species vary in both demographic rates and fitness (Zhang and Lin 1997; Yu et al. 1998; Zhou and Zhang 2009)). These recent studies produced mixed results about whether fitness-equalized life history variation matters for structural properties of the community and perhaps for that reason have gone largely unnoticed by most ecologists interested in neutral theory. Here, I use a more flexible birth-death tradeoff model to consider how assumptions about speciation dynamics influence the community. In particular, the scaling of speciation rate with birth and death rates has been shown to vary (e.g. Marzluff and Dial 1991; Owens et al. 1999; Liow et al. 2008), and I demonstrate that this scaling has a critical influence on the apportionment of abundance and species richness across life history strategies, and on the total species richness and species abundance distribution. In one case, these properties are consistent with the predictions of current neutral models, but in all others there are important differences. Hence, I explain how the discrepancies between previous studies arose and show that there are many more possibilities for the structure of fitness-equalized communities than even those studies considered. I also provide a new framework for predicting those varied structures, and hence a new starting point for the development of neutral models for communities. Elements of the framework I develop may also be useful in the development of stochastic niche models with speciation dynamics.

The model

In this section, I first consider the dynamics of any community of differing species and provide a differential equation for the probability of a given configuration of the whole community. I then specify this differential equation for the case where species differ only in birth and death rates, but are equal in fitness (i.e., the case of a fitness-equalizing birth-death tradeoff). Next, I present a "non-interactive" approximation to the dynamics of this birth-death tradeoff community, which should apply well when the community size is large. Finally, I specify the speciation dynamics part of my tradeoff model in detail. I then obtain a differential equation for the probability that a species of a given life history type has a given abundance at a given time. From this differential equation, I am able to derive predictions for various equilibrium properties of the community.

Dynamics of joint distribution when species differ in type

In this paper, I focus on the properties of a “metacommunity”, i.e., the large pool of species that might disperse to any local community, and ignore the potential influence of dispersal limitation within the metacommunity (Chave and Leigh 2002; Rosindell and Cornell 2007). Hence the only process adding species in the model here is speciation. I will refer to this metacommunity simply as a “community”. I begin by writing down a differential equation for the distribution, $P(n_1, n_2, \dots, n_S, t)$, defined as the probability for the community to have the configuration $\{n_1, \dots, n_S\}$, where n_k is the abundance of species k , and the time t is the time since species 1 speciated. Note some important things which are implicit to this configuration. Firstly, each species has a type vector \mathbf{T}_k associated with it, where multiple species can have the same type vector (there is no reason in principle why a given set of trait values could not arise more than once in multiple species. Secondly, I set the time to 0 when species 1 speciates, and the species listed in the configuration $\{n_1, \dots, n_S\}$ are all species who were either in existence at the time that species 1 speciated, or arose since then. Clearly, the number of species in the list increases over time and as the list grows, the probability associated with configurations where abundance values early in the list are zero will tend to be higher. Finally, the species other than species 1 are listed in the order in which they speciated (species 1 is an exception because some of the other species in the list may have been in existence at the time species 1 speciated).

Although this approach to specifying the configuration of the community may seem complex, its advantage is that it enables us to handle the speciation dynamics in a very straightforward way. In particular, in deriving the species abundance distribution, we do not need to approximate speciation as immigration in the infinite community size limit as has often been done by developers of neutral theory (Volkov et al. 2003; Etienne et al. 2007). In particular, I will use the alternative approach (Vallade and Houchmandzadeh 2003) of expressing the species abundance distribution in terms of the marginal probability distribution for a species to have abundance n a time t after it arose through speciation. Placing the species determining the time variable t at the beginning of the configuration will enable me to use the simplest notation in deriving the differential equation for this marginal probability distribution.

The differential equation for $P(n_1, n_2, \dots, n_S, t)$ is

$$\begin{aligned} & \frac{dP(n_1, \dots, n_S, t)}{dt} \\ &= \sum_k l_{n_k+1}^k P(n_1, \dots, n_k+1, \dots, t) \\ &\quad + \sum_k g_{n_k-1}^k P(n_1, \dots, n_k-1, \dots, t) \\ &\quad - \sum_k (l_{n_k}^k + g_{n_k}^k) P(n_1, \dots, n_k, \dots, t) \\ &\quad + \sum_k \rho(n_k+1, \mathbf{T}_k, \mathbf{T}_S) \\ &\quad \times \delta_{n_S,1} P(n_1, \dots, n_k+1, \dots, n_{S-1}, t) \\ &\quad - \sum_k \sum_{\mathbf{T}_{S+1}} \rho(n_k, \mathbf{T}_k, \mathbf{T}_{S+1}) P(n_1, \dots, n_k, \dots, n_S, t). \quad (1) \end{aligned}$$

The first three lines in Eq. 1 reflect events in which a species loses or gains an individual through birth and death events. (Note the l_n^k and g_n^k reflect loss and gain rates, respectively.) The last two terms reflect speciation events, in which I assume one species loses an individual when it speciates and the new species arises with one individual (reflected in the presence of n_k+1 and $\delta_{n_S,1}$ in the second to last term). I use this assumption for consistency with the widely used version of neutral theory in ecology, but it could be generalized (Allen and Savage 2007; Haegeman and Etienne 2009). These terms involve $\rho(n_k, \mathbf{T}_k, \mathbf{T}_S)$, which is the rate at which a species of type \mathbf{T}_k with abundance n_k gives rise to a daughter species of type \mathbf{T}_S . The last term also involves a sum over possible types for the daughter species.

Fitness-equalizing birth–death tradeoff

In the rest of the paper, I explore a more specific model captured by Eq. 1 that has a fitness-equalizing interspecific birth–death tradeoff. I build this into a model that has “zero-sum” dynamics analogous to the Moran model in population genetics (Hubbell 2001; Blythe and McKane 2007). Under “zero-sum” dynamics, each death event is immediately followed by a birth event. Although other approaches have been used for neutral models in both the population genetics and community contexts most seem to lead to similar results in the completely neutral case (Blythe and McKane 2007; Haegeman and Etienne 2008) (although the more realistic case of density-dependent population or community regulation is relatively unexplored), and hence I

take this approach as a good starting point for studying the impact of introducing fitness-equalized life history variation.

Specifically, I define the transition rates l_n^k and g_n^k in Eq. 1 as:

$$l_n^k = d_k n \left(\frac{\sum_{k'} b_{k'} n_{k'} - b_k n}{\sum_{k'} b_{k'} n_{k'}} \right) \quad (2)$$

$$g_n^k = \left(\sum_{k'} d_{k'} n_{k'} - d_k n \right) \left(\frac{b_k n}{\sum_{k'} b_{k'} n_{k'}} \right), \quad (3)$$

where b_k and d_k are the per-capita birth and death rates, respectively, of species k . In Eq. 2, the first factor reflects the rate at which individuals of species k die, and the second the probability that the replacing individual is of a species other than k . Similarly, in Eq. 3, the first factor reflects the rate at which individuals of species other than k die, and the second the probability that the replacing individual is from species k . Since the model is essentially only keeping track of adult individuals, the birth rate b_k is really the rate of recruitment into the adult stage for species k . Furthermore, the rate b_k reflects the inherent reproductive potential of the species k . Specifically, it is the per-capita recruitment rate species k would obtain in a completely available, favorable habitat. Equations 2 and 3 assume that these per-capita rates in an open, favorable habitat accurately reflect the relative likelihood of species capturing a single available patch for which they are competing. In this model, the type of each species is specified by a vector of length two: $\mathbf{T}_k = (b_k, d_k)$.

I assume species vary and tradeoff in their per-capita “birth” and “death” rates, or more exactly in their per-capita rates of adult recruitment and adult survival. Specifically, I assume that species have equal fitness, where I define equal fitness as the case where the rate of loss of individuals from each species is equal to the rate of gain, regardless of the abundance of the species or the overall configuration of the community, i.e., the case where

$$l_n^k = g_n^k \quad \text{for all } k \text{ and all } \{n_1, \dots, n_s, \dots, n_S\}. \quad (4)$$

This leads to the following condition on the birth and death rates:

$$b_k = c d_k \quad \text{for all } k. \quad (5)$$

In words, equal fitness requires that each species has its birth rate proportional to their death rate according to the same constant, c . This constant reflects how

closely balanced recruitment and mortality of any of the species would be in an open spaced environment. Most species would produce more adults per unit time than would die per unit time if given plenty of favorable habitat, so $c > 1$ is expected. I take the assumption of equal fitness across species from here on, in which case I no longer need a vector \mathbf{T}_k to specify the type of each species, and can instead use one parameter $T_k = d_k = b_k/c$.

Note that equal fitness will cause species’ average abundances to be constant in time in the absence of speciation dynamics. Consider the expectation value of the abundance of species 1 at time t , $E[n_1(t)]$ (noting that any species can be thought of as species 1), which can be obtained from the joint distribution by

$$E[n_1(t)] = \sum_{\text{configs}} n_1 P(n_1, \dots, n_s, t) \quad (6)$$

where \sum_{configs} is the sum over all possible configurations of the community. This includes a sum over the possible values for the number of species in the community configuration, integration over the possible types (presuming b_k and d_k are continuous variables) for each species (except for species 1) and a sum over the possible abundances for all the species. Under equal fitness, species’ abundances will on average be neither increasing nor decreasing in the absence of speciation dynamics (i.e., in the absence of the last two terms of Eq. 1):

$$\begin{aligned} \frac{dE[n_1(t)]}{dt} &= E[(g_{n_1}^1(t) - l_{n_1}^1(t))] - \text{speciation terms} \\ &= 0 - \text{speciation terms}, \\ \text{if } l_{n_1}^1 &= g_{n_1}^1 \text{ for all } \{n_1, \dots, n_s\}. \end{aligned} \quad (7)$$

Note that eventually every species will either go extinct or fix in the community (i.e., have an abundance equal to the total community size), but the relative probabilities of these events under equal fitness should be such that the average abundance of each species is fixed at one after it arises with one individual through speciation, just as in the completely neutral model (Blythe and McKane 2007). Furthermore, note that the addition of speciation dynamics causes each species to on average decline in abundance over time, and eventually go extinct.

Non-interactive approximation

To derive community properties from the complex dynamics in Eq. 1 for the fitness-equalizing birth-death

tradeoff case, a useful approximation is to assume abundances n of the focal species are small compared with the total number of individuals in the community, N . This approximation has been shown to work well in the completely neutral case (Alonso and McKane 2004; Chave 2004; Etienne et al. 2007). Under this assumption, Eqs. 2 and 3 can be written as:

$$l_n^k = d_k n \left(1 - \frac{b_k n}{\langle b \rangle N}\right) \approx d_k n = T_k n \quad (8)$$

$$g_n^k = (\langle d \rangle N - d_k n) \left(\frac{b_k n}{\langle b \rangle N}\right) \approx b_k n \frac{\langle d \rangle}{\langle b \rangle} = T_k n \quad (9)$$

Hence under this approximation the species are essentially “non-interactive”, meaning that the probability of loss or gain of an individual of any species through birth or death is independent of the abundance of the other species. This approximation allows consideration of the birth–death dynamics of each species separately, a key step towards decoupling the complex dynamics in Eq. 1.

Speciation dynamics

The complexity of speciation dynamics (i.e., the last two terms in Eq. 1) must also be simplified for the tradeoff model to be tractable. However, because here I use Eq. 1 as my starting point, I incorporate more flexibility in speciation dynamics than previous approaches to community tradeoff models. There are two aspects of the speciation dynamics I will consider: (1) how the rate at which a species speciates depends on its life history strategy, and (2) how quickly new species of a given life history strategy arise through speciation.

The first of these, the dependence of the rate at which a species speciates on its life history type T , is one component of the function $\rho(n, T, T_k)$, defined as above in Eq. 1 as the rate at which species of type T and abundance n give rise to species of type T_k . In the analysis that follows, I take this function to have the form:

$$\rho(n, T, T_k) = f_T^{\text{loss}} v n \rho'(T, T_k) \quad (10)$$

In Eq. 10, $f_T^{\text{loss}} v n$ reflects the rate at which the species of abundance n and type T speciates, where v is the community-average per-capita speciation rate, and $\rho'(T, T_k)$ reflects the probability for a species of type T_k to arise from a parent species of type T that is speciating. Hence, I am taking the simplification that the rate at which a species speciates is determined entirely by its abundance and life history and not the abundance

and types of the rest of the species in the community. In particular, I take the rate at which a species speciates to be linearly proportional to its abundance. This is consistent with most neutral models used in ecology, but variation from this assumption does influence predictions (Etienne et al. 2007). More importantly to the focus of this paper, I have used a dimensionless scaling factor f_T^{loss} to encapsulate how the rate at which a species speciates depends on its life history type T , i.e., how it depends on its birth or death rate. Here, I allow this factor to have any dependence on T . Previous studies (Ostling 2004; Etienne et al. 2007; Lin et al. 2009; Allouche and Kadmon 2009) implicitly assumed a form for f_T^{loss} .

Studies point to faster rates of molecular evolution among taxa with faster life history strategies (Bromham et al. 1996; Smith and Donoghue 2008). However, the rate at which a species speciates may or may not have a similar relationship with life history, depending on whether it is determined primarily by the rate of genetic divergence, the likelihood for geographic isolation, or the prevalence of ecological opportunity, or all three (Futuyma 1997; Webster et al. 2003). Fossil record and phylogenetic studies point to a variety of relationships between speciation rate or diversification rate (speciation rate minus extinction rate) and life history (Marzluff and Dial 1991; Owens et al. 1999; Liow et al. 2008).

This leaves open a wide variety of possibilities, and the likelihood of a great deal of system specificity, for the scaling of the rate at which a species speciates with its life history, f_T^{loss} . If the rate of molecular evolution does determine speciation rate, one would expect f_T^{loss} to be linear in T , since the rate of molecular evolution is inversely proportional to generation time. However, if other factors dominate, or if they influence speciation rates in concert with the rate of molecular evolution, then f_T^{loss} could increase, remain constant or decrease with T (and the increase or decrease could be linear or non-linear).

I now turn to the second key aspect of speciation dynamics, how quickly new species of a given life history type T arise through speciation. I will derive an expression for this dependence in terms of f_T^{loss} and then demonstrate that this dependence can be different than the scaling of the rate at which a species speciates encapsulated in f_T^{loss} . Take $p_T(t)$ to be the rate at which species of type T are arising at time t . This rate can be calculated from the distribution $P(n_1, \dots, n_S, t)$ by:

$$p_T(t) = \sum_{\text{configs}} \sum_k \rho(n_k, T_k, T) P(n_1, \dots, n_S, t). \quad (11)$$

Using Eq. 10 and converting the sum over species k into an integral over types T' this expression for the speciation rate becomes

$$p_T(t) = \int_{T_{\min}}^{T_{\max}} dT' f_{T'}^{\text{loss}} v \rho'(T', T) N_{T'}(t), \quad (12)$$

where $N_{T'}(t)$ is the expected total abundance across species of type T' at time t , i.e., $N_{T'}(t) = \sum_k \delta(T_k - T')$ $E[n_k(t)]$ (See Appendix S1 in the [Electronic supplementary material](#)). So $p_T(t)$ depends on the current distribution of abundance across types in the community ($N_{T'}(t)$), how the rate at which they speciate depends on their type ($f_{T'}^{\text{loss}}$), and the degree of correlation between parent and daughter types ($\rho(T', T)$). It is the large t behavior of $p_T(t)$ that matters for equilibrium community properties, i.e., what matters is $p_T = \lim_{t \rightarrow \infty} p_T(t)$, the behavior some long time after any particular starting configuration of the community or particular speciation event. In particular, what matters here is how p_T scales with T . For convenience I define the dimensionless scaling factor $f_T^{\text{gain}} = \frac{p_T \eta}{v N}$ where η is the range of possible T values of the community, N and v are defined as above. The relationship between the scaling factors f_T^{loss} and f_T^{gain} is then:

$$f_T^{\text{gain}} = \int_{T_{\min}}^{T_{\max}} dT' f_{T'}^{\text{loss}} \rho'(T', T) \frac{N_{T'}}{N/\eta}, \quad (13)$$

where $N_{T'} = \lim_{t \rightarrow \infty} N_{T'}(t)$.

One can see from Eq. 13 that f_T^{gain} can be different than f_T^{loss} . In particular, consider the relationship between these two scaling factors in two extremes for the relationship between parent and daughter life history types, $\rho'(T', T)$. Firstly, if parent and daughter types are equal, i.e., if $\rho'(T', T) = \delta(T' - T)$, the historical relative abundance of different types in the community will be maintained (see Appendix A) and will determine the equilibrium $N_{T'}$. Hence any historical bias in $N_{T'}$ will cause f_T^{gain} to differ from f_T^{loss} . Secondly, if the relationship between daughter and parent species' traits is very weak, i.e., if $\rho'(T', T)$ is relatively independent of T' , then f_T^{gain} is simply equal to $\rho'(T', T)$ and hence is unrelated to f_T^{loss} . A weak relationship like this might arise because the daughter type T is heavily determined by fundamental physiological or genetic constraints, or even ecological opportunity (there is the possibility that niche space availability has had a larger influence on the speciation dynamics of the community than it is currently having on the birth-death dynamics, or one may want to separate the evolutionary- and ecological-

time-scale influences of niche space). Ultimately, the model is completely specified by specifying $\rho'(T', T)$, f_T^{loss} (which together determine $N_{T'}$ (see Appendix A) and f_T^{gain}), and, if $\rho'(T', T) = \delta(T' - T)$, the historical value of $N_{T'}$. However, it is complex to solve for $N_{T'}$ in situations other than the two extremes just mentioned, and all of the community properties I study here are ultimately just dependent on f_T^{loss} and f_T^{gain} . Hence later in this paper when I study the community properties predicted by this model, I take the approach of studying some cases delineated by the form of f_T^{loss} and f_T^{gain} , and providing very basic insight into how these cases could arise by considering them in the two extremes of the relationship between parent and daughter traits.

Species abundance distribution for each type

Taking the “non-interactive” approximation, and modelling speciation dynamics as described above, the following differential equation for the probability for a species of type T to have abundance n at time t , $P_T(n, t)$ can be obtained either by intuition or by summing Eq. 1 for the joint distribution over the configurations of species other than species 1 (the species that speciated at time $t = 0$) (see Appendix S2):

$$\begin{aligned} \frac{dP_T(n, t)}{dt} = & w_{n+1}^T(t) P_T(n+1, t) + z_{n-1}^T(t) P_T(n-1, t) \\ & - (w_n^T(t) + z_n^T(t)) P_T(n, t). \end{aligned} \quad (14)$$

where

$$w_n^T = l_n^T + f_T^{\text{loss}} v n \quad (15)$$

and I have now used T in place of k in labeling l_n^k and g_n^k for species 1. Note that there can be multiple species of type T present, and that Eq. 14 would capture the behavior of any of them.

The equilibrium of the distribution $P_T(n, t)$ is obvious without solving Eq. 14. On average, all species are declining in abundance because they are loosing individuals to speciation events, eventually all species go extinct, and the equilibrium of $P_T(n, t)$ is $\delta_{n,1}$ regardless of the value of T . But it is not just the equilibrium of $P_T(n, t)$ that determines the species abundance distribution but its value at all times. To derive the species abundance distribution (SAD) of species of type T , meaning the expected number of species of type T with abundance n at time t (which we'll write as $S_T(n, t)$), we must write down an expression for it in

terms of the behavior of $P_T(n, t)$ at all times, and then apply that expression to Eq. 14 to obtain a differential equation for it. Ultimately we will not need to know the full time-dependent behavior of $P_T(n, t)$ to get at the equilibrium SAD, but the approach of initially writing it in terms of the time-dependent behavior enables us to solve for the SAD without approximating speciation as the infinite community size limit of immigration dynamics (the approach taken by Volkov et al. (2003) and Etienne et al. (2007), and others). The relationship between the SAD of each type and $P_T(n, t)$ is Vallade and Houchmandzadeh (2003):

$$S_T(n, t) = \int_0^t dt' p_T(t') P_T(n, t - t') + \text{terms from species present at } t = 0. \quad (16)$$

Equation 16 integrates over the possible times t' that each type T species might have arisen in the community. Specifically it integrates over the rate at which type T species are arising at time t' , $p_T(t')$, multiplied by the probability that a species of type T has n individuals at time $t - t'$ after it arose through speciation. This integral, when added to terms from type T species that are present at time $t = 0$ that now have abundance n , gives the SAD of each type.

I'll consider the large t behavior of the SAD, i.e., the equilibrium $S_T(n, t)$ would approach a long time after any starting configuration of the community. In that limit the terms from species initially present in the community are negligible, and the time dependence of the speciation rate is also negligible. At large t the SAD of each type can be approximated by

$$S_T(n, t) \approx p_T \int_0^t dt' P_T(n, t - t'), \quad (17)$$

where $p_T = \lim_{t' \rightarrow \infty} p_T(t')$. Carrying out the integration in Eq. 17 on both sides of Eq. 14 leads to (see Appendix S3 in the [Electronic supplementary material](#) for details):

$$\frac{dS_T(n, t)}{dt} = w_{n+1}^T S_T(n+1, t) + z_{n-1}^T S_T(n-1, t) - (w_n^T + z_n^T) S_T(n, t) + \delta_{n,1} p_T \quad (18)$$

The equilibrium solution of Eq. 18 is (see SI in the [Electronic supplementary material](#) for details):

$$S_T(n) = \frac{f_T^{\text{gain}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta} \frac{N}{n} \frac{\left(\left(1 + \frac{f_T^{\text{loss}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta} \right)^{-1} \right)^n}{n} \quad (19)$$

In Eq. 19, $\langle T \rangle$ is the average life history type across individuals of the community, i.e., $\langle T \rangle = (1/N) \sum_T S_T(n) n T$. Although $\langle T \rangle$ actually cancels out of Eq. 19, I introduce it for conceptual value, to emphasize dependence on the speciation rate per average death rate, $v/\langle T \rangle$. Note that Eq. 19 is simply a log-series distribution, i.e., $S_T(n) = \alpha_T \frac{(x_T)^n}{n}$ with $x_T = (1 + \frac{f_T^{\text{loss}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta})^{-1}$ and $\alpha_T = \frac{f_T^{\text{gain}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta} \frac{N}{n}$, so the scaling factors f_T^{loss} and f_T^{gain} in comparison to linear scaling with birth and death rates, i.e., $T/\langle T \rangle$, along with the speciation rate per average death rate $v/\langle T \rangle$ and the total community size N are all that are needed to determine the properties of the community.

I now use Eq. 19 to calculate equilibrium expectations for a variety of community structure properties. Firstly, the expected total number of individuals across all species of life history strategy T , N_T , is:

$$N_T = \sum_{n=1}^{\infty} S_T(n) \cdot n = \alpha_T \frac{x_T}{1 - x_T} = \frac{f_T^{\text{gain}}}{f_T^{\text{loss}}} \frac{N}{\eta} \quad (20)$$

Next, the total number of species of life history strategy T , S_T , follows:

$$S_T = \sum_{n=1}^{\infty} S_T(n) = -\alpha_T \log(1 - x_T) = \frac{f_T^{\text{gain}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta} \frac{N}{\log \left(\frac{1 + \frac{f_T^{\text{loss}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta}}{\frac{f_T^{\text{loss}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta}} \right)} \quad (21)$$

Finally, the average abundance of a species of life history strategy T directly follows from these two properties:

$$\langle n_T \rangle = \frac{N_T}{S_T} = \frac{1}{\frac{f_T^{\text{loss}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta} \log \left(\frac{1 + \frac{f_T^{\text{loss}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta}}{\frac{f_T^{\text{loss}}}{T/\langle T \rangle \langle T \rangle} \frac{v}{\eta}} \right)} \quad (22)$$

Sensitivity of predictions to speciation dynamics

Here, I use Eqs. 19–22 to examine the sensitivity of these community properties to the scaling of speciation rates with birth and death rates as reflected in f_T^{loss} and f_T^{gain} . Firstly, through study of these expressions for the community properties one can see when they are the same as the naive predictions from current neutral models with equal demographic rates across all

individuals of all species. $S_T(n)$ and S_T , the average number of type T species with abundance n and the average total number of species of type T , respectively, reduce to the completely neutral prediction only when $f_T^{\text{gain}} = f_T^{\text{loss}} = T/\langle T \rangle$. In that case, Eq. 19 is the log series with $\alpha = \frac{v}{\langle T \rangle} \frac{N}{\eta}$ and $x = (1 + \frac{v}{\langle T \rangle})^{-1}$, which is the completely neutral prediction for the species abundance distribution of a randomly chosen fraction $1/\eta$ of the species in a community with an average death rate of $\langle T \rangle$ (see Appendix S4 in the [Electronic supplementary material](#)). N_T , the total abundance across all species of type T , is independent of T , and in that sense consistent with the completely neutral case, in a wider variety of circumstances, namely as long as the two scaling factors f_T^{gain} and f_T^{loss} depend on T in the same way. Finally, $\langle n_T \rangle$ is independent of T , and in that sense consistent with the completely neutral case, whenever $f_T^{\text{loss}} = T/\langle T \rangle$. Hence, it is only sensitive to the scaling of the rate at which species of type T speciate.

Next, I plot the expected form of the properties in Eqs. 20–22 (Fig. 1), as well as the total species richness and total species abundance distribution (SAD) of the community (Fig. 2) under five cases for the form of f_T^{loss} and f_T^{gain} that demonstrate a wide range of behavior in community structure (see Box 1 for a list of the cases and insight into how each one might arise). I use community size $N = 1$ million, life history parameter T ranging over integer values 1–100, and a speciation rate per average death rate of 5×10^{-4} . Restriction to integer values of T simplifies the calculation and is analogous to binning predictions on the T axis as would be done for real data. The two order of magnitude range in T is comparable to the range of seed outputs even within gap-specialist species in tropical forests (R. Condit, personal communication). These plots are based on Eqs. 19–22 and hence the non-interactive approximation. However, I verified for *case 2* that the predicted community properties are indistinguishable

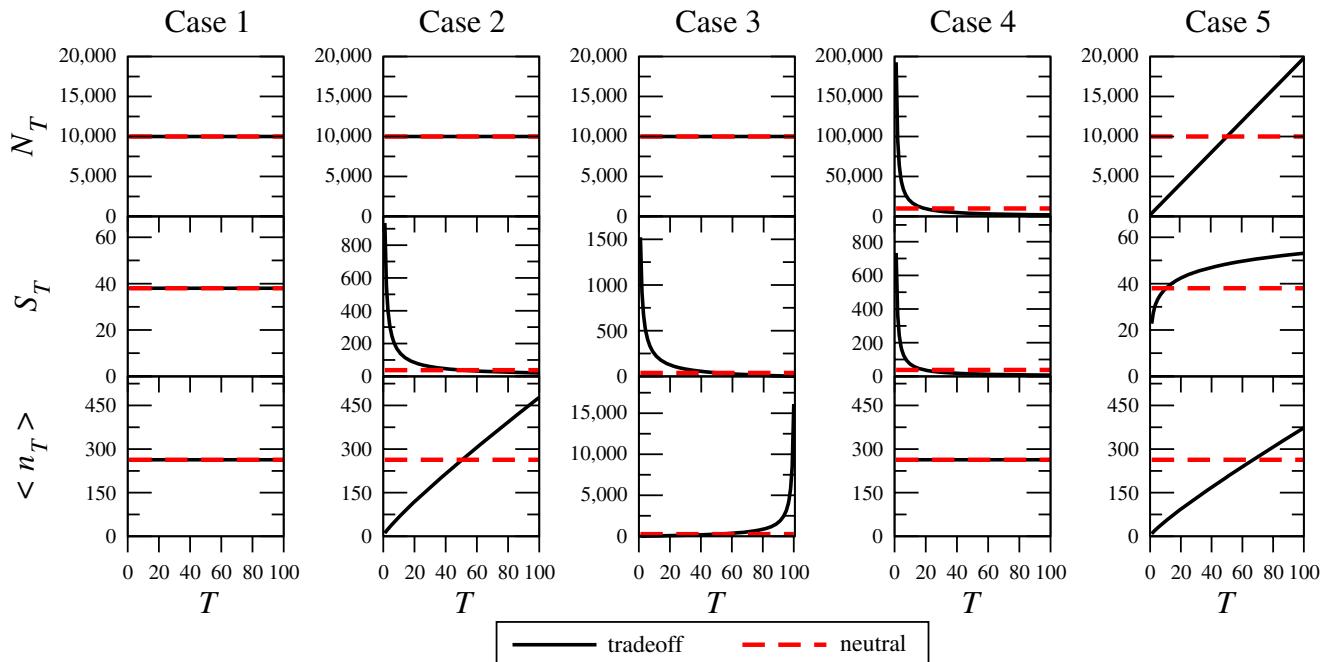


Fig. 1 Apportionment of abundance and species richness across life history types in the tradeoff model. Community structure properties are shown under the five different cases of the scaling of speciation rates with life history. Shown for each case are the expected equilibrium values of total abundance across all species of a given life history type, $N_T = \sum_n S_T(n)n$ (top graphs, based on Eq. 20, but also implicit to the speciation dynamics assumptions of each case), the number of species present in the community with a given life history type, $S_T = \sum_n S_T(n)$ (middle graphs, based on Eq. 21), and the average abundance of species present with a given life history type, $\langle n_T \rangle = N_T/S_T$ (bottom graphs, based on Eq. 22). I used a community size $N = 1$ million,

life history parameter T ranging over integer values 1–100, and a speciation rate per average death rate of 5×10^{-4} . Solid lines are tradeoff model properties; dashed red lines are naive expectations from neutral theory (i.e., equal apportionment of abundance and species richness across types). *Case 1:* f_T^{loss} and f_T^{gain} linearly proportional to T . *Case 2:* f_T^{loss} and f_T^{gain} independent of T . *Case 3:* f_T^{loss} and f_T^{gain} decreasing linearly with T . *Case 4:* f_T^{loss} linearly proportional to T , but f_T^{gain} independent of T . *Case 5:* f_T^{loss} independent of T , but f_T^{gain} linearly proportional to T . See Box 1 for insight into how each case might arise

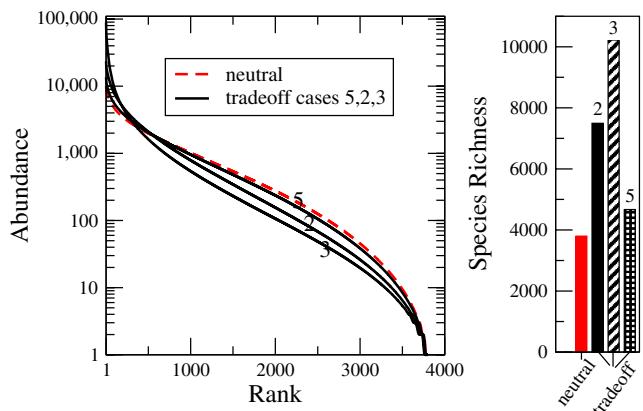


Fig. 2 Species abundance distribution and species richness in the tradeoff model. The *left graph* compares rank abundance curves (RACs) (calculated by drawing without replacement the abundance n for each of S species with probability $S(n)/S = \sum_T S_T(n)/S$), and the *right graph* species richness, of the tradeoff and neutral models for communities of the same parameter values and speciation rate scaling cases as specified in the caption of Fig. 1. To remove drastic differences in the RACs caused by differences in species richness rather than relative abundance, speciation rates were decreased in the tradeoff RACs so that species richness matched the neutral case. Tradeoff RACs reflect more unevenness, and tradeoff species richness tends to be higher, than the neutral case (except for tradeoff model *cases 1* and *4* which match neutral predictions and are not shown). Note that the abundance of the most dominant species (i.e., the species of rank 1, the left intercept on the graph) is highest in *case 1*, next highest in *case 2*, then *case 5*, and lowest in the neutral case

from those predicted by simulation of a Moran-style or “zero-sum” model (see Appendix S5 in the [Electronic supplementary material](#)). In addition, I verified that the same qualitative differences between the tradeoff and completely neutral cases arise when the community size N , per-capita speciation rate ν , and range in T are varied from the values used to generate the plots shown here.

These plots show that different forms for the scaling factors f_T^{loss} and f_T^{gain} lead to very different apportionment of abundance and species richness across life history strategies (Fig. 1), many of which are quite different from a naive application of neutral theory to a community containing different life history strategies (i.e., equal apportionment across all strategies). Furthermore, in the presence of a fitness-equalizing tradeoff, total species richness can be much higher and the total species abundance distribution much more uneven than in the completely neutral model (see SI in the [Electronic supplementary material](#) for completely neutral model calculations) (Fig. 2). Note in particular that the plots in Fig. 1 verify the direct analysis of the equations for the community properties made above, in that S_T is independent of T only in *case 1*, where both

scaling factors are linear in T , N_T is independent of T in *cases 1–3*, where the two scaling factors take the same form, and $\langle n_T \rangle$ is independent of T in *cases 1* and *4*, where f_T^{loss} is linear in T .

These effects can to some degree be understood intuitively. Consider in particular *case 2*, where f_T^{loss} and f_T^{gain} are constant with respect to T . In this case the total abundance across all species of given life history type is homogeneous across types (top graph in Fig. 1). This makes sense because there is equal fitness across life history types and $f_T^{\text{loss}} = f_T^{\text{gain}}$ means each life history type is losing and gaining individuals through speciation events at the same rate. However, in this case there is a declining relationship between species richness and life history strategy (middle graph in Fig. 1). This is because species of the faster life history types go extinct more quickly due to larger fluctuations in abundance from demographic stochasticity. This means that for each life history type, the same total abundance ($N_T = N/\eta$) is spread over fewer species (S_T) for the faster life history types, leading to higher abundance per extant species ($\langle n_T \rangle$) for those faster life history types (bottom graph for *case 2* in Fig. 1). Although this result makes intuitive sense, it is at the same time surprising. Even in a community in which the different types present have the same fitness, there can be a relationship between abundance and type! Given this relationship, it makes sense that the total SAD tends to be more uneven than the completely neutral case (Fig. 2), but why the species richness is higher than in the neutral case is not obvious.

These results explain why Etienne et al. (2007) and Allouche and Kadmon (2009), who looked at a birth-death tradeoff model, but essentially assumed $f_T^{\text{gain}} = f_T^{\text{loss}} = T/\langle T \rangle$, found no difference between the SAD of their fitness-equalized birth-death tradeoff model and that of the completely neutral case. Two other studies of a birth-death tradeoff model (Ostling 2004; Lin et al. 2009) reported a relationship between $\langle n_T \rangle$ and T , which will arise when f_T^{loss} is not linear in T . Surprisingly, the dynamics described in these studies seem to instead imply an f_T^{loss} linear in T . (They each describe the speciation process as occurring in a fraction ν of the death events, in which case species with higher death rates will be proportionally more likely to speciate.) However, one of these studies was my own (Ostling 2004), and in that study the actual simulations used a slightly different speciation algorithm to improve computation time (I mention this very briefly in the study). Namely they carried out $N\nu$ speciation events after every N death events, where N is the metacommunity size. Species were not selected for speciation according to their death rate, but instead independent of their

Box 1 Speciation rate scaling cases in Figs. 1 and 2.

There are two key aspects of the speciation dynamics that determine the community properties under this fitness-equalized tradeoff model (see Eq. 19): f_T^{loss} , which describes how the rate at which species speciate (and loose and individual to the new species) scales with their birth or death rate (or their life history type $T = d = b/c$ where b and d are the birth and death rates respectively and the constancy of c across species in this equality enforces equal fitness); and f_T^{gain} , which describes how the rate at which new species arise scales with their birth or death rate (or life history type T). In Figs. 1 and 2, I selected five cases for the form of these two scaling factors that demonstrate a range of behavior in community properties, but there are likely many biologically plausible possibilities. Here I provide some very basic insight into how each case could arise in the two extremes for the relationship between parent and daughter traits: a very strong relationship or a very weak one. A very strong relationship is when $\rho'(T', T) = \delta(T' - T)$ where $\rho'(T', T)$ is the probability density for a species of type T to arise from a parent species of type T' that is speciating. Under a strong relationship, the relationship between f_T^{loss} and f_T^{gain} is determined by any historical biases in the relative abundance of types (meaning the relative total abundance across all species with that type: $N_T = \lim_{t \rightarrow \infty} \sum_k \delta(T_k - T) E[n_k(t)]$) (See Appendix A). In particular, f_T^{gain} is simply the product of the historical bias in the relative abundance of types and f_T^{loss} , i.e., $f_T^{\text{gain}} = N_{T, \text{historical}} f_T^{\text{loss}}$ (see Eq. 13), so these two scaling factors will have the same form whenever the historical relative abundance of types is uniform. A very weak relationship is when $\rho'(T', T)$ independent of T' . Under a weak relationship, f_T^{gain} is simply equal to the dependence of $\rho'(T', T)$ on T , which may be determined by fundamental mechanisms influencing speciation (e.g. physiological or genetic constraints, or ecological opportunity). See Appendix B for calculation of constants of proportionality in the scaling factors f_T^{loss} or f_T^{gain} in each case based on consistency conditions.

Case 1: f_T^{loss} and f_T^{gain} linearly proportional to T .

Linear f_T^{loss} could arise if the rate at which species speciate is largely determined by rate of molecular evolution, which should scale linearly with the life history type T . This same form for f_T^{gain} will arise under a tight relationship between parent and daughter traits if the historical relative abundance of types is uniform. Alternatively, it could arise under no relationship between parent and daughter traits if there is some fundamental bias for species with faster life history strategies to arise in a given community. For example, ecological opportunity might favor species with faster life history strategies if there is a lot of disturbance.

Case 2: f_T^{loss} and f_T^{gain} independent of T .

An f_T^{loss} that is independent of T could arise if the rate at which species speciate is largely determined by the opportunity for geographic isolation, and if that opportunity is relatively similar across life history strategies. f_T^{gain} could then be the same as f_T^{loss} under a tight relationship between parent and daughter traits and a uniform historical relative abundance of types, or under a weak relationship between parent and daughter types if there is no bias towards a given life history in the fundamental mechanisms governing the rate at which different life histories arise through speciation.

Case 3: f_T^{loss} and f_T^{gain} decreasing linearly with T .

An f_T^{loss} that decreases with T could arise for example if the rate at which species speciate is largely determined by the opportunity for geographic isolation, and if species with bigger body sizes have greater opportunity for this, perhaps because they are more wide ranging. f_T^{gain} could have the same scaling as f_T^{loss} under a strong parent–daughter-type relationship due to no historical bias in the relative abundance of types, or under a weak parent–daughter-type relationship due to for example greater ecological opportunity for species with larger body sizes because the environment is relatively undisturbed.

Case 4: f_T^{loss} linearly proportional to T , but f_T^{gain} independent of T .

As in Case 1, linear f_T^{loss} could arise if the rate at which a species speciates is largely determined by the rate of molecular evolution, which should scale linearly with life history type T . The different, constant behavior of f_T^{gain} could then arise under a strong parent–daughter type relationship if there is a historical bias in the relative abundance of types towards slower life history types, perhaps simply because the community happened to be first colonized by slow life history strategies due to prior environmental conditions, or under a weak parent–daughter relationship and no life history bias in the mechanisms governing which types of species are likely to arise through speciation.

Case 5: f_T^{loss} independent of T , but f_T^{gain} linearly proportional to T .

As in Case 2, an f_T^{loss} that is independent of T could arise if the rate at which species speciate is largely determined by the opportunity for geographic isolation, and if that opportunity is relatively similar across life history strategies. The different, linear behavior in f_T^{gain} could then arise under a strong parent–daughter relationship if there is a historical bias towards faster life history strategies (they might be more likely to be the first colonists of a community), or under a weak parent–daughter type relationship due to for example ecological opportunity favoring faster life history strategies arising through speciation due to high disturbance rates.

death rate. Essentially the simulation took f_T^{loss} to be independent of T . The result was an approximately linear relationship between $\langle n_T \rangle$ and T , as expected according to Eq. 22, as well as an SAD differing from the original neutral model. Lin et al. (2009) may have used

a similar simulation short cut but just didn't report it. In the context of my more flexible speciation dynamics framework in this paper, it is clear that these previous studies explored only a small number of the many possibilities for the structure of tradeoff communities.

Discussion

Species differ and tradeoff in demographic rates like adult recruitment and survival (e.g. Gunderson 1997; Saether and Bakke 2000; Forbis and Doak 2004; Moles et al. 2004). Hence neutral theory's strict assumption of demographic equivalence is clearly violated. Can neutral theory provide robust insight into communities where species have the same fitness but differ in demographic rates? Here I have expanded neutral theory to a theory of communities with a fitness-equalizing “birth–death” tradeoff to resolve this fundamentally important issue. I find that the structure of these types of communities depends on how speciation rates scale with birth and death rates, and that in many cases this structure can vary substantially from the predictions of current neutral theory.

Since its beginnings, ecologists have criticized neutral theory for its strict assumption of demographic equivalence, but there has been only limited exploration of the implications of demographic variation for community structure. A key problem with early studies (Zhang and Lin 1997; Yu et al. 1998) was that they allowed for demographic variation without enforcing a tradeoff across species. Hence, the phenomena they found seemed due to the resulting fitness differences across species, which are counter to the spirit of neutral theory and not so clearly justifiable by empirical work except in special cases. More recent studies have focused on the fitness-equalized case (Ostling 2004; Etienne et al. 2007; Lin et al. 2009; Allouche and Kadmon 2009). (Note that although what constitutes equal fitness in a stochastic context can be subtle in some model frameworks (Parsons and Quince 2007; Parsons et al. 2008; Turnbull et al. 2008), these recent studies and my own here do indeed consider the case of equal fitness.) However, these recent studies have differed in their conclusions. My work here identifies the key difference between them: their assumptions about how speciation rates scale with life history. Furthermore it shows that the speciation dynamics cases these studies considered are just two of many possibilities, across which community structure patterns vary considerably.

These results indicate that differences between real communities and the predictions of current neutral theory might arise due to demographic variation across species and the scaling of speciation rates with demography rather than the presence of stabilizing mechanisms. The uncertainty in our knowledge of the scaling of speciation rates means neutral theory is currently of limited use as a null model for tests for stable coexistence. Empirical analysis testing for stabilization must

either be based on patterns that are insensitive to demographic variation, or consider the potential influence of demographic variation and speciation dynamics. This realization adds to a growing awareness that speciation dynamics can have an important influence on community structure and must be factored into tests of community assembly theory (Allen and Savage 2007; Etienne et al. 2007; Haegeman and Etienne 2009). It is possible that the effect of demographic variation across speciation might be incorporated simply through some sort of effective parameters (although the speciation rate per average death rate is multiplied by different scaling factors in different places where it appears in Eqs. 19–22 and so this may not be so simple). But even if the original neutral theory fits are valid through the use of effective parameters, consideration of demographic variation will be vital if we aim to verify that neutral theory predicts the correct patterns for realistic values of the speciation rate and metacommunity size.

Although information about speciation dynamics may be difficult to obtain, the results of this study suggest that if it can be obtained, the signature of stabilizing mechanisms may be clearer than expected. In particular, stabilization and fitness equalization might be distinguishable through patterns of apportionment of abundance and species richness across types like those examined here. For example, ecologists might infer the means of coexistence in a forest from the relative abundance and diversity of gap-specialist versus shade tolerant species. If speciation rates are homogeneous across these differing life history strategies, fitness equalization would predict community patterns as shown for *Case 2* above, with higher abundance per species among species with faster life history strategies. This prediction could be directly compared with observed relationships between abundance and life history traits. Although it is possible to get a wide variety of species richness and species abundance patterns from both neutral and niche models under uncertainty in total speciation and dispersal rates (Chave et al. 2002), trends in abundance with traits may provide greater power to distinguish models even under such parameter uncertainty if at least the scaling of speciation rates can somehow be inferred. Note however that life history tradeoffs are typically more complex than modeled here, involving differences in the size and age-dependence of demographic rates. Hence in order to develop an empirically useful null model of fitness-equalized communities, a framework like the one here might need to be combined with recently developed size structured neutral models (O'Dwyer et al. 2009).

Acknowledgements I thank R. Condit, J.M. Levine, J. Harte, D. Alonso, A.J. McKane, E.P. White, C. Moritz, S.P. Hubbell, D. Goldberg, and A.P. Allen, for helpful conversations related to this work and Adnrew Noble and Bart Haegeman for their thorough reviews. This work was partially supported by the Class of 1935 Endowed Chair at UC Berkeley, by the EPA Science to Achieve Results (STAR) Graduate Fellowship, and by the University of Michigan Elizabeth C. Crosby Research Fund. This work also benefited from my participation in the Santa Fe Institute Complex Systems Summer School, the Institute for Theoretical Physics Program on Physics and Biological Information, and the Unifying Theories in Ecology Working Group at the National Center for Ecological Analysis and Synthesis.

Appendix A: N_T at equilibrium

Here, I show that $\lim_{t \rightarrow \infty} N_T(t)$ is determined by f_T^{loss} and $\rho(T', T)$. To see this, first note that an alternative way of expressing the expected total abundance across all species of type T , $N_T(t)$ (which we originally defined as $N_T(t) = \sum_k \delta(T_k - T) E[n_k(t)]$) is

$$N_T(t) = \sum_n S_T(n, t) \cdot n \quad (23)$$

where $S_T(n, t)$ is the expected number of species of type T with abundance n at time t and comes from Eqs. 16 and 17 and take this sum over the differential equation for $S_T(n)$ (Eq. 16 from the main text) in order to obtain a differential equation for N_T . The result is

$$\frac{dN_T(t)}{dt} = p_T(t) - v f_T^{\text{loss}} N_T(t) \quad (24)$$

$$= v \int_{T_{\min}}^{T_{\max}} dT' f_{T'}^{\text{loss}} \rho'(T', T) N_{T'}(t) \\ - f_T^{\text{loss}} N_T(t) \quad (25)$$

So at equilibrium

$$f_T^{\text{loss}} N_T = \int_{T_{\min}}^{T_{\max}} dT' f_{T'}^{\text{loss}} \rho'(T', T) N_{T'} \quad (26)$$

Note that if parent and daughter species traits are exactly equal, i.e., if $\rho'(T', T) = \delta(T' - T)$ then any N_T and f_T^{loss} can provide a solution to this equation, so any historical influences on N_T will be preserved, and f_T^{gain} as defined by Eq. 13 can be different than f_T^{loss} if history produced a bias in N_T (i.e., an N_T that depends on T). If instead the relationship between parent and daughter species is very weak (i.e., $\rho'(T', T)$ is independent of T'), then $N_T = \rho'(T', T)/f_T^{\text{loss}}$ (and as discussed in the main text f_T^{gain} is simply $\rho'(T', T)$). The integral equation Eq. 26 is more complex when the parent and

daughter species traits are related by not exactly. It is also useful (in particular for Appendix B) to note that at equilibrium N_T can be expressed as

$$N_T = \frac{f_T^{\text{gain}}}{f_T^{\text{loss}}} \frac{N}{\eta} \quad (27)$$

So by specifying the model parameters f_T^{loss} and f_T^{gain} one essentially specifies the equilibrium value of N_T . This expression for N_T makes it obvious that one will have an inhomogeneous N_T at equilibrium in cases where f_T^{gain} is different in form from f_T^{loss} .

Appendix B: Constants of proportionality for cases 1–5

Here, I provide some details of the five different speciation rate scaling cases used in the main text. In particular, I show how I calculated the specific parameter values of the speciation rate scalings from constraints on the total size of the community and total speciation rate, and how the average death rate could be calculated in each case. The two constraints I used to calculate proportionality constants of the scalings of f_T^{loss} and f_T^{gain} with T are:

1. $\sum_T N_T = N$
2. $\sum_T p_T = vN$

where N_T is the expectation value of the total number of individuals of type T , and p_T is the rate at which species of type T are arising in the community. Note that here I am using sums over the possible death rates T because in these example cases I took T to range over integer values. I did this for convenience and because the output is then more analogous to a real community, where abundance and diversity would be measured within discrete bins of the life history characteristics of the species. Also, note that a second constraint one might imagine on the speciation rate, namely on the total rate at which species are speciating leads to the same condition on the speciation rate scaling factors as constraint (2) above on the total rate at which species are arising.

These two constraints can be translated into constraints on the scaling factors f_T^{loss} and f_T^{gain} as follows. Firstly, as shown in the previous section the equilibrium expectation for N_T is

$$N_T = \frac{f_T^{\text{gain}}}{f_T^{\text{loss}}} \frac{N}{\eta} \quad (28)$$

Table 1 Constraints on scaling factor parameters for the five cases in Fig. 1 of the main text

Case	Scaling factors	Constraints	$\langle T \rangle$
1	$f_T^{\text{loss}} = bT, f_T^{\text{gain}} = b'T$	(1) $b' = b$, (2) $b' = 1/\bar{T}$	$\langle T \rangle = \bar{T}$
2	$f_T^{\text{loss}} = a, f_T^{\text{gain}} = a'$	(1) $a' = a$, (2) $a' = 1$	$\langle T \rangle = \bar{T}$
3	$f_T^{\text{loss}} = a - bT, f_T^{\text{gain}} = a - bT$	(1) Satisfied, (2) $a = 1 + b\bar{T}$	$\langle T \rangle = \bar{T}$
4	$f_T^{\text{loss}} = bT, f_T^{\text{gain}} = a$	(1) $b/a = \bar{T}^{-1}$, (2) $a = 1$	$\langle T \rangle = (\bar{T}^{-1})^{-1}$
5	$f_T^{\text{loss}} = a, f_T^{\text{gain}} = bT$	(1) $b/a = (\bar{T})^{-1}$, (2) $b = (\bar{T})^{-1}$	$\langle T \rangle = \bar{T}^2/\bar{T}$

Here, $\langle T \rangle$ refers to the average death rate across individuals in the community, whereas $\bar{T} = \sum_T T$ is the mean of all possible death rate types in the community, and \bar{T}^{-1} and \bar{T}^2 are the mean values of T^{-1} and T^2 , respectively, across all possible death rate types in the community

The first constraint above then becomes:

$$1. \frac{1}{\eta} \sum_T \frac{f_T^{\text{gain}}}{f_T^{\text{loss}}} = 1$$

The second constraint can be written in terms of the speciation rate scaling factors simply by using $p_T = f_T^{\text{gain}} \frac{\nu N}{\eta}$. The result is:

$$2. \frac{1}{\eta} \sum_T f_T^{\text{gain}} = 1$$

Table 1 below shows the scaling factor parameter values resulting when each of these two constraints is applied to the five different speciation rate scaling cases in Fig. 1 of the main text. It also shows the expected average death rate across individuals in the community for each case, which I calculated according to

$$\langle T \rangle = \frac{1}{N} \sum_T N_T T \quad (29)$$

The information in Table 1, plus the range of values for T (which I took to be from 1 to 100) are all that is needed to generate predictions for the apportionment of abundance and species richness across life history types using Eq. 17–20 of the main text.

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