

## Origination and extinction components of taxonomic diversity: general problems

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*Abstract.*—Mathematical modeling of cladogenesis and fossil preservation is used to explore the expected behavior of commonly used measures of taxonomic diversity and taxonomic rates with respect to interval length, quality of preservation, position of interval in a stratigraphic succession, and taxonomic rates themselves. Particular attention is focused on the independent estimation of origination and extinction rates. Modeling supports intuitive and empirical arguments that single-interval taxa, being especially sensitive to variation in preservation and interval length, produce many undesirable distortions of the fossil record. It may generally be preferable to base diversity and rate measures on estimated numbers of taxa extant at single points in time rather than to adjust conventional interval-based measures by discarding single-interval taxa.

A combination of modeling and empirical analysis of fossil genera supports two major trends in marine animal evolution. (1) The Phanerozoic decline in taxonomic rates is unlikely to be an artifact of secular improvement in the quality of the fossil record, a point that has been argued before on different grounds. (2) The post-Paleozoic rise in diversity may be exaggerated by the essentially complete knowledge of the living fauna, but this bias is not the principal cause of the pattern. The pattern may partly reflect a secular increase in preservation nevertheless.

Apparent temporal variation in taxonomic rates can be produced artificially by variation in preservation rate. Some empirical arguments suggest, however, that much of the short-term variation in taxonomic rates observed in the fossil record is real. (1) For marine animals as a whole, the quality of the fossil record of a higher taxon is not a good predictor of its apparent variability in taxonomic rates. (2) For a sample data set covering a cross-section of higher taxa in the Ordovician, most of the apparent variation in origination and extinction rates is not statistically attributable to independently measured variation in preservation rates. (3) Previous work has shown that standardized sampling to remove effects of variable preservation and sampling yields abundant temporal variation in estimated taxonomic rates. While modeling suggests which rate measures are likely to be most accurate in principle, the question of how best to capture true variation in taxonomic rates remains open.

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Accepted: 21 June 2000

### Interval Estimates of Diversity and Taxonomic Rates

Do changes in taxonomic diversity tend to be associated preferentially with changes in origination rate or with changes in extinction rate? This rather simple empirical question, which I address in a companion paper (Foote 2000), involves a number of methodological problems that I will consider here: (1) How are interval estimates of diversity and taxonomic rates affected by interval length? (2) How do true rates affect our ability to estimate rates? (3) How are diversity and rate estimates affected by incompleteness of the fossil record? (4) How are they affected by the finite stratigraphic extent of the fossil record? (5) How do the foregoing factors affect our ability to mea-

sure origination and extinction rates independently? This paper focuses on measuring diversity and rate changes over discrete stratigraphic or temporal intervals, rather than in calculating long-term average rates (cf. Foote in press a).

Using mathematical modeling of cladogenesis and fossil preservation, I will explore the behavior of several interval measures of diversity and taxonomic rates. This exercise points to a number of undesirable properties of single-interval taxa. The difficulties discussed here stand in addition to those that arise from differences in species abundance and, consequently, in preservation probability (Buzas et al. 1982). Taxa confined to single intervals are problematic even if preservation is complete or if all taxa and time intervals are

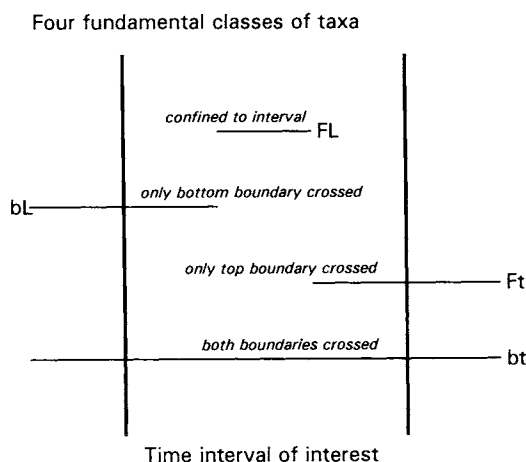


FIGURE 1. Illustration of four fundamental classes of taxa present during a stratigraphic interval.  $N_{FL}$  is the number of taxa confined to the interval,  $N_{bL}$  is the number that cross the bottom boundary only,  $N_{Ft}$  is the number that cross the top boundary only, and  $N_{bt}$  is the number that cross both boundaries.

characterized by the same quality of preservation. It is therefore advantageous to base measures on taxa that cross between stratigraphic or temporal intervals. Simply modifying conventional measures by discarding single-interval taxa may not be the best approach, however. Instead, it is preferable under a wide range of circumstances to use measures for which single-interval are simply irrelevant by the very nature of the measures.

#### Four Fundamental Classes of Taxa

Any taxon known or inferred from a stratigraphic interval can be classified into one of four mutually exclusive categories (Fig. 1) (see Barry et al. 1995 for a similar classification): (1) taxa confined to the interval, i.e., taxa whose first and last appearance are both within the interval; (2) taxa that cross the bottom boundary and make their last appearance during the interval; (3) taxa that make their first appearance during the interval and cross the top boundary; and (4) taxa that range through the entire interval, crossing both the top and bottom boundaries. Using *b* and *t* to refer to crossing the bottom and top boundaries of an interval and using *F* and *L* to refer to first and last appearance within the interval, I will denote the numbers of taxa in the four categories  $N_{FL}$ ,  $N_{bL}$ ,  $N_{Ft}$ , and  $N_{bt}$ . The term

*singleton* is commonly used to refer to species represented by a single specimen (Buzas and Culver 1994, 1998). I will denote as a *singleton* any taxon that is confined to a single stratigraphic interval at the given level of resolution (any member of the *FL* category). Although I will refer to boundaries, these need not be times of major biotic turnover; any recognizable temporal or stratigraphic division can serve as a point of reference. As I will discuss below, there are many useful combinations of these categories of taxa. Two that are especially important are the total number of taxa crossing the bottom boundary,  $N_b$  ( $= N_{bL} + N_{bt}$ ), and the total number crossing the top boundary,  $N_t$  ( $= N_{Ft} + N_{bt}$ ).

All measures of diversity and taxonomic rates for an interval are derived from combinations of the numbers of taxa in the four fundamental classes. The numbers denoted by *N* with subscripts are the true numbers of taxa with the given properties. Although these are useful for modeling, in the fossil record we always deal with observed numbers, which I will denote by *X* with the corresponding subscripts (Foote 1999: Appendix 7). The relationships between true and observed numbers are central to what will be developed below (see Appendix for details). Of course, taxa can shift categories when filtered through incomplete preservation. For example, a taxon that truly belongs to the *bt* category can contribute to  $X_{FL}$ ,  $X_{bL}$ ,  $X_{Ft}$ , or  $X_{bt}$ , depending on how much of its range is truncated. It should also be kept in mind that observed taxa (*X*) in the first three categories must necessarily be found within the interval, while the last category includes taxa that are found before and after, but not necessarily during, the interval.

#### Measures of Diversity and Rate

Numerous measures of diversity and rate have been applied to paleontological data, and their intuitive advantages and disadvantages have been discussed at length (Gingerich 1987; Gilinsky 1991; Foote 1994; Harper 1996; Sepkoski and Koch 1996). Rather than review all of them, I will explore the properties of some commonly used measures that have been proposed to solve particular problems or to take advantage of particular aspects

TABLE 1. Definitions of taxonomic diversity measures and taxonomic rate metrics for intervals of length  $\Delta t$ . Measures are expressed in terms of numbers belonging to the four fundamental classes of taxa,  $N_{FL}$ ,  $N_{bL}$ ,  $N_{FI}$ , and  $N_{bI}$  (Fig. 1), or combinations derived from them (Appendix).

| Diversity measures                                 |                                                                                                                                   |
|----------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------|
| Measure                                            | Definition                                                                                                                        |
| Total diversity, $N_{tot}$                         | $N_{FL} + N_{bL} + N_{FI} + N_{bI}$                                                                                               |
| Total diversity minus singletons                   | $N_{bL} + N_{FI} + N_{bI}$                                                                                                        |
| Bottom-boundary crossers, $N_b$                    | $N_{bL} + N_{bI}$                                                                                                                 |
| Top-boundary crossers, $N_t$                       | $N_{FI} + N_{bI}$                                                                                                                 |
| Number of originations, $N_o$                      | $N_{FL} + N_{FI}$                                                                                                                 |
| Number of extinctions, $N_e$                       | $N_{FL} + N_{bL}$                                                                                                                 |
| Estimated mean standing diversity                  | $(N_b + N_t) / 2$<br>$= (N_{bL} + N_{FI} + 2N_{bI}) / 2$<br>$= (N_{tot} - N_o / 2 - N_e / 2)$                                     |
| Rate measures                                      |                                                                                                                                   |
| Measure                                            | Definition                                                                                                                        |
| Per-taxon rate                                     | Origination: $(N_{FL} + N_{FI}) / (N_{tot}) / \Delta t$<br>Extinction: $(N_{FL} + N_{bL}) / (N_{tot}) / \Delta t$                 |
| Van Valen metric                                   | Origination: $(N_{FL} + N_{FI}) / [(N_b + N_t) / 2] / \Delta t$<br>Extinction: $(N_{FL} + N_{bL}) / [(N_b + N_t) / 2] / \Delta t$ |
| Van Valen metric without singletons                | Origination: $(N_{FI}) / [(N_b + N_t) / 2] / \Delta t$<br>Extinction: $(N_{bI}) / [(N_b + N_t) / 2] / \Delta t$                   |
| Estimated per-capita rate, $\hat{p}$ and $\hat{q}$ | $\hat{p}$ : $-\ln(N_{bI} / N_t) / \Delta t$<br>$\hat{q}$ : $-\ln(N_{bI} / N_b) / \Delta t$                                        |

of data. I will not discuss the well-known problems associated with poor constraints on interval length (Gilinsky 1991; McGhee 1996; Sepkoski and Koch 1996). Long-term averages, appropriately calculated, are not very sensitive to errors in interval length (Foote 1999: Appendix 7). It is often short-term variation that is of interest, however, and the fundamental distortion is that an overestimate of interval length yields an underestimate of taxonomic rates, and conversely for an underestimate of interval length. Thus, while dating error may produce spurious extremes in taxonomic rates, it is unlikely to produce long-term secular patterns. The diversity measures differ in whether they seek an estimate of standing diversity at a point in time or of the total number of taxa that exist during any part of an interval. Most rate metrics start with a tabulation of the number of events within an interval and normalize this number by some measure of diversity and by the length of the interval. The goal of these normalizations is to obtain an estimate of the instantaneous, per-capita rates of origination and extinction,  $p$  and  $q$ , per lineage-million-years (Lmy) (Raup 1985). The per-capita rate estimates advocated here,  $\hat{p}$  and  $\hat{q}$  (Table 1), are derived directly

from branching theory rather than as a normalization of the number of events observed within an interval.

Table 1 gives definitions of diversity and rate measures in terms of the four fundamental classes of taxa and the interval length,  $\Delta t$ . The expected values of these measures under various conditions of completeness are derived in the Appendix. Expressing these expectations in terms of fundamental parameters such as origination and extinction rates, rather than counts of number of events, helps to make sense of their behavior. Since the Appendix contains exact expressions for a number of quantities that have sometimes been derived less directly with Monte Carlo methods, it is hoped that it will be of some use to the paleontologist. Table 2 provides a "road map" to the Appendix.

The first two sections that follow will discuss measures of diversity and rate in terms of true numbers of taxa ( $N$ ) in order to emphasize problems that would exist even if the fossil record were complete. The discussion will then switch to observed numbers ( $X$ ) in order to emphasize problems related to paleontological incompleteness.

### Effects of Interval Length

For the problems discussed here, it is natural and convenient to measure time in multiples of  $1/q$ , the average taxon duration. This yields in effect a dimensionless expression of time. Similarly, expressing origination and preservation rates relative to  $q$  yields dimensionless rate measures. Thus, an increase in interval length with taxonomic rates held constant has the same effect as an increase in taxonomic rates with interval length held constant. The number of top- or bottom-boundary crossers may be larger or smaller depending on where we choose our time lines, and if origination is concentrated shortly after boundaries and extinction shortly before them, average standing diversity may be underestimated (Raup 1991; Alroy 1992; Foote 1994). Nevertheless, the number of boundary crossers is not systematically affected by interval length (Fig. 2) (Bambach 1999). This is just one potential advantage of measuring diversity using boundary crossers (see below).

The per-taxon rates have been used as a way to normalize the number of origination or extinction events by total diversity and interval length. As interval length increases, a progressively larger proportion of total diversity consists of singletons (Fig. 2). Because these taxa first appear and last appear within the same interval, proportional origination and extinction asymptotically approach unity as  $\Delta t$  increases, and the per-taxon rates consequently decline as interval length increases (Fig. 3; Appendix, section 2) (Gingerich 1987; Foote 1994).

Van Valen (1984) used a rate metric designed to normalize the number of originations and extinctions by estimated average standing diversity,  $(N_b + N_t)/2$ , since this number rather than total diversity better expresses the number of taxa susceptible to origination or extinction at an instant in time (Harper 1975; Van Valen 1984). This normalization implicitly assumes a linear change in standing diversity, a change that is expected to be exponential if rates are constant within an interval. As  $\Delta t$  increases, the linear approximation becomes progressively worse, and  $(N_b + N_t)/2$  overestimates mean standing

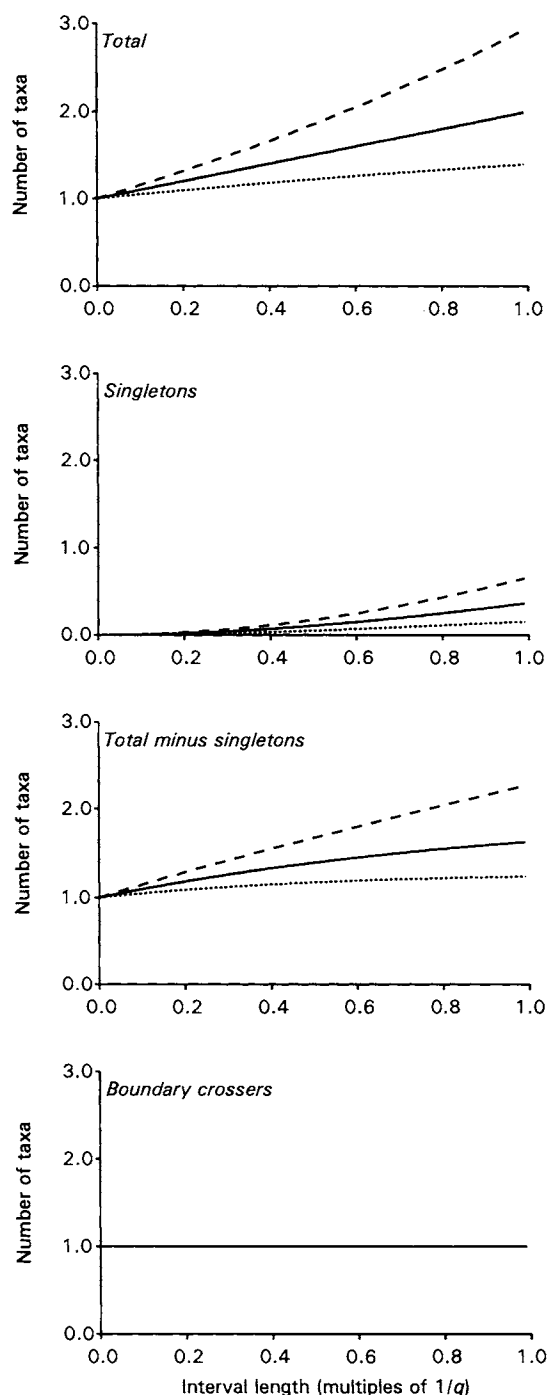


FIGURE 2. Effect of interval length on number of taxa within an interval. Rates are time-homogeneous and fossil record is complete. Interval length is expressed as multiples of  $1/q$ . Solid lines,  $p = q$ ; dashed lines,  $p = 1.5q$ ; dotted lines,  $p = 0.5q$ . In this and subsequent figures, diversity at the start of the interval is unity. Only the number of boundary crossers is independent of interval length.

TABLE 2. Guide to equations in Appendix.

|                                            | Quantity of interest | Preservation |  | Edge effect? | Equations*                     |  |
|--------------------------------------------|----------------------|--------------|--|--------------|--------------------------------|--|
|                                            |                      |              |  |              |                                |  |
| 1A. Total diversity                        | Complete             |              |  | —            | 9                              |  |
| 1B. Total diversity                        | Constant             |              |  | No           | 24c,25c,26–29,34,35e           |  |
| 1C. Total diversity                        | Constant             |              |  | Yes          | 24b,25b,26–29,34,35e           |  |
| 1D. Total diversity                        | Variable             |              |  | Yes          | 24a,25a,26–29,34,35e           |  |
| 2A. Taxa crossing bottom boundary only     | Complete             |              |  | —            | 4                              |  |
| 2B. Taxa crossing bottom boundary only     | Constant             |              |  | No           | 24c,25c,27,31b,32a,34b,37d     |  |
| 2C. Taxa crossing bottom boundary only     | Constant             |              |  | Yes          | 24b,25b,27,31b,32a,34b         |  |
| 2D. Taxa crossing bottom boundary only     | Variable             |              |  | Yes          | 24a,25a,27,31b,32a,34b         |  |
| 3A. Taxa crossing top boundary only        | Complete             |              |  | —            | 5                              |  |
| 3B. Taxa crossing top boundary only        | Constant             |              |  | No           | 24c,25c,28,31c,33a,34c,37e     |  |
| 3C. Taxa crossing top boundary only        | Constant             |              |  | Yes          | 24b,25b,28,31c,33a,34c         |  |
| 3D. Taxa crossing top boundary only        | Variable             |              |  | Yes          | 24a,25a,28,31c,33a,34c         |  |
| 4A. Total taxa crossing bottom boundary    | Complete             |              |  | —            | 1                              |  |
| 4B. Total taxa crossing bottom boundary    | Constant             |              |  | No           | 24c,25c,30c,35a                |  |
| 4C. Total taxa crossing bottom boundary    | Constant             |              |  | Yes          | 24b,25b,30b,35a                |  |
| 4D. Total taxa crossing bottom boundary    | Variable             |              |  | Yes          | 24a,25a,30a,35a                |  |
| 5A. Total taxa crossing top boundary       | Complete             |              |  | —            | 2                              |  |
| 5B. Total taxa crossing top boundary       | Constant             |              |  | No           | 24c,25c,30c,35b                |  |
| 5C. Total taxa crossing top boundary       | Constant             |              |  | Yes          | 24b,25b,30b,35b                |  |
| 5D. Total taxa crossing top boundary       | Variable             |              |  | Yes          | 24a,25a,30a,35b                |  |
| 6A. Taxa crossing both boundaries          | Complete             |              |  | —            | 3                              |  |
| 6B. Taxa crossing both boundaries          | Constant             |              |  | No           | 24c,25c,30c,31a,34a,37c        |  |
| 6C. Taxa crossing both boundaries          | Constant             |              |  | Yes          | 24b,25b,30b,31a,34a,36c        |  |
| 6D. Taxa crossing both boundaries          | Variable             |              |  | Yes          | 24a,25a,30a,31a,34a            |  |
| 7A. Singletons                             | Complete             |              |  | —            | 6                              |  |
| 7B. Singletons                             | Constant             |              |  | No           | 24c,25c,29,31d,32b,33b,34d,38b |  |
| 7C. Singletons                             | Constant             |              |  | Yes          | 24b,25b,29,31d,32b,33b,34d     |  |
| 7D. Singletons                             | Variable             |              |  | Yes          | 24a,25a,29,31d,32b,33b,34d     |  |
| 8A. Number of originations or extinctions  | Complete             |              |  | —            | 7,8                            |  |
| 8B. Number of originations or extinctions  | Constant             |              |  | No           | 35c; lines 2B,3B,7B            |  |
| 8C. Number of originations or extinctions  | Constant             |              |  | Yes          | 35c; lines 2C,3C,7C            |  |
| 8D. Number of originations or extinctions  | Variable             |              |  | Yes          | 35c; lines 2D,3D,7D            |  |
| 9A. Proportional origination or extinction | Complete             |              |  | —            | 10,11                          |  |
| 9B. Proportional origination or extinction | Constant             |              |  | No           | 10,11; line 8B                 |  |
| 9C. Proportional origination or extinction | Constant             |              |  | Yes          | 10,11; line 8C                 |  |
| 9E. Proportional origination or extinction | Variable             |              |  | Yes          | 10,11; line 8D                 |  |
| 10A. Per taxon rate metric                 | Complete             |              |  | —            | 12,13                          |  |
| 10B. Per taxon rate metric                 | Constant             |              |  | No           | 12,13; line 8B                 |  |
| 10C. Per taxon rate metric                 | Constant             |              |  | Yes          | 12,13; line 8C                 |  |
| 10D. Per taxon rate metric                 | Variable             |              |  | Yes          | 12,13; line 8D                 |  |
| 11A. Van Valen rate metric                 | Complete             |              |  | —            | 14,15,16,17                    |  |
| 11B. Van Valen rate metric                 | Constant             |              |  | No           | 39                             |  |
| 11C. Van Valen rate metric                 | Constant             |              |  | Yes          | 14a; lines 4C,5C,8C            |  |
| 11D. Van Valen rate metric                 | Variable             |              |  | Yes          | 14a; lines 4D,5D,8D            |  |

TABLE 2. Continued.

| Quantity of interest                                                 | Preservation             |                          | Edge effect? | Equations*                |
|----------------------------------------------------------------------|--------------------------|--------------------------|--------------|---------------------------|
|                                                                      | Complete                 | Constant                 |              |                           |
| 12A. Van Valen rate metric (minus singletons)                        | Complete                 | Constant                 | —            | 18, 19, 20, 21            |
| 12B. Van Valen rate metric (minus singletons)                        | Constant                 | Constant                 | No           | 18a; lines 2B, 3B, 4B, 5B |
| 12C. Van Valen rate metric (minus singletons)                        | Variable                 | Variable                 | Yes          | 18a; lines 2C, 3C, 4C, 5C |
| 12D. Van Valen rate metric (minus singletons)                        | Complete                 | Complete                 | —            | 18a; lines 2D, 3D, 4D, 5D |
| 13A. Estimated per-capita rates                                      | Constant                 | Constant                 | No           | 22, 23                    |
| 13B. Estimated per-capita rates                                      | Constant                 | Constant                 | No           | 22, 23; lines 4B, 5B, 6B  |
| 13C. Estimated per-capita rates                                      | Variable                 | Variable                 | Yes          | 22, 23; lines 4C, 5C, 6C  |
| 13D. Estimated per-capita rates                                      | Constant                 | Constant                 | Yes          | 22, 23; lines 4D, 5D, 6D  |
| 14A. Probability of preservation before boundary                     | Constant                 | Constant                 | No           | 24c                       |
| 14B. Probability of preservation before boundary                     | Variable                 | Variable                 | Yes          | 24b                       |
| 14C. Probability of preservation before boundary                     | Constant                 | Constant                 | No           | 24a                       |
| 15A. Probability of preservation after boundary                      | Constant                 | Constant                 | No           | 25c                       |
| 15B. Probability of preservation after boundary                      | Constant                 | Constant                 | Yes          | 25b                       |
| 15C. Probability of preservation after boundary                      | Variable                 | Variable                 | Yes          | 25a                       |
| 16A. Probability of preservation during interval                     | Constant during interval | Constant during interval | —            | 26—29                     |
| 16B. Probability of being observed to cross a boundary               | Constant                 | Constant                 | No           | 30c                       |
| 16C. Probability of being observed to cross a boundary               | Constant                 | Constant                 | Yes          | 30b                       |
| 17A. Probability of being observed to cross a boundary               | Variable                 | Variable                 | Yes          | 30a                       |
| 18. Probability that singleton is observed                           | Constant within interval | Constant within interval | —            | 29                        |
| 19A. Probability that <i>bl</i> taxon is observed as such            | Constant                 | Constant                 | No           | 24c, 27, 32a              |
| 19B. Probability that <i>bl</i> taxon is observed as such            | Constant                 | Constant                 | Yes          | 24b, 27, 32a              |
| 19C. Probability that <i>bl</i> taxon is observed as such            | Variable                 | Variable                 | Yes          | 24a, 27, 32a              |
| 20A. Probability that <i>bl</i> taxon is observed as singleton       | Constant                 | Constant                 | No           | 24c, 27, 32b              |
| 20B. Probability that <i>bl</i> taxon is observed as singleton       | Constant                 | Constant                 | Yes          | 24b, 27, 32b              |
| 20C. Probability that <i>bl</i> taxon is observed as singleton       | Variable                 | Variable                 | Yes          | 24a, 27, 32b              |
| 21A. Probability that <i>Ft</i> taxon is observed as such            | Constant                 | Constant                 | No           | 25c, 28, 33a              |
| 21B. Probability that <i>Ft</i> taxon is observed as such            | Constant                 | Constant                 | Yes          | 25b, 28, 33a              |
| 21C. Probability that <i>Ft</i> taxon is observed as such            | Variable                 | Variable                 | Yes          | 25a, 28, 33a              |
| 22A. Probability that <i>Ft</i> taxon is observed as singleton       | Constant                 | Constant                 | No           | 25c, 28, 33b              |
| 22B. Probability that <i>Ft</i> taxon is observed as singleton       | Constant                 | Constant                 | Yes          | 25b, 28, 33b              |
| 22C. Probability that <i>Ft</i> taxon is observed as singleton       | Variable                 | Variable                 | Yes          | 25a, 28, 33b              |
| 23A. Probability that <i>bt</i> taxon is observed as such            | Constant                 | Constant                 | No           | 24c, 25c, 31a             |
| 23B. Probability that <i>bt</i> taxon is observed as such            | Constant                 | Constant                 | Yes          | 24b, 25b, 31a             |
| 23C. Probability that <i>bt</i> taxon is observed as such            | Variable                 | Variable                 | Yes          | 24a, 25a, 31a             |
| 24A. Probability that <i>bt</i> taxon is observed as <i>bl</i> taxon | Constant                 | Constant                 | No           | 24c, 25c, 26, 31b         |
| 24B. Probability that <i>bt</i> taxon is observed as <i>bl</i> taxon | Constant                 | Constant                 | Yes          | 24b, 25b, 26, 31b         |
| 24C. Probability that <i>bt</i> taxon is observed as <i>bl</i> taxon | Variable                 | Variable                 | Yes          | 24a, 25a, 26, 31b         |
| 25A. Probability that <i>bt</i> taxon is observed as <i>Ft</i> taxon | Constant                 | Constant                 | No           | 24c, 25c, 26, 31c         |
| 25B. Probability that <i>bt</i> taxon is observed as <i>Ft</i> taxon | Constant                 | Constant                 | Yes          | 24b, 25b, 26, 31c         |
| 25C. Probability that <i>bt</i> taxon is observed as <i>Ft</i> taxon | Variable                 | Variable                 | Yes          | 24a, 25a, 26, 31c         |
| 26A. Probability that <i>bt</i> taxon is observed as singleton       | Constant                 | Constant                 | No           | 24c, 25c, 26, 31d         |
| 26B. Probability that <i>bt</i> taxon is observed as singleton       | Constant                 | Constant                 | Yes          | 24b, 25b, 26, 31d         |
| 27C. Probability that <i>bt</i> taxon is observed as singleton       | Variable                 | Variable                 | Yes          | 24a, 25a, 26, 31d         |

\* Lines in lists of equations refer to numbered lines in this table.

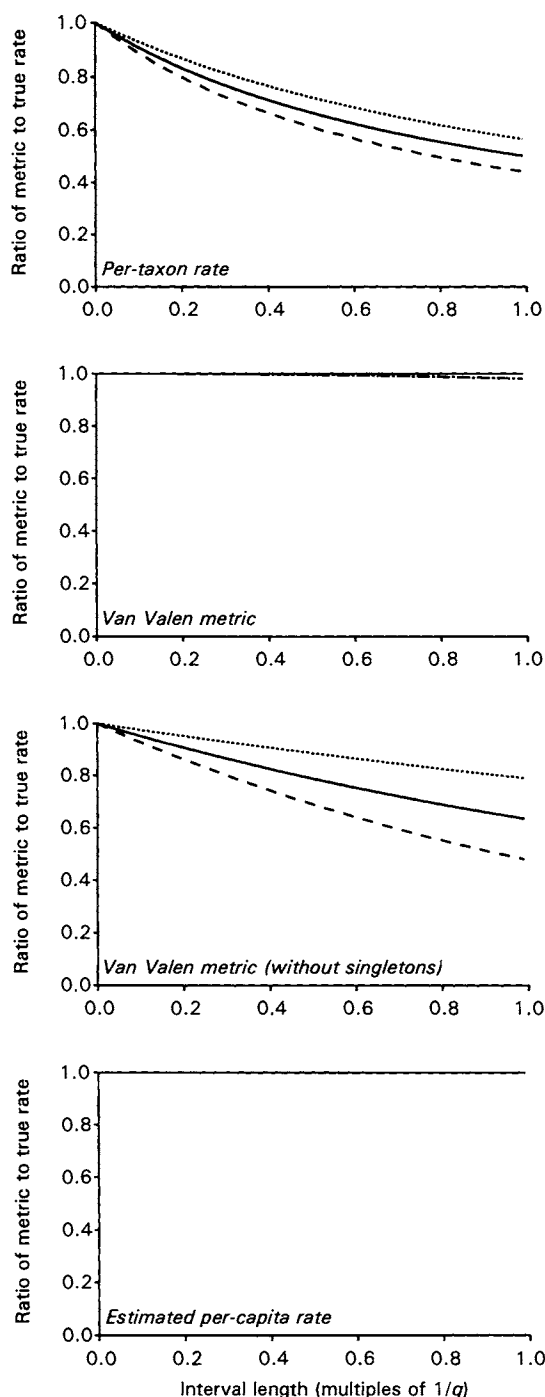


FIGURE 3. Effect of interval length on extinction metrics with time-homogeneous rates and complete record. Similar effects result for origination metrics. See Figure 2 for explanation. Dotted and dashed lines coincide for the Van Valen metric. The per-capita rate estimated from numbers of boundary crossers is independent of interval length. This is also the only metric for which origination rate does not affect the estimation of extinction rate and vice versa.

diversity when  $p \neq q$ . The Van Valen metric therefore underestimates true rates more as  $\Delta t$  increases (Fig. 3), although the error is relatively small if  $p$  and  $q$  are not very different. Recognizing potential problems with singletons, Harper (1996) suggested a variation on Van Valen's metric in which singletons are omitted. As interval length increases, more of the extinctions and originations are singletons. Discarding them completely therefore leads to an underestimate of taxonomic rates that becomes worse as the interval length increases (Fig. 3).

The estimates of per-capita rates advocated here,  $\hat{p}$  and  $\hat{q}$ , are unaffected by interval length.  $N_{bt}/N_b$  gives the proportion of lineages extant at the start of the interval that survive to the end, and  $N_{bt}/N_t$  gives the proportion of lineages extant at the end that were already extant at the start. These ratios decay exponentially with time if rates are constant within the interval; thus the logarithm of each ratio declines linearly with time. The magnitude of the slope of this decline is exactly equal to the extinction rate in the first case and the origination rate in the second case. In fact, even if rates are not constant,  $\hat{p}$  and  $\hat{q}$  provide unbiased estimates of the mean rate within an interval (Appendix, section 2).

Alroy (1996b) independently proposed rate metrics similar to Van Valen's and Harper's, normalizing by  $N_b$  rather than  $(N_b + N_t)/2$ . When  $p = q$ , Alroy's metrics are expected to be identical to those of Van Valen and Harper (since  $N_b = N_t$  in this case). Moreover, if  $p = q$ , if  $p\Delta t$  and  $q\Delta t$  are relatively low, and if singletons are ignored, Alroy's metric and Van Valen's metric are approximately equal to  $\hat{p}$  and  $\hat{q}$  (see Appendix, section 2, and Alroy et al. 2000).

In some cases, for example those involving deep-sea microfossils or Neogene macroinvertebrates, temporal resolution may be sufficiently fine that equal-length intervals can be established relatively easily (Wei and Kennett 1983, 1986; Pearson 1992, 1996; Budd et al. 1994; Budd and Johnson 1999). Alroy (1992, 1996b, 1998, 1999) has developed an alternative approach to circumventing the problem of unequal interval lengths. Using an exhaustive compilation of faunal lists, he has ordi-

nated first and last appearance data of North American Cenozoic mammals and has used this ordination to interpolate between well-constrained absolute ages. This has allowed an arbitrarily fine, equal-interval temporal grid to be superimposed on the data. Although Alroy's approach is labor-intensive, it holds great promise for avoiding problems associated with uneven and uncertain interval lengths.

In general, the only measures of diversity and taxonomic rates that are expected to be independent of interval length are those based exclusively on boundary crossers. This suggests that, if interval length varies substantially, it is a good idea to measure diversity as  $N_b$  or  $N_i$  and to measure taxonomic rates as  $\hat{p}$  and  $\hat{q}$ . It is nevertheless often the case empirically that there is ample true variation in diversity and rates, with the result that most of the apparent variation in rates is not attributable to variation in interval length (Raup 1986; Gingerich 1987; Collins 1989; Foote 1994; Patzkowsky and Holland 1997).

### Effects of Rates on Rate Estimation

For certain rate metrics, true rates of taxonomic evolution affect our ability to estimate rates in two principal ways, concerning the magnitude of rates and the difference between origination and extinction rates.

Because an increase in taxonomic rates has the same effect as an increase in interval length, the per-taxon rate and the Van Valen metric, with or without singletons, become less accurate as taxonomic rates increase. The only exception to this is that the Van Valen metric is insensitive to interval length and taxonomic rates if  $p = q$  and if singletons are included.

The greater the difference between  $p$  and  $q$ , the greater the discrepancy between the true taxonomic rates and the estimates given by the per-taxon rate and the Van Valen metric, with or without singletons (Fig. 3). This is largely because of the increasing discrepancy between an exponential diversity change within an interval and the linear change implicit in the normalization by  $(N_b + N_i)/2$ . The per-taxon rate and the singleton-free Van Valen metric exhibit a more serious problem. Suppose that extinction rate is held fixed. As origina-

tion rate increases (from the dotted to the solid to the dashed lines in Fig. 3), the estimate of extinction rate decreases when either of these rate metrics is used. (Likewise, if origination rate is constant and extinction rate changes, the estimate of origination rate changes in the opposite direction.) The reason the per-taxon rate behaves this way can be seen by inspecting equations (8a) and (9a) in the Appendix, which give the numerator and denominator of the rate metric. The normalization makes sense only if  $p \approx q$ . The reason for the bias in the singleton-free Van Valen metric is different. Equation (21) shows that this metric approximates the extinction rate only when  $p \approx q$  and when both rates are low. With these two rate metrics, true variation in rates will therefore contribute to a spurious negative correlation between origination and extinction. This will complicate the independent measurement of origination and extinction rates.

In contrast to the other rate metrics,  $\hat{p}$  is unaffected by extinction rate, while  $\hat{q}$  is unaffected by origination rate. This makes  $\hat{p}$  and  $\hat{q}$  especially useful if one desires independent estimates of origination and extinction rates.

### Incomplete Preservation

Preservation can be modeled in a number of realistic ways that include variation in time and space (Shaw 1964; Koch and Morgan 1988; Marshall 1994; Holland 1995; Holland and Patzkowsky 1999; Weiss and Marshall 1999). As a heuristic tool for understanding the behavior of diversity and rate measures, it is convenient to focus on the temporal aspect and to start by assuming time-homogeneous fossil preservation at a constant per-capita rate  $r$  per Lmy (Paul 1982, 1988; Pease 1985; Strauss and Sadler 1989; Marshall 1990; Foote and Raup 1996; Solow and Smith 1997; Foote 1997). This simple assumption will be relaxed below. In the time-homogeneous case, the proportion of lineages preserved is equal to  $r/(q + r)$  if  $p = q$  and if the fossil record is of effectively infinite length (Pease 1985; Solow and Smith 1997) (see Edge Effects, below). It is therefore natural for many problems to express preservation rate as a multiple of  $q$ . Throughout this discussion I will assume tax-



onomic homogeneity of taxonomic and preservational rates. For modeling, this assumption can easily be relaxed by performing calculations for an arbitrary number of rate classes and combining the results (see Buzas et al. 1982, Koch and Morgan 1988, Holland 1995, Holland and Patzkowsky 1999, and Weiss and Marshall 1999 for explicit treatments of taxonomic heterogeneity of preservation).

As preservation rate decreases, there is a regular decrease in observed numbers in nearly all categories of taxa within an interval. The sole exception is singletons, whose behavior is especially problematic. This is shown in Figure 4, which portrays the observed number of taxa relative to the true number. As preservation rate decreases, singletons constitute an ever greater proportion of observed taxa. For a certain range of values of preservation rate and interval length, the observed number of singletons is not only relatively high but also absolutely greater than the true number. In general, the observed excess of singletons causes the per-taxon rate and the Van Valen metric to increase as preservation rate decreases (Fig. 5). Because all categories of boundary crossers are diminished in the same proportion by incomplete, time-homogeneous preservation, however,  $\hat{p}$ ,  $\hat{q}$ , and the Van Valen metric without singletons are unaffected by incomplete preservation, as are other metrics based only on boundary crossers (Alroy 1996b). This result is related to the fact that the observed age distribution of taxa, exclusive of singletons, is expected to be identical to the true age distribution (Foote and Raup 1996; Foote 1997; Solow and Smith 1997). Without independent estimates of preservation rate, it may be difficult to distinguish a truly high number of singletons (reflecting high taxonomic rates) from a preservational artifact.

I have been unable to develop a measure of absolute diversity that is insensitive to incomplete preservation. It is nevertheless possible to estimate changes in diversity accurately if we accept the point that a proportional or logarithmic scale is a natural one with which to measure diversity (Sepkoski 1991). The quantity  $\ln(N_i/N_b)$  gives the proportional change in diversity through an interval, i.e., the fundamental growth rate ( $p - q$ ) times the inter-

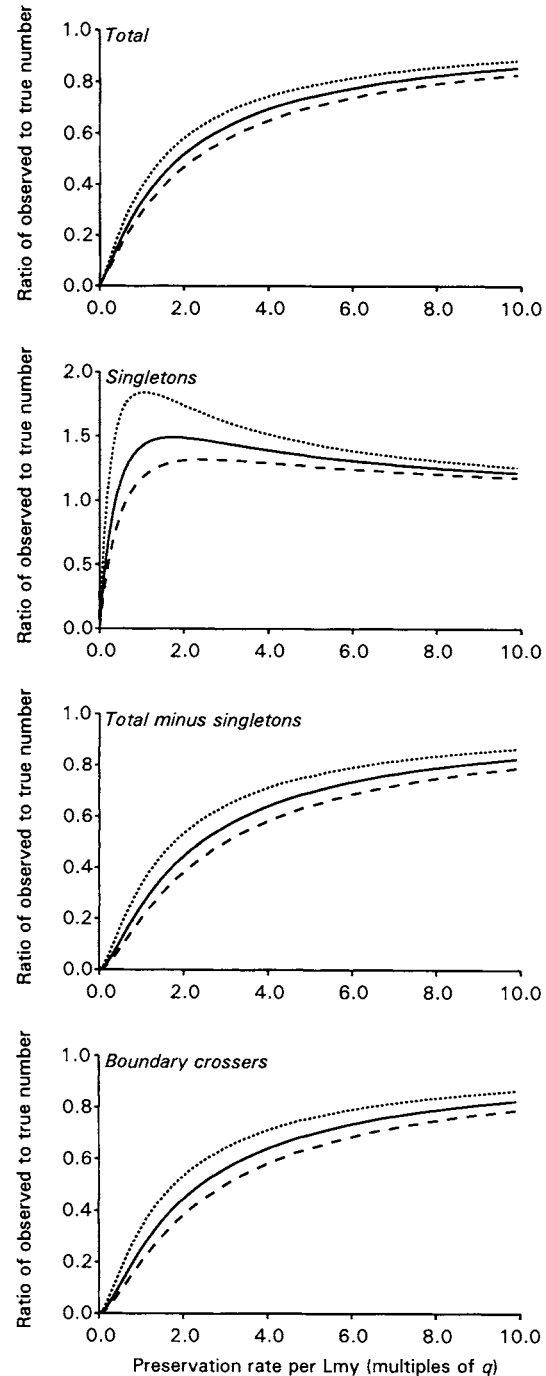


FIGURE 4. Effect of preservation rate on observed numbers of taxa within an interval. Preservation is time-homogeneous and there are no edge effects. Interval length is fixed at  $0.5/q$ , and preservation rate  $r$  is expressed as multiples of extinction rate  $q$ . Solid, dashed, and dotted lines are as in Figure 2. Most categories of observed taxa increase monotonically with preservation rate, but the number of observed singletons is disproportionately large when preservation rate is low.

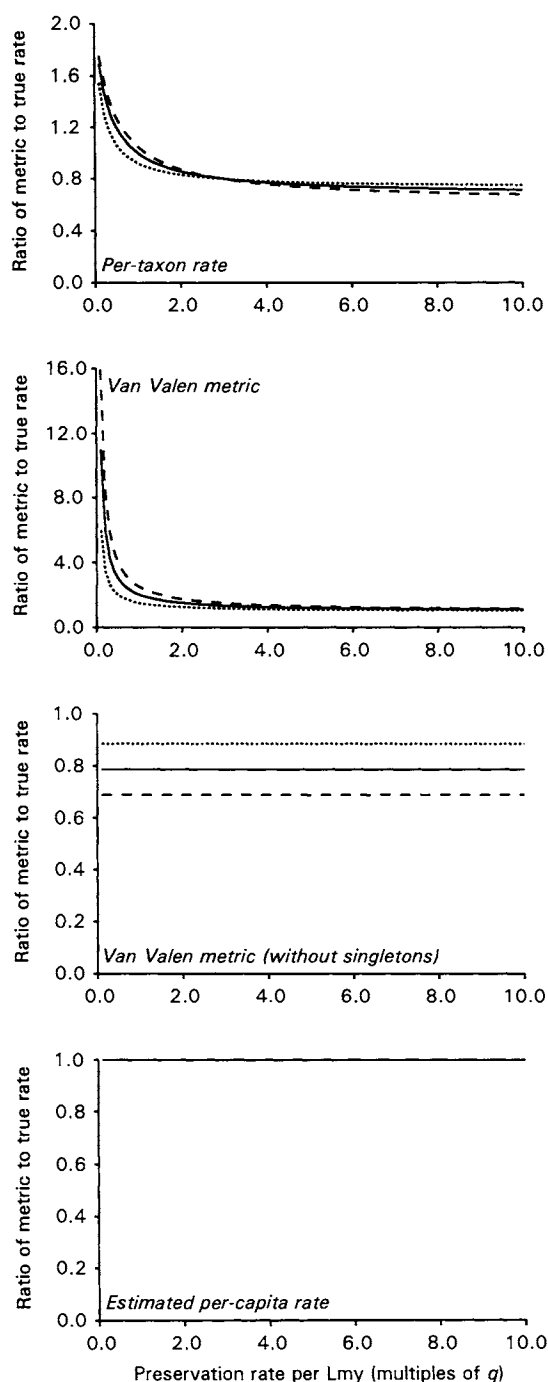


FIGURE 5. Effects of preservation rate on extinction metrics. Similar effects obtain for origination metrics. See Figure 4 for explanation. Because of the inclusion of singletons, the per-taxon rate and the Van Valen metric are strongly influenced by preservation. If singletons are excluded, the Van Valen metric is independent of preservation rate, but it is sensitive to the difference between origination and extinction rates.

val length  $\Delta t$ . In the time-homogeneous case, this quantity is unaffected by incomplete preservation.

If one has estimates of preservation rate and is interested in true levels of diversity, then it is a relatively straightforward matter to adjust observed numbers of boundary crossers in the time-homogeneous case: the true number is equal to the observed number times  $[(p + r)(q + r)]/r^2$  (see Appendix, section 5). The case of variable rates is more realistic, however. How to adjust diversity measures in the face of variable preservation remains an important problem. Rarefaction and other approaches involving standardized resampling and subsampling of data have been used extensively (Hessler and Sanders 1967; Sanders 1968; Jackson et al. 1993; Rex et al. 1993, 1997; Raymond and Metz 1995; Alroy 1996a,b, 1998, 1999; Miller and Foote 1996; Markwick 1998; Marshall et al. 1999), as have methods that rely on an estimated phylogeny to identify and fill gaps (Norell 1992; Benton 1994; Johnson 1998). The relative performance of these various approaches under different conditions still needs further exploration.

In summary, many effects of incompleteness can be overcome in the case of time-homogeneous preservation if taxonomic rates and changes in diversity are measured on the basis of relative numbers of boundary crossers.

### Edge Effects

The fossil record as a whole, or any part of it we investigate, has a discrete beginning and end. During any interval of measurement, whether coarse or fine, the presence of a taxon can be inferred because the taxon is actually preserved during the interval or because it is preserved before and after the interval; this is the standard range-through approach. As the interval in question falls toward either edge of the record, our ability to infer the presence of taxa by the range-through method diminishes. This creates a series of related edge effects (Figs. 6, 7). Apparent diversity declines. The number of first appearances is high toward the lower edge (as taxa that truly extend below the beginning of the record make their first appearance) and the number of last appearances is high toward the top. The number of

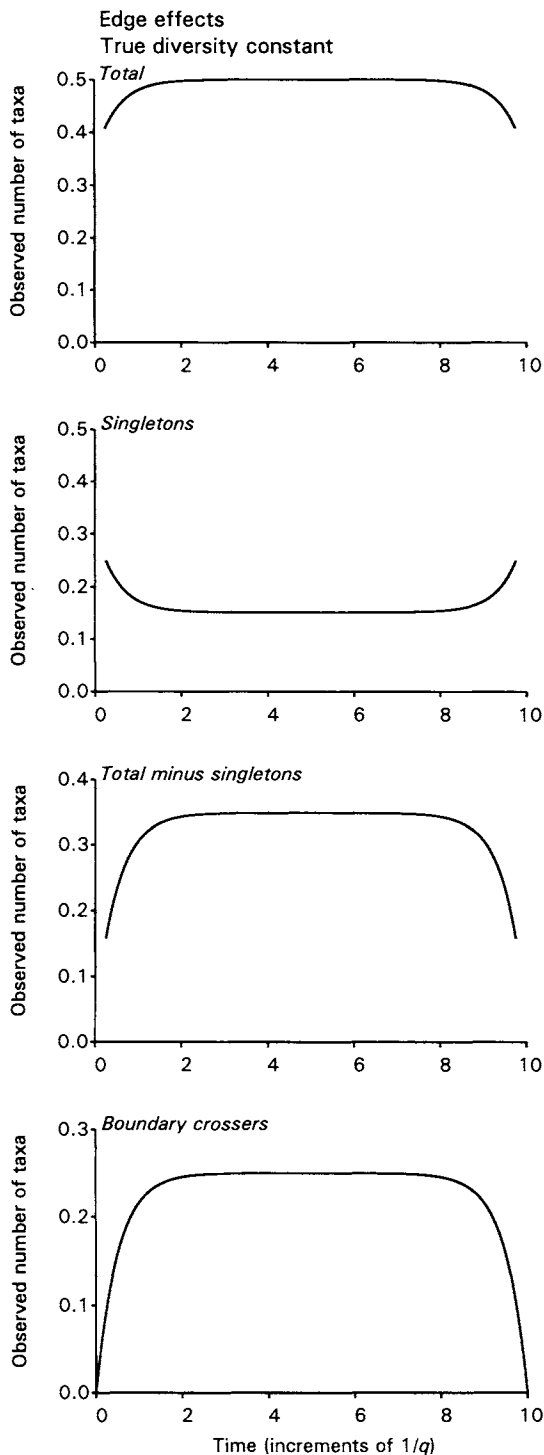


FIGURE 6. Edge effects on taxonomic diversity. Figure shows number of observed taxa in relation to distance of the interval from beginning or end of fossil record. In all cases  $p = q$ ,  $r = q$ , and interval length is equal to  $0.5/q$ . The height of curves depends on the value of  $r$ . The effect decays exponentially and the distance from the edge at which the curves level off is a function of the taxonomic rates (see text for further explanation).

singletons increases, as taxa that would have been observed to cross a boundary are now less likely to be found before the interval (near the lower edge) or after the interval (near the upper edge). The singletons contribute heavily to counts of origination and extinction. As a result of these edge effects, the per-taxon rate and the Van Valen metric with singletons are inflated toward the edges. Note that estimates of both origination and extinction rate for these metrics are inflated near both edges.

The increase in first and last appearances relative to total numbers also means that  $\hat{p}$  and the Van Valen origination metric without singletons are inflated toward the beginning of the record, while the corresponding extinction metrics are inflated toward the end. Note that the total number of last appearances is low near the beginning of the record and that the apparent change in standing diversity (the difference between  $X_i$  and  $X_b$ ) can be substantial within a single interval near an edge. Because the Van Valen metric without singletons compares a reduced number of events to an estimate of average standing diversity that is changing substantially near the edges, the extinction metric is also depressed near the beginning of the record while the origination metric is also depressed near the end. In contrast to the three other metrics,  $\hat{p}$  and  $\hat{q}$  are affected only toward the beginning or end of the record, respectively.

Edge effects are significant only to the extent that a taxon extant at some point in time is likely to intersect either edge. At a distance  $t$  from the bottom edge, the edge is no longer felt when  $e^{-qt}$  is acceptably small; near the top edge, the relevant quantity is  $e^{-pt}$ . For example, suppose  $p = q$  and the interval is placed near the bottom edge. If the interval is separated from the edge by 2.3 times the mean taxon duration ( $2.3/q$ ), then  $e^{-qt}$  is about 0.10, and  $\hat{p}$ ,  $\hat{q}$ ,  $X_{FL}$ ,  $X_{bL}$ ,  $X_{FL}$ ,  $X_{bL}$ ,  $X_{FL}$ , and  $X_{bL}$  are within about 1% of the values they would have in the absence of edge effects. Practically speaking, then, an edge is no longer felt within about two or so average taxon lengths.

I have presented edge effects that result from incomplete preservation within the window of observation as if they were created only by the termination of the fossil record at

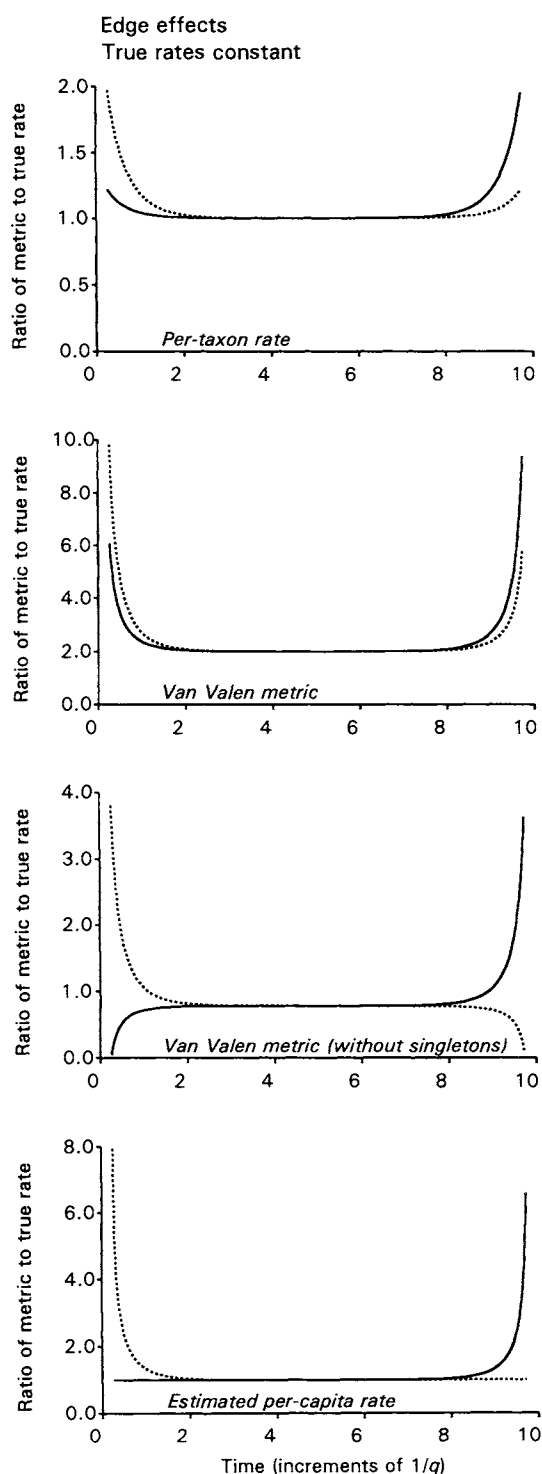


FIGURE 7. Edge effects on taxonomic rate metrics. In all cases  $p = q$ ,  $r = q$ , and interval length is equal to  $0.5/q$ . Solid line, extinction metric; dotted line, origination metric. All rate metrics except estimated per-capita rate are affected at both edges.

either end. Qualitatively different but mathematically identical edge effects are also created by sudden drops in preservation rate (Holland 1995) and by major changes in evolutionary rates such as mass extinctions and evolutionary radiations (Signor and Lipps 1982). Gilinsky and Bambach (1987) discuss an edge effect that results from the definition of certain rate metrics even if preservation is complete; proportional origination and extinction (number of events divided by total diversity) must be unity in the first and last intervals, respectively. Similarly,  $\hat{p}$  and  $\hat{q}$  are undefined in the first and last intervals.

A different kind of edge effect is created by a singular increase in preservation rate. This is obviously relevant to the effects of Recent taxa on patterns of diversity and taxonomic rates (Raup 1972, 1979; Pease 1988a,b, 1992). Because the Recent fauna of skeletonized marine animals is very well known, taxa that lack a late Cenozoic fossil record can have their ranges pulled forward, with the result that apparent diversity is likely to be inflated toward the Recent and apparent extinction rate is likely to decline (Figs. 8, 9). Whether apparent origination rate increases, decreases, or is unaffected depends on which rate metric is used (Fig. 9).

For fossil marine animal genera, a substantial number of taxa extend from the Recent back into the early to mid Tertiary. It is thus conceivable that the rise in diversity and decline in background rates seen during the Phanerozoic (Raup and Sepkoski 1982; Van Valen 1984; Sepkoski 1996, 1997, 1998) are partly artificial (Raup 1972; Pease 1985, 1988a,b, 1992). As Sepkoski (1997) showed, however, the increase in genus diversity, measured as total non-singleton genera in an interval, persists even when Recent genera are included only if they are known to have a Pliocene-Pleistocene fossil record. Figure 10 shows the same result for boundary-crossing diversity. (For the sake of completeness, Figures 10 and 11 also show the effect of removing all genera that extend to the Recent, a culling that is unreasonably extreme since many of these genera have a fossil record near the Recent.) The decline in extinction rate is seen in both the Paleozoic and post-Paleozoic even when Re-

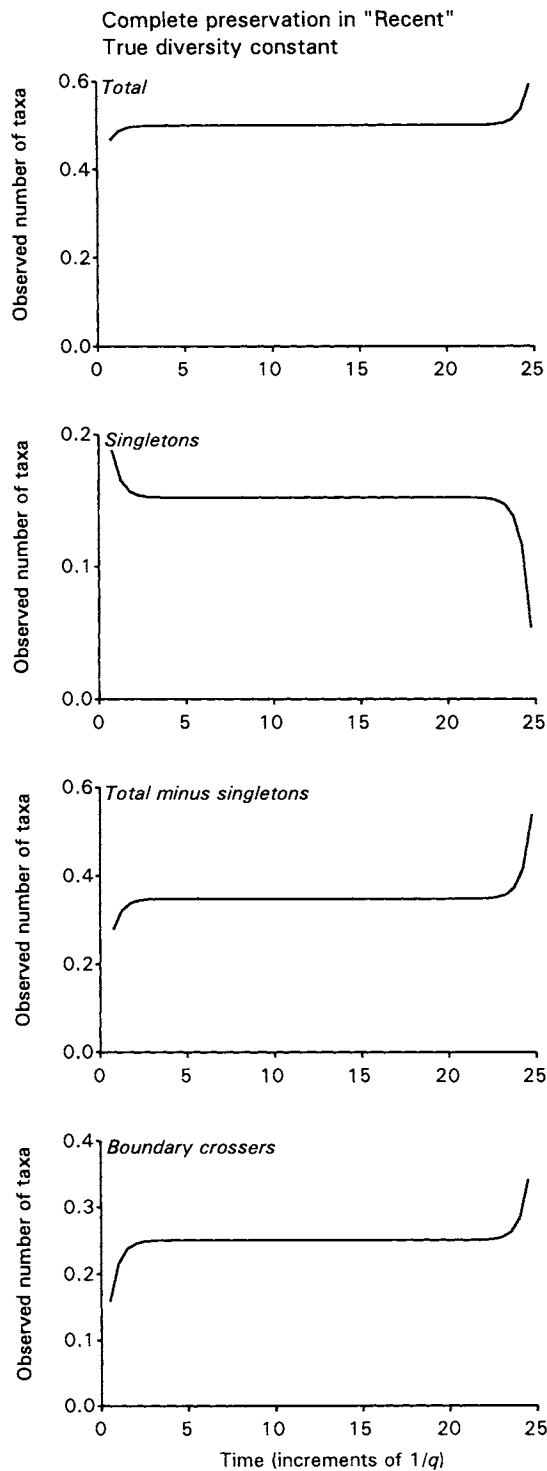


FIGURE 8. Effects of complete preservation at end of fossil record on observed numbers of taxa. Interval length is equal to  $0.5/q$ ,  $p = q$ , and  $r = q$ . As with other edge effects, the edge is no longer relevant beyond about two taxon lengths.

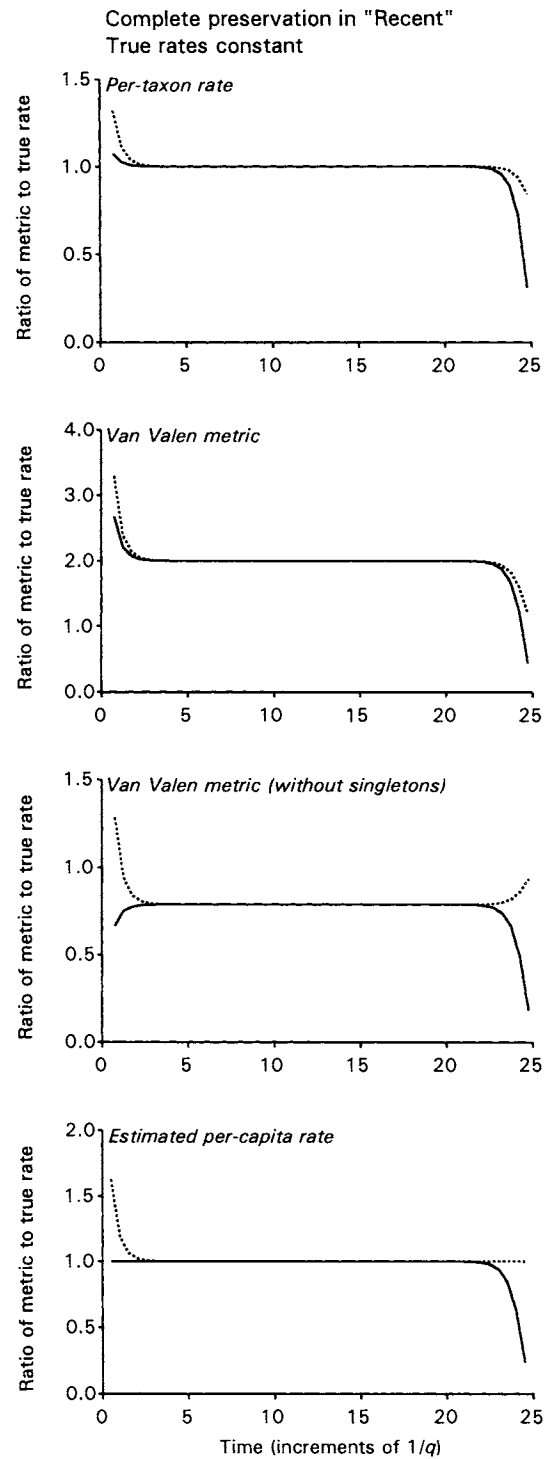


FIGURE 9. Effects of complete preservation at end of fossil record on taxonomic rate metrics. See Figure 8 for explanation. Solid line, extinction metric; dotted line, origination metric.

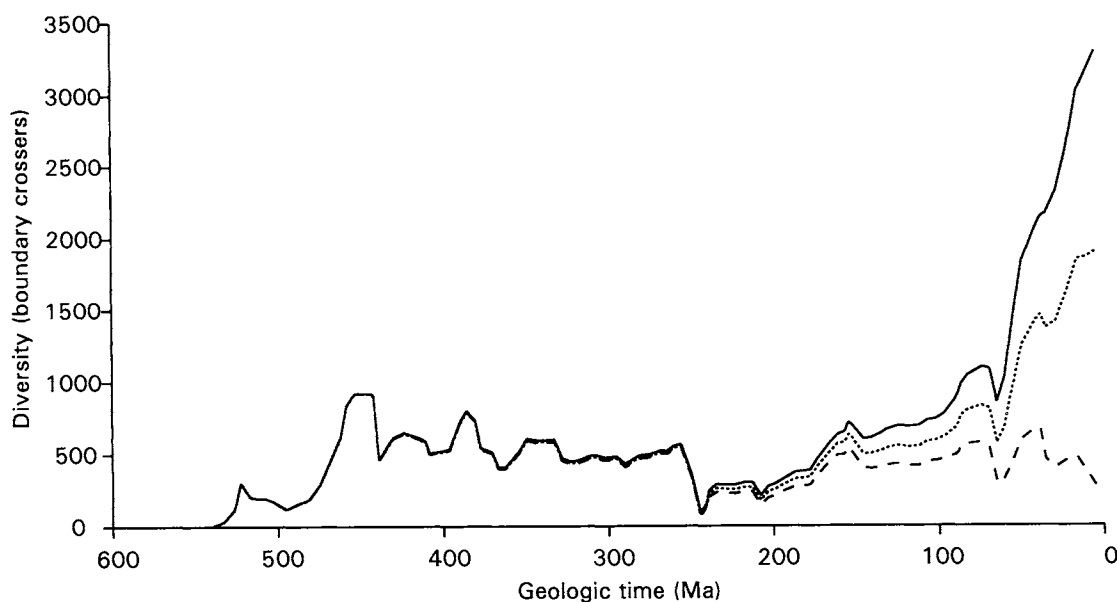


FIGURE 10. Genus diversity through the Phanerozoic. Data are from Sepkoski's unpublished compendium (Sepkoski 1996). Diversity curves show number of boundary crossers based on 25,049 fossil genera whose first and last appearances are fully resolved to one of 107 stratigraphic intervals of about 5.1 m.y. average duration (Foote and Sepkoski 1999; ages based mainly on Harland et al. 1990, Tucker and McKerrow 1995, and Bowring and Erwin 1998). Solid curve, all fossil genera included. Dashed curve, 3759 fossil genera still extant today are excluded. This is an overly extreme culling, since many extant genera do in fact have a fossil record near the Recent. Dotted curve, 1630 extant genera that are known to have a Plio-Pleistocene fossil record are included (Sepkoski 1997). Dotted curve is an absolute minimum, since it is unknown to what extent Sepkoski had documented Plio-Pleistocene occurrences. Curves have similar shapes except for the Tertiary portions. The Cenozoic rise in diversity may be exaggerated by nearly complete knowledge of the Recent fauna, but it is unlikely to be a complete artifact of this bias. Similar results hold for total diversity (Sepkoski 1997).

cent genera lacking a Plio-Pleistocene record are omitted (Fig. 11). Moreover, the decline in origination rate is seen, at least in the Paleozoic, with  $\hat{p}$ , a metric that is not expected to feel the upper edge of the fossil record (Fig. 11), and with the singleton-free Van Valen metric (data not presented), which is expected to increase as a result of essentially complete preservation in the Recent. The early Paleozoic decline in origination rate may be exaggerated by the left-hand edge effect, but the decline continues far beyond the point where this edge has a substantial influence. These results suggest that the Cenozoic increase in diversity and the Phanerozoic decline in taxonomic rates seen in marine animals are not artifacts of our relatively complete knowledge of the Recent fauna.

#### Temporal Variation in Taxonomic Rates

Consider the effect of an increase in extinction rate that lasts for one stratigraphic inter-

val (Fig. 12). (An increase in origination rate yields converse results.) Because of incomplete preservation, the last appearances are smeared back in time (Signor and Lipps 1982; Raup 1989; Meldahl 1990; Koch 1991; Stanley and Yang 1994; Rampino and Adler 1998). The estimate of extinction rate in the interval is therefore lower than it should be, while it is higher than it should be in earlier intervals. As discussed above, changes in one rate affect estimates of both rates with the per-taxon metric, the Van Valen metric, and the singleton-free Van Valen metric. Incompleteness and the correlation of rate estimates combine to produce complicated signals in apparent origination and extinction rates even if only one rate varies. With  $\hat{p}$  and  $\hat{q}$ , however, a change in one rate leaves the estimate of the other unaffected, even in the case of incomplete but homogeneous preservation. This property, lacking in other rate metrics, should lead us to favor  $\hat{p}$  and  $\hat{q}$ , especially in cases where inde-

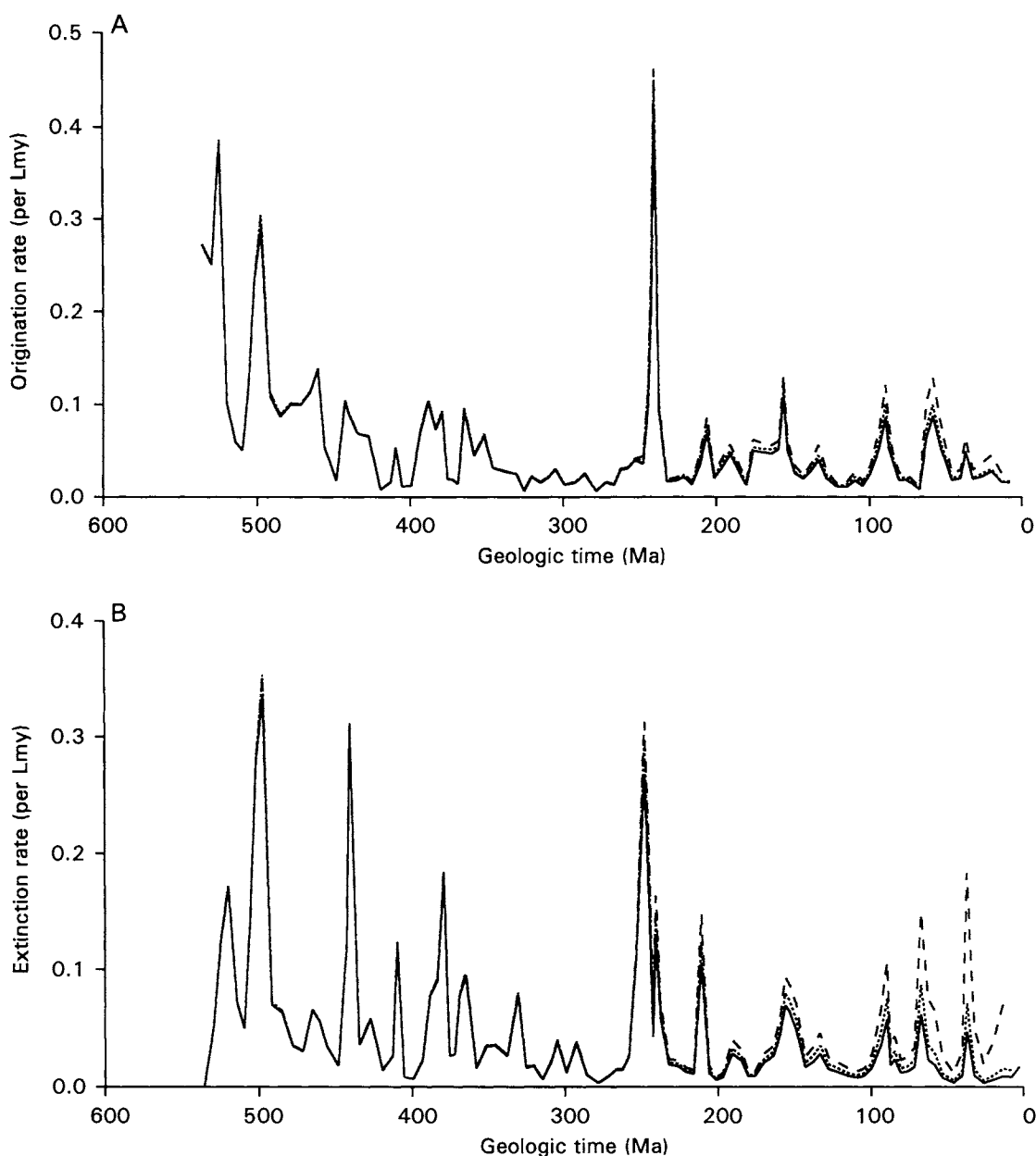


FIGURE 11. Per-capita origination rate (A) and extinction rate (B) for genus data portrayed in Figure 10. Solid, dashed, and dotted curves as in Figure 10. Complete culling of extant taxa yields extinction rates that rise toward the Recent (exhibiting the edge effect of Figure 7), but this culling is unreasonably extreme (see Fig. 10). The similarity of solid and dotted curves suggests that the Phanerozoic decline in rates is not a consequence of nearly complete knowledge of the living fauna.

pendent estimates of origination and extinction are desired.

#### Temporal Variation in Rate of Preservation

If preservation rate increases or decreases gradually over time while taxonomic rates re-

main constant, the number of singletons will gradually change in the opposite direction. Thus, the per-taxon rate and the Van Valen metric will show spurious secular changes (Fig. 13). Partly for this reason, Pease (1988a,b, 1992) argued that the Phanerozoic decline in

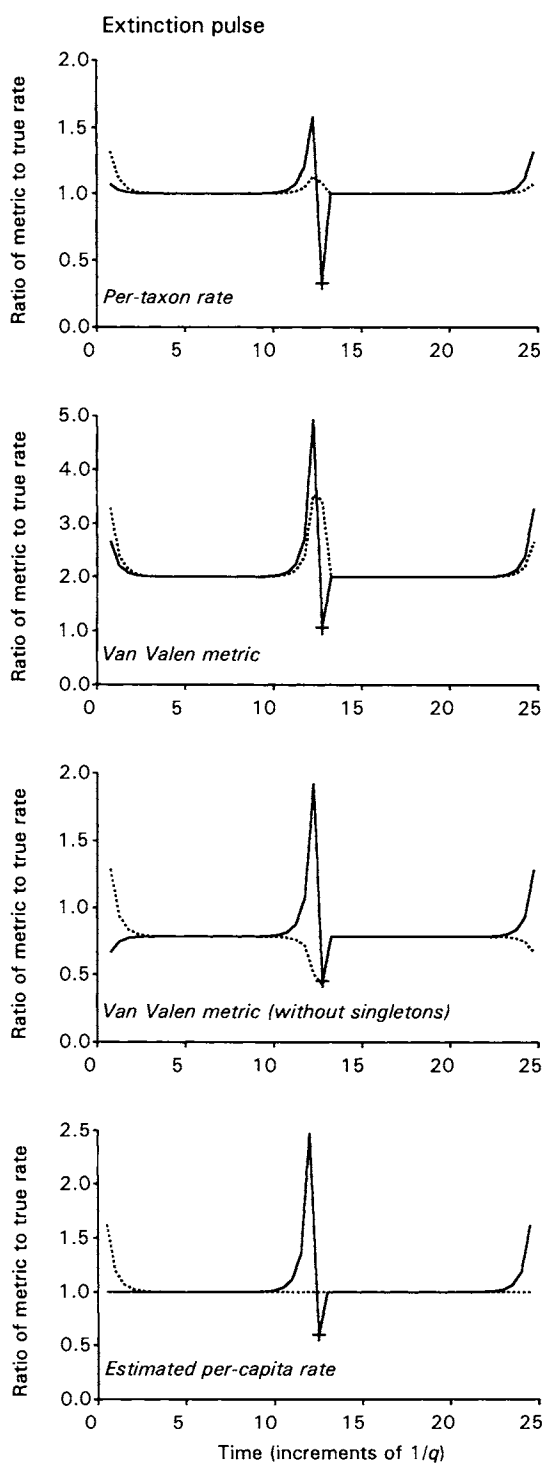


FIGURE 12. Effect of short-lived increase in extinction rate on taxonomic rate metrics. Solid line, extinction metric; dotted line, origination metric. Extinction rate  $q$  is constant except for a fivefold increase that lasts for one interval (indicated by the cross). Interval length is equal to  $0.5/q$ , and  $r = p = q$ . Because the record is incomplete, extinction rate appears lower than it should

taxonomic rates may be an artifact of increasing completeness of the fossil record. If the change in preservation rate is smooth, however, then top- and bottom-boundary crossers will not experience significantly different preservational histories. Thus, rate metrics based on boundary crossers should barely be affected by long-term secular changes in preservation rate. The fact that the Phanerozoic decline in rates is seen in the singleton-free Van Valen metric and in  $\hat{p}$  and  $\hat{q}$  (Fig. 11) suggests that this decline is not an artifact of a secular increase in the quality of the fossil record. Holman (1985) also argued that the decline in rates is real, since the frequency of gaps, estimated from the stratigraphic ranges of lower-level taxa within the ranges of the higher taxa containing them, does not show an obvious decrease through the Phanerozoic.

Figures 14 and 15 illustrate the more complicated effects of a sudden increase in preservation rate. (A sudden decrease has converse effects.) All categories of taxa of course increase. Top- and bottom-boundary crossers are affected equally only if origination and extinction rates are equal. When diversity is truly increasing, the magnitude of the increase is exaggerated, and conversely when diversity is decreasing (Appendix, section 5). Taxa that would have been singletons in adjacent intervals had preservation been homogeneous now extend into the interval in question; the number of singletons in adjacent intervals therefore declines. The number of first and last appearances increases with the increase in preservation rate, so that both the origination and extinction rates appear to increase. In preceding intervals, the number of taxa that would have made their last appearance is reduced because they now appear last in the interval with better preservation. The same is true of

in the interval of the extinction spike, and the extra extinctions are spread backward in time. With all metrics except estimated per-capita rate, the estimate of origination rate is also affected (see Fig. 3). As with related edge effects (Fig. 7), the effect of a transient rate pulse decays exponentially until it is no longer detectable after about two taxon lengths. A transient increase in origination rate has converse effects, which propagate in the opposite direction in time.



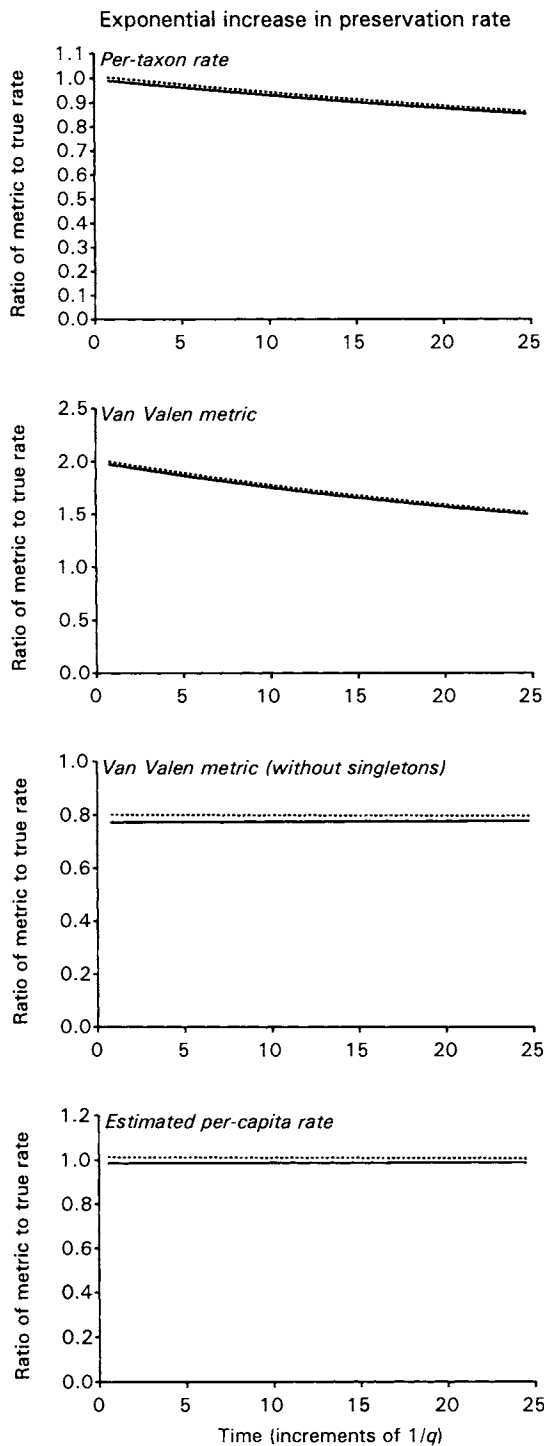


FIGURE 13. Effect of secular trend in preservation rate on taxonomic rate metrics. Interval length is equal to  $0.5/q$ , and  $p = q$ . Dotted line, origination; solid line, extinction. Preservation rate increases exponentially from  $q$  to  $2q$ . There are no edge effects. Results for linear change in preservation rate are similar. Metrics that disregard singletons are barely affected by a smooth change in preservation rate.

first appearances in succeeding intervals. As a result, all metrics underestimate extinction rate before the interval of increased preservation and underestimate origination rate afterwards. In addition, the per-taxon rate and the Van Valen metric underestimate origination beforehand, while they underestimate extinction afterwards. This is because they include singletons in the origination and extinction counts. The singleton-free Van Valen metric overestimates origination before the pulse in preservation and overestimates extinction afterwards. A strength of the proposed estimates of per-capita rates is that  $\hat{p}$  is affected only during and after the interval of unusually high (or low) preservation, and  $\hat{q}$  is affected only during and before this interval.

It is often observed that certain intervals of time appear to have unusually high rates of both origination and extinction (Allmon et al. 1993). Because apparent rates increase when preservation increases, abrupt variation in preservation rates can induce a spurious positive correlation between origination and extinction metrics even if the two rates are in fact independent. This effect is especially strong for the per-taxon rate and the Van Valen metric, since both rates also apparently decrease before and after an interval with better preservation. The effect is quite evident empirically as well. Mark and Flessa (1977) and Alroy (1996b, 1998) showed that apparent origination and extinction rates are less strongly correlated if singletons are removed. For Phanerozoic marine animal genera, the per-taxon rate and the Van Valen metric tend to show higher correlations than do the singleton-free Van Valen metric and  $\hat{p}$  and  $\hat{q}$  (Table 3). The correlations tend to be lowest for the singleton-free Van Valen metric, but this may partly reflect the fact that true, independent variation in origination and extinction rates tends to yield a spurious negative correlation between the apparent rates with this metric (Fig. 3).

More generally, variation in preservation rate can artificially create patterns that resemble true temporal variation in origination and extinction rates. This is a fundamental problem that has long plagued paleontology. The extreme case of Lagerstätten is relatively easy

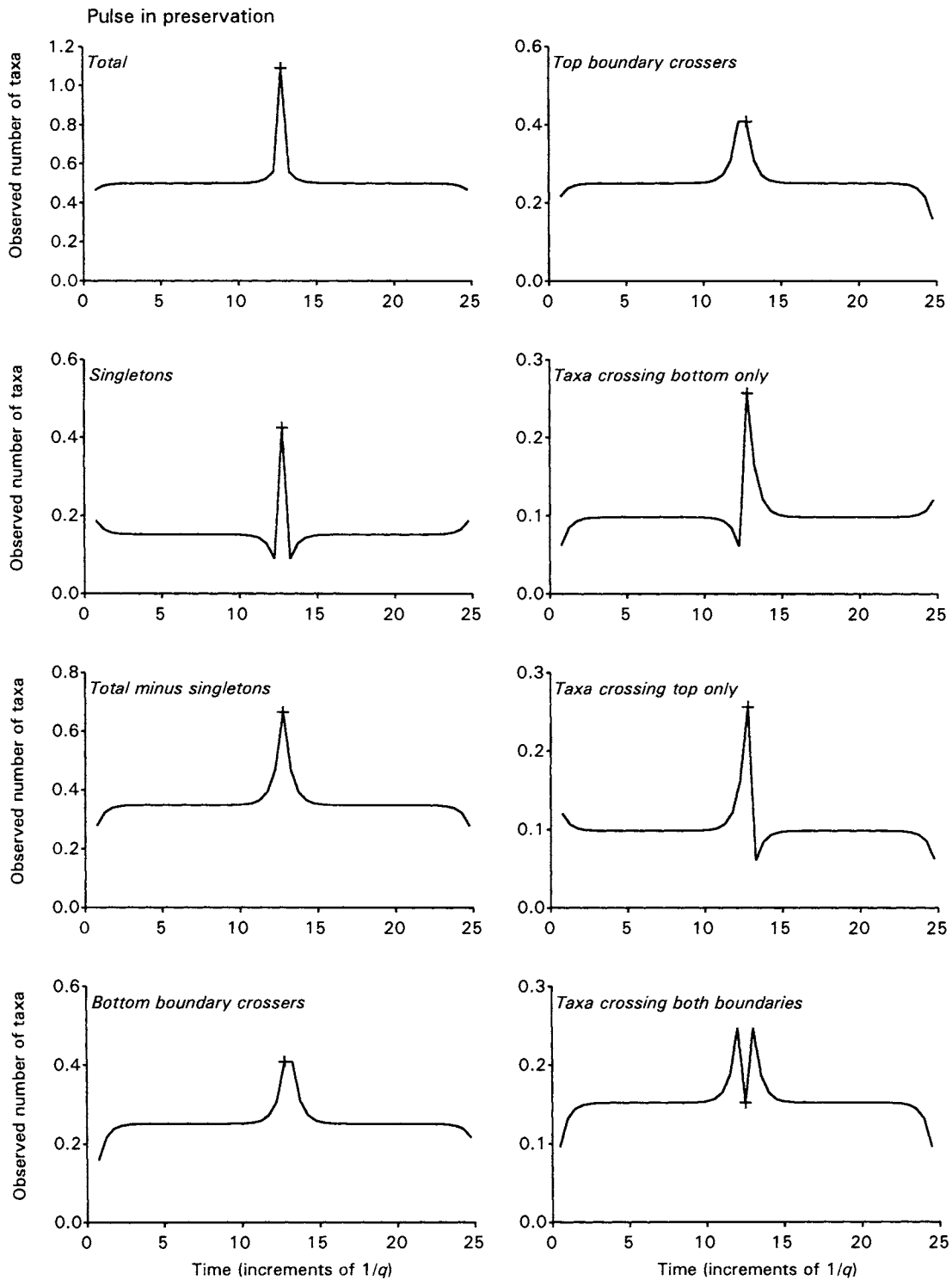


FIGURE 14. Effect of short-lived increase in preservation rate on number of observed taxa. Preservation rate  $r$  is constant except for a fivefold increase that lasts for one interval (indicated by the cross). Interval length is equal to  $0.5/q$ , and  $r = p = q$ . Transient decrease in preservation rate has opposite effects.

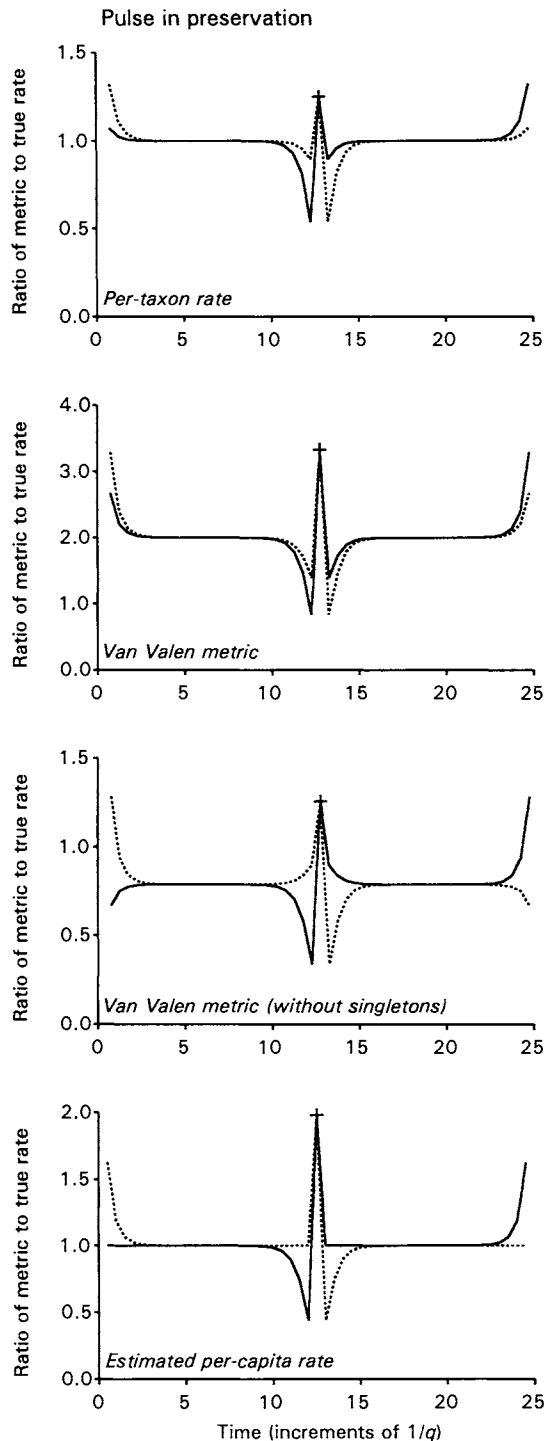


FIGURE 15. Effect of short-lived increase in preservation rate on taxonomic rate metrics. Solid line, extinction metric; dotted line, origination metric. Preservation rate  $r$  is constant except for a fivefold increase that lasts for one interval (indicated by the cross). Interval length is equal to  $0.5/q$  and  $r = p = q$ . All metrics increase artificially as a result of spike in preservation. Because singletons are depressed on both sides of the preservation-

to identify, but more subtle variation in preservation rate is likely to be less obvious.

### Distinguishing Variation in Taxonomic Rates from Variation in Rates of Preservation

To what extent is apparent variation in origination and extinction rates real, and to what extent is it an artifact of variation in preservation rate? This question must be addressed case by case (Koch and Morgan 1988; Koch 1991; Alroy 1996b). I will offer two arguments, suggestive but certainly not conclusive, that there is a real signal of variation in taxonomic rates for marine animal genera as a whole. First, if the apparent variation in taxonomic rates were an artifact of variable preservation, groups with lower preservation potential should have more apparent variation in taxonomic rates. This is because the effect of changes in preservation rate is greater when preservation rate on average is lower (Appendix, section 3). There are diminishing returns, such that an increment in preservation rate has a substantial effect if the record is poor but a negligible effect if the record is good. Figure 16 compares the estimated probability of preservation per genus per stratigraphic interval, measured as the *FreqRat* (Foote and Raup 1996; Wagner 1997; Cheetham and Jackson 1998; Foote and Sepkoski 1999), with the variability in taxonomic rates, measured as the median absolute difference in log rate between adjacent stratigraphic intervals, for a number of higher taxa of animals. The data are those used in Figures 10 and 11. Contrary to the expectations of the artifact hypothesis, the correlations between preservability and rate variability are in fact positive (though not significantly so). Clearly, overall quality of preservation is not a good predictor of apparent variation in taxonomic rates.

←

al spike (Fig. 14), rate metrics that include singletons are depressed on both sides of the spike. Note that with the estimated per-capita rate, apparent origination is affected only during and after the preservational spike, while extinction is affected only before and during the spike. With other metrics, both rates are affected in both directions. Transient decrease in preservation rate has opposite effects.

TABLE 3. Correlation between change in origination metric and change in extinction metric for Phanerozoic marine animal genera (unpublished data from Sepkoski; see Sepkoski 1996, 1997, and Figs. 10 and 11 of this paper). First differences are used in order to detrend the data. Correlation coefficient is Kendall's  $\tau$ .

| Metric                                                | Correlation |
|-------------------------------------------------------|-------------|
| Per-taxon rate                                        | 0.599       |
| Van Valen metric                                      | 0.669       |
| Van Valen metric (without singletons)                 | 0.256       |
| Estimated per-capita rate ( $\hat{p}$ and $\hat{q}$ ) | 0.381       |

The second argument concerns the proportion of variation in apparent taxonomic rates that is potentially attributable to variation in preservation rates. This last quantity is most directly estimated not with first and last appearance data alone, but rather with occurrences within stratigraphic ranges. I have used data on occurrences of Ordovician brachiopods, mollusks, and trilobites kindly supplied by Arnold I. Miller of the University of Cincinnati. The data are part of an ongoing effort to analyze temporal, geographic, and environmental patterns of diversity, origination, and extinction through the Ordovician (Miller and Mao 1995, 1998; Miller and Foote 1996; Miller 1997a,b, 1998). At the time of writing, the data mainly cover Laurentia, China, Baltica, East Avalonia, Bohemia, Australia, and South America (including the Precordillera). I analyzed occurrences and ranges at the sub-series level of resolution and ignored occurrences that could not be adequately resolved. All told, I included 1075 genera and 7461 occurrences.

I first used gap analysis (Paul 1982, 1998) to estimate the preservation probability,  $R_i$ , for each Ordovician subseries. I tallied the number of genera,  $X_{bt}$ , known both before and after the interval in question and the number of these genera actually sampled during the interval,  $X_{bt,samp}$ , and estimated  $R_i$  as  $X_{bt,samp}/X_{bt}$ . (Note that first and last occurrences of genera are necessarily discarded by this approach. To include them, as Paul did, would bias the estimate of  $R_i$  upward [see Holman 1985; Maas et al. 1995; Foote and Raup 1996; Markwick 1998; Foote in press b].) As is usually the case,  $R_i$  is the joint probability that a taxon is preserved, collected, published, and entered into

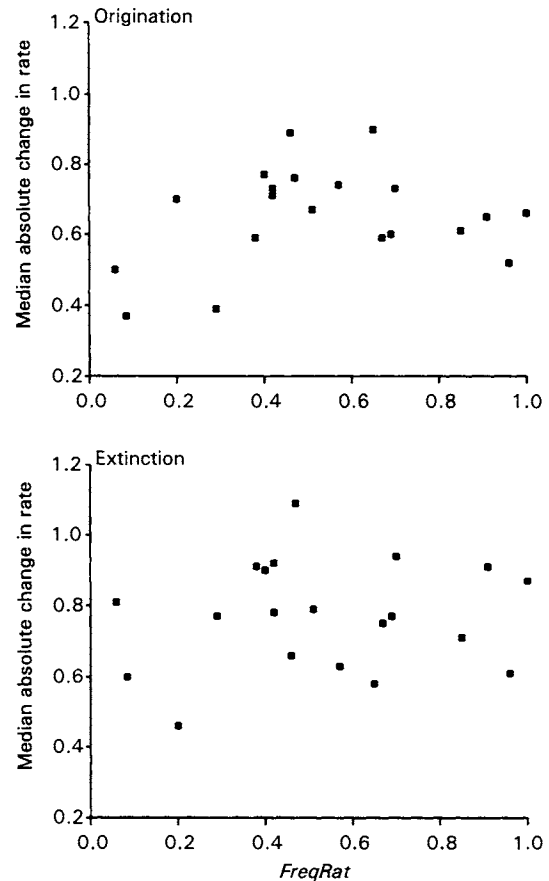


FIGURE 16. Quality of preservation versus apparent variability in per-capita origination and extinction rates for genera within higher taxa. The *FreqRat* (Foote and Raup 1996) is used to estimate probability of genus preservation within stratigraphic intervals of about 5.1 m.y. duration (Foote and Sepkoski 1999). Data are from Sepkoski (see Figs. 10, 11). To measure abrupt rather than long-term variation, variability is measured as the median absolute difference in log taxonomic rates between adjacent stratigraphic intervals. Quality of preservation is not a good predictor of apparent variability in rates, suggesting that this variability may be at least partly real. Taxa analyzed are Ammonoidea, Anthozoa, Asterozoa, Bivalvia, Blastozoa, Brachiopoda, Bryozoa, Cephalopoda, Chondrichthyes, Conodonta, Crinoidea, Echinoidea, Gastropoda, Graptolithina, Malacostraca, Nautiloidea, Osteichthyes, Ostracoda, Polychaeta, Porifera, and Trilobita. Note that Cephalopoda contains Ammonoidea and Nautiloidea; thus not all points are independent.

the database. Since  $R_i$  is expected to be equal to  $1 - \exp(-r_i \Delta t)$ , the preservation rate  $r_i$  is estimated as  $-\ln(1 - R_i)/\Delta t$  (Appendix: eq. 26). Because Miller's data cover the Ordovician only, it would be impossible to estimate preservation probability in this way for the first and last intervals of the Ordovician. I there-

fore also used Sepkoski's genus data to tabulate Cambrian first occurrences and post-Ordovician last occurrences of genera present in Miller's data. Even though I have used data outside the Ordovician, it is still likely that there are edge effects. Of 1187 total genera in Miller's data, 108 (9.1%) are not found at all in Sepkoski's data.

If variation in apparent taxonomic rates were dominated by variation in preservation rates, then correlations between  $r$  and  $\hat{p}$  and between  $r$  and  $\hat{q}$  should both be large and positive. In fact, the first is negative and the second is positive, and neither is statistically significant (product-moment correlation coefficients:  $r_{r,\hat{p}} = -0.10$ ;  $r_{r,\hat{q}} = 0.36$ ). (Results are similar if the Kendall's  $\tau$  is used, except that  $\tau_{r,\hat{p}}$  is small and positive rather than small and negative.) It is possible that an effect of preservation rates is obscured because all three rates show temporal trends (Fig. 17). If we take first differences, there is a weak negative effect of change in preservation rate on change in apparent origination rate, while the effect of change in preservation rate on change in apparent extinction rate is significant and positive ( $r_{\Delta r, \Delta \hat{p}} = -0.16$ ;  $r_{\Delta r, \Delta \hat{q}} = 0.66$ ). Even though this last correlation is statistically significant ( $p < 0.05$ ), the proportion of variation in apparent extinction rate that can be explained by variation in preservation rate is less than 40%. These results certainly argue against taking all variation in taxonomic rates at face value, but at the same time they suggest that there is substantial variation in estimated origination and extinction rates that is not an artifact of variation in preservation rate.

### Discussion

Using boundary crossers to estimate origination and extinction rates is relatively insensitive to secular trends in the quality of preservation. Except very near the Recent, this approach is also affected but little by the nearly complete knowledge of the living fauna. Why is it then that Pease (1988a,b, 1992) interpreted the Phanerozoic decline in taxonomic rates as an artifact of improving preservation and of the Pull of the Recent? There seem to be at least two reasons. First, he used origination and extinction metrics, such as the per-taxon

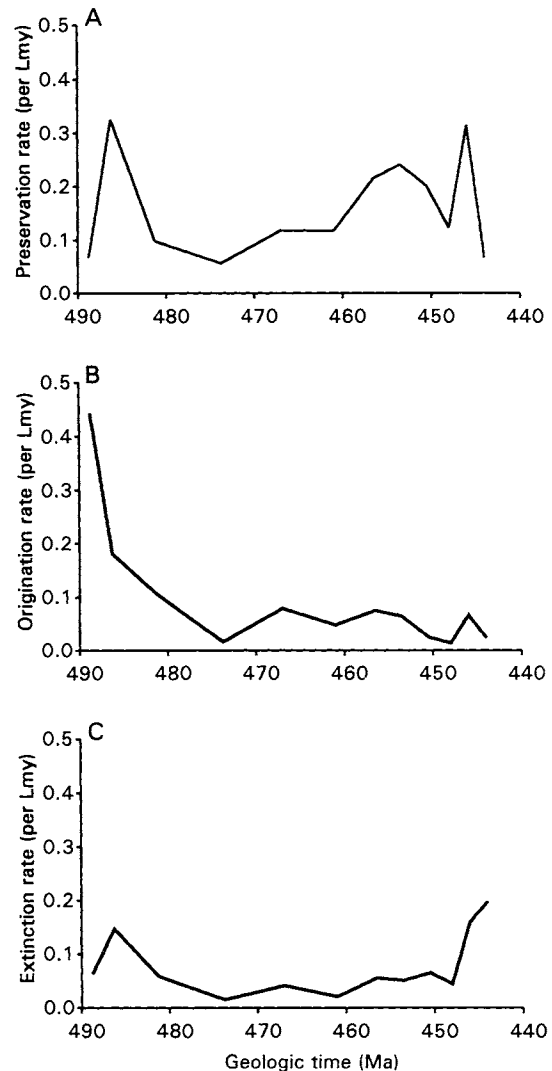


FIGURE 17. Estimated preservation rate (A), per-capita origination rate (B), and per-capita extinction rate (C) during the Ordovician. Data are from A. I. Miller, supplemented from Sepkoski for pre- and post-Ordovician occurrences of genera in Miller's data set. Probability of preservation  $R_i$  for each interval is estimated as inverse of ratio of number of genera known both before and after the interval to the number of these genera actually occurring within the interval.  $R_i$  is converted to a rate per Lmy:  $r_i = -\ln(1 - R_i)/\Delta t$ . See text for discussion.

rate, that are sensitive to secular changes in preservability. Second, some of his arguments were based on analysis of bivalve families. Because families tend to be long-lived taxa in general, and bivalve taxa are especially long-lived, the edge effect of the Recent extends far back in time in this case.

Because variation in preservation can mimic

variation in taxonomic rates, it is important to consider how much true variation in taxonomic rates is contained in stratigraphic range data and how this variation may be distorted (Koch and Morgan 1988). For the Phanerozoic as a whole, the magnitude of apparent variation in taxonomic rates is not correlated with a group's preservation potential. This suggests that there is substantial, short-term variation in taxonomic rates that is potentially measurable. The same conclusion is indicated by the correlations among preservation rate and apparent rates of origination and extinction in Ordovician invertebrates. If the results for marine animals are typical, then apparent variation in origination and extinction may be largely real. But knowing that the variation is largely real in a statistical sense is not the same as knowing the exact pattern of this variation. There are at least two obvious approaches to uncovering this pattern: (1) We can exploit occurrence data to adjust first and last appearances in a way that takes variable preservation and sampling into consideration. For example, by basing origination and extinction metrics on sampling-standardized first and last appearances, Alroy (1996b, 1998) has estimated the pattern of origination and extinction in North American Cenozoic mammals that one would likely have observed if preservation and sampling had been uniform through time. This approach has shown considerable variation in taxonomic rates that is not easily attributable to variation in the quality of the record or our knowledge of it. Extensive data of the sort that Miller has collected for the Ordovician and Alroy for the Cenozoic have not yet been compiled for most of geologic time, so we are far from being able to follow the approach of after-the-fact, standardized resampling of the entire fossil record. Such a comprehensive compilation has been started for Phanerozoic marine animals, however (Marshall et al. 1999), and preliminary results suggest that there are some similarities between genus origination and extinction curves based on raw data and those based on sampling-standardized data (J. Alroy et al. unpublished). (2) We can seek to develop methods that enable preservation rates to be estimated and first and last appearances

to be correspondingly adjusted given only the more readily available data on range endpoints, with no information on occurrences within ranges. I hope to report on one such method in a future contribution to this journal.

### Conclusion

Incomplete preservation and variation in interval length cause most diversity measures and origination and extinction metrics to be inaccurate. Moreover, some metrics of taxonomic rate by their very nature preclude the independent estimation of origination and extinction rates even under the ideal assumption of a complete record. Modeling of cladogenesis and preservation supports previous intuitive and empirical arguments that diversity and rates are best estimated if single-interval taxa are disregarded (Sepkoski 1990, 1993; Buzas and Culver 1994, 1998; Raymond and Metz 1995; Alroy 1996b, 1998, 1999; Harper 1996; Sepkoski and Koch 1996; Bambach 1999; see also Pease 1985). Using measures for which singletons are simply irrelevant is preferable to adapting conventional measures by discarding singletons. Thus it appears advantageous in principle to measure relative changes in diversity using the proportional difference between the number of taxa crossing into an interval and the number crossing out, and to measure taxonomic rates using the number of taxa that range completely through the interval relative to the total number that cross into or out of the interval. Although the fossil record is incomplete to an extent that varies substantially over time, past and current developments aimed at coping with this variability suggest that it may be possible to extract true signals of origination rate, extinction rate, and taxonomic diversity through time, provided that one avoids the dual pitfalls of taking the record at face value and assuming that it is so distorted as to be uninformative. The fact that methods for uncovering these signals are still being developed attests to the vibrancy of paleontology today.

### Acknowledgments

I am especially grateful to R. H. Foote for years of discussing this work and for sug-

gesting substantial improvements in analysis and presentation. This work also benefited from discussions with J. Alroy, D. Jablonski, A. I. Miller, and the late J. J. Sepkoski Jr. A. I. Miller and J. J. Sepkoski Jr. generously provided data. J. Alroy, R. H. Foote, A. I. Miller, and M. Newman read and improved the manuscript. This research was supported by the National Science Foundation (grant EAR 95-06568).

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### Appendix

#### Equations Regarding True and Apparent Taxonomic Rates and Diversity

This appendix develops equations for observed measures of diversity and taxonomic rates given true taxonomic rates and rates of fossil preservation. The basic equations for branching theory are taken mainly from Kendall (1948), Raup (1985), and Foote (in press a), while those for preservation are based upon Foote (1997) and simplifications of Pease (1985). A header file in C, containing library functions for all relevant calculations, is available from the author.

A time window over which observations can be made extends from time  $T = 0$  to  $T = w$ . In cases where a discrete interval of time is of interest, it has bottom and top boundaries  $T = t_b$  and  $T = t_t$  and duration  $\Delta t = t_t - t_b$ .  $p(T)$ ,  $q(T)$ , and  $r(T)$  are the time-specific, per-capita rates of origination, extinction, and preservation at an instant in time  $T$ . For simplicity, I will assume that rates are constant within a discrete interval, although they may vary among intervals. Interval rates will be denoted  $p_i$ ,  $q_i$ , and  $r_i$ . This assumption greatly reduces computational time for the time-heterogeneous numerical integrations, but it can easily be relaxed by allowing intervals to be arbitrarily short.

#### 1. True Numbers of Taxa in a Stratigraphic Interval

There are four fundamental, exclusive kinds of lineages that can exist during an interval (see Barry et al. 1995 for a similar classification): (1) those that have both first and last appearances within the interval, i.e., singletons; (2) those that cross into the interval and last appear within it; (3) those that first appear within the interval and extend beyond it; and (4) those that cross into the interval from below and extend beyond the top of the interval. Let the corresponding numbers be denoted  $N_{FL}$ ,  $N_{BL}$ ,  $N_{FT}$ , and  $N_{BT}$ , where the subscripts refer to *first-last*, *bottom-last*, *first-top*, and *bottom-top*. These numbers can be combined to yield several composite groups: (5) all lineages that cross into the interval,  $N_b = N_{BL} + N_{BT}$ ; (6) all lineages that cross out of the interval,  $N_i = N_{FT} + N_{FL}$ ; (7) lineages that become extinct during the interval,  $N_e = N_{BL} + N_{FL}$ ; (8) lineages that originate during the interval,  $N_o = N_{FT} + N_{BT}$ ; and (9) all lineages,  $N_{tot} = N_{BL} + N_{BT} + N_{FT} + N_{FL}$ .

Let  $\rho(t)$  be the accumulated difference between origination and extinction from  $T = 0$  until  $T = t$ :

$$\rho(t) = \int_0^t \{p(T) - q(T)\} dT.$$

Let  $N(t)$  be the expected diversity at time  $t$ . Then

$$N(t) = N(0)e^{\rho(t)}.$$

For simplicity, I will take  $N(0)$  to be equal to unity. Thus, the number of taxa extant at the start of the interval is given by

$$N_b = N(t_b) = e^{\rho(t_b)}. \quad (1a)$$

In the special case where rates are constant, this is equal to

$$N_b = N(t_b) = e^{(p-q)t_b}. \quad (1b)$$

Similarly,

$$N_i = N_b e^{(p_i - q_i)\Delta t}. \quad (2)$$

The probability that a lineage entering the interval will still be extant at the end is equal to  $e^{-q_i\Delta t}$ . Likewise, the probability that a lineage leaving the interval was already extant at the start of the interval is equal to  $e^{-p_i\Delta t}$ . Thus,

$$N_{BL} = N_b e^{-q_i\Delta t} = N_i e^{-p_i\Delta t}, \quad (3)$$

$$N_{BL} = N_b(1 - e^{-q_i\Delta t}), \quad \text{and} \quad (4)$$

$$N_{FL} = N_i(1 - e^{-p_i\Delta t}) = N_b e^{(p_i - q_i)\Delta t}(1 - e^{-p_i\Delta t}). \quad (5)$$

The number of lineages confined to the interval is found by integrating the expected number of originations at any time during the interval (i.e., origination rate times standing diversity), multiplied by the probability of not surviving from the time of origination to the end of the interval. Thus,

$$N_{FL} = N_b \int_0^{\Delta t} p_i e^{(p_i - q_i)T} [1 - e^{-q_i(\Delta t - T)}] dT. \quad (6a)$$

This is equal to

$$N_{FL} = N_b(e^{-q_i\Delta t} + p_i\Delta t - 1) \quad \text{if } p_i = q_i, \quad \text{and} \quad (6b)$$

$$N_{FL} = N_b \frac{q_i e^{(p_i - q_i)\Delta t} + (p_i - q_i)e^{-q_i\Delta t} - p_i}{p_i - q_i} \quad \text{if } p_i \neq q_i. \quad (6c)$$

The number of originations during the interval is the integral of the origination rate times the standing diversity. Thus

$$N_o = N_b \int_0^{\Delta t} p_i e^{(p_i - q_i)T} dT, \quad (7a)$$

which is equal to

$$N_o = \begin{cases} N_b p_i \Delta t & \text{if } p_i = q_i \quad \text{and} \\ N_b \frac{p_i [e^{(p_i - q_i)\Delta t} - 1]}{p_i - q_i} & \text{if } p_i \neq q_i. \end{cases} \quad (7b)$$

Similarly,

$$N_e = N_b \int_0^{\Delta t} q_i e^{(p_i - q_i)T} dT, \quad (8a)$$

which is equal to

$$N_e = \begin{cases} N_b q_i \Delta t & \text{if } p_i = q_i \quad \text{and} \\ N_b \frac{q_i [e^{(p_i - q_i)\Delta t} - 1]}{p_i - q_i} & \text{if } p_i \neq q_i. \end{cases} \quad (8b)$$

Finally, the total number of lineages within the interval (the total progeny of Kendall 1948) is equal to

$$N_{tot} = N_b \left( 1 + \int_0^{\Delta t} p_i e^{(p_i - q_i)T} dT \right), \quad (9a)$$

which is equal to

$$N_{tot} = \begin{cases} N_b(1 + p_i \Delta t) & \text{if } p_i = q_i \text{ and} \\ N_b \frac{p_i e^{(p_i - q_i) \Delta t} - q_i}{p_i - q_i} & \text{if } p_i \neq q_i. \end{cases} \quad (9b)$$

## 2. Taxonomic Rate Metrics for an Interval, Assuming Complete Preservation

Various metrics have been devised to measure taxonomic rates over some extended interval of time, usually by counting originations and extinctions and normalizing by diversity and / or interval length. One problem that has been noted (Gilinsky 1991) is that some normalizations implicitly assume constancy of rates within an interval. Inspection of the foregoing equations shows that  $N_o$ ,  $N_e$ ,  $N_{TL}$ , and  $N_{tot}$  are affected by variation in rates within an interval, not just by mean rates over the interval. In contrast,  $N_b$ ,  $N_i$ ,  $N_{bu}$ ,  $N_{bi}$  ( $= N_b - N_{bi}$ ), and  $N_{fi}$  ( $= N_i - N_{bi}$ ) depend only on the average rates within the interval. Therefore, measures of taxonomic rate that are based only on  $N_b$ ,  $N_i$ , and  $N_{bi}$  are, at least in theory, insensitive to rate variation within an interval and capable of accurately estimating average rates.

Proportional origination is the ratio of number of originations to total diversity. Substituting into the equations for  $N_o$  and  $N_{tot}$  yields

$$P_o = \begin{cases} \frac{p_i \Delta t}{1 + p_i \Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{p_i [e^{(p_i - q_i) \Delta t} - 1]}{p_i e^{(p_i - q_i) \Delta t} - q_i} & \text{if } p_i \neq q_i. \end{cases} \quad (10)$$

Similarly, for proportional extinction

$$P_e = \begin{cases} \frac{q_i \Delta t}{1 + p_i \Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{q_i [e^{(p_i - q_i) \Delta t} - 1]}{p_i e^{(p_i - q_i) \Delta t} - q_i} & \text{if } p_i \neq q_i. \end{cases} \quad (11)$$

Normalizing these expressions by interval length yields the so-called per-taxon rates:

$$P_{o/m.y.} = \begin{cases} \frac{p_i}{1 + p_i \Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{p_i [e^{(p_i - q_i) \Delta t} - 1]}{[p_i e^{(p_i - q_i) \Delta t} - q_i] \Delta t} & \text{if } p_i \neq q_i \end{cases} \quad (12)$$

and

$$P_{e/m.y.} = \begin{cases} \frac{q_i}{1 + q_i \Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{q_i [e^{(p_i - q_i) \Delta t} - 1]}{[p_i e^{(p_i - q_i) \Delta t} - q_i] \Delta t} & \text{if } p_i \neq q_i. \end{cases} \quad (13)$$

Clearly,  $P_o$  and  $P_e$  increase nonlinearly with  $\Delta t$ , whereas  $P_{o/m.y.}$  and  $P_{e/m.y.}$  decrease nonlinearly with  $\Delta t$ . This nonlinear dependence on  $\Delta t$ , which cannot be eliminated by a simple normalization, complicates the use of proportional origination and extinction when interval length varies (Gilinsky 1991; Foote 1994).

Van Valen proposed a measure of taxonomic rates that normalizes the observed number of events by the estimated standing diversity within the interval, which is simply the mean of  $N_b$  and  $N_i$  (algebraically identical to  $N_{tot} - N_o/2 - N_e/2$ ; [see Table 1 and Harper 1975, 1996]). The corresponding origination metric is given by

$$V_o = \frac{N_o}{(N_b + N_i)/2} \quad (14a)$$

which is equal to

$$V_o = \begin{cases} p_i \Delta t & \text{if } p_i = q_i \text{ and} \\ \frac{2p_i [e^{(p_i - q_i) \Delta t} - 1]}{(p_i - q_i)[1 + e^{(p_i - q_i) \Delta t}]} & \text{if } p_i \neq q_i. \end{cases} \quad (14b)$$

The time-normalized origination metric is thus equal to

$$V_{o/m.y.} = \begin{cases} p_i & \text{if } p_i = q_i \text{ and} \\ \frac{2p_i [e^{(p_i - q_i) \Delta t} - 1]}{(p_i - q_i)[1 + e^{(p_i - q_i) \Delta t}]} & \text{if } p_i \neq q_i. \end{cases} \quad (15)$$

The corresponding extinction metrics are given by

$$V_e = \begin{cases} q_i \Delta t & \text{if } p_i = q_i \text{ and} \\ \frac{2q_i [e^{(p_i - q_i) \Delta t} - 1]}{(p_i - q_i)[1 + e^{(p_i - q_i) \Delta t}]} & \text{if } p_i \neq q_i, \end{cases} \quad (16)$$

and

$$V_{e/m.y.} = \begin{cases} q_i & \text{if } p_i = q_i \text{ and} \\ \frac{2q_i [e^{(p_i - q_i) \Delta t} - 1]}{(p_i - q_i)[1 + e^{(p_i - q_i) \Delta t}]} & \text{if } p_i \neq q_i. \end{cases} \quad (17)$$

Thus, if origination and extinction rates are equal, Van Valen's metric provides an accurate estimate of these rates that is independent of interval length. The Van Valen metric progressively underestimates origination and extinction rates as the true difference between these rates increases.

Harper (1996) used a number of measures of origination and extinction that disregard singletons. Harper's modification of the Van Valen metric is given by

$$V_o^* = \frac{N_o - N_{TL}}{(N_b + N_i)/2} = \frac{N_{fi}}{(N_b + N_i)/2} \quad (18a)$$

which is equal to

$$V_o^* = \begin{cases} 1 - e^{-p_i \Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{2[e^{(p_i - q_i) \Delta t} - e^{-p_i \Delta t}]}{1 + e^{(p_i - q_i) \Delta t}} & \text{if } p_i \neq q_i. \end{cases} \quad (18b)$$

Thus, when origination and extinction rates are equal, the singleton-free Van Valen metric before time-normalization gives the probability that a lineage present at either boundary will extend all the way through the interval. (Alroy [1996b] also used a similar approach, normalizing by  $N_b$  rather than by  $(N_b + N_i)/2$ . The two metrics are equivalent if  $p_i = q_i$ .) Normalizing by interval length yields

$$V_{o/m.y.}^* = \begin{cases} \frac{1 - e^{-p_i \Delta t}}{\Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{2[e^{(p_i - q_i) \Delta t} - e^{-p_i \Delta t}]}{[1 + e^{(p_i - q_i) \Delta t}] \Delta t} & \text{if } p_i \neq q_i. \end{cases} \quad (19)$$

The corresponding extinction metrics are given by

$$V_e^* = \begin{cases} 1 - e^{-q_i \Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{2(1 - e^{-q_i \Delta t})}{1 + e^{(p_i - q_i) \Delta t}} & \text{if } p_i \neq q_i, \end{cases} \quad (20)$$

and

$$V_{e/m.y.}^* = \begin{cases} \frac{1 - e^{-q_i \Delta t}}{\Delta t} & \text{if } p_i = q_i \text{ and} \\ \frac{2(1 - e^{-q_i \Delta t})}{[1 + e^{(p_i - q_i) \Delta t}] \Delta t} & \text{if } p_i \neq q_i. \end{cases} \quad (21)$$

In the general case,  $V_{o/m.y.}^*$  and  $V_{e/m.y.}^*$  do not provide accurate rate estimates. They decrease nonlinearly with interval length, and they deviate more from  $p_i$  and  $q_i$  as the true rates increase and as the difference between them increases. Because  $1 - e^{-x}$

$\approx x$  for small  $x$ , however,  $V_{o/m,y}^* = V_{e/m,y}^* \approx p_i = q_i$  in the special case where  $p_i = q_i$  and  $p_r, q_r$  and  $\Delta t$  are not too large. The same is true of Alroy's (1996b) metrics when singletons are disregarded (see Alroy et al. 2000).

The number of lineages extending through the entire interval depends only on the mean taxonomic rates for the interval. Rearranging the simple equivalence  $N_{bi} = N_b e^{-q_i \Delta t} = N_b e^{-p_i \Delta t}$  yields estimates of per-capita rates:

$$\hat{p} = \frac{-\ln(N_{bi}/N_i)}{\Delta t} \quad \text{and} \quad (22)$$

$$\hat{q} = \frac{-\ln(N_{bi}/N_i)}{\Delta t}. \quad (23)$$

$\hat{p}$  and  $\hat{q}$  reduce to  $p_i$  and  $q_i$ , but, in contrast to the singleton-free Van Valen metric, this is true regardless of the magnitude of the rates. If origination and extinction rates are unequal, then, in contrast to the Van Valen metrics, with or without singletons, one rate is not expected to affect the estimation of the other. Note that  $\hat{p}$  and  $\hat{q}$  do not rely on counting events within the interval and normalizing by total diversity or estimated standing diversity. Also, as with the singleton-free Van Valen metric, single-interval taxa play no role. This will be important when the incompleteness of the fossil record is taken into consideration.

### 3. Fundamental Preservation Probabilities

A lineage with time-specific preservation rate  $r(T)$  per m.y. and duration  $t$  from  $t_1$  to  $t_2$  has a net probability of preservation equal to  $1 - e^{-\int_{t_1}^{t_2} r(T) dT}$ . In the case of constant preservation rates, this is equal to  $1 - e^{-r}$ . This relationship and the probability distribution of taxon durations are used to calculate probabilities of preservation for taxa spanning all or part of relevant intervals of time.

*Probability of Preservation before a Point in Time.*—The duration of a lineage before any arbitrary point in time depends on prior rates of origination and on the span of time. The probability of preservation before time  $t$ , assuming that the lineage is in fact extant at time  $t$  (not assuming that we know this fact), is therefore equal to

$$P_B = \int_0^t \left( p(T) \exp \left[ - \int_0^T p(x) dx \right] \left[ 1 - \exp \left[ - \int_0^T r(x) dx \right] \right] \right) dT. \quad (24a)$$

In the special case where  $p$  and  $r$  are constant, this reduces to

$$P_B = \frac{r}{p+r} [1 - e^{-(p+r)t}]. \quad (24b)$$

In the special case where  $p$  and  $r$  are constant and the time span  $t$  is effectively infinite (i.e., the probability that a lineage extends from  $T = 0$  to  $T = t$  is approximately nil), this reduces to

$$P_B = \frac{r}{p+r}. \quad (24c)$$

The corresponding probability of preservation after an arbitrary point in time, given that the lineage is extant at that point, depends on the extinction and preservation rates and the span of time after that point. Thus

$$P_A = \int_t^w \left( q(T) \exp \left[ - \int_t^T q(x) dx \right] \left[ 1 - \exp \left[ - \int_t^T r(x) dx \right] \right] \right) dT. \quad (25a)$$

where, as above,  $w$  is the upper bound of the stratigraphic window over which observations can be made. If  $q$  and  $r$  are constant, this reduces to

$$P_A = \frac{r}{q+r} [1 - e^{-(q+r)(w-t)}]. \quad (25b)$$

If  $q$  and  $r$  are constant and the time span  $(w - t)$  is effectively infinite, this reduces to

$$P_A = \frac{r}{q+r}. \quad (25c)$$

Equations (24c) and (25c) are the backward and forward preservation probabilities of Pease (1985).

*Probability of Preservation during an Interval.*—The probability of preservation depends on whether a lineage (1) spans the entire interval, (2) crosses into it from below and terminates within it, (3) originates within it and extends beyond it, or (4) originates and becomes extinct during the interval. For lineages that span the entire interval, we have

$$P_{D|bi} = 1 - e^{-q_i \Delta t}. \quad (26)$$

For lineages that originate before the interval and terminate within it, the probability of preservation depends on how far into the interval they extend, which is a function of the extinction rate. Thus

$$P_{D|bl} = \frac{\int_0^{\Delta t} q_i e^{-q_i T} (1 - e^{-r_i T}) dT}{1 - e^{-q_i \Delta t}}. \quad (27a)$$

The denominator in this equation is a normalization reflecting the probability of extinction during the interval if the lineage is extant at the start. This equation reduces to

$$P_{D|bl} = \left\{ \frac{[r_i + q_i e^{-(q_i+r_i)\Delta t}] - e^{-q_i \Delta t}}{q_i + r_i} \right\} / (1 - e^{-q_i \Delta t}). \quad (27b)$$

For lineages that originate during the interval and extend beyond it, the preservation probability is analogous to the foregoing, except that the origination rate is the relevant parameter:

$$P_{D|rl} = \frac{\int_0^{\Delta t} p_i e^{-p_i T} (1 - e^{-r_i T}) dT}{1 - e^{-p_i \Delta t}}. \quad (28a)$$

This reduces to

$$P_{D|rl} = \left\{ \frac{[r_i + p_i e^{-(p_i+r_i)\Delta t}] - e^{-p_i \Delta t}}{p_i + r_i} \right\} / (1 - e^{-p_i \Delta t}). \quad (28b)$$

For lineages that originate and become extinct during the same interval, we need to consider the density of origination at any point during the interval (which is uniform only if  $p_i = q_i$ ). This is obtained by multiplying the origination rate  $p_i$  by the standing diversity at time  $T$  within the interval,  $N_i e^{(p_i-q_i)T}$ , and normalizing by the total number of single-interval lineages,  $N_{iL}$ . The density of origination is then weighted by the density of a given duration, which depends on the extinction rate  $q_r$  and the probability of preservation given that duration. Thus

$$P_{D|rl} = \int_0^{\Delta t} \frac{N_i p_i e^{(p_i-q_i)T}}{N_{iL}} \left[ \int_0^{\Delta t-T} q_i e^{-q_i x} (1 - e^{-r_i x}) dx \right] dT. \quad (29a)$$

If  $p_i = q_i$ , this is equal to

$$P_{D|rl} = \frac{N_b p_i}{N_{iL}} \left[ \frac{r_i \Delta t}{p_i + r_i} - \frac{1 - e^{-p_i \Delta t}}{p_i} - \frac{p_i (1 - e^{-(p_i+r_i)\Delta t})}{(p_i + r_i)^2} \right]. \quad (29b)$$

If  $p_i \neq q_i$ , this is equal to

$$P_{D|rl} = \frac{N_b}{N_{iL}} \left\{ \frac{p_i r_i [e^{(p_i-q_i)\Delta t} - 1]}{(q_i + r_i)(p_i - q_i)} + \frac{p_i q_i e^{-(q_i+r_i)\Delta t} [e^{(p_i+r_i)\Delta t} - 1]}{(p_i + r_i)(q_i + r_i)} - e^{-q_i \Delta t} (e^{p_i \Delta t} - 1) \right\}. \quad (29c)$$

In equations (29b) and (29c),  $N_b$  and  $N_{FL}$  are from equations (1b) and (6b).

#### 4. Compound Probabilities of Preservation

Probabilities of preservation before, during, and after an interval can be combined to yield probabilities of observed ranges given true durations. Because I am interested in the relationship between true and observed durations and rates, I will not present equations expressing the probability of not being preserved at all. These are easily derived from the fundamental probabilities (see Pease 1985; Foote and Raup 1996; Foote 1997; Solow and Smith 1997). The probabilities depend on a particular span of time. To avoid ambiguities, I will use notations such as  $P_b(t)$  to indicate, for example, the probability of preservation before a point in time when there is a time span  $t$  over which preservation can occur. Let  $P_{\times| \times}$  denote the probability that a lineage is observed to cross a particular time line, given that the lineage truly crosses it. This probability is simply the product of the probabilities of preservation before and after:

$$P_{\times| \times} = P_b P_a. \quad (30a)$$

If the rates are constant and  $t_b$  and  $t_a$  are the time spans before and after the time line, then this is equal to

$$P_{\times| \times} = \frac{r^2}{(p+r)(q+r)} [1 - e^{-(p+r)t_b}] [1 - e^{-(q+r)t_a}]. \quad (30b)$$

If the rates are constant and  $t_b$  and  $t_a$  are effectively infinite, then this reduces to

$$P_{\times| \times} = \frac{r^2}{(p+r)(q+r)}. \quad (30c)$$

In the time-homogeneous case, the foregoing expression gives the ratio of observed to true standing diversity at any point in time. Note that this is substantially smaller than the proportion of taxa preserved (see below).

Lineages that truly span an entire interval can appear a number of different ways. They can appear to span the entire interval, to cross the bottom boundary only, to cross the top boundary only, or to be confined to the interval. The corresponding probabilities are

$$P_{b|b} = P_b(t_b) \cdot P_a(w - t_i), \quad (31a)$$

$$P_{bL|b} = P_b(t_b) \cdot P_{D|b} \cdot [1 - P_a(w - t_i)], \quad (31b)$$

$$P_{tL|b} = [1 - P_b(t_b)] \cdot P_{D|b} \cdot P_a(w - t_i), \quad \text{and} \quad (31c)$$

$$P_{tL|b} = [1 - P_b(t_b)] \cdot P_{D|b} \cdot [1 - P_a(w - t_i)]. \quad (31d)$$

Note that the relevant time span for  $P_{D|b}$  is  $\Delta t$  in all cases. The probabilities that a lineage will appear to cross the bottom boundary (whether or not it also crosses the top) or that it will appear to cross the top boundary (whether or not it also crosses the bottom) are given by

$$P_{b|b} = P_b(t_b) \cdot P_a(w - t_i + \Delta t) \quad \text{and} \quad (31e)$$

$$P_{t|t} = P_b(t_b + \Delta t) \cdot P_a(w - t_i). \quad (31f)$$

Lineages that truly cross only the bottom boundary of an interval can appear to cross that boundary or to be confined to the interval. The corresponding probabilities are

$$P_{bL|bL} = P_b(t_b) \cdot P_{D|bL} \quad \text{and} \quad (32a)$$

$$P_{tL|bL} = [1 - P_b(t_b)] \cdot P_{D|bL}. \quad (32b)$$

Similarly, lineages that truly cross only the top boundary can appear to cross that boundary or to be confined to the interval. The probabilities are

$$P_{tL|tL} = P_{D|tL} \cdot P_a(w - t_i), \quad \text{and} \quad (33a)$$

$$P_{bL|tL} = P_{D|tL} \cdot [1 - P_a(w - t_i)]. \quad (33b)$$

Lineages truly confined to an interval can be preserved only in that interval. The corresponding preservation probability was given above as  $P_{D|FL}$  (eq. 29).

#### 5. Observed Numbers of Taxa in an Interval

Given the expected true numbers of taxa from section 1 above and the probabilities of preservation from section 4, it is easy to derive expressions for the number of taxa in various categories that are observed in an interval. For a taxon to appear to span the entire interval, it must have done so in reality. The number of taxa that are observed to cross both top and bottom boundaries is thus equal to

$$X_{bt} = N_{bt} P_{b|b}. \quad (34a)$$

A taxon that appears to cross the bottom boundary only may have crossed only that boundary in reality, or it may have spanned the entire interval. The number of taxa observed to cross the bottom boundary only is thus equal to

$$X_{bL} = N_{bt} P_{bL|b} + N_{bL} P_{bL|bL}. \quad (34b)$$

Similarly, the number of taxa observed to cross only the top boundary is equal to

$$X_{tL} = N_{bt} P_{tL|b} + N_{tL} P_{tL|tL}. \quad (34c)$$

Taxa that are observed to be confined to the interval may truly have been confined to the interval, or they may in fact have crossed either or both boundaries. The number of observed single-interval taxa is thus equal to

$$X_{FL} = N_{bt} P_{FL|b} + N_{bL} P_{FL|bL} + N_{tL} P_{FL|tL} + N_{FL} P_{FL|FL}. \quad (34d)$$

The four fundamental classes of observed lineages can be combined in a number of ways to yield the total observed taxa crossing the bottom and top boundaries, the number of taxa first appearing (apparently originating) within the interval, the number last appearing (apparently becoming extinct) within the interval, and the total number of taxa known from the interval (including those preserved before and after but not during the interval). Thus,

$$X_b = X_{bt} + X_{bL}. \quad (35a.i)$$

Note that this is also equal to

$$X_b = N_b P_b(t_b) \cdot P_a(w - t_i + \Delta t). \quad (35a.ii)$$

Similarly,

$$X_t = X_{tL} + X_{tL}, \quad (35b.i)$$

which is equal to

$$X_t = N_t P_b(t_b + \Delta t) \cdot P_a(w - t_i). \quad (35b.ii)$$

Finally,

$$X_o = X_{bL} + X_{tL}, \quad (35c)$$

$$X_e = X_{tL} + X_{bL}, \quad \text{and} \quad (35d)$$

$$X_{tot} = X_{bt} + X_{bL} + X_{tL} + X_{FL}. \quad (35e)$$

Section 2 discussed methods for estimating taxonomic rates that use only boundary-crossing lineages. The observed numbers of boundary crossers,  $X_b$ ,  $X_t$ , and  $X_{bt}$ , are given by simple expressions in the case of constant rates:

$$X_b = N_b \frac{r^2}{(p+r)(q+r)} [1 - e^{-(p+r)t_b}] [1 - e^{-(q+r)(w-t_r+\Delta t)}], \quad (36a)$$

$$X_t = N_t \frac{r^2}{(p+r)(q+r)} [1 - e^{-(p+r)t_b+\Delta t}] [1 - e^{-(q+r)(w-t_r)}], \quad (36b)$$

and

$$X_{bt} = N_{bt} \frac{r^2}{(p+r)(q+r)} [1 - e^{-(p+r)t_b}] [1 - e^{-(q+r)(w-t_r)}]. \quad (36c)$$

As the interval in question gets farther from the beginning or end of the window of observation, the exponential terms in these equations become less important. When the interval is far enough from the edges that  $t_b$  and  $w - t_r$  are effectively infinite, the exponential terms vanish and we have

$$X_b = N_b \frac{r^2}{(p+r)(q+r)}, \quad (37a)$$

$$X_t = N_t \frac{r^2}{(p+r)(q+r)}, \quad \text{and} \quad (37b)$$

$$X_{bt} = N_{bt} \frac{r^2}{(p+r)(q+r)}. \quad (37c)$$

From these it follows that

$$X_{bt} = N_{bt} \frac{r^2}{(p+r)(q+r)}, \quad \text{and} \quad (37d)$$

$$X_{bt} = N_{bt} \frac{r^2}{(p+r)(q+r)}. \quad (37e)$$

If we add the further constraint that  $p = q$ , then we have simple relationships for  $X_o$ ,  $X_e$  and  $X_{FL}$  as well:

$$X_o = X_e = N_b p \Delta t \frac{r}{p+r} = N_b q \Delta t \frac{r}{q+r} \quad \text{and} \quad (38a)$$

$$X_{FL} = N_b \left[ p \Delta t \frac{r}{p+r} + (e^{-p\Delta t} - 1) \frac{r^2}{(p+r)^2} \right]. \quad (38b)$$

Note that  $[r/(p+r)] (= [r/(q+r)])$  in this case is simply the proportion of lineages preserved (Solow and Smith 1997).

Equations (37a) through (37e) have important implications. The ratios of observed numbers of boundary crossers are identical to the ratios of actual numbers of boundary crossers. If preservation rate is constant and the rates are calculated for an

interval that is far from the beginning or end of the window of observation, the rate estimates of equations (22) and (23) are unaffected by incompleteness of the fossil record. This result is related to fact that the observed age distribution of taxa exclusive of singletons is identical to the true age distribution in the time-homogeneous case (Foote and Raup 1996; Foote 1997). Several authors have advocated excluding single-interval taxa from measures of taxonomic rates (Pease 1985; Sepkoski 1990; Alroy 1996b, 1998, 1999; Harper 1996), and many have advocated measuring diversity as the number of taxa crossing time lines rather than the number accumulated over an interval (Raymond and Metz 1995; Alroy 1996b, 1998, 1999; Bambach 1999). Whether the exclusion of singletons is seen as an adjustment of a conventional metric (Harper 1996) or part of a less conventional approach to rate estimation, the practice has much to recommend it, at least in the time-homogeneous case. The text explores behavior of the proposed metric and other metrics when taxonomic rates and preservation rates vary and when the interval is close enough to the beginning or end of the window of observation to experience a noticeable edge effect.

The singleton-free Van Valen metrics discussed above are also insensitive to rate of preservation in the time-homogeneous case when edge effects are absent. As shown earlier, however, these metrics yield inaccurate estimates of origination and extinction rates, and the degree of inaccuracy increases as the magnitude of rates or the difference between them increases.

Because the Van Valen metric and the per-taxon rate include singletons in the count of originations and extinctions, these metrics increase as the rate of preservation decreases. Combining equations (37a), (37b), and (38a) yields a simple and striking result. When origination and extinction rates are constant and equal and when there are no edge effects, the normalized Van Valen metric is equal to

$$V_{o/m.y.} = V_{e/m.y.} = p \frac{p+r}{r} = q \frac{q+r}{r}. \quad (39)$$

Since  $r/(p+r) = r/(q+r)$  is the proportion of lineages preserved, the observed Van Valen metric in this special case is simply the true taxonomic rate divided by proportion of lineages preserved. Thus, in practice, the average ratio of  $\hat{p}$  to  $V_{o/m.y.}$  or of  $\hat{q}$  to  $V_{e/m.y.}$  may provide a measure of the completeness of the fossil record. To my knowledge, this possibility has not yet been explored in detail.