Assessing temporal variations in diversification rates from phylogenies: estimation and hypothesis testing

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SUMMARY

A new method to estimate the diversification rate of a lineage from a phylogeny of recent species is presented. This uses survival models to analyse the ages of the species as derived from the phylogeny. Survival models can analyse missing data where the exact date of death is unknown (censoring). This approach allows us to include missing data (species not included in a detailed phylogenetic study) in the analysis, provided a minimum age is known for these species. Three models are presented, with emphasis on temporal variation in diversification rates. The maximum likelihood method and the Akaike information criterion are used to derive estimators and tests of hypotheses. A simulation study demonstrates that the method is able to detect a temporal variation in diversification rate only when it is present, avoiding type I and type II errors. A lineage with ten species may be sufficient to detect a temporal variation in diversification rate even with 50% of missing data. An application is presented with data from a phylogeny of birds of the genus *Ramphocelus*.

1. INTRODUCTION

All theories in evolutionary biology have the ultimate goal of explaining the patterns of diversity through time in terms of different evolutionary success and their causes (Cracraft 1985). The diversity in species of a given evolutionary lineage is the result of speciation and extinction events. Evolutionary diversification has been classically investigated by the study of fossils and their variations in diversity through time (Raup *et al.* 1973). This approach is limited to a restricted range of phyla (mainly mammals and some groups of invertebrates). On the other hand, phylogenies based only on recent species are becoming more and more widespread, especially with the use of molecular techniques. Some alternative approaches have been proposed recently to evaluate patterns of diversification using phylogenies of recent species (Harvey *et al.* 1994; Nee *et al.* 1994a; Kubo & Iwasa 1995; Sanderson & Donoghue 1996). However, practical use of these methods seems limited for the moment. Large numbers of species have been used by Nee *et al.* (1992) to estimate diversification patterns in birds, and by Harvey *et al.* (1994) and Kubo & Iwasa (1995) in their simulations. Nee *et al.* (1994b) extended their approach to situations in which the phylogeny is based on a sample of a lineage, but the power to detect temporal variations in diversification is unknown. Accurate reconstruction of the phylogeny with all extant species is required by these methods, which limits severely their application to comparing diversification across lineages since exhaustive molecular phylogenies are still limited to

very few lineages (Nee *et al.* 1994b).

In this paper I develop a method, inspired by statistical models of survival (Cox & Oakes 1984), to estimate diversification rate with a phylogeny of recent species. This method can be used even with a small number of species. Temporal variation in diversification rate can be evaluated and statistical significance of this time effect can be tested against the alternative of a constant diversification rate. Finally, use of the statistical methodology for survival data allows use of data on species that were not included in a detailed phylogenetic study. An example is given to illustrate the method with molecular data on the tanagers of the genus *Ramphocelus* (Aves). Emphasis is given throughout the paper to time variation in diversification rates.

2. MODELS AND ESTIMATION

The present method assumes that there exists, for a lineage, an instantaneous diversification rate $\delta(t)$ which has two components, the instantaneous speciation rate $\sigma(t)$ and the instantaneous extinction rate $\epsilon(t)$, so that $\delta(t) = \sigma(t) - \epsilon(t)$. This means that at each time unit t all species are exposed to extinction and to speciation. No assumption is required on the pattern of splitting during speciation (bifurcation or multifurcation). It is also assumed that it is not possible to separately estimate $\sigma(t)$ and $\epsilon(t)$.

Consider the lineage depicted in figure 1a. Among the eight species (denoted A to H) that have been described, six have been included in a phylogenetic study resulting in estimates of their time of divergence. However, independent data allow us to estimate the minimum age of

Figure 1. (a) Hypothetical phylogeny of eight species. The plain lines symbolize the reliable parts of the phylogeny (for instance, inferred from DNA sequences); dashed lines symbolize the uncertain parts (see details in text). (b) Translation of the phylogeny in terms of survival events (F: failure, C: censoring), and derived contributions to the likelihood function. Note that one species does not contribute to the likelihood because it was already living when the lineage originated (by definition of a monophyletic lineage). We have for these data: $k = 5$ and $u = 2$ ($k + u = n - 1$).

species C and D which were not included in this phylogenetic study. For instance, we could have some biogeographic data suggesting that species C did not appear before one unit of time in figure 1a. Also, we may know that species D is closely related to species E and F but these latter are sibling species and are more closely related to each other than they are to D. Consequently, the age of the divergence between species E and F gives an estimate of the minimum age of species D.

A reconstructed phylogeny has the property that its number of species increases with time (see Harvey *et al.* (1994) for details). If one reverses the time axis of such a phylogeny, the graph could be seen as the representation of survival data, one species dying at each dichotomous node, two species dying at each trichotomous node, etc. These are called failure events in survival data analysis. Survival analysis is centred on a group or groups of individuals for each of which there is a failure event after a length of time, called the 'failure time' (Cox & Oakes 1984). For some individuals, the failure time may be unknown, but the time when they were still living could be known and is called the censoring time. The important statistical parameter is the hazard rate $h(t)$ or instantaneous failure rate. The failure time can be modelled as a random variable with density $f(t)$:

$$f(t) = h(t) \exp \left[- \int_0^t h(u) du \right]. \quad (1)$$

The probability of being censored at time t is the proba-

bility of surviving at least until time t and is given by

$$c(t) = \exp \left[- \int_0^t h(u) du \right]. \quad (2)$$

For instance, if the hazard rate is constant through time then the failure time follows an exponential distribution $f(t) = \rho \exp(-\rho t)$, and $c(t) = \exp(-\rho t)$, where ρ is the failure rate. Given a sample with k observations of failure times t_i ($i = 1, \dots, k$) and u observations of censoring times t_j ($j = 1, \dots, u$), the likelihood is given by

$$L = \prod_{i=1}^k f(t_i) \prod_{j=1}^u c(t_j), \quad (3)$$

and the log likelihood is

$$\log L = \sum_{i=1}^k \log f(t_i) + \sum_{j=1}^u \log c(t_j). \quad (4)$$

The survival models can be used with data from a phylogeny using the ages of the nodes as failure times and the minimum ages of unknown nodes as censoring times (figure 1b). When reversing the time axis to its original direction, the hazard rate can be viewed as equivalent to the diversification rate of the phylogeny. The failure rate, $h(t)$, is the probability of failure at time t conditioned on survival until this time (Cox & Oakes 1984, p. 14). Analogously, a node observed on a phylogenetic tree of recent species is a speciation event conditioned on future survival. So the estimated diversification rate, $\delta(t)$, with such phylogenies is the estimated probability of speciation and subsequent survival until present.

Three models are considered in this paper: a constant δ model (model A), a model with δ varying through time and modelled with a Weibull distribution (model B) and a model with a breakpoint in time and two different diversification rates before and after this point (model C). The choice of these models is motivated by hypothesis testing on variations in diversification through time as illustrated below. All formulae (log likelihood, maximum likelihood estimators and their variances) are given in Appendix 1. In model B, the diversification rate is modelled by $\delta(t) = \beta \alpha (\alpha t)^{(\beta-1)}$. When the hazard rate is modelled in this way in a survival analysis the failure times follow a Weibull distribution (Antle & Bain 1988). This distribution displays a great variety of shape in relation to its two parameters α and β . It is interesting to note that $\delta(t)$ decreases through time if $\beta > 1$, and increases through time if $\beta < 1$ (keeping in mind that the time axis is reversed in the present framework, this corresponds to the inverse trends in a survival analysis). The exponential distribution is a particular case of the Weibull distribution with $\beta = 1$. This latter competes with the gamma distribution as a generalization of the exponential distribution (Antle & Bain 1988), but its formulation makes the Weibull distribution easier to handle and is usually preferred in survival analyses (Cox & Oakes 1984).

These three models are only examples of how survival models can be used in the analysis of diversification. Other models are described in Cox & Oakes (1984).

3. CONFIDENCE IN THE ESTIMATES AND HYPOTHESIS TESTING

(a) Normal approximation

Estimates obtained by the maximum likelihood method are usually asymptotically normally distributed (Cox & Oakes 1984), allowing for the fol-

lowing estimator of variance:

$$\text{var}(\hat{\delta}) = \left(\left[-\frac{\partial^2 \log L}{\partial \delta^2} \right]_{\hat{\delta}} \right)^{-1}. \quad (5)$$

A 95% confidence interval could be constructed using

$$\hat{\delta} \pm 1.96 \sqrt{\text{var}(\hat{\delta})}. \quad (6)$$

However, Cox & Oakes (1984) warn against the use of this symmetric confidence interval with censored data because in such situations the log likelihood is asymmetric.

(b) Bootstrap

The bootstrap has been adapted to estimate variance of failure rate with censored data by Efron (1981a), and follows the same general guidelines described in Efron (1981b).

(c) Comparing models

Likelihood ratio tests (LRTs) provide a rigorous way of testing statistical hypotheses. LRTs can be used to compare nested models. Here, model A is nested in models B and C, but there is no relationship of nestedness between B and C. The LRT is computed by the logarithm of the ratio of both likelihoods with the most general model on the denominator multiplied by -2 . This LRT follows asymptotically a χ^2 distribution with Δnp degrees of freedom, where Δnp is the difference in the number of identifiable parameters of both models. Two models, whatever their relationship of nestedness, can be compared with the Akaike information criterion (AIC, Akaike 1973). This criterion is computed for each model by:

$$\text{AIC} = -2 \log L + 2np,$$

where np is the number of identifiable parameters of the model. The model with the lowest AIC is selected as the one that best describes the data.

4. SIMULATION STUDY

The power of the method was investigated with simulations of extinctions and speciations within a lineage. Here species defines a line in the phylogeny, and lineage means a set of related species. At each time-step of the simulation, each species has a probability σ of splitting into two species, and a probability ϵ of disappearing. Speciation and extinction were simulated successively in this order, so that a species may give birth to a daughter species and disappear at the same time-step. This process of evolution was simulated during 2000 time-steps with one species as the initial condition. Since the simulations were stochastic, so were the number of species surviving after 2000 time units. This simulation study aimed to evaluate whether the present method is able to detect a temporal variation in diversification. For simplicity, only speciation rate was assumed to vary with time. Two basic scenarios were considered: (i) constant

Figure 2. Results of the simulation study described in the text. The top charts display the simulated values of diversification rates. The middle charts display the results of the likelihood ratio tests (LRTs) comparing model A and model B with respect to the number of species, n , living at the end of the simulation. Each dot represents the LRT for one simulated phylogeny. The bottom charts display the difference in the Akaike information criterion (AIC) for models A and B. Speciation events are dichotomous. The dashed lines in the middle and bottom charts indicate the critical value of the statistics: model A is accepted below the line, model B is accepted above the line.

speciation and extinction rates; and (ii) time-varying speciation rate defined by $\sigma(t) = \beta \alpha (\alpha t)^{(\beta-1)}$ and constant extinction rate. The parameter values were chosen to result in numbers of living species n after the 2000 time-steps that have similar distributions with both scenarios. These values were: (i) $\sigma = 0.0013$, and $\epsilon = 0.00001$; and (ii) $\beta = 2.5$, $\alpha = 0.00075$, and $\epsilon = 0.00001$, for both scenarios, respectively. To calculate $\sigma(t)$ in the second scenario, t was measured from present ($t = 0$) to the past ($t = 2000$), so $\sigma(t)$ decreased with time (figure 2). After the simulations, the ages of the n surviving species were analysed with the models described above. To simulate some species not being included in a phylogenetic study, 50% of the surviving species were selected randomly and their ages were considered as known approximately during model fitting. The minimum ages of these species were taken as 80% of their real ages. Model C was difficult to evaluate in this context as the choice of the time threshold t_C is critical to fit it to the data. This model is not considered here. Before analysis, the data were divided by ten to avoid frequent overflows while fitting model B. For each simulation, the LRT comparing models A and B and AIC for both models were computed. Three hundred replications were per-

Figure 3. Same as in figure 2 except that the speciation events are trichotomous or tetrachotomous with equiprobability.

formed. In 53 and 37 cases (for both scenarios, respectively), two, one, or zero species survived after 2000 time units, leaving 247 and 263 cases for analysis. The mean numbers of species produced were 14.7 and 15.5, respectively. These means were not significantly different ($t = -0.65$, d.f. = 508, $p = 0.517$), nor were the distributions (Mann–Whitney U-test: $U = 31\,739$, $p = 0.656$). When the diversification rate was constant, the tests (LRT or AIC) did not vary much with n : the correct model was identified for any sample size (figure 2). By contrast, when diversification varied with time, both the values of LRT and the difference in AIC were positively associated with n (figure 2). The LRT selected correctly model B in all cases for $n \geq 15$, and the AIC did so for $n \geq 10$.

To evaluate the robustness of the method when speciation events are not dichotomous, the same simulations were made but speciations were now assumed to be either trichotomous or tetrachotomous with the same probability. The same basic scenarios were studied and the parameters were: (i) $\sigma = 0.001$ and $\epsilon = 0.0006$; and (ii) $\beta = 1.75$, $\alpha = 0.000\,75$ and $\epsilon = 0.0006$. The number of replications was 500. In 227 and 198 cases (for both scenarios, respectively), two, one, or zero species survived after 2000 time units, leaving 273 and 302 cases for analysis. The mean numbers of species produced were 76.3 and 66.1, respectively. These means were not significantly different ($t = -1.50$, d.f. = 573, $p = 0.134$), nor were the distributions (Mann–Whitney U-test: $U = 38\,832$, $p = 0.205$). Broadly, the same results were observed with dichotomous speciations, with a noticeable difference: larger sample sizes were necessary to detect a temporal variation in diversification rate (figure 3). Both LRT and AIC correctly selected model B when $n \geq 40$.

5. EXAMPLE

A recent study on the phylogeny of the tanagers of the genus *Ramphocelus* (Aves) provides molecular data for six species among the eight of this genus (Hackett 1996). I extracted from GenBank the complete sequences of the cytochrome *b* of eight individuals (accession numbers U15717–15724) belonging to six species. I analysed the aligned sequences with the program DNAMLK in PHYLIP (Felsenstein 1993): this program performs maximum likelihood analysis of DNA sequences under the assumption that there is a molecular clock, i.e. all tips of the tree are assumed to be equally distant from the root. The reconstructed phylogeny has the same topology as the one obtained by Hackett (1996) with parsimony methods. Using a calibration of mitochondrial DNA evolutionary rate in birds of 2% divergence per million years (Shields & Helm-Bychowski 1988), it is possible to draw a temporal scale on this phylogeny. Two species of *Ramphocelus* were not studied by Hackett (1996): *R. dimidiatus* and *R. melanogaster*. Isler & Isler (1987, in Hackett (1996)) considered both species as being closely related to *R. carbo* and *R. bresilius*. It is so possible to estimate the minimum age of *R. dimidiatus* and *R. melanogaster* at 852 000 years, which is also the age of the youngest node in the phylogeny. This procedure of estimating these minimum ages is disputable as the speciating events leading to *R. dimidiatus* and *R. melanogaster* could have occurred at any time between 1 089 500 years ago (the origin of the *carbo*–*bresilius* lineage) and the present; however, the present analysis has mainly an illustrative purpose. Note here that I assume that *Ramphocelus* is monophyletic (all extant descendants of the lineage are included in the genus). Therefore for this lineage $k = 5$ and $u = 2$.

In a hypothesis testing framework, one can formulate predictions with respect to the present analysis. It has been hypothesized that diversification of birds has slowed down since the onset of the Pleistocene (see Zink & Slowinski 1995). This can be tested with the present method. Specifically, if the diversification rate was higher before the Pleistocene, then we should observe $\hat{\beta} > 1$ with model B, $\hat{\delta}_1 < \hat{\delta}_2$ with model C, and a superiority (in terms of LRT and AIC) of both models B and C compared to model A in explaining the present data. The maximum log likelihoods and AIC for each model are indicated in table 1. Model B is the best one as is indicated by both the AIC and the LRT of model B versus model A: $\chi^2 = 6.652$, d.f. = 1, $p = 0.01$. The estimated parameters according to model B are: $\hat{\alpha} = 5.68 \times 10^{-4}$ and $\hat{\beta} = 3.05$. As $\hat{\beta} > 1$, this result provides evidence for a decrease in diversification rate through time for the genus *Ramphocelus*. Model C does not provide any improvement of fit compared to model A, as is indicated by the AIC (table 1) and the LRT: $\chi^2 = 0.598$, d.f. = 1, $p > 0.4$. The estimated parameters of model C are: $\hat{\delta}_1 = 4.75 \times 10^{-4}$ and $\hat{\delta}_2 = 1.24 \times 10^{-3}$. It is possible to change the parameter t_C and select the value that gives the highest likelihood. This was obtained for

Table 1. *Results of fitting three models to the Ramphocelus data*(Models are described in the text: log L , log likelihood; np , number of identifiable parameters; AIC, Akaike information criterion.)

model	log L	np	AIC	parameter	estimated variance	
					normal approximation	bootstrap
A	-46.605	1	87.210	δ	5.87×10^{-8}	1.58×10^{-8}
B	-39.279	2	82.558	β	0.796	7.58
				α	8.20×10^{-9}	1.58×10^{-8}
C	-42.306	2	88.612	δ_1	5.64×10^{-8}	2.66×10^{-8}
				δ_2	1.53×10^{-6}	3.52×10^{-7}

$t_C = 1.8$ My, which corresponds roughly to the onset of the Pleistocene period.

The estimated variances with the normal approximations and the bootstrap for the three models are indicated in table 1. The estimated variance of $\hat{\beta}$ is particularly high with the bootstrap which is explained by the fact that with the present sample the estimate of β was very sensitive to sampling variations, leading to a particularly high variance. Bootstrap estimate of this parameter should be taken with care when sample size is small.

6. DISCUSSION

Investigating the rates of diversification of evolutionary lineages requires knowledge of the temporal sequence of speciation and extinction events. Use of molecular data allows us, under some conditions, to draw a temporal scale on phylogenies of recent species. The present paper deals with a method that estimates the diversification rate of a lineage given a temporally scaled phylogeny for at least some of the species belonging to this lineage. One may think that a limitation of the method can come from the fact that in a survival model the failure events are considered to be independent, which is not true for the ages of species read on a phylogeny, because of the hierarchical nature of the latter. However, there are two reasons to think this does not limit the method. First, the ages are all measured from the present and not relatively to each other. Second, nodes are not assumed to be dichotomous, so two sister species may originate at the same time.

The impossibility of distinguishing speciation and extinction is a limitation of the approach that uses phylogenies of recent species to estimate diversification rates (Kubo & Iwasa 1995). This is a serious limitation compared to methods based on the analysis of fossils. An important line of future research is in the use of molecular data to try to distinguish speciation and extinction rates (Nee *et al.* 1994*a, b*).

The present method assumes that, through time, a species experiences an instantaneous diversification rate that is the result of instantaneous speciation

and extinction rates (the Markovian assumption; Losos & Adler 1995). This seems unrealistic: speciation and extinction are likely to operate on different time-scales and have different patterns of temporal variations. Losos & Adler (1995) simulated a model of diversification where the speciation events are not instantaneous. They showed that their model makes predictions that are notably different from those made from a Markovian model. Similar departures from the Markovian model were observed when speciation was assumed to occur simultaneously in all species (Losos & Adler 1995). Temporal variations in diversification have rarely been investigated, though they are thought to be important (Mayr 1963; Cracraft 1985). The method introduced in this paper offers a framework for the analysis of temporal variations in diversification rate. An appropriate function $\delta(t)$ can be formulated and used in equations (1) and (2), giving a theoretical distribution of splitting events in a phylogenetic tree. The statistical framework developed above could allow investigation of temporal changes in diversification.

It should be noted that the topology of the tree is not important here; only the times of splitting are analysed. Nevertheless, hypotheses on the shape of trees can be tested using survival models with covariates (Conroy *et al.* 1996). These models allow one to test for the influence of individual variables (age, sex, habitat, etc.) on survival. These models can be adapted to the present framework by considering the influence of some internal (e.g. evolutionary novelties) or external (e.g. habitat or climate) covariates on diversification rate. This is currently under development.

The simulation study showed that the proposed method is able to detect a time variation in diversification rate with a lineage of ten species. Remembering that only half of the species were considered for inclusion in a detailed phylogeny, this result is encouraging as it suggests that a phylogeny of five species and indirect information on the dates of origin of five others could be sufficient to detect a time variation in diversification. The method has less

power when speciation is trichotomous or tetrachotomous, but it is still statistically consistent and the correct model is selected when sample size increases. Assuming this multifurcating pattern of speciation, a lineage with 40 species is necessary to detect a time variation in diversification rate corresponding to a detailed phylogeny of 20 species; this is not insurmountable as more and more phylogenies with more than 20 species become available.

It is essential that analytical methods provide a statistical framework for hypothesis testing. Methods of estimation and hypothesis testing based on likelihood methods (Thompson 1975; Hey 1992; Nee *et al.* 1994a; this study) allow for a diversity of models (and so for a diversity of hypotheses) to be tested. A definite advantage of the present method is that it can accommodate the presence of missing data in the phylogeny under study. Furthermore, these missing data can be included in the analysis and contribute to the computation of the likelihood functions.

The results obtained with the *Ramphocelus* data show the potentialities of the method. Model B provided the best fit to the data; this is not surprising because it is based on a Weibull distribution of the diversification rate which is very flexible (Antle & Bain 1988). The analyses revealed a decrease in diversification through time for *Ramphocelus*, which is consistent with previous studies on North American Passerines (Zink & Slowinski 1995). Because the method presented here is based on a large family of explicitly statistical methods from survival studies (Cox & Oakes 1984), it should prove useful in framing hypotheses regarding this decline in avian diversification rates.

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APPENDIX 1.

(a) Model A

This is similar to the exponential model mentioned above. The log likelihood is given by

$$\log L = k \log \delta - \left(\sum_{i=1}^k t_i + \sum_{j=1}^u t_j \right). \quad (7)$$

The maximum likelihood estimator (MLE) of δ is obtained by deriving the log likelihood on δ and solving this partial derivative as equal to zero, which gives

$$\hat{\delta} = k / \left(\sum_{i=1}^k t_i + \sum_{j=1}^u t_j \right). \quad (8)$$

The variance of this estimator is found with equation (5):

$$\text{var}(\hat{\delta}) = (\hat{\delta}^2/k). \quad (9)$$

(b) Model B

The log likelihood is

$$\log L = k(\log \beta - \beta \log \alpha) + (\beta - 1) \sum_{i=1}^k \log t_i - \alpha^\beta \left(\sum_{i=1}^k t_i^\beta + \sum_{j=1}^u t_j^\beta \right). \quad (10)$$

Respective MLEs for β and α are found by taking the appropriate partial derivatives:

$$\frac{1}{\hat{\beta}} - \frac{\sum_{i=1}^k t_i^{\hat{\beta}} \log t_i + \sum_{j=1}^u t_j^{\hat{\beta}} \log t_j}{\sum_{i=1}^k t_i^{\hat{\beta}} + \sum_{j=1}^u t_j^{\hat{\beta}}} + \frac{\sum_{i=1}^k \log t_i}{k} = 0, \quad (11)$$

$$\hat{\alpha} = \left(k / \left(\sum_{i=1}^k t_i^{\hat{\beta}} + \sum_{j=1}^u t_j^{\hat{\beta}} \right) \right)^{1/\hat{\beta}}. \quad (12)$$

The MLE of β is searched iteratively using equation (11) and is then used in equation (12) to calculate the MLE of α . The variance estimators are

$$\text{var}(\hat{\alpha}) = \left[\frac{k\hat{\beta}}{\hat{\alpha}^2} + \hat{\beta}(\hat{\beta} - 1)\hat{\alpha}^{\hat{\beta}-2} \left(\sum_{i=1}^k t_i^{\hat{\beta}} + \sum_{j=1}^u t_j^{\hat{\beta}} \right) \right]^{-1}, \quad (13)$$

$$\text{var}(\hat{\beta}) = \left[\frac{k}{\hat{\beta}^2} + \sum_{i=1}^k (\hat{\alpha} t_i)^{\hat{\beta}} \log(\hat{\alpha} t_i) + \sum_{j=1}^u (\hat{\alpha} t_j)^{\hat{\beta}} \log(\hat{\alpha} t_j) \right]^{-1}. \quad (14)$$

(c) Model C

Consider a point in time noted t_C . For $t \leq t_C$, the diversification rate is constant and noted δ_1 , and for $t > t_C$, the diversification rate is constant and noted δ_2 (with $\delta_1 \neq \delta_2$). The log likelihood is

$$\begin{aligned} \log L = & k_1 \log \delta_1 - \delta_1 \sum_{i=1}^{k_1} t_{1i} + k_2 \log \delta_2 \\ & + k_2 t_C (\delta_2 - \delta_1) - \delta_2 \sum_{i=1}^{k_2} t_{2i} - \delta_1 \sum_{j=1}^{u_1} t_{1j} \\ & + u_2 t_C (\delta_2 - \delta_1) - \delta_2 \sum_{j=1}^{u_2} t_{2j}, \end{aligned} \quad (15)$$

where the subscripts 1 and 2 denote the numbers and times before and after t_C , respectively. Deriving partially on δ_1 and δ_2 , respectively, gives the MLEs

$$\hat{\delta}_1 = k_1 / \left(\sum_{i=1}^{k_1} t_{1i} + \sum_{j=1}^{u_1} t_{1j} + (k_2 + u_2) t_C \right), \quad (16)$$

$$\hat{\delta}_2 = k_2 / \left(\sum_{i=1}^{k_2} t_{2i} + \sum_{j=1}^{u_2} t_{2j} - (k_2 + u_2) t_C \right). \quad (17)$$

The variance estimators are:

$$\text{var}(\hat{\delta}_1) = (\hat{\delta}_1^2/k_1), \quad (18)$$

$$\text{var}(\hat{\delta}_2) = (\hat{\delta}_2^2/k_2). \quad (19)$$

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