

# ESTIMATING SPECIATION AND EXTINCTION RATES FROM DIVERSITY DATA AND THE FOSSIL RECORD

Rampal S. Etienne<sup>1,2</sup> and M. Emile F. Apol<sup>1</sup>

<sup>1</sup>Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

<sup>2</sup>E-mail: r.s.etienne@rug.nl

Received December 21, 2007

Accepted September 17, 2008

Understanding the processes that underlie biodiversity requires insight into the evolutionary history of the taxa involved. Accurate estimation of speciation, extinction, and diversification rates is a prerequisite for gaining this insight. Here, we develop a stochastic birth–death model of speciation and extinction that predicts the probability distribution of both extinct and extant numbers of species in a clade. We present two estimation methods based on this model given data on the number of extinct species (from the fossil record) and extant species (from diversity assessments): a multivariate method of moments approach and a maximum-likelihood approach. We show that, except for some special cases, the two estimation methods produce very similar estimates. This is convenient, because the usually preferred maximum-likelihood approach is much more computationally demanding, so the method of moments can serve as a proxy. Furthermore, we introduce a correction for possible bias that can arise by the mere fact that we will normally only consider extant clades. We find that in some cases the bias correction affects the estimates profoundly. Finally, we show how our model can be extended to incorporate incomplete preservation. Preservation rates can, however, not be reliably estimated on the basis of numbers of extant and extinct species alone.

**KEY WORDS:** Birth–death model, cladogenesis, conditioning, diversification, maximum likelihood, method of moments, stochastic model.

A thorough understanding of the processes that shape biodiversity is a common objective of evolutionary biology and ecology. Many macroevolutionary explanations of diversity within a taxon or clade use simple models of speciation (origination) and extinction, where species may give birth to new species and eventually die, leading to extinction, with rates that usually does not depend on species identity (Nee 2004, 2006 and references therein). These birth–death models at the species level have received a warm welcome, at least as useful null models of diversification. They are often used to estimate speciation, extinction, and diversification rates from phylogenies only (Hey 1992; Nee et al. 1994; Nee 2001), so without fossil data, because the fossil record is often considered incomplete and the fossil species concept problematic (Smith 1994; Kidwell and Flessa 1995; Strait and Wood 1999;

but see Kidwell 2001; Valentine et al. 2006). However, in many cases complete or undisputed phylogenies are (still) not available. Moreover, it has been shown that inferences based solely on phylogenies may be flawed (Wagner 2000; Paradis 2004). Therefore, there is certainly a merit in obtaining estimates of speciation, extinction, and diversification rates from data on extinct and extant species only, even if they would eventually be used only as a quick way to provide a null expectation or, in Bayesian terms, prior distribution of these rates.

A birth–death model that predicts the number of extinct and extant species has been provided by Rosenzweig and Vetault (1992), commenting on an earlier model by Vrba (1987) who in turn follows Stanley (1979). We will refer to this model by Rosenzweig and Vetault (1992) as the RV model. The RV model

is deterministic and treats the number of extinct and extant species as real numbers rather than as integers. This would be reasonable if the number of extinct and extant species were high, but in most examples they are not (see for example Table 1, where we reanalyze the data used by RV and Vrba). One of the consequences of using a deterministic formulation is that a clade can never go extinct within a finite time. To model this more realistically, we must use a stochastic formulation that predicts the probability distribution of the (integer) number of extinct and extant species. Stochastic models form a scientific way to represent the many uncertainties about the systems under study (Clark et al. 2007), and they are therefore amenable to likelihood analyses, which are generally the preferred statistical methods. By being probabilistic they can also properly incorporate dependences between different variables (here numbers of extant and extinct species), as we will discuss below. Furthermore, they allow for probabilistic conditioning by which one can account for the way in which the data are sampled. For example, when the data consist of phylogenies, one can incorporate the mere fact that we are looking at a tree (not a single lineage) and the fact that we have no extinct species in a phylogeny (Nee 2001).

In this article we present the stochastic counterpart of the RV model and we formulate two approaches to estimate speciation and extinction rates on the basis of data on extinct (from the fossil record) and extant (from biodiversity surveys) species in a clade and the clade's age. One approach is an extension of the deterministic estimation procedure in which the observed and expected numbers of extinct and extant species are set equal to one another. This is a multivariate version of the method of moments (the first moment of each of two variables, number of extant and number of extinct species). The other approach is maximum-likelihood estimation. We compare the results of both estimation approaches and apply them to the data used by Rosenzweig and Vetault (1992). Because we usually only carry out analyses for clades with extant taxa, this bias may have an impact on our parameter estimates. The stochastic model formulation allows us to account for this by proper probabilistic conditioning on at least one species of a clade being still extant (Bokma 2003). We show how this can be done and what effect it has on parameter estimates. We end with a discussion, in which we show that our model allows for the incorporation of preservation rates, but parameter estimation becomes more difficult.

## Model

### THE DETERMINISTIC ROSENZWEIG AND VETAULT 1992 (RV) MODEL

The RV model is a deterministic birth–death model that describes the number of extant species  $N_L$  and the number of extinct species  $N_E$  at time  $t$  when the per species speciation rate  $S$  and the ex-

tingtion rate  $E$  are constant. It is determined by the following set of ordinary differential equations and initial conditions:

$$\frac{dN_L(t)}{dt} = (S - E)N_L(t) \quad (1a)$$

$$\frac{dN_E(t)}{dt} = EN_L(t) \quad (1b)$$

$$N_L(0) = N_0 \quad (1c)$$

$$N_E(0) = 0, \quad (1d)$$

where the initial condition applies to the common ancestors of the clade (usually  $N_0 = 1$ , e.g., for monophyletic clades). This set of equations is easily solved:

$$N_L(t) = \begin{cases} N_0 e^{(S-E)t} & \text{for } S \neq E \\ N_0 & \text{for } S = E \end{cases} \quad (2a)$$

$$N_E(t) = \begin{cases} \frac{N_0 e^{(S-E)t} - 1}{\frac{S}{E} - 1} & \text{for } S \neq E \\ N_0 Et & \text{for } S = E. \end{cases} \quad (2b)$$

If we know the number of extinct species  $N_E$  (estimated from the fossil record), and the current number of extant species  $N_L$  of a clade and we also have an estimate of the age  $T$  of the clade, then one can calculate the speciation and extinction rates by solving this system of equations for  $S$  and  $E$

$$\widehat{S}_{RV} = \begin{cases} \frac{\ln\left(\frac{N_L}{N_0}\right)}{T} \left(1 + \frac{N_E}{N_L - 1}\right) & \text{for } N_L \neq N_0 \\ \frac{N_E}{N_0 T} & \text{for } N_L = N_0 \end{cases} \quad (3a)$$

$$\widehat{E}_{RV} = \begin{cases} \frac{\ln\left(\frac{N_L}{N_0}\right)}{T} \left(\frac{N_E}{N_L - 1}\right) & \text{for } N_L \neq N_0 \\ \frac{N_E}{N_0 T} & \text{for } N_L = N_0, \end{cases} \quad (3b)$$

where the subscript RV refers to the Rosenzweig and Vetault (1992) model. The estimated net diversification rate,  $\widehat{D} = \widehat{S} - \widehat{E}$ , is therefore

$$\widehat{D}_{RV} = \frac{\ln\left(\frac{N_L}{N_0}\right)}{T} \quad (4)$$

which does not depend on the number of extinct species  $N_E$ .

### THE STOCHASTIC MODEL

The alternative stochastic model proposed in this article describes the dynamics of the probability  $P(N_E, N_L, t)$  of the number of

**Table 1.** Estimates of per species rates of speciation ( $S$ ), extinction ( $E$ ), and net diversification ( $D$ ) for the mammal clades given in Vrba (1987) and Rosenzweig and Veltault (1992); these clades are aged  $T$  and have  $N_E$  extinct species and  $N_L$  extant species. In all calculations it is assumed that  $N_0 = 1$ . Subscripts denote the estimation method: MM, unconditional method of moments, ML, unconditional maximum likelihood, MMC, conditional method of moments, MLC, conditional maximum likelihood. The MM estimates are identical to those reported by Rosenzweig and Veltault (1992) using the deterministic model. The figures between parentheses denote standard errors as computed from the observed information matrix. These values are not available (meaningless) when  $N_L = 1$  and  $N_E = 0$ .

Clade	$T$ (Ma)	$N_E$	$N_L$	$\hat{S}_{MM}$ ( $\text{Ma}^{-1}$ )	$\hat{E}_{MM}$ ( $\text{Ma}^{-1}$ )	$\hat{D}_{MM}$ ( $\text{Ma}^{-1}$ )	$\hat{S}_{ML}$ ( $\text{Ma}^{-1}$ )	$\hat{E}_{ML}$ ( $\text{Ma}^{-1}$ )	$\hat{D}_{ML}$ ( $\text{Ma}^{-1}$ )	$\hat{S}_{MMC}$ ( $\text{Ma}^{-1}$ )	$\hat{E}_{MMC}$ ( $\text{Ma}^{-1}$ )	$\hat{D}_{MMC}$ ( $\text{Ma}^{-1}$ )	$\hat{S}_{MLC}$ ( $\text{Ma}^{-1}$ )	$\hat{E}_{MLC}$ ( $\text{Ma}^{-1}$ )	$\hat{D}_{MLC}$ ( $\text{Ma}^{-1}$ )
Taurotragus	7	2	1	0.286	0.286	0	0.197 (0.145)	0.197 (0.145)	0 (0.197)	0.143	$\infty$	$-\infty$	0.143 (0.101)	$\infty$	$-\infty$
Tragelaphus	7	9	7	0.695	0.417	0.278	0.538 (0.196)	0.323 (0.136)	0.215 (0.184)	0.514	0.378	0.139	0.516 (0.187)	0.380 (0.174)	0.136 (0.205)
Aepyceros	5	1	1	0.200	0.200	0	0.159 (0.162)	0.159 (0.162)	0 (0.225)	0.100	$\infty$	$-\infty$	0.100 (0.100)	$\infty$	$-\infty$
Alecephini	5	27	7	2.141	1.751	0.389	1.283 (0.404)	1.049 (0.351)	0.233 (0.234)	1.233	1.244	-0.0109	1.255 (0.386)	1.274 (0.497)	-0.0188 (0.397)
Connochaetes	4	11	4	1.617	1.271	0.347	1.044 (0.390)	0.821 (0.327)	0.224 (0.377)	0.962	1.093	-0.130	0.982 (0.357)	1.133 (0.603)	-0.151 (0.581)
Damaliscus	4	12	3	1.923	1.648	0.275	1.110 (0.412)	0.951 (0.368)	0.159 (0.406)	1.013	1.420	-0.407	1.049 (0.376)	1.556 (1.058)	-0.507 (0.961)
Syncerus	5	3	1	0.600	0.600	0	0.372 (0.229)	0.372 (0.229)	0 (0.304)	0.300	$\infty$	$-\infty$	0.300 (0.173)	$\infty$	$-\infty$
Oreotragus	3	1	1	0.333	0.333	0	0.265 (0.269)	0.265 (0.269)	0 (0.376)	0.167	$\infty$	$-\infty$	0.167 (0.167)	$\infty$	$-\infty$
Kobus	6	11	5	1.006	0.738	0.268	0.690 (0.253)	0.506 (0.202)	0.184 (0.240)	0.645	0.634	0.0109	0.654 (0.236)	0.647 (0.311)	0.00661 (0.313)
Anatidorcas	3	3	1	1.000	1.000	0	0.620 (0.381)	0.620 (0.381)	0 (0.506)	0.500	$\infty$	$-\infty$	0.500 (0.289)	$\infty$	$-\infty$
Pelea	2	0	1	0	0	0	0 (n.a.)	0 (n.a.)	0 (n.a.)	0	0	0	0 (n.a.)	0 (n.a.)	0 (n.a.)
Phacochoerus	3	7	1	2.333	2.333	0	1.103 (0.487)	1.103 (0.487)	0 (0.589)	1.167	$\infty$	$-\infty$	1.167 (0.441)	$\infty$	$-\infty$
Potamochoerus	3	0	1	0	0	0	0 (n.a.)	0 (n.a.)	0 (n.a.)	0	0	0	0 (n.a.)	0 (n.a.)	0 (n.a.)
Giraffa	5	8	1	1.600	1.600	0	0.721 (0.304)	0.721 (0.304)	0 (0.360)	0.800	$\infty$	$-\infty$	0.800 (0.282)	$\infty$	$-\infty$
Orycteropus	15	5	1	0.333	0.333	0	0.177 (0.088)	0.177 (0.088)	0 (0.111)	0.167	$\infty$	$-\infty$	0.167 (0.074)	$\infty$	$-\infty$
Loxodonta	5	2	1	0.400	0.400	0	0.276 (0.203)	0.276 (0.203)	0 (0.276)	0.200	$\infty$	$-\infty$	0.200 (0.141)	$\infty$	$-\infty$
Elephas	5	10	1	2.000	2.000	0	0.829 (0.326)	0.829 (0.326)	0 (0.371)	1.000	$\infty$	$-\infty$	1.000 (0.316)	$\infty$	$-\infty$
Pedetes	4	0	1	0	0	0	0 (n.a.)	0 (n.a.)	0 (n.a.)	0	0	0	0 (n.a.)	0 (n.a.)	0 (n.a.)

extinct ( $N_E$ ) and extant ( $N_L$ ) species at time  $t$ , given per species speciation rate  $S$  and extinction rate  $E$ . The dynamics is governed by a master equation, that is, an ordinary differential equation, and initial conditions and boundary conditions

$$\frac{dP(N_E, N_L, t)}{dt} = E(N_L + 1)P(N_E - 1, N_L + 1, t) + S(N_L - 1)P(N_E, N_L - 1, t) - (E + S)N_L P(N_E, N_L, t) \quad (5a)$$

$$P(N_E = 0, N_L = N_0, 0) = 1 \quad (5b)$$

$$P(N_E \neq 0, N_L \neq N_0, 0) = P(N_E \neq 0, N_L = N_0, 0) = P(N_E = 0, N_L \neq N_0, 0) = 0 \quad (5c)$$

$$P(N_E < 0, N_L, t) = P(N_E, N_L < 0, t) = 0 \quad (5d)$$

This is the exact stochastic counterpart of the RV model. It describes how the probability  $P(N_E, N_L, t)$  changes due to transitions between states of the system at a rate proportional to the per species speciation ( $S$ ) and extinction ( $E$ ) rates, the number of extant species in the state of origin ( $N_L - 1, N_L$ , or  $N_L + 1$ , depending on the state), and the probability of the state of origin at time  $t$ . Not only does this stochastic method provide expressions for the expectations (first moments), first and foremost it gives the probability  $P(N_E, N_L, t)$  for each combination of  $N_L$ - and  $N_E$ -values at time  $t$ . This probability can be obtained by solving the master equation for the probability generation function  $G(z, s, t)$ , a transform of  $P(N_E, N_L, t)$  which is defined as

$$G(z, s, t) := \sum_{N_E=0}^{\infty} z^{N_E} \sum_{N_L=0}^{\infty} s^{N_L} P(N_E, N_L, t). \quad (6)$$

When the probability-generation function  $G(z, s, t)$  is known, the probability distribution can be recovered by taking partial derivatives:

$$P(N_E, N_L, t) = \frac{1}{N_E! N_L!} \left. \frac{\partial^{N_E} \partial^{N_L} G(z, s, t)}{\partial z^{N_E} \partial s^{N_L}} \right|_{z=s=0} \quad (7)$$

In Appendix S1 of the Supporting information we show that in our model  $G(z, s, t)$  has the form

$$G(z, s, t) = \left( \frac{(A^2 - B - 2As)(e^{-St\sqrt{B}} - 1) - 2s\sqrt{B}(e^{-St\sqrt{B}} + 1)}{(2A - 4s)(e^{-St\sqrt{B}} - 1) - 2\sqrt{B}(e^{-St\sqrt{B}} + 1)} \right)^{N_0} \quad (8a)$$

$$A := 1 + \frac{E}{S} \quad (8b)$$

$$B := \left(1 + \frac{E}{S}\right)^2 - 4z \frac{E}{S}. \quad (8c)$$

The probability  $P(N_E, N_L, t)$  can be used in likelihood-based estimation methods. Below we give estimates using maximum-likelihood estimation, that is, those values of  $S$  and  $E$  that maximize this probability  $P(N_E, N_L, t)$  for given  $N_E, N_L$ , and  $T$ . We will indicate these estimates (e.g., in Table 1) by the subscript ML. Evaluating the derivatives of (7) generally leads to a long expression without a closed-form analytical generalization. Therefore, one must resort to numerical methods, of which automatic differentiation techniques seem to be the most suitable. We have included a program code for such automatic differentiation using the freely available software COSY Infinity ([http://bt.pa.msu.edu/index\\_files/cosy.htm](http://bt.pa.msu.edu/index_files/cosy.htm)) in the Supporting information. In some special cases (7) reduces to relatively simple expressions (see Appendix S3). The maximum-likelihood method also allows for computation of the standard error in the estimates by means of the observed information matrix  $I_o$ . The variance-covariance matrix  $M$  at the likelihood optimum (where  $\frac{\partial \ln P}{\partial S} = \frac{\partial \ln P}{\partial E} = 0$ ) is given by

$$M = I_o^{-1} = \begin{pmatrix} -\frac{\partial^2 \ln P}{\partial S^2} & -\frac{\partial^2 \ln P}{\partial S \partial E} \\ -\frac{\partial^2 \ln P}{\partial S \partial E} & -\frac{\partial^2 \ln P}{\partial E^2} \end{pmatrix} = \frac{1}{\left(\frac{\partial^2 \ln P}{\partial S^2}\right)\left(\frac{\partial^2 \ln P}{\partial E^2}\right) - \left(\frac{\partial^2 \ln P}{\partial S \partial E}\right)^2} \times \begin{pmatrix} -\frac{\partial^2 \ln P}{\partial E^2} & \frac{\partial^2 \ln P}{\partial S \partial E} \\ \frac{\partial^2 \ln P}{\partial S \partial E} & -\frac{\partial^2 \ln P}{\partial S^2} \end{pmatrix} \quad (9)$$

where the derivatives are evaluated at the ML parameter values. Square roots of the diagonal elements (the variances) are the standard errors for the two parameters  $S$  and  $E$ . The off-diagonal elements (the covariances) are needed to compute the standard error in the net diversification rate  $D = S - E$ .

Using the definition of the probability-generating function (6) it is straightforward to show that the expectations for  $N_E$  and  $N_L$  are given by

$$\langle N_L(t) \rangle = \sum_{N_L=0}^{\infty} \sum_{N_E=0}^{\infty} N_L P(N_E, N_L, t) = \left. \frac{\partial G(z, s, t)}{\partial s} \right|_{z=1, s=1} = \begin{cases} N_0 e^{(S-E)t} & \text{for } S \neq E \\ N_0 & \text{for } S = E \end{cases} \quad (10a)$$

$$\langle N_E(t) \rangle = \sum_{N_L=0}^{\infty} \sum_{N_E=0}^{\infty} N_E P(N_E, N_L, t) = \left. \frac{\partial G(z, s, t)}{\partial z} \right|_{z=1, s=1} = \begin{cases} \frac{N_0 e^{(S-E)t} - 1}{S} & \text{for } S \neq E \\ \frac{E}{N_0 E t} & \text{for } S = E \end{cases} \quad (10b)$$

and these expressions are identical to those for  $N_L(t)$  and  $N_E(t)$  in the deterministic model (as expected in a linear model). The estimates for the speciation, extinction, and net diversification rates based on these expectation values are therefore identical to the RV model, equations (3) and (4). That is, given observations of  $N_L$  extant and  $N_E$  extinct species at time  $T$ , we have the estimates:

$$\widehat{S}_{MM} = \begin{cases} \frac{\ln\left(\frac{N_L}{N_0}\right)}{T} \left(1 + \frac{N_E}{N_L - 1}\right) & \text{for } N_L \neq N_0 \\ \frac{N_E}{N_0 T} & \text{for } N_L = N_0 \end{cases} \quad (11a)$$

$$\widehat{E}_{MM} = \begin{cases} \frac{\ln\left(\frac{N_L}{N_0}\right)}{T} \left(\frac{N_E}{N_L - 1}\right) & \text{for } N_L \neq N_0 \\ \frac{N_E}{N_0 T} & \text{for } N_L = N_0 \end{cases} \quad (11b)$$

$$\widehat{D}_{MM} = \frac{\ln\left(\frac{N_L}{N_0}\right)}{T} \quad (11c)$$

where the subscript MM indicates that the estimation has been done by the method of moments, that is equating observed and expected numbers.

In the course of selecting clades we usually choose only those that are still extant. Even if we also allow for clades that may have gone extinct, such clades are often underrepresented. This may cause a serious bias. In the stochastic model we can correct for this by conditioning our probability and the expected number of extinct and extant species on the fact that  $N_L > 0$ . For this, we need the following auxiliary quantities:

$$P(N_L > 0, t) = 1 - \sum_{N_E=0}^{\infty} P(N_E, N_L = 0, t) = 1 - G(1, 0, t)$$

$$= \begin{cases} 1 - \left(\frac{\frac{E}{S}(1 - e^{-(S-E)t})}{1 - \frac{E}{S}e^{-(S-E)t}}\right)^{N_0} & \text{for } S \neq E \\ 1 - \left(\frac{Et}{1 + Et}\right)^{N_0} & \text{for } S = E \end{cases} \quad (12)$$

$$\langle N_E(t) | N_L(t) = 0 \rangle = \frac{\partial G(z, s, t)}{\partial z} \Big|_{z=1, s=0}$$

$$= \begin{cases} N_0 \left(\frac{\frac{E}{S}(1 - e^{-(S-E)t})}{1 - \frac{E}{S}e^{-(S-E)t}}\right)^{N_0-1} \frac{E e^{2(S-E)t} - \left(\frac{E}{S}\right)^2 - \left(1 - \frac{E}{S}\right)\left(\frac{E}{S} + 1 + 2Et\right) e^{(S-E)t}}{\left(1 - \frac{E}{S}\right)\left(e^{(S-E)t} - \frac{E}{S}\right)^2} & \text{for } S \neq E \\ N_0 \left(\frac{Et}{1 + Et}\right)^{N_0-1} \frac{1 + Et - \frac{1}{(1 + Et)^2}}{3} & \text{for } S = E \end{cases} \quad (13)$$

The conditional probability of observing  $N_L$  extant species and  $N_E$  extinct species is simply given by

$$P(N_L, N_E, t | N_L > 0) = \frac{P(N_L, N_E, t)}{P(N_L > 0)}$$

$$= \begin{cases} \frac{\frac{1}{N_E! N_L!} \frac{\partial^{N_E} \partial^{N_L} G(z, s, t)}{\partial z^{N_E} \partial s^{N_L}} \Big|_{z=s=0}}{\left(\frac{\frac{E}{S}(1 - e^{-(S-E)t})}{1 - \frac{E}{S}e^{-(S-E)t}}\right)^{N_0}} & \text{for } S \neq E \\ \frac{\frac{1}{N_E! N_L!} \frac{\partial^{N_E} \partial^{N_L} G(z, s, t)}{\partial z^{N_E} \partial s^{N_L}} \Big|_{z=s=0}}{1 - \left(\frac{Et}{1 + Et}\right)^{N_0}} & \text{for } S = E \end{cases} \quad (14)$$

This conditional probability can again be used in likelihood-based estimation procedures. We will indicate estimates using conditional maximum likelihood by the subscript MLC.

The conditional expectations of  $N_L$  extant species and  $N_E$  extinct species are:

$$\langle N_L(t) | N_L(t) > 0 \rangle = \sum_{N_E=0}^{\infty} \sum_{N_L=1}^{\infty} N_L P(N_E, N_L, t | N_L > 0)$$

$$= \sum_{N_E=0}^{\infty} \sum_{N_L=0}^{\infty} N_L \frac{P(N_E, N_L, t)}{P(N_L > 0, t)}$$

$$= \frac{\langle N_L(t) \rangle}{P(N_L > 0, t)} = \begin{cases} \frac{N_0 e^{(S-E)t}}{\left(\frac{\frac{E}{S}(1 - e^{-(S-E)t})}{1 - \frac{E}{S}e^{-(S-E)t}}\right)^{N_0}} & \text{for } S \neq E \\ \frac{N_0}{1 - \left(\frac{Et}{1 + Et}\right)^{N_0}} & \text{for } S = E \end{cases} \quad (15a)$$

$$\begin{aligned}
 & \langle N_E(t) \mid N_L(t) > 0 \rangle \\
 &= \sum_{N_E=0}^{\infty} \sum_{N_L=1}^{\infty} N_E P(N_E, N_L, t \mid N_L > 0) = \sum_{N_E=0}^{\infty} \sum_{N_L=1}^{\infty} N_E \frac{P(N_E, N_L, t)}{P(N_L > 0, t)} \\
 &= \frac{\sum_{N_E=0}^{\infty} N_E \left( \left( \sum_{N_L=0}^{\infty} P(N_E, N_L, t) \right) - P(N_E, N_L = 0, t) \right)}{P(N_L > 0, t)} \\
 &= \frac{\sum_{N_E=0}^{\infty} N_E P(N_E, t) - \sum_{N_E=0}^{\infty} N_E P(N_E, N_L = 0, t)}{P(N_L > 0, t)} \\
 &= \frac{\langle N_E(t) \rangle - \langle N_E(t) \mid N_L(t) = 0 \rangle}{P(N_L > 0, t)} \\
 &= \begin{cases} \frac{N_0 e^{(S-E)t} - 1}{\frac{S}{E} - 1} - N_0 \left( \frac{\frac{E}{S} (1 - e^{-(S-E)t})}{1 - \frac{E}{S} e^{-(S-E)t}} \right)^{N_0-1} \frac{E e^{2(S-E)t} - \left(\frac{E}{S}\right)^2 - \left(1 - \frac{E}{S}\right) \left(\frac{E}{S} + 1 + 2Et\right) e^{(S-E)t}}{S \left(1 - \frac{E}{S}\right) \left(e^{(S-E)t} - \frac{E}{S}\right)^2} & \text{for } S \neq E \\ 1 - \left( \frac{\frac{E}{S} (1 - e^{-(S-E)t})}{1 - \frac{E}{S} e^{-(S-E)t}} \right)^{N_0} & \\ N_0 \frac{Et - \left(\frac{Et}{1+Et}\right)^{N_0-1} \frac{1+Et - \frac{1}{(1+Et)^2}}{3}}{1 - \left(\frac{Et}{1+Et}\right)^{N_0}} & \text{for } S = E \end{cases} \quad (15b)
 \end{aligned}$$

By setting both expressions equal to observed values of  $N_L$  and  $N_E$  for a known clade age  $T$ , estimates for  $\hat{S}$  and  $\hat{E}$  can be obtained, but only numerically, except for some special cases in which analytical closed-form expressions are available (see Appendix S3). However, one does observe that  $T$  factors out, so:

$$\hat{S}_{\text{MMC}} = \frac{f_1(N_E, N_L, N_0)}{T} \quad (16a)$$

$$\hat{E}_{\text{MMC}} = \frac{f_2(N_E, N_L, N_0)}{T} \quad (16b)$$

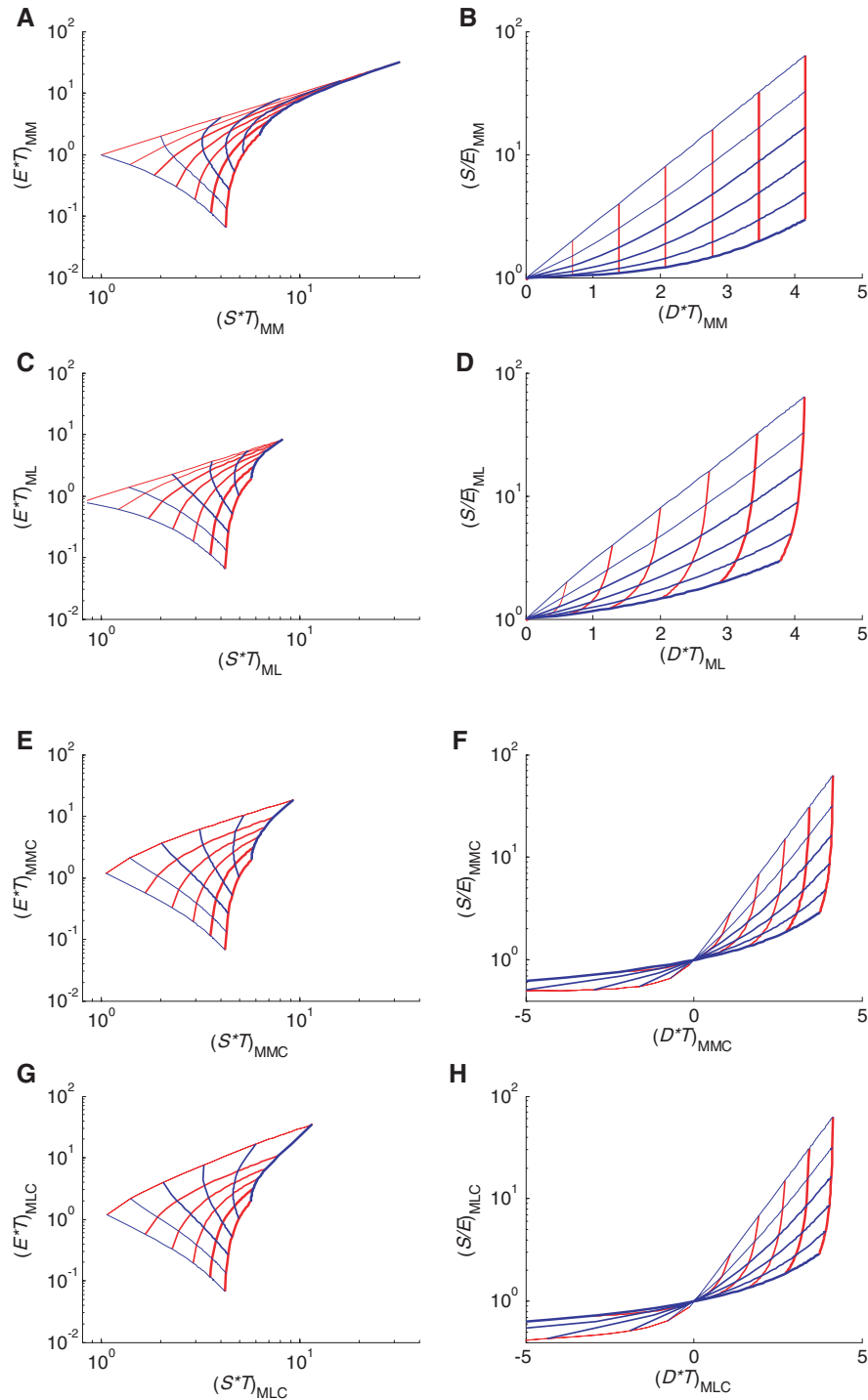
$$\hat{D}_{\text{MMC}} = \frac{f_1(N_E, N_L, N_0) - f_2(N_E, N_L, N_0)}{T} \quad (16c)$$

where MMC indicates that these estimates are based on the conditional method of moments, and where  $f_1$  and  $f_2$  are functions of  $N_E$ ,  $N_L$ , and  $N_0$ . Numerical examples are given below.

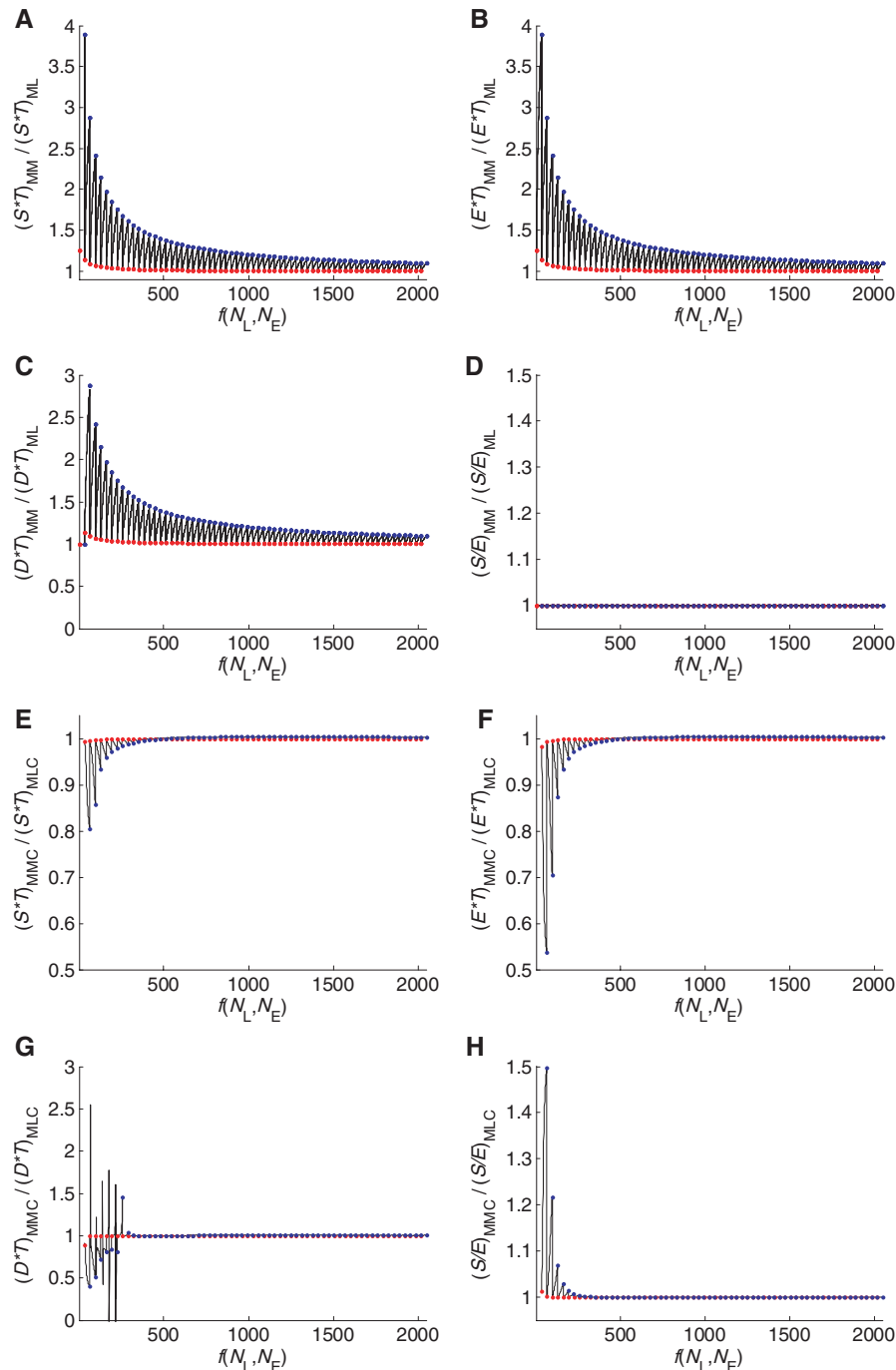
### Results

We compare in general the parameter estimates for  $\hat{S}$  and  $\hat{E}$  using the method of moments and maximum-likelihood approaches for various values of  $N_L$  and  $N_E$ . Figure 1 shows these estimates and also of the dependent quantities  $\hat{D} = \hat{S} - \hat{E}$  and  $\frac{\hat{S}}{\hat{E}}$ , where each rate is multiplied by  $T$  to make the estimates dimensionless and

general. Figure 1(A–D) shows the estimates obtained with the unconditional approaches, whereas Figure (E–H) shows the estimates for the conditional approaches. Overall the two approaches give fairly similar estimates, especially in the conditional case, but discrepancies arise for low  $N_L$  and high  $N_E$ . The reason for this is that for this particular situation the probability distribution is highly asymmetric (i.e., mode and mean differ substantially), a situation in which it is actually surprising that the clade under consideration still exists, that is the probability that it would have gone extinct is high. Figure 2 presents a more detailed comparison by showing how the ratio of estimates using the two different methods behaves when  $N_L$  and  $N_E$  are increased. Indeed, these ratios deviate substantially from 1 only for low  $N_L$  and high  $N_E$ . In the unconditional case the estimates for  $\hat{S}$  and  $\hat{E}$  are both higher when obtained with the method of moments than with maximum likelihood, whereas in the conditional case they are both lower. Perhaps surprisingly the ratio of speciation and extinction rates is exactly the same for both approaches in the unconditional case, which also always has a lower diversification rate  $\hat{D}$  when obtained with maximum likelihood than with the method of moments. This suggests that estimates based on the method of moments, which are much easier to compute than those based on maximum likelihood,



**Figure 1.** Estimates of speciation and extinction rates for varying numbers of extinct and extant species plotted as  $ET$  versus  $ST$  (left-hand column) or as  $\frac{ST}{E} = \frac{S}{E}$  versus  $DT$  (right-hand column) and assuming  $N_0 = 1$ . (A–D): Unconditional method of moments (A and B) and unconditional maximum likelihood (C and D). (E–H) Conditional method of moments (E and F) and conditional maximum likelihood (G and H). Red curves connect points with equal numbers of extant species ( $N_L = 1, 2, 4, 8, 16, 32, 64$ ), blue curves connect points with equal number of extinct species ( $N_E = 1, 2, 4, 8, 16, 32$ ). The thickness of the curves increase with the number of extinct or extant species they correspond to. For example, the top (i.e., thinnest) blue curve in B connects points where  $N_E = 1$ , whereas the rightmost (i.e., thickest) red curve in B connects points with  $N_L = 64$ . These curves intersect in the top right corner which therefore represents the parameter estimates for  $N_E = 1$  and  $N_L = 64$ . The case  $N_L = 1$  is not shown for the conditional estimates (E–H) because this case has an infinite estimate for the extinction rate. Note the similarity (except for small  $N_L$  and large  $N_E$ ) of the figures for expectations and maximum likelihood. See Figure 2 for a better comparison.



**Figure 2.** Comparison of multivariate method of moments and maximum likelihood; the panels show the ratio of estimates of the two different approaches as a function of  $f(N_L, N_E) = 32(N_L - 1) + N_E$  where  $N_L$  runs through the values from 1 (2 in the conditional approach) to 64 and, for each value of  $N_L$ ,  $N_E$  loops through the values 1 to 32.  $N_E = 1$  is indicated with a red dot, whereas  $N_E = 32$  is indicated with a blue dot. The zigzag behavior is therefore due to an increase of  $N_L$  by 1 and  $N_E$  jumping from 32 back to 1 (i.e., from a blue dot to a red dot). (A–D) Unconditional approach. (E–H) conditional approach.

can be used as proxies for maximum likelihood based estimates for sufficiently high  $N_L$  and sufficiently low  $N_E$ .

For comparison with the literature, Table 1 lists the parameter estimates for the data considered by Vrba (1987) and Rosenzweig and Vetault (1992). Again, it is clear that the two approaches yield

very similar estimates (except for  $N_L = 1$ ) and particularly for the conditional estimates. For the ML parameter values we have added error estimates, calculated with the observed information matrix  $I_o$ . The method of moments does not allow error estimates in this way. Errors can be obtained by parametric bootstrap, but

**Table 2.** Maximum-likelihood parameter estimates of speciation ( $S$ ), extinction ( $E$ ), and net diversification ( $D$ ) rates resulting from combining the four pairs of sister clades of Table 1. Subscript denote the estimation method: ML = unconditional maximum likelihood, MLC = conditional maximum likelihood. The figures between parentheses denote standard errors as computed from the observed information matrix.

Clade	$T$ (Ma)	$N_E$ –	$N_L$ –	$\hat{S}_{ML}$ ( $\text{Ma}^{-1}$ )	$\hat{E}_{ML}$ ( $\text{Ma}^{-1}$ )	$\hat{D}_{ML}$ ( $\text{Ma}^{-1}$ )	$\hat{S}_{MLC}$ ( $\text{Ma}^{-1}$ )	$\hat{E}_{MLC}$ ( $\text{Ma}^{-1}$ )	$\hat{D}_{MLC}$ ( $\text{Ma}^{-1}$ )
Taurotragus		2	1						
Tragelaphus	7	9	7	0.412 (0.122)	0.266 (0.092)	0.145 (0.130)	0.382 (0.115)	0.352 (0.142)	0.030 (0.160)
Aepyceros		1	1						
Alcelaphini	5	27	7	0.826 (0.191)	0.680 (0.163)	0.146 (0.194)	0.778 (0.180)	0.853 (0.231)	–0.075 (0.221)
Connochaetes		11	4						
Damaliscus	4	12	3	1.077 (0.284)	0.885 (0.246)	0.205 (0.277)	1.012 (0.243)	1.306 (0.508)	–0.294 (0.522)
Loxodonta		2	1						
Elephas	5	10	1	0.574 (0.188)	0.574 (0.188)	0 (0.234)	0.600 (0.173)	$\infty$	$-\infty$

they do not properly indicate the range of parameter values that would give the same number of extinct and extant taxa; rather they indicate the range of values that are most likely to produce other numbers of extinct and extant taxa that could have been produced by the ML parameter estimates. Therefore we chose not to report the bootstrap errors.

Comparing unconditional with conditional estimates, one observes that these differ substantially as may be expected. The unconditional diversification rate is always nonnegative by definition, whereas the conditional diversification rates may well be negative. The conditional diversification rates are always lower than the unconditional ones due to a lower speciation rate and higher extinction rate. This can be understood as follows. Consider the probability distribution of all clades for a particular set of speciation and extinction rates. Low speciation rate and high extinction rate are likely to lead to rapid extinction of the entire clade. This heavily affects the unconditional probability distribution, so in order for the observed data to be likely, speciation rate must be high and extinction rate must be low. By conditioning on nonextinction of the clade, one removes from the probability distribution all clades that are extinct at time  $T$ , so these no longer affect the parameter estimates.

So far we have estimated  $S$  and  $E$  for a single clade, using only two quantities for this clade,  $N_L$  and  $N_E$ . One may also attempt to estimate these parameters for multiple, similar, clades, assuming that the clades have the same  $S$  and  $E$ . For two sister clades, one thus uses four quantities to estimate two parameters. The ML method can also accommodate this, if one assumes the likelihoods of the clades to be independent. Table 2 shows some examples for the sister clades of Table 1. The estimates are roughly the average of the estimates for each clade separately and the error in the estimates is smaller, as may be expected. More certainty on parameter values can thus be obtained at the expense of additional assumptions on equality of rates across clades.

## Discussion

In this article we have introduced a stochastic analog of the Rosenzweig and Vetault (1992) model and we have established two methods to estimate speciation, extinction, and diversification rates, one based on equating expectations to observed values and one on maximum likelihood given the observed data, where we can condition on the fact that we actually observe the clade as being extant (if it were not, we would most probably not be considering it). Kendall (1948) already considered such a model, but apart from the number of extant species, he was interested in what he called the cumulative population, that is, the sum of extinct and extant species, rather than just the number of extinct species. This can be converted into our model, for which we have provided an alternative derivation. Kendall, however, did not consider parameter estimation and conditioning.

The maximum-likelihood approach is preferable over the multivariate method of moments, which simply equates expectations to observed values, because the former can take into account that the number of extinct and extant species are not independent. With the formulas for the expected number of extant species, one effectively averages over all the possible values of the number of extinct species, and vice versa. A more consistent way of using expectations would be to use the formula for the expected number of extant species (which is independent of the number of extinct species) in combination with a formula for the expected number of extinct species conditional on the number of extant species. This formula would read

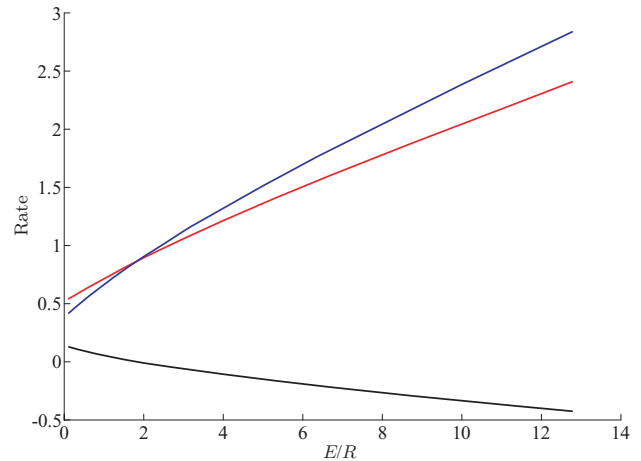
$$\langle N_E(t) | N_L(t) \rangle = \frac{1}{N_L!} \left. \frac{\partial^{N_L} \partial G(z, s, t)}{\partial s^{N_L} \partial z} \right|_{z=1, s=0} \quad (17)$$

which in general does not simplify further. Hence, the advantage of using the method of moments—computational simplicity—no longer applies.

However, we have observed that, except for low  $N_L$  and high  $N_E$ , the parameter estimates based on the method of moments are similar to those based on maximum likelihood. This is convenient, because numerical inaccuracies rapidly cumulate in evaluating the high-order derivatives required for the maximum-likelihood approach, and a proxy for this likelihood is therefore more than welcome. We therefore suggest that for low  $N_L$  (e.g.,  $N_L \leq 50$ ) the exact estimates based on the likelihood are used and for higher values ( $N_L > 50$ ) the approximations based on the method of moments are used.

The question whether one should condition or not is mainly a philosophical one. For phylogenies, Nee (2001) argues that the fact that in phylogenetic analyses we will be only considering a real phylogenetic tree rather than a single lineage must be taken into account by conditioning. In our case, the fact that we would normally not be computing speciation and extinction rates for already extinct clades implies that we should condition on the existence of the clade (see also Bokma 2003). The consequences are ambiguous. On the one hand, this allows negative diversification rates. Although clades with negative diversification rates are short-lived, they do occur. Also, the model assumes constant rates, whereas in reality they may fluctuate over time; negative estimates thus might indicate that even though initially there was true radiation (positive diversification rates), the clade may now be deterministically on its way to extinction, for example due to (human-induced) changes in the biotic and abiotic environment of the clade's species. On the other hand, for  $N_L = 1$ , one obtains (negative) infinite estimates for the extinction and diversification rates (unless  $N_E = 0$ ), an unpleasant result. However, in the unconditional case, we would similarly obtain (negative) infinite estimates when  $N_L = 0$ .

In our analysis of the data with the model, we made an important assumption: cladogenesis occurs within the punctuated equilibrium model of speciation (Eldredge and Gould 1972). That is, every new species found in the fossil record forms a new clade (branch). This is in contrast to the phyletic gradualism model of speciation, where new species can slowly evolve out of older ones (anagenesis). Branching can also occur, but there are no clear periods of stasis, which means that fossils identified as new species may be either a continuation of an earlier species or a newly born one that could, in principle, coexist for long periods of time with its ancestor and other descendants. We will not enter the discussion on which model of speciation is more appropriate (see e.g., Dennett 1995), but only wish to indicate this underlying assumption. A model incorporating phyletic speciation as well as branching would be more involved (Foote 1996). It would contain two speciation rates: a phyletic speciation rate and a branching speciation rate. It will be impossible to estimate these rates on the basis of numbers of extinct and extant species only, unless one uses temporal (stratigraphic) data.



**Figure 3.** Conditional maximum-likelihood estimates for speciation rate  $S$  (red), extinction rate  $E$  (blue), and diversification rate  $D$  (black) as a function of the ratio of extinction and preservation rates ( $\frac{E}{R}$ ) for the *Tragelaphus* clade of Table 1.

The model can also be extended to incorporate rates of preservation (Foote 2000) to correct for incompleteness of and biases in the fossil record. The model presented here assumes that every species will be preserved, that is, the preservation probability  $p_R$  equals unity. If, more realistically,  $p_R < 1$ , then the probability-generating function has the same form as in (8) but with  $B = (1 + \frac{E}{S})^2 - 4\frac{E}{S}(zp_R + (1 - p_R))$ , see Appendix S2 of Supporting information. Because the preservation probability depends on the longevity of a species which in turn depends on the extinction rate  $E$ , the preservation probability also depends on  $E$ . In Appendix S2 we analyze a model for this dependence that is a variation in the model explored by Foote and Raup (1996), Solow and Smith (1997), and Foote (1997). Assuming a constant preservation rate  $R$ , it yields  $p_R = \frac{R}{E+R}$ . Figure 3 shows how the conditional maximum-likelihood estimates for speciation, extinction, and diversification rates depend on the ratio of extinction and preservation rates for the *Tragelaphus* clade of Table 1. For  $\frac{E}{R} = 0$  (i.e., when all extinct species are preserved in the fossil record) one retrieves the values reported in Table 1. With only data on  $N_L$  and  $N_R$  where  $N_R$  is the number of preserved extinct species, the method of moments can no longer be used, as it provides only two instead of the required three equations to estimate the three parameters  $S$ ,  $E$ , and  $R$ . The maximum-likelihood method can still be used, but finding the ML parameter estimation becomes computationally demanding. More importantly, the likelihood surface will be very flat, so the maximum-likelihood parameters will have very wide confidence intervals (we analyzed various combinations of  $N_L$  and  $N_R$  which all showed this result). The reason is simple: high extinction rates and high preservation rates can lead to a similar number of species in the fossil record ( $N_R$ ) as low extinction rates and low preservation rates. More

information is clearly needed to distinguish between these parameter combinations.

For example, one could consider a much larger clade, for example, all North American mammals, which may show a more peaked likelihood surface (this cannot currently be evaluated because of numerical problems with large values of  $N_L$  and  $N_R$ ). Note that the corresponding reduction of the uncertainty in the parameter estimates comes at the cost of an increase in the fundamental model uncertainty due to the assumption that the rates of speciation and extinction are equal for all taxa in the clade. Alternative information to separate extinction and preservation rates could come from the fossil record itself: the stratigraphic range combined with a model of extinction and preservation provides estimates of extinction and preservation rates, when properly accounting for possible biases (Solow and Smith 1997; Foote 1997; Solow 2003). The model presented here can in principle be extended to incorporate such information along the lines of the probabilistic models developed by the aforementioned authors. Alternative information could also be phylogenetic information, as mentioned in the Introduction, but this is beyond the scope of the current article. The purpose of this article was to see how far one would get with the most parsimonious model requiring the smallest amount of data, for a quick assessment of diversification rates, as commonly used (e.g., Coyne and Orr 2004). It provides lower bounds to the real speciation and extinction rates when preservation probability is less than unity (see Figure 3).

Birth–death models at the species level as we used in this article have been criticized for ignoring species' population sizes, because population size may well affect speciation and extinction rates (Hubbell 2001). Birth–death models at the individual level (Hubbell 2001) can account for the effect of population size on speciation and extinction rates, and can also incorporate immigration. However, these models focus on diversity within an ecological community rather than within a clade. The two types of models share the property that they are neutral, that is, they do not assume dependence of the various rates on individual or species identity. The neutral models at the individual level, despite incorporating more mechanism, have met with more resistance than the models at the species level (e.g., McGill 2003; Ricklefs 2003; Nee 2005), but are increasingly recognized as null models for diversity on regional and local scales (Alonso et al. 2006; Adler et al. 2007; Leigh 2007). Interestingly, in these models, the possibility of probabilistic conditioning has also been noted: when the data consist of not only number of species but also species abundances, one needs to specify and condition on the sampling design, for example, whether a certain number of species or a certain number of individuals is sampled, to allow for proper model comparisons (Etienne and Olf 2005). Although these models generally provide a better description of species abundance distributions than models where the speciation rate is a per species rate (Etienne

et al. 2007), the latter models may perform better for high abundances (Etienne et al. 2007). Thus, there is merit in using and further developing both types of models. We hope that this article will contribute to this.

#### ACKNOWLEDGMENTS

We acknowledge the financial support of the Netherlands Organisation for Scientific Research (NWO). We thank F. Weissing, B. Sommeijer, B. Fornberg, M. El-Mikkawy, A. Phares, R. Neidinger, and particularly M. Berz for suggestions on the fast computation of higher order derivatives. We thank A. McKane for discussions on solving multidimensional master equations, and D. Vanpeteghem, J. O'Dwyer, M. Foote and one anonymous reviewer for constructive comments on the manuscript. Part of the work for this article was done while RSE was a Courtesy Research Associate at the University of Oregon.

#### LITERATURE CITED

- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecol. Lett.* 10:95–104.
- Alonso, D., R. S. Etienne, and A. J. McKane. 2006. The merits of neutral theory. *Trends Ecol. Evol.* 21:451–457.
- Bokma, F. 2003. Testing for equal rates of cladogenesis in diverse taxa. *Evolution* 57:2469–2474.
- Clarke, J., M. Dietze, S. Chakraborty, P. Agrawal, I. Ibanez, S. LaDeau, and M. Wolosin. 2007. Resolving the biodiversity paradox. *Ecol. Lett.* 10:647–662.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer, Sunderland MA.
- Dennett, D. 1995. *Darwin's dangerous idea*. Simon & Schuster, New York, NY.
- Eldredge, N., and S. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82–115 in T. Schopf, ed., *Models in paleobiology*. Freeman, Cooper and Company, San Francisco, CA.
- Etienne, R. S., and H. Olf. 2005. Confronting different models of community structure to species-abundance data: a Bayesian model comparison. *Ecol. Lett.* 8:493–504.
- Etienne, R. S., M. E. F. Apol, H. Olf, and F. J. Weissing. 2007. Modes of speciation and the neutral theory of biodiversity. *Oikos* 116:241–258.
- Foote, M. 1996. On the probability of ancestors in the fossil record. *Paleobiology* 22:141–151.
- . 1997. Estimating taxonomic durations and preservation probability. *Paleobiology* 23:278–300.
- . 2000. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology* 26:74–102.
- . 2003. Origination and extinction through the Phanerozoic: a new approach. *J. Geo.* 111:125–148.
- Foote, M., and D. M. Raup. 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 22:121–140.
- Hey, J. 1992. Using phylogenetic trees to study speciation and extinction. *Evolution* 46:627–640.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton Univ. Press, Princeton, NJ.
- Kendall, D. G. 1948. On some modes of population growth giving rise to R.A. Fisher's logarithmic series distribution. *Biometrika* 35:6–15.
- Kidwell, S. 2001. Preservation of species abundance in marine death assemblages. *Science* 294:1091–1094.
- Kidwell, S., and K. Flessa. 1995. The quality of the fossil record: populations, species, and communities. *Annu. Rev. Ecol. Syst.* 26:269–299.
- Leigh, E. G. 2007. The neutral theory: a historical perspective. *J. Evol. Biol.* 20:2075–2091.

- McGill, B. J. 2003. Strong and weak tests of macroecological theory. *Oikos* 102:679–685.
- Nee, S. 2001. Inferring speciation rates from phylogenies. *Evolution* 55:661–668.
- . 2004. Extinct meets extant: simple models in paleontology and molecular phylogenetics. *Paleobiology* 30:172–178.
- . 2005. The neutral theory of biodiversity: do the numbers add up? *Funct. Ecol.* 19:173–176.
- . 2006. Birth-death models in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* 37:1–17.
- Nee, S., R. May, and P. Harvey. 1994. The reconstructed evolutionary process. *Philos. Trans. R. Soc. Lond. B* 344:305–311.
- Paradis, E. 2004. Can extinction rates be estimated without fossils? *J. Theor. Biol.* 229:19–30.
- Ricklefs, R. E. 2003. A comment on Hubbell's zero-sum ecological drift model. *Oikos* 100:185–192.
- Rosenzweig, M., and S. Vetaut. 1992. Calculating speciation and extinction rates in fossil clades. *Evol. Ecol.* 6:90–93.
- Smith, A. 1994. *Systematics and the fossil record*. Blackwell, Oxford, UK.
- Solow, A. R. 2003. Estimation of stratigraphic ranges when fossil finds are not randomly distributed. *Paleobiology* 29:181–185.
- Solow, A. R., and W. Smith. 1997. On fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 23:271–277.
- Stanley, S. M. 1979. *Macroevolution: pattern and process*. Freeman, San Francisco, CA.
- Strait, D. S., and B. A. Wood. 1999. Early hominid biogeography. *Proc. Natl. Acad. Sci. USA* 96:9196–9200.
- Valentine, J., D. Jablonski, S. Kidwell, and K. Roy. 2006. Assessing the fidelity of the fossil record by using marine bivalves. *Proc. Natl. Acad. Sci. USA* 103:6599–6604.
- Vrba, E. S. 1987. Ecology in relation to speciation rates: some case histories of Miocene-Recent mammal clades. *Evol. Ecol.* 1:283–300.
- Wagner, P. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Syst. Biol.* 49:45–86.

Associate Editor: M. Van Baalen

## Supporting Information

The following supporting information is available for this article:

**Appendix S1.** Derivation of the probability-generating function (8).

**Appendix S2.** Results are shown when the probability of preservation is less than unity.

**Appendix S3.** Some analytical closed-form expressions for the probability distribution and estimates based on conditional expectations.

**EstimateSED.fox** gives maximum-likelihood estimates for speciation, extinction and diversification rates given numbers of extinct and extant species at a certain time. It runs under COSY Infinity, a free program downloadable (after registration) from [http://bt.pa.msu.edu/index\\_files/cosy.htm](http://bt.pa.msu.edu/index_files/cosy.htm).

**EstimateSED.txt** gives the parameter estimates for the cases in Figure 1.

Supporting Information may be found in the online version of this article.

(This link will take you to the article abstract).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting informations supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.