ADAPTS (ANALYSIS OF DIVERSITY, ASYMMETRY OF PHYLOGENETIC TREES, AND SURVIVORSHIP): A NEW SOFTWARE TOOL FOR ANALYSING STRATIGRAPHIC RANGE DATA

Alistair J. McGowan and **Paul N. Pearson**

ABSTRACT

In order to automate analysis of stratigraphic range data, a new software tool ADAPTS (Analysis of Diversity, Asymmetry of Phylogenetic Trees and Survivorship) has been developed. This software runs analyses of three broad types; taxonomic evolutionary rate metrics, survivorship analyses and tests for biases in rates of speciation and extinction between ancestors and descendants, such as cause asymmetrical branching in phylogenetic trees. To carry out all of these tests, ADAPTS needs only five data items about each taxon in a group: an identification number (I.D.) number, first appearance datum (FAD), last appearance datum LAD, its stratigraphic range, and the I.D. number of its ancestor. These data may be entered into any standard spreadsheet program. The ADAPTS software automatically reads in these data in activated and the results output to a spreadsheet. To test the performance of ADAPTS, a known random phylogeny was generated with the TREE GROWTH program, and the output analysed. This test confirmed that ADAPTS was capable of detecting a known random signal and of handling large data sets rapidly.

A demonstration version of ADAPTS is available at:
http://geosci.uchicago.edu/paleo/csource/
http://palaeo.gly.bris.ac.uk/personnel/Pearson/ADAPTS.html.
A final version will be made available in the future.

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KEY WORDS: stratigraphic ranges, survivorship, evolutionary rates

Submission: 30 December 1998, Acceptance: 23 February 1999

INTRODUCTION

The palaeontological literature is full of questions and debates that could be illuminated by the application of quantitative methods and considerable effort has been expended developing such techniques since the advent of microcomputer technology (Kitchell 1990). Unfortunately, many tests that have been developed are underused due to the need for labourious hand calculation. To remedy this, a new software tool to implement analysis of stratigraphic range data in three broad categories (taxonomic evolutionary rate metrics, survivorship analysis, and tests for asymmetry in phylogenetic trees) has been created. The program code for the software, named ADAPTS (Analysis of Diversity, Asymmetry of Phylogenetic Trees and Survivorship) is included in Appendix I.

ADAPTS requires only five pieces of data for each taxon, which are initially entered into a standard spreadsheet program. These allow use of all of the procedures offered.

Data Required

- (First Column) Taxon I.D. Number (Taxa are numbered 1 to n);
- (Second Column) First Appearance Datum (FAD) in time (e.g. myr);
- (Third Column) Last Appearance Datum (LAD) in time (e.g. myr);
- (Fourth Column) Stratigraphic Range (FAD-LAD). (This calculation can easily be automated on a spreadsheet.);
- (Fifth Column) I.D. Number of Ancestral Taxon. (This information is only required for the A-D tests, if not a column of zeros should be entered.)

These data are then highlighted in the spreadsheet and copied. When ADAPTS is opened the program automatically reads these data in. The user then specifies calculation parameters and which tests they wish to perform via a series of dialogue boxes. The order of the procedures is as follows:

Taxonomic Evolutionary Rate Metrics; after Sepkoski (1978), Lasker (1978) and Wei and Kennett (1986)

For each calculation interval, which is user specified and can be changed, ADAPTS computes:

- Diversity (D = species richness), using the methods of Wei and Kennett (1986).
- Number of originations (S).
- Number of extinctions (E).
- Per taxon rate of origination (r_o).
- Per taxon rate of extinction (r_e).
- Rate of diversification (r_d).
- Rate of turnover (r_t).

- Rate of change in diversity (delta D).

Survivorship Analysis

Three methods of survivorship analysis are offered:

- Dynamic survivorship as used by Van Valen (1973a).
- Corrected Survivorship Score (CSS) Pearson (1992,1995).
- Extinction Intensity Survival Score (EISS) as suggested by Pearson, 1995, p. 122.

The taxonomic durations are evaluated using Epstein's Test (Epstein 1960a, b), which is a statistical test for detecting departure from linearity in survivorship curves.

Ancestor-Descendant (A-D) Tests (Pearson 1998)

These tests are used to quantify asymmetry in phylogenetic trees:

- A-D Extinction Test.
- Survivorship Control Test
- A-D Speciation Test.
- A-D Speciation Test (Restricted).

The rationale behind ADAPTS is to unite these tests into a single package that can thoroughly evaluate palaeobiological data, rather than carry out piecemeal investigations. The results are output to a spreadsheet, to make further data manipulation easy. Spreadsheet files are also simple to update and distribute. The ADAPTS software can be used to calculate taxonomic evolutionary rate metrics, or only the A-D tests. By offering this flexibility the usefulness of ADAPTS can be extended to users not so keenly focused on the particular problems that some of the procedures were designed to investigate.

The combination of computing power and statistical tests has changed palaeontological debate, by enabling large data sets to be handled and quantitative conclusions to be drawn from them (Kitchell 1990). This does not remove the onus from the user to be discerning about their data. ADAPTS is, after all, only a series of algorithms. Rather, it frees the palaeobiologist to be a palaeobiologist and use their particular skills to enhance and expand our knowledge of the fossil record.

The ADAPTS software was tested with a random dataset, generated using a random branching model. The program TREE GROWTH was based on the branching model presented in Pearson (1998; Figure 3). A random tree of 986 taxa was analysed to verify that ADAPTS can identify known random patterns and those results are presented in this paper. Currently ADAPTS is available for limited public use and the source code can be found in Appendix I and at:

http://geosci.uchicago.edu/paleo/csource/
http://paleo.gly.bris.ac.uk/micropal/micropalaeo/

This is a demonstration version and developmental work is continuing with the aim of creating a downloadable application for distribution as freeware. Updates on progress will be posted at the two websites listed.

Sources of Data

The first edition of The Fossil Record appeared in 1967 (Harland et al. 1967). Since then the efforts of Sepkoski (1982 1992) and Benton (1993) have been of particular note in terms of the compilation of large scale databases. The advent of the World Wide Web has also increased the amount of potential access to taxonomic range data. These data represent a great resource, and a problem. New information is appearing at a sometimes bewildering rate and there are already vast amounts of data available in the technical literature. This situation makes a software tool for analysing evolutionary patterns in the fossil record desirable.

The availability and widespread use of spreadsheet-based packages for both data storage and statistical analysis served as a starting point for the development of ADAPTS. It was considered vital for ADAPTS to be able to interface with such programs, as they have the virtues of ease of updating and the capacity to cut, paste and copy data at will. These virtues had to be matched by the user interface of ADAPTS, which consists of a series of windows and check boxes of the sort familiar to most computer users. Similarly, when the run is finished a dialogue box appears to explain how to transfer the data into a spreadsheet, which is a simple case of opening a spreadsheet and using the "paste" command to transfer the data into the designated cells.

The selection of the three groups of tests was a balance between those that were thought to be of the widespread use to the palaeontological community, such as the diversity-based metrics and the need to automate Epstein's Test and the A-D tests, that are extremely time consuming to perform by hand. A glance at the current literature shows widespread use of diversity-related metrics and plots of diversity. By automating all of the procedures listed under taxonomic evolutionary rate metrics, a user may clarify the underlying factors that are shaping diversity plots. By incorporating the power to vary the calculation interval (which permits investigation of timescale effects) the question of whether origination and extinction peaks are artifacts can be explored in successive runs (Foote, 1997).

While stratigraphic range data are widely available, and such data are all that is required if only taxonomic evolutionary rates and/or survivorship analysis are to be performed, ancestor-descendant hypotheses are scarcer. Without such information it is not possible to use the A-D tests. The lack of such data is really a combination of two factors. One is that many groups do not possess the continuous, well sampled fossil record that Gingerich (1976) based the stratophenetic method upon. The groups that were targeted in Pearson (1998) are all biostratigraphically important, and are hence well sampled and well described. This is clearly not the case with many groups.

The other factor is the widespread use of cladistics by many systematists. This method is based on the search for common ancestry and has no need for hypotheses of ancestral relationships. Smith (1994) presented a discussion of integrating stratigraphic data and cladograms to produce evolutionary trees to generate A-D relationships.

METHODS

Spreadsheet Format

Table 1 shows part of the dataset generated by TREE GROWTH that has been analysed with ADAPTS. It shows the five columns of data required to use all the tests that ADAPTS offers. ADAPTS uses the Taxon I.D. number to track the taxa in calculations, but it is possible to add taxon names into the spreadsheet when working with real groups. The first taxon has ’0’ in the ancestor column. This is a device to signify taxa whose ancestry is unknown or equivocal and such taxa are labeled as unknown by the ADAPTS output. This option becomes more important in the analysis of real groups, as there are more cases of questionable ancestry. Once a database has been prepared, all the user has to do is highlight the cells with the information and copy them. Once ADAPTS is opened the data are automatically read into the relevant program arrays.

Taxonomic Evolutionary Rate Metrics

These metrics are taken from Sepkoski (1978) and Lasker (1978). The ADAPTS software uses the diversity calculation procedure of Wei and Kennett (1986). This involves weighting each taxa by the proportion of the calculation interval for which it is present. A taxon that is present for all of a calculation interval adds one to the diversity for that interval and one that is present for only half of an interval adds 0.5 to the value of diversity for that interval. Figure 1 shows a simple case. Taxon A would contribute 1.0 to the diversity of interval 4, taxon B would contribute 0.5, and taxon C would contribute 0.75. In a simple count, as used by Sepkoski (1978), diversity would be measured as 3.0. The problem with this method is that measured diversity is positively correlated wirth the arbitrarily chosen calculation interval. The Wei and Kennett (1986) method gives a diversity of 2.25. Once the diversity, D, has been

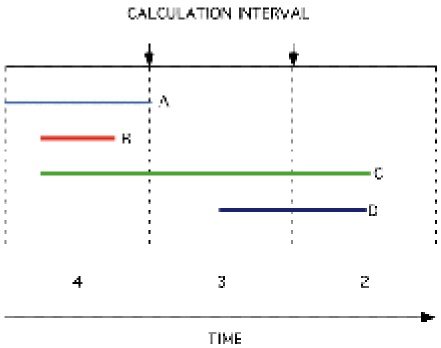

Figure 1.

recorded the number of originations (S), and extinctions (E) within each interval are calculated. On Table 1, S=3.0 for interval 4, S=1.0 for interval 3 and S=0.0 for interval 2. The values for E are 2.0, 0.0 and 2.0 for the same intervals. The ADAPTS software allows the user to set the calculation interval to whatever values are appropriate.

Rate Calculations. A rate calculation is a measure of the amount of change in a variable in a given interval of time. The values of D, S and E are used to calculate the taxonomic evolutionary rate metrics, using the following equations from Sepkoski (1978) and Lasker (1978);

- Rate of Speciation (r_s). $r_s = 1/D \times S/\text{delta } t$ (1)
- Rate of Extinction (r_e). $r_e = 1/D \times E/\text{delta } t$ (2)
- Rate of Diversification (r_d). $r_d = r_s - r_e$ (3)
- Rate of Turnover (r_t) (Lasker (1978). $r_t = r_s + r_e$ (4)
- Rate of Change in Diversity (delta D). delta $D = r_d \times D$ (5)

Raup and Boyajian (1988), Benton (1995), and Jablonski (1995) considered the various methods of quantifying extinction rates, but their comments apply to all diversity related metrics. They observed that using the absolute number of extinctions per interval is flawed, as it fails to take into account the number of taxa present. Correcting for diversity introduces errors in diversity estimation. Using a per interval approach (E/t) introduces timescale errors. Per taxon rates are in favour amongst theoreticians (Raup and Boyajian 1988; Gilinsky 1991; Hallam and Wignall 1997) and give a probability of extinction for each taxon in each period. However, this method combines the problems of errors in diversity and timescale measurements. Pease (1985, 1988a, 1988b, 1992) has considered potential problems with the mathematical expressions used in the calculation of extinction rates. Pease notes that as diversity, the denominator, approaches zero more rapidly in the geological past than the number of extinctions, the numerator, which could cause the reported decline in extinction rate as the Recent is approached, because dividing by a smaller denominator will give in a larger result. Pease (1992) pointed out that the "Pull of the Recent" (Raup 1979) could compound the problem, by inflating diversity close to the Recent, which could result in an artificial decline in extinction rates due to inflated estimates of diversity.

Survivorship Analysis

All methods of survivorship analysis used by ADAPTS require the generation of life tables (see Table 2). The first column shows the age classes, the second column contains the number of taxa that went extinct in that interval, the third column shows the survivors at the start of the interval, and the final column is the extinction rate for that interval. The mortality rate is calculated with the expression $q_x = d_x/l_x$. This example was designed to show a constant probability of extinction. The survivorship curve is constructed as a log-linear plot of age class against the log of the number of survivors at the start of each interval, after Van Valen (1973a). Van Valen proposed "The Law of Constant Extinction" based upon the linear nature of the survivorship curves that he generated from data. Linearity implies a constant rate of extinction and hence the probability of extinction of a taxon should be invariant with respect to its age.

Raup (1975) named this hypothesis "Van Valen's Law". However, he also noted that there were some methodological problems with Van Valen's analysis. Raup's analysis of the ammonoid Family data indicated a nonlinear extinction pattern, as shown by his use of Epstein's Test. In trying to account for the discrepancy Raup observed that although the first x value in life tables is 0.0, most of Van Valen's plots do not start at 0.0, but at 1.0, effectively underweighting the lack of extinctions amongst short lived taxa. Raup manipulated the ammonoid Family data by adding a number of short-lived taxa and this modified data "passed" Epstein's Test. Sepkoski (1975) demonstrated that the distribution of stage lengths was log-normal with a positive skew (Sepkoski 1975; Figures 1 A-D). Plotting survivorship curves on this framework generated curves with flat tops and near-linear sloping limbs (Sepkoski 1975; Figures 2 A-C). Many of Van Valen's plots have this shape. Modern timescales, such as Harland et al. (1990), try to standardize stage lengths, thus removing much of this bias. Sepkoski also estimated the preservation potential of the shape of survivorship curves and found that it was possible for the true shape to be reconstructed with only 20% of taxa in a group, if preservation potential was sufficiently high (>97%). However, once preservation potential started to decrease, the shape became distorted, unless sampling improved. This effect was most pronounced for concave survivorship curves, that recorded an age-decreasing risk of extinction.

Corrected Survivorship Score (CSS). One of the drawbacks of the dynamic survivorship method is that for the shape of the curve to reflect an age-dependent pattern extinction rates must be stochastically constant in real time. To correct for variation in real time extinction rates, Pearson (1992, 1995) introduced the CSS. The CSS is calculated with this formula:

$$\text{CSS} = L \times R_e\ (\text{extant}) / R_e\ (\text{total}) \quad (6)$$

where L is the longevity of the taxon, Re (extant) is the average rate of extinction for the duration of the taxon and Re (total) is the average rate of extinction for the whole dataset. The CSS for each taxon is calculated and then the survivorship analysis proceeds as normal. As R_e (extant) and R_e (total) are required to calculate the CSS, ADAPTS will automatically engage the taxonomic diversity routines if the user requests the CSS.

Extinction Intensity Survival Score (EISS). The use of time-averaged rates for examining patterns of extinction presents a problem. Although the time when an extinction took place is instantaneous, its influence is spread across the whole calculation interval. Taxa that originate after, or go extinct before, an event, but within the same calculation interval, are treated as though they were present during the event, thus adding "noise" to the CSS calculations. Pearson (1995, p. 122) suggested a refinement of the CSS, whereby longevity is measured in extinction events survived, with each extinction event adding 1/D to the longevity of each taxon surviving the event. This is basically equivalent to the CSS, except it has the advantage of cutting down the "noise" arising from not specifiying the order of extinctions in each calculation interval. This method scores each taxon by of the number of extinctions it survives. The general scoring procedure follows (Figure 2):

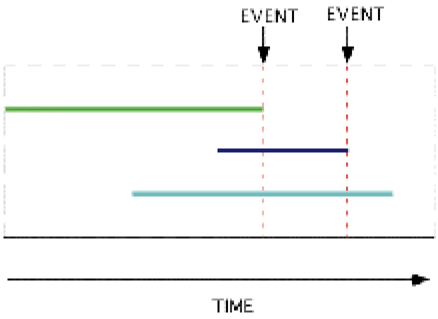

Figure 2.

- The taxon adds 0 to its EISS. A does not increase its EISS, while, as diversity is 3 at the time of A's demise B and C both add 1/D = 1/3. When B becomes extinct B adds 0 whereas C adds 1/2. In this simple case, the EISSs for B and C are 1/3 and 5/6 respectively.

- The taxon that goes extinct scores 0. All other taxa extant at the time of the event score 1/D. In this example, both B and C survive the extinction of A. A gains an EISS of 0.0, while, as diversity is 3.0 at the time of A's demise B and C both score 1/D = 0.33. When B becomes extinct B scores 0.0 while C scores 0.5. The EISSs for B and C are 0.33 and 0.83 respectively. Although B is much shorter lived it has an higher EISS, as it outlived A.

There is the special case in which two or more taxa go extinct simultaneously. This requires a modified procedure. This is illustrated in Figure 3.

- The diversity is calculated for the instant of the extinction event.
- In Case A the victims are awarded the mean score for all the taxa involved. Taxa A, B and C have the same LAD and each one scores (0+2/3+1/2)/3. The reasoning behind this is that although all three taxa have the same LOD, its is assumed that there is an order to the extinction of the three taxa, but that the order is unknown
- Any taxa that survive a multiple extinction event are scored as though the extinctions were ordered, as in Case B . If a fourth taxon D is present the EISS for A, B and C would now be (0 + 2/4 +1/3)/3. D would score 1/4+1/3+1/2. This is consistent with the statement that the extinctions are ordered, but the order is unknown.

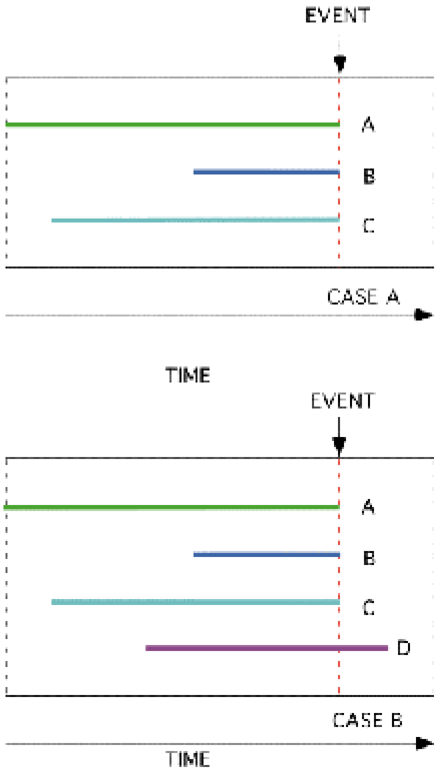

Figure 3.

The scoring methods presented here are not the only options. Another way of handling multiple extinctions would be to give a score of 0 to every taxon that becomes extinct during a multiple event. However, this would act only to systematically lower the scores of these taxa by a uniform amount, affecting the slope, but not the linear/nonlinear nature of the survivorship curve.

Epstein’s Total Life Method (Epstein’s Test). Test 3 of Epstein (1960a), is better known as Epstein’s Test in the palaeontological literature, after its use by Raup (1975). It is a statistical method for determining whether survivorship curves are linear. Epstein’s Test has been used in several previous studies, but some of these contain misprints of the actual equations (Wei and Kennett 1983; Pearson 1992, 1995, 1996). We also note that the program previously used by Pearson (1995) contained an error that caused the volume presented for the total lives to be inflated, but did not affect the efficacy of the test or the interpretation of the results. However, this error does not affect the scientific conclusion of that earlier work. Reference to Epstein (1960a) or Raup (1975) is recommended. The "total life" of a taxon is the summation of the longevities of all taxa that become extinct before the taxon becomes extinct. Longevities are ranked as shown below:

$$d_1 =< d_2 =< .... =< d_r$$

The total lives (T) are calculated as follows;

$T_1 = rd_1$
$T2 = d_1 + (n-1)d_2$
$T_3 = d_1 + d_2 + (n - 3 +1)d_3$
....
$Tr = d_1 + d_2 + ...+ (n - r +1)d_r$ (7)

To illustrate how the calculations are done take T_3 above and let $n = 50$, $d_1 = 5$ $d_2 = 6$, and $d_3 = 7$;

$T_3 = 5 + 6 + (50 - 3 +1) \times 7$
$= 5 + 6 + (48 \times 7)$
$= 347$

If the taxa under consideration exhibit linear survivorship, Epstein (1960a) proved that the sum of (r - 1) total lives will have a normal distribution. The theoretical mean is calculated thus;

$(r-1)T_r / 2$ (8)

Standard deviation is calculated by;

$[(r-1)T_r^2/12]^{1/2}$ (9)

The null hypothesis is tested by comparing the sum of (r-1) lives with the theoretical range, calculated thus;

theoretical mean ± (1.96) x standard deviation (10)

If the sum of (r-1) lives lies within the theoretical range, then the null hypothesis of duration-independent extinction is accepted at the 5% significance level. A worked example from Epstein (1960b) verified that ADAPTS carries out this test correctly.

The use of Epstein's Test removes the subjectivity of "fitting a line" on the survivorship curve. Cumulative curves can look very regular and thus be interpreted as linear by those unused to viewing them (Raup, 1975). However, statistical methods are not infallible and there will be cases where slightly nonlinear curves will pass as linear. Hoffman and Kitchell (1984) found that Epstein's Test can be sensitive to variation in the lower right hand portion of a survivorship plot, and that, for both simulated and real data sets, this could result in a curve that is linear for all but the last few points to be assessed as non-linear by Epstein's Test.

Ancestor-Descendant (A-D) Tests

The following tests are the ancestor-descendant (A-D) tests of Pearson (1998). They are used to quantify asymmetry in phylogenetic trees. The premise of the tests is that if there have been systematic variations in rates of extinction and/or speciation in a group this has the potential to be recorded as tree asymmetry.

A-D Extinction Test. This test is concerned with whether the ancestor or descendant of an A-D pair tends to go extinct first. The LODs of the pair are compared to see which one became extinct first. There are four possible outcomes (Figure 4):

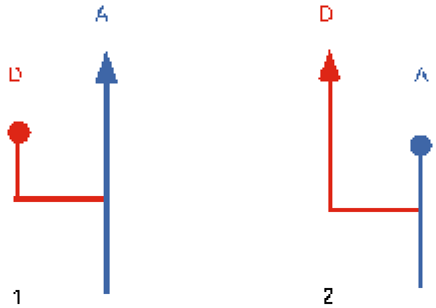

Figure 4.

1. Ancestor outlives descendant. (Figure 4, 1);
2. Descendant outlives ancestor. (Figure 4, 2);
3. Simultaneous extinction;
4. Indeterminate, as ancestor is unknown.

Only nodes that exhibit the first two cases are summed and subjected to a chi-squared analysis. If evolution is random then no statistically significant departure from the null hypothesis (that in half of the cases the ancestor should die before the descendant and vice versa) should occur.

Survivorship Control Test. This test represents a "control" on the A-D extinction test. If a pattern of age-dependent extinction exists in the data this would skew the chi-squared result. If this restricted test produces a similar chi-squared result then the age-dependency pattern is probably responsible for the bias (Pearson 1998). Each taxon is randomly assigned a new ancestor from the set of all taxa that were present at its time of origin. This procedure can select the actual ancestor as the random ancestor. Taxa whose ancestor is unknown retain this status, as it is assumed that there is a good taxonomic reason for this status. The altered data set is then analysed as above.

A-D Speciation Test. This test also compares A-D pairs, but in this case to look for bias in patterns of origination. All taxa in the tree are examined in turn and checked to see whether the taxon is descended from the ancestor or descendant of the previous branching event. This generates four possible outcomes (Figure 5):

1. Descended from a descendant (Figure 5, 1);
2. Descended from an ancestor (Figure 5, 2);
3. Unknown, due to ancestor being unknown;
4. Unknown, due to the ancestor of the A-D pair being subject to Case 3 above.

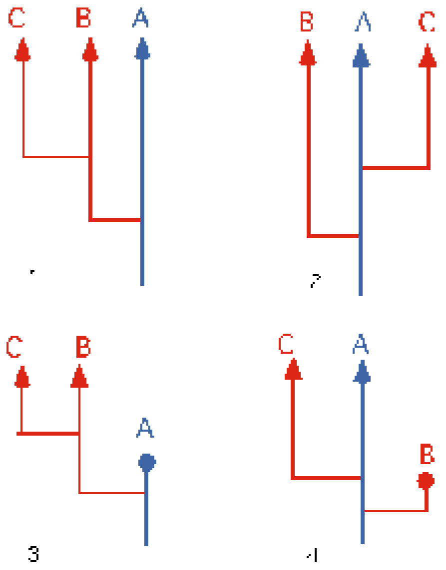

Figure 5.

As in the A-D extinction test, only cases 1 and 2 are used in the chi-squared calculation. The null hypothesis is that both members of the A-D pair are equally likely to give rise to new taxa in future.

A-D Speciation Test (Restricted). The speciation and extinction tests are not necessarily independent of each other. If a strong pattern emerges in the extinction test, this would result in a systematic bias in the speciation test. Greater longevity would result in more chances to give rise to daughter taxa, due to the fact that the surviving taxa are systematically longer-lived (Pearson 1998). To investigate this possibility the A-D speciation test (restricted) is used. The "restriction" criterion is that both the ancestor and descendant of the previous branching event must survive until the appearance of the third taxon. Cases in which this criterion is not met are excluded from the chi squared test. The possible cases for a taxon are:

1. Descended from descendant, with both ancestor and descendant of the previous branching still in existence. (Figure 5, 1);
2. Descended from ancestor, with both ancestor and descendant of the previous branching still in existence. (Figure 5, 2);
3. Indeterminate, due to ancestor being unknown;
4. Indeterminate, due to the ancestor of the A-D pair being subject to case 3 above;
5. Indeterminate due to the extinction of either the ancestor or descendant of the previous branching (Figure 5, 3-4).

Random Branching Model

To verify the ability of ADAPTS to detect known random patterns, a program for generating random phylogenetic trees, TREE GROWTH, was written, which can be found in Appendix 2. The power of stochastic models to generate patterns that resemble those from the fossil record was first highlighted by Raup et al. (1973) and has become a major area of interest, although the most ambitious attempt at interpreting the history of clades as random walks (Gould et al. 1977) was refuted by Stanley et al. (1981). The TREE GROWTH software uses a model in which the probabilities of speciation and extinction are constant, based upon the time homogeneous models of Simberloff et al. (1981), Raup (1985) and Pearson (1998). Such models are know as time homogeneous models. This program started with one taxon in the "clade" and the probabilities of branching and extinction were set at **p**=0.01. If a new taxon arose at time t, its ancestor was noted and it was then subjected to the branching/extinction algorithm at time t+1. A target zone for the number of taxa was defined and the program was designed to return only trees in which all taxa were "extinct" by the time the target number of taxa was reached, to avoid problems with censorship of ranges (Furbish et al. 1990). Once a suitable tree was generated, it was analysed with ADAPTS.

RESULTS

The results of the analysis of the random tree generated by TREE GROWTH are presented here as an example of the capabilities of ADAPTS both to analyse and identify a known random dataset and to demonstrate the utility of having a program that can interface with spreadsheet/graphing packages. The tree had 986 taxa, spread across 575 myr of simulation time and was analysed in 1 myr intervals. Results are broken down into the three main areas of analysis: taxonomic evolutionary rates, survivorship and tree asymmetry tests.

Taxonomic Evolutionary Rate Results

Figure 6 shows the results of the diversity of the random dataset through time and serves as a reminder of the power of such random walks to produce deterministic-looking patterns!

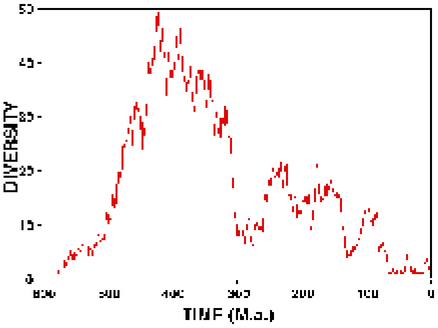

Figure 6.

Survivorship Results

Dynamic Survivorship. If there is no age-dependency and a stochastically constant rate of extinction, a linear survivorship curve should result. Figure 7 shows the curve for the 986 taxa and the value for Epstein’s Test (Table 3) is within the expected range of values.

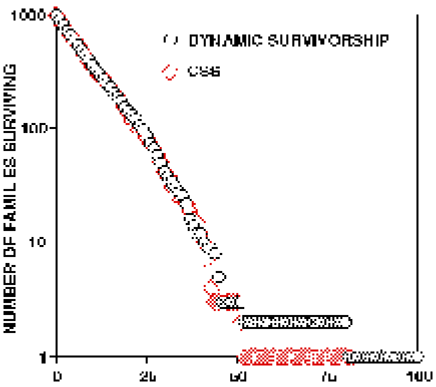

Figure 7.

Corrected Survivorship. The CSS corrects for systematic variation in real time extinction rates. Fluctuations in the per taxon rate exist in the model, as Figure 7 shows. However, these are a known random signal. Since the random model contains no non-stochastic variation in the extinction rate, the CSS will not be significantly different in shape to the dynamic survivorship curve.

Extinction Intensity Survival Score. The EISS is shown on a different plot (Figure 8), as it is not directly comparable to the other two measures of survivorship. A linear curve from this test means that there is no variation in the probability of a taxon becoming extinct, relative to the number of extinction events that it has experienced. The EISS curve is indistinguishable for linear by Epstein’s Test.

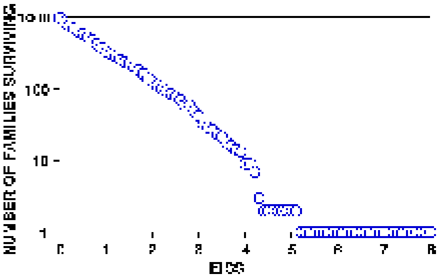

Figure 8.

Ancestor-Descendant (A-D) Test Results (Table 4)

A-D Extinction Test. The null model expectation for this test is that there is no significant difference in the number of ancestors that become extinct before their descendants and vice versa. The result generated for this test does not depart from the null hypothesis.

Survivorship Control Test. Pearson (1998) introduced this test as a control for age-dependent effects in a dataset. If all variation in survivorship was attributable to survivorship effects then the chi-squared results for the A-D extinction test and the Survivorship Control Test should be very similar. For the random tree, this was indeed the case, suggesting that any departure from a 50:50 ratio is the result of differential survivorship. The fact that this test performed as expected on a large random dataset confirms that it is capable of discriminating between genuine bias and the effects of differential survival.

A-D Speciation Test. If there is no bias for new taxa to preferentially arise from ancestors or descendants then no departure from the null model should appear. The results from the random tree are very close to the expected 50:50 ratio.

A-D Speciation Test (Restricted). The purpose of this test is to correct for any bias introduced into the unrestricted test by the non-independence of the extinction and speciation tests. However, if there is no bias there should be no large difference between the chi-squared values for the two speciation tests. The difference is 0.01 between this test and the unrestricted test.

DISCUSSION

The preceding section has reported the results of an ADAPTS analysis of a large dataset that was randomly generated. The main purpose of this exercise was to demonstrate that ADAPTS was able to identify known random patterns. From the results, which were all well within the expected ranges, it is clear that ADAPTS is functioning correctly. By manipulating a dataset of considerable size, the speed and efficacy of ADAPTS has been demonstrated. In a study of ammonoid Families, the data set comprised 243 taxa; around a quarter of the size of this test dataset. The automation of the A-D tests has also allowed confirmation of that the two control tests are performing as predicted. This increases confidence in the results published in Pearson (1998).

While the trials of ADAPTS have been successful, the fact that the QuickBasic language is incompatible with new Macintosh operating systems is a major problem. This state of affairs necessitates a conversion of ADAPTS to another language, preferably one that is suitable for IBM-PC as well as Macintosh users. This article allows some canvassing of the palaeontological community to gauge the level of potential support that might exist for further development of such a tool. The source code for ADAPTS and TREE GROWTH is available in Appendices I and II respectively and at:
http://geosci.uchicago.edu/paleo/csource/
http://palaeo.gly.bris.ac.uk/personnel/Pearson/ADAPTS.html.

These web locations also have a basic user manual. Any questions on the use of either of the programs should be addressed to the first author.

CONCLUSIONS

The ADAPTS software is a functional tool capable of taking much of the drudgery out of examining patterns of evolution in the fossil record. Testing of ADAPTS, through the use of a known random phylogeny has confirmed that the program functions as expected, as well as demonstrating the capability of ADAPTS to rapidly analyse large data sets.

ACKNOWLEDGMENTS

We would like to thank C.W. Stearns and R.T. Patterson for organising the session at the 1998 GSA Annual Meeting, Toronto, in which a summary of this work was presented. We are grateful to D. Henderson, M. Wills and S.J. Braddy for help with various programming matters and discussions. This manuscript was improved by comments from two anonymous reviewers. A. McGowan wishes to thank the Department of Earth Sciences, University of Bristol, where ADAPTS was written as part of a M.Sc. thesis, for extending support and facilities during the project and the Department of Geophysical Sciences, University of Chicago, where most of the paper was written. Some of this work was presented and discussed during a "Brown Bag" talk at the University of Chicago. Thanks to all those who took part in that seminar for the ensuing discussion.

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Table 1. Sample data table to illustrate how a spreadsheet should be set up for ADAPTS.

TAXON I.D.	FIRST APPEARANCE DATUM	LAST APPEARANCE DATUM	RANGE	ANCESTOR
1	575	564.1	10.9	0
2	574.4	555.7	18.7	1
3	565	542.9	22.1	1
4	564.6	563.8	0.8	2
5	564.1	563.7	0.4	1
6	562.3	552.7	9.6	2
7	560.2	551.9	8.3	2
8	558.4	552.6	5.8	2
9	557.4	556.5	0.9	7
10	555.2	554.9	0.3	8

Table 2. A hypothetical life table, showing constant probability of extinction, after Raup (1975).

Age class (x)	No. of extinctions in interval (dx)	Survivors at start of interval (lx)	Mortality rate (qx)
0	4000	10000	0.4
1	2400	6000	0.4
2	1440	3600	0.4
3	860	2160	0.4
4	526	1300	0.4
5	312	774	0.4
6	186	462	0.4
7	114	276	0.4
8	66	162	0.4
9	42	96	0.4
>=10	54	54	_ _

Table 3. Table showing the results of Epstein's Test for the three survivorship curves for the random tree.

ST	n	SUM (r-1) lives	UPPER LIMIT	LOWER LIMIT	LINEAR?
DYNAMIC	986	4787477.2	4940824.06	4596930.34	Y
CSS	986	4805056.27	4934671.26	4591206.38	Y
EISS	986	452943.89	475359.31	442273.17	Y

Table 4. Results of the A-D tests for the TREE GROWTH data. For the extinction tests, the "A" and "D" columns refer to the numbers of ancestors that outlive their descendants and vice versa. For the speciation tests the "A" and "D" columns tally the number of ancestors, in the previous branching event that gave rise to the next taxon, and vice versa.

ST	n	"A"	"D"	CHI SQUARED (df=1)	ACCEPT NULL HYPOTHESIS?
EXTINCTION	986	506	473	1.11	Y (p>0.1)
SURVIVORSHIP "CONTROL"	986	473	507	1.18	Y (p>0.1)
SPECIATION	986	489	495	0.04	Y (p>0.1)
SPECIATION (RESTRICTED)	986	334	328	0.05	Y (p>0.1)

APPENDIX I
LISTING OF THE ADAPTS PROGRAM CODE

The entire program listing for ADAPTS is reproduced here.
If you have a functioning version of QBasic on your Macintosh,
then you should be able to paste and cut this straight into a program file.
Words in block capitals, outside of quotation marks, are
commands in the QBasic language. Any line with REM at the start
is a note that has no effect on what the program does.
Due to the page size constraints some program lines are "wrapped around".
This is a demonstration version, and as such has no error trapping.
A basic user manual is available at:

        http://geosci.uchicago.edu/paleo/csource/
        http:/paleo.gly.bris.ac.uk/micropal/micropalaeo/

which will explain what the contents of all the output columns are.

```
10 CLS
20 REM INTRO BOX
30 SH=SYSTEM (6) ’height
40 SW=SYSTEM (5) ’WIDTH
50 h% = 250
60 w% = 400
70 WINDOW 2,"WELCOME TO ADAPTS VERSION 1.0",((SW-w%)/1.5, (SH-h%)/1.5)-((SW-
w%)/1.5 +w%, (SH-h%)/1.5+h%),1
80 TEXTFONT 20:TEXTSIZE 36:TEXTFACE(30): MOVETO 80,30: PRINT "A.D.A.P.T.S."
90 TEXTFONT 4:TEXTSIZE 10:TEXTFACE(1): MOVETO 5,50: PRINT "Analysis of
Diversity, Asymmetry of Phylogenetic Trees"
100 MOVETO 120,65: PRINT " and Survivorship."
110 TEXTFONT 4 :TEXTSIZE 12: TEXTFACE(5): MOVETO 130,80:PRINT "INTRODUCTION"
120 TEXTSIZE 10: TEXTFACE (0): PRINT "ADAPTS is a program for analysing;"
130 PRINT "Taxonomic evolutionary rates."
140 PRINT "Taxonomic survivorship."
150 PRINT  "Phylogentic tree symmetry."
160 PRINT
170 PRINT "ADAPTS was written by Alistair McGowan as part"
180 PRINT "of a MSc. project (1998) supervised by Paul Pearson,
190 PRINT "at the Department of Earth Sciences, University of Bristol "
200 PRINT "VISIT OUR WEBSITE at www.
210 PRINT "A full user manual is available at this site."
220 BUTTON 1,1,"PROCEED", (150,225)-(240,245),1
230 WHILE DIALOG(0)<>1 :WEND
240     IF DIALOG (1)=1 THEN WINDOW CLOSE 2
250     CLS
260 REM  SET UP BOX
270 SH=SYSTEM (6) ’height
280 SW=SYSTEM (5) ’WIDTH
290 h% = 250
300 w% = 400
310 WINDOW 2,"SET-UP PARAMETERS",((SW-w%)/1.5, (SH-h%)/1.5)-((SW-w%)/1.5 +w%,
(SH-h%)/1.5+h%),1
320 TEXTFONT 4 :TEXTSIZE 12: TEXTFACE(5): MOVETO 130,20:PRINT "SET-UP
PARAMETERS"
330 PRINT
340 TEXTSIZE 10: TEXTFACE (0): PRINT "The series of windows that follows will
help
```

```
350 PRINT "you to set up the parameters for your analysis."
360 PRINT "When you are finished on each screen click on  ’proceed’."
370 PRINT "Consult the ADAPTS manual FOR further help."
380 PRINT
390 PRINT "Enter the number of taxa in your dataset below."
400 PRINT
410 INPUT "NUMBER OF TAXA",n%
420 BUTTON 1,1,"PROCEED", (150,225)-(240,245),1
430 WHILE DIALOG(0)<>1 :WEND
440     IF DIALOG (1)=1 THEN WINDOW CLOSE 2
450     CLS
460 REM  calculation interval BOX
470 SH=SYSTEM (6) ’height
480 SW=SYSTEM (5) ’WIDTH
490 h% = 250
500 w% = 400
510 WINDOW 2,"SET-UP THE CALCULATION INTERVAL",((SW-w%)/1.5, (SH-h%)/1.5)-
((SW-w%)/1.5 +w%, (SH-h%)/1.5+h%),1
520 TEXTFONT 4 :TEXTSIZE 12: TEXTFACE(5): MOVETO 100,20:PRINT "SET THE
CALCULATION INTERVAL"
530 PRINT
540 TEXTSIZE 10: TEXTFACE (0): PRINT "This window allows you to define the
calculation interval."
550 REM PRINT "If you only want to use the A-D tests just hit ’return’."
560 REM PRINT "Otherwise a value MUST be entered."
570 PRINT "Fractions (e.g. 0.5) are permissible."
580 PRINT "If the calculation interval is set to more than ’1’"
590 PRINT "the value of start point-minus end point"
600 PRINT "(the NEXT two parameters you will be asked for)"
610 PRINT "must be EXACTLY divisible by the value of"
620 PRINT"the calculation interval or else the output may be incomplete."
630 PRINT
640 PRINT "Enter the calculation interval."
650 PRINT
660 INPUT "CALCULATION INTERVAL",timestep
670 BUTTON 1,1,"PROCEED", (150,225)-(240,245),1
680 WHILE DIALOG(0)<>1 :WEND
690     IF DIALOG (1)=1 THEN WINDOW CLOSE 2
700     CLS
710 REM  start point BOX
720 SH=SYSTEM (6) ’height
730 SW=SYSTEM (5) ’WIDTH
740 h% = 250
750 w% = 400
760 WINDOW 2,"SET THE START POINT",((SW-w%)/1.5, (SH-h%)/1.5)-((SW-w%)/1.5
+w%, (SH-h%)/1.5+h%),1
770 TEXTFONT 4 :TEXTSIZE 12: TEXTFACE(5): MOVETO 100,20:PRINT"SET THE
STARTING POINT"
780 PRINT
790 TEXTSIZE 10: TEXTFACE (0): PRINT "This window allows you to define the
start point."
800 REM PRINT "If you only want to use the A-D tests just hit ’return’."
810 PRINT "Set the start point"
820 PRINT "equal to or greater than the oldest FAD in your dataset."
830 PRINT
```

```
840 INPUT "START POINT",start
850 BUTTON 1,1,"PROCEED", (150,225)-(240,245),1
860     WHILE DIALOG(0)<>1 :WEND
870     IF DIALOG (1)=1 THEN WINDOW CLOSE 2
880 CLS
890 REM  end point BOX
900 SH=SYSTEM (6) 'height
910 SW=SYSTEM (5) 'WIDTH
920 h% = 250
930 w% = 400
940 WINDOW 2,"SET THE END POINT",((SW-w%)/1.5, (SH-h%)/1.5)-((SW-w%)/1.5 +w%,
(SH-h%)/1.5+h%),1
950 TEXTFONT 4 :TEXTSIZE 12: TEXTFACE(5): MOVETO 100,20:PRINT"SET THE END
POINT"
960 PRINT
970 TEXTSIZE 10: TEXTFACE (0): PRINT "This window allows you to define the
end point."
980 REM PRINT "If you only want to use the A-D tests just hit 'return'."
990 REM PRINT "Otherwise set the end point"
1000 PRINT "Remeber that the start point minus the end point"
1100 PRINT "must be exactly divisible by the calculation interval."
1110 PRINT "Check this now before entering the end point"
1120 PRINT
1130 PRINT "Calculation interval:"timestep
1140 PRINT
1150 PRINT "Start point:"start
1160 PRINT
1170 PRINT "Now enter your end point value"
1180 PRINT
1190 INPUT "END POINT",ends
1200 BUTTON 1,1,"PROCEED", (150,225)-(240,245),1
1300 WHILE DIALOG(0)<>1 :WEND
1400 IF DIALOG (1)=1 THEN WINDOW CLOSE 2
1410 CLS
1420 REM  procedure selection BOX
1430 DIM routines$(8)
1440 SH=SYSTEM (6) 'height
1450 SW=SYSTEM (5) 'WIDTH
1460 h% = 250
1470 w% = 400
1480 WINDOW 2,"PROCEDURE SELECTION WINDOW",((SW-w%)/1.5, (SH-h%)/1.5)-((SW-
w%)/1.5 +w%, (SH-h%)/1.5+h%),1
1490 TEXTFONT 4 :TEXTSIZE 12: TEXTFACE(5): MOVETO 150,20:PRINT"SELECT
PROCEDURES"
1500 PRINT
1510 TEXTSIZE 10: TEXTFACE (0): PRINT "This window allows you to choose the
procedures you want."
1520 BUTTON 1,1, "TAXONOMIC EVOLUTIONARY RATES", (20,60)-(400,75),2
1530 BUTTON 2,1, "DYNAMIC SURVIVORSHIP", (20,80)-(400,95),2
1540 BUTTON 3,1, "CSS", (20,100)-(400,115),2
1550 BUTTON 4,1, "ESS", (20,120)-(400,135),2
1560 BUTTON 5,1, "A-D EXTINCTION TEST", (20,140)-(400,155),2
1570 BUTTON 6,1, "A-D SURVIVORSHIP CONTROL TEST", (20,160)-(400,175),2
1580 BUTTON 7,1, "A-D SPECIATION TEST", (20,180)-(400,195),2
1590 BUTTON 8,1, "A-D SPECIATION (RESTRICTED) TEST", (20,200)-(400,215),2
```

```
1600 BUTTON 9,1,"PROCEED", (150,225)-(240,245),1
1610 WHILE BUTTON (9)<>2
1620 WHILE DIALOG(0)<>1:WEND
1630 x= DIALOG (1)
1640 IF x =1 THEN
1650     IF BUTTON (x) = 1 THEN
1660        BUTTON x,2
1670        routines$(x) = "y"
1680     GOTO 1610
1690 END IF
1700 END IF
1710 IF x = 1 THEN
1720     IF BUTTON (x) = 2 THEN
1725         IF BUTTON(3) = 1 THEN
1730             BUTTON x,1
1740             routines$(x) = ""
1750             GOTO 1610
1755         END IF
1760     END IF
1770 END IF
1780 IF x =2 THEN
1790     IF BUTTON (x) = 1 THEN
1800         BUTTON x,2
1810         routines$(x) = "y"
1820         GOTO 1610
1830     END IF
1840 END IF
1850 IF x = 2 THEN
1860     IF BUTTON (x) = 2 THEN
1870         BUTTON x,1
1880         routines$(x) = ""
1890         GOTO 1610
1900     END IF
1910 END IF
1920 IF x =3 THEN
1930     IF BUTTON (x) = 1 THEN
1940         BUTTON x,2
1950         BUTTON 1,2
1960         routines$(x) = "y"
1970         routines$(1) = "y"
1980         GOTO 1610
1990     END IF
2000 END IF
2010 IF x = 3 THEN
2020     IF BUTTON (x) = 2 THEN
2030         BUTTON x,1
2040         BUTTON 1,1
2050         routines$(x) = ""
2060         routines$(1)=""
2070         GOTO 1610
2080    END IF
2090 END IF
2100 IF x =4 THEN
2110     IF BUTTON (x) = 1 THEN
2120         BUTTON x,2
```

```
2130         routines$(x) = "y"
2140         GOTO 1610
2150     END IF
2160 END IF
2170 IF x = 4 THEN
2180     IF BUTTON (x) = 2 THEN
2190         BUTTON x,1
2200         routines$(x) = ""
2210         GOTO 1610
2220     END IF
2230 END IF
2240 IF x =5 THEN
2250     IF BUTTON (x) = 1 THEN
2260         BUTTON x,2
2270         routines$(x) = "y"
2280         GOTO 1610
2290     END IF
2300 END IF
2310 IF x = 5 THEN
2320     IF BUTTON (x) = 2 THEN
2330         BUTTON x,1
2340         routines$(x) = ""
2350         GOTO 1610
2360     END IF
2370 END IF
2380 IF x =6 THEN
2390     IF BUTTON (x) = 1 THEN
2400         BUTTON x,2
2410         routines$(x) = "y"
2420         GOTO 1610
2430     END IF
2440 END IF
2450 IF x = 6 THEN
2460     IF BUTTON (x) = 2 THEN
2470         BUTTON x,1
2480         routines$(x) = ""
2490         GOTO 1610
2500     END IF
2510 END IF
2520 IF x =7 THEN
2530     IF BUTTON (x) = 1 THEN
2540         BUTTON x,2
2550         routines$(x) = "y"
2560         GOTO 1610
2570     END IF
2580 END IF
2590 IF x = 7 THEN
2560     IF BUTTON (x) = 2 THEN
2570         BUTTON x,1
2580         routines$(x) = ""
2590         GOTO 1610
2600     END IF
2610 END IF
2620 IF x =8 THEN
2630     IF BUTTON (x) = 1 THEN
```

```
2640         BUTTON x,2
2650         routines$(x) = "y"
2660         GOTO 1610
2670     END IF
2680 END IF
2690 IF x = 8 THEN
2700     IF BUTTON (x) = 2 THEN
2710         BUTTON x,1
2720         routines$(x) = ""
2730         GOTO 1610
2740      END IF
2750 END IF
2760 IF x = 9 THEN
2770     BUTTON x,2
2780 END IF
2790 WEND
2800 WINDOW CLOSE 2
2810 backcolor 273
2820 forecolor 38
2830 TEXTFONT 8
2840 TEXTSIZE 20


3000 REM arrays for clipboard data
3010 DIM SHARED number(n%)
3020 DIM SHARED ancestor (n%)
3030 DIM SHARED fad(n%)
3040 DIM SHARED lod(n%)
3050 DIM SHARED ranges(n%)
3060 CLS
3070 REM transfers data from clipboard
3080 OPEN "clip:" FOR INPUT AS #1
3090 REM loops until all clipboard data moved
3100 WHILE NOT EOF(1)
3110  INPUT #1, a,b,c,d,e
3120    counter = counter+1
3130    number (counter) = a
3140    fad(counter) = b
3150    lod(counter) = c
3160    ranges(counter) = d
3170    ancestor(counter) = e
3180 WEND
3190 CLOSE #1
3200 REM dimensions arrays for time dependent routines
3210 slots = (start - ends)/timestep
3220 IF slots >= 12 AND slots >=n% THEN
3230 o = slots
3240 ELSEIF n% >= 12 AND n% >= slots THEN
3250     o = n%
3260 ELSE
3270   o = 12
3280 END IF
3290 REM output arrays for routines
3300 DIM SHARED in (o)
3310 DIM SHARED div (o)
```

```
3320 DIM SHARED sp (o)
3330 DIM SHARED ex (o)
3340 DIM SHARED rs (o)
3350 DIM SHARED re (o)
3360 DIM SHARED rd (o)
3370 DIM SHARED rt(o)
3380 DIM SHARED delt (o)
3390 DIM SHARED csss(o)
3400 DIM SHARED cep(n%)
3410 DIM SHARED fsss(o)
3420 DIM SHARED sur(o)
3430 DIM SHARED fep(n%)
3440 DIM SHARED ade$ (o)
3450 DIM SHARED ran (o)
3460 DIM SHARED ader$ (o)
3470 DIM SHARED ads$ (o)
3480 DIM SHARED adsr$ (o)
3490 DIM SHARED chi(o)
3500 IF routines$(1) = "y" THEN
3510  CALL metrics
3520 END IF
3530 REM arrays for dynamic survivorship
3540 DIM SHARED acvv(o)
3550 DIM SHARED ltvv (o)
3560 DIM SHARED vvf (o)
3570 DIM SHARED rvv (o)
3580 DIM SHARED epvv(o)
3590 IF routines$(2) ="y" THEN
3600  CALL vanvalen
3610  CALL epsteinvv
3620 END IF
3630 REM dimensions arrays for CSS
3640 DIM SHARED accss (o)
3650 DIM SHARED cssf(o)
3660 DIM SHARED ltc (o)
3670 DIM SHARED rcss (o)
3680 DIM SHARED epc(o)
3690 IF routines$(3) = "y" THEN
3700    REM calculate average rate of extinction for entire period for use in
CSS
3710    FOR g = 1 TO slots
3720        sum = sum + re(g)
3730    NEXT g
3740    avre = sum/slots
3750  CALL CSS
3760  CALL csstable
3770  CALL epsteincss
3780 END IF
3790 REM set up arrays for FSS
3800 DIM SHARED cfss(o)
3810 DIM SHARED fssf(o)
3820 DIM SHARED ltf(o)
3830 DIM SHARED rfss(o)
3840 DIM SHARED epf(o)
3850 IF routines$(4) = "y" THEN
```

```
3860    CALL fss
3870    CALL fsstable
3880    CALL epsteinfss
3890 END IF
3900 IF routines$(5) = "y" THEN
3910   CALL adetest
3920 END IF
3930 IF routines$(6) = "y" THEN
3940   CALL random
3950   CALL adertest
3960 END IF
3970 IF routines$(7) = "y" THEN
3980    CALL adstest
3990 END IF
4000 IF routines$(8) = "y" THEN
4100   CALL adsrtest
4200 END IF
4210 CLS
4220 OPEN "clip:" FOR OUTPUT AS #1
4230 FOR z = 1 TO o
   WRITE #1,
in(z),div(z),sp(z),ex(z),rs(z),re(z),rd(z),rt(z),delt(z),acvv(z),vvf(z),ltvv(
z),rvv(z),epvv(z),csss(z),accss(z),
cssf(z),ltc(z),rcss(z),epc(z),fsss(z),sur(z),cfss(z),fssf(z),ltf(z),rfss(z),e
pf(z),ade$(z),ran(z),ader$(z), ads$(z),adsr$(z),chi(z)
4240 NEXT z
4250 CLOSE #1
42600 CLS
4270 REM  output BOX
4280 SH=SYSTEM (6) ’height
4290 SW=SYSTEM (5) ’WIDTH
4300 h% = 250
4310 w% = 400
4320 WINDOW 2,"OUTPUT",((SW-w%)/1.5, (SH-h%)/1.5)-((SW-w%)/1.5 +w%, (SH-
h%)/1.5+h%),1
4330 TEXTFONT 4 :TEXTSIZE 12: TEXTFACE(5): MOVETO 150,20:PRINT"OUTPUT"
4340 PRINT
4350 TEXTSIZE 10: TEXTFACE (0): PRINT "Follow this procedure to transfer your
results to a spreadsheet."
4360 PRINT
4370 PRINT "1. Quit ADAPTS"
4380 PRINT "2. Open the spreadsheet package of your choice."
4390 PRINT "3. Once your worksheet is open use the PASTE command."
4400 BUTTON 1,1,"PROCEED", (150,225)-(240,245),1
4410 WHILE DIALOG(0)<>1 :WEND
4420 IF DIALOG (1)=1 THEN WINDOW CLOSE 2

5000 REM subroutines follow
5010 REM carries out diversity related calculations
5020 SUB metrics STATIC
5025 PRINT "calculating taxonomic evolutionary rates"
5030 SHARED n%,start,slots,in,timestep,div,sp,ex,rs,re,rd,rt,delt
5040 REM loop for each time step
5050 FOR loop = 1 TO slots
5060    interval = start -timestep*c
```

```
5070    REM activates diversity calculations
5080    w = w+1
5090    c=c+1
5100    in(w) = interval
5110    REM calculates absolute diversity
5120 diversity=0
5130     FOR taxa = 1 TO n%
5140        IF fad (taxa) =< interval AND fad (taxa) > interval-timestep THEN
5150            IF lod (taxa) >interval-timestep THEN
5160                diversity = diversity + (fad(taxa) -
lod(taxa))*(1/timestep)
5170            END IF
5180        END IF
5190    IF fad (taxa) =< interval AND fad (taxa) > interval-timestep THEN
5200        IF lod (taxa) =< interval-timestep THEN
5210            diversity=diversity + (fad (taxa) - (interval-
timestep))*(1/timestep)
5220        END IF
5230    END IF
5240    IF fad (taxa) > interval THEN
5250        IF lod (taxa) =< interval-timestep THEN
5260            diversity=diversity + (timestep)*(1/timestep)
5270        END IF
5280    END IF
5290    IF fad (taxa) > interval THEN
5300        IF lod (taxa) < interval AND lod (taxa) >interval-timestep THEN
5310             diversity=diversity + (interval - lod (taxa))*(1/timestep)
5320        END IF
5330    END IF
5340 NEXT taxa
5350 div(w) = diversity

5360 REM sums number of originations in interval
5370 origins =0
5380 FOR taxa= 1 TO n%
5390     IF  fad(taxa)>interval-timestep AND fad(taxa)=<interval THEN
5400         origins = origins +1
5500     ELSE
5510         origins  = origins
5520     END IF
5530 NEXT taxa
5540 sp(w) = origins

5550 REM sums number of extinctions in each time interval
5560 extinctions = 0
5570 FOR taxa = 1 TO n%
5580     IF lod(taxa) < interval AND lod (taxa) >= interval-timestep THEN
5590         extinctions = extinctions +1
5600     ELSE
5610         ext = extinctions
5620     END IF
5630 NEXT taxa
5640 ex(w) = extinctions

5650 REM calculates rate of speciation
```

```
5660 IF diversity=0 THEN
5670     Rspec = 0
5680 ELSE
5690     Rspec = (1/diversity)*(origins/timestep)
5710 END IF
5720 rs(w) = Rspec

5730 REM calculates total rate of extinction
5740 IF diversity = 0 THEN
5750     Rext = 0
5760 ELSE
5770     Rext = (1/diversity)*(extinctions/timestep)
5780 END IF
5790 re(w) = Rext

5800 REM calculates the rate of diversification of taxa
5810 df= Rspec-Rext
5820 rd (w) = df

5830 REM calculates the turnover of taxa in each interval
5840 turn= Rspec+Rext
5850 rt(w) = turn

5860 REM calculates change in diversity per interval
5870 delta = diversity*df
5880 delt(w) = delta
5890 NEXT loop
5900 PRINT "taxonomic evolutionary rates completed"
5905 PRINT
5910 END SUB

6000 REM calculates lifetable and rates for van valen
6010 SUB vanvalen STATIC
6015 PRINT "calculating dynamic survivorship lifetable"
6020 SHARED n%,slots,ltvv,timestep,vvf,acvv,rvv
6030 REM calculates life table
6040 FOR class = 1 TO slots
6050 failures = 0
6060 acvv(class) = (class*timestep)-timestep
6070     FOR taxa = 1 TO n%
6080        IF ranges(taxa)>= (class*timestep) -timestep AND ranges
(taxa)<class*timestep THEN
6090            failures = failures + 1
6100            totals = totals+1
6110        ELSE
6120            failures = failures
6130            totals = totals
6140        END IF
6150    NEXT taxa
6160     vvf(class) = failures
6170     ltvv(class) = (n%-totals)+failures
6180        IF (n%-totals)+failures = 0 THEN
6190            rate = 0
6200        ELSE
6210            rate = failures/((n%-totals)+failures)
```

```
6200        END IF
6210        rvv (class) = rate
6220 NEXT class
6230 PRINT"dynamic survivorship lifetable completed"
6235 PRINT
6240 END SUB

6250 REM epstein’s test for dynamic surviorship data
6260 SUB epsteinvv STATIC
6265 PRINT "calculating Epstein’s Test (dynamic survivorship)"
6270 SHARED n%,epvv
6280 REM calculate total lives
6290 unsort = 0
6300 FOR i = 1 TO (n%-1)
6310    x = ranges(i)
6320    y = ranges (i+1)
6330    IF y<x THEN
6340        ranges(i+1) =x
6350        ranges(i) = y
6360    END IF
6370 NEXT i
6380 FOR i = 1 TO (n%-1)
6390    x = ranges(n%-i)
6400    y = ranges(n%+1-i)
6410    IF y<x THEN
6420        ranges(n%+1-i) = x
6430        ranges(n%-i) = y
6440        unsort = unsort+1
6450    END IF
6460 NEXT i
6470 IF unsort >0 THEN
6480    GOTO 6290
6490 END IF
6500 total = 0
6510 FOR ep = 1 TO n%
6520    IF (ep) = 1 THEN
6530        term = n%*ranges(1)
6540    END IF
6550    IF (ep) = 2 THEN
6560        term = ranges(1)+(n%-1)*ranges(2)
6570    END IF
6580    IF (ep) >2 THEN
6590        dsum = 0
6600        FOR j = 1 TO ep-1
6610            dsum = dsum + ranges(j)
6620        NEXT j
6630        term = dsum + (n%-ep+1)*ranges(ep)
6640    END IF
6650    total = total+term
6660 NEXT ep
6670 sum = total-term
6680 epvv (1) = sum
6690 mean = ((n%-1)*term/2)
6700 epvv (4) = mean
6710 sd = SQR(((n%-1)*(term^2))/12)
```

```
6720 epvv (5) = sd
6730 con = 1.96*sd
6740 epvv (6) =con
6750 ucl = mean+con
6760 epvv (3) = ucl
6770 lcl = mean - con
6780 epvv (2) = lcl
6790 PRINT "Epstein’s Test (dynamic survivorship) completed"
6795 PRINT
6800 END SUB

7000 REM CSS CALCULATIONS
7010 SUB CSS STATIC
7015 PRINT "calculating CSS"
7020 SHARED n%,slots,start,timestep,csss,cep,avre
7030 FOR taxon = 1 TO n%
7040    FOR sum = 1 TO slots
7050    fract = 0
7060    value = 0
7070    interval = start-timestep*c
7080        IF fad(taxon)=<interval AND fad(taxon)>interval-timestep THEN
7090            IF lod(taxon)>interval-timestep THEN
7100                fract = fract+(fad(taxon)-lod(taxon))
7110            END IF
7120        END IF
7130    IF fad (taxon)=< interval AND fad(taxon)>interval-timestep THEN
7140        IF lod(taxon)=<interval-timestep THEN
7150            fract = fract+(fad(taxon)-(interval-timestep))
7160        END IF
7170    END IF
7180    IF fad(taxon)>interval THEN
7190        IF lod(taxon)=< interval-timestep THEN
7200            fract = fract+(timestep)
7210        END IF
7220    END IF
7230    IF fad(taxon)> interval THEN
7240        IF lod (taxon) < interval AND lod(taxon)>interval-timestep THEN
7250            fract =fract + (interval-lod(taxon))
7260        END IF
7270    END IF
7280    value = fract*re(sum)
7290    score = score+value
7300    c = c+1
7310    NEXT sum
7320    range = ranges(taxon)
7330    extant = score/range
7340    corrected  = range*(extant/avre)
7350    csss(taxon) = corrected
7360    cep(taxon) = corrected
7370    score = 0
7380    c =0
7390 NEXT taxon
7400 PRINT "CSS completed"
7405 PRINT
7410 END SUB
```

```
7420 REM CREATES LIFETABLE FOR CSS DATA
7430 SUB csstable STATIC
7435 PRINT "calculating CSS lifetable"
7440 SHARED n%,slots,ltc,timestep,cssf,accss,rcss
7450 REM calculates life table
7460 FOR class = 1 TO slots
7470 fails = 0
7480 accss(class) = (class*timestep)-timestep
7490 FOR taxa = 1 TO n%
7500    IF csss(taxa)>= (class*timestep)-timestep AND csss
(taxa)<class*timestep THEN
7510        fails = fails + 1
7520        totals = totals+1
7530    ELSE
7540        fails = fails
7550        totals = totals
7560    END IF
7570 NEXT taxa
7580 ltc(class) = (n%-totals)+fails
7590 cssf(class) = fails
7600 IF (n%-totals)+fails = 0 THEN
7610     rate = 0
7620 ELSE
7630     rate = fails /((n%- totals)+fails)
7640 END IF
7650 rcss(class) = rate
7660 NEXT class
7670 PRINT "CSS lifetable completed"
7675 PRINT
7680 END SUB

7690 REM epstein’s test for CSS data
7700 SUB epsteincss STATIC
7705 PRINT "calculating Epstein’s Test (CSS)"
7710 SHARED n%,epc
7720 REM try to remove line numbers
7730 unsort = 0
7740 FOR i = 1 TO (n%-1)
7750    x = cep(i)
7760    y = cep (i+1)
7770    IF y<x THEN
7780        cep(i+1) =x
7790        cep(i) = y
7800    END IF
7810 NEXT i
7820 FOR i = 1 TO (n%-1)
7830    x = cep(n%-i)
7840    y = cep(n%+1-i)
7850    IF y<x THEN
7860        cep(n%+1-i) = x
7870        cep(n%-i) = y
7890        unsort = unsort+1
7900    END IF
7910 NEXT i
```

```
7920 IF unsort >0 THEN
7930    GOTO 7730
7940 END IF
7950 total = 0
7960 FOR ep = 1 TO n%
7970    IF (ep) = 1 THEN
7980        term = n%*cep(1)
7990    END IF
8000    IF (ep) = 2 THEN
8010        term = cep(1)+(n%-1)*cep(2)
8020    END IF
8030    IF (ep) >2 THEN
8040        dsum = 0
8050        FOR j = 1 TO ep-1
8060            dsum = dsum + cep(j)
8070        NEXT j
8080        term = dsum + (n%-ep+1)*cep(ep)
8090    END IF
8100    total = total+term
8110 NEXT ep
8120 sum = total-term
8130 epc(1) =sum
8140 mean = ((n%-1)*term/2)
8150 epc(4) =mean
8160 sd = SQR(((n%-1)*(term^2))/12)
8170 epc(5) = sd
8180 con = 1.96*sd
8190 epc(6) = con
8200 ucl = mean+con
8210 epc(3) = ucl
8220 lcl = mean - con
8230 epc (2) = lcl
8240 PRINT "Epstein’s Test (CSS) completed"
8245 PRINT
8250 END SUB

8300 REM calculates ESS
8310 SUB fss STATIC
8315 PRINT "calculating ESS"
8320 SHARED n%,fsss,fep,sur
8330 FOR taxon = 1 TO n%
8340 fad = fad(taxon)
8350 lod =lod(taxon)
8360 suma=0
8370 sumb=0
8380 sumc=0
8390 count = 0
8400 d=0
8410 ds=0
8420 w=0
8430 sur = 0
8440    FOR taxa = 1 TO n%
8450            div = 0
8460        IF lod(taxa)=<fad AND lod(taxa)>=lod THEN
8470             comp =lod(taxa)
```

```
8480            FOR tax = 1 TO n%
8490                 IF fad(tax)>=comp AND lod(tax) =< comp THEN
8500                     div = div +1
8510                 END IF
8520             NEXT tax
8530         di = div
8540        IF lod(taxa) = comp THEN
8550            FOR ta = 1 TO n%
8560                IF lod(ta) = comp THEN
8570                c=c+1
8580                END IF
8590            NEXT ta
8600        IF div=c  AND c>1 THEN
8610            div = div-ds
8620            ds=ds+1
8630            IF div =< 0 THEN
8640                even = 0
8650            ELSEIF ds>c THEN
8660                even = 0
8670            ELSE
8680                even = (1/div)*(c-ds)
8690            END IF
8700            count = count+even
8710            suma =  count/di
8720            sur = sur+(1/c*.5)*(c-1)
8730        ELSEIF lod(taxon) = comp AND c>1 THEN
8740            div = div-w
8750            w=w+1
8760            IF div =<0 THEN
8770                even =0
8780            ELSEIF w>c THEN
8790                even = 0
8800            ELSE
8810                even = (1/div)*(c-w)
8820            END IF
8830            count = count+even
8840            suma = count /c
8850            sur = sur+(1/c*.5)*(c-1)
8860        END IF
8870        IF lod(taxon) < comp AND c=1 THEN
8880            IF div=<0 THEN
8890                score = 0
8900            ELSE
8910                score =1/div
8920            END IF
8930            sumb =sumb+score
8940            sur = sur+1
8950        ELSEIF lod(taxon) < comp AND c>1 THEN
8960        high =0
8970        FOR phena = 1 TO n%
8980            IF lod(phena) = comp THEN
8990                nu = number (phena)
9000                    IF nu > high THEN
9010                        high = nu
9020                    ELSE
```

```
9030                        high = high
9040                    END IF
9050            END IF
9060        NEXT phena
9070        IF taxa < high THEN
9080            score =0
9090        ELSEIF taxa = high THEN
9100            FOR f = 1 TO c
9110                score = 1/(div-d)
9120                d = d+1
9130                total = total+score
9140            NEXT f
9150                d = 0
9160                sur = sur+c
9170            END IF
9180            sumc = sumc+total
9190            total = 0
9200        END IF
9210    END IF
9220 END IF
9230    score = 0
9240    c = 0
9250    sum = suma+sumb+sumc
9260    NEXT taxa
9270    fsss(taxon) = sum
9280    fep (taxon) = sum
9290    sur(taxon) = sur
9300 NEXT taxon
9310 PRINT "ESS completed"
9315 PRINT
9320 END SUB

9400 REM creates FSS lifetable
9410 SUB fsstable STATIC
9415 PRINT "calculating ESS lifetable"
9420 SHARED n%,o,ltf,timestep,fssf,cfss,rfss
9430 REM calculates life table
9440 FOR class = 1 TO o
9450 failures = 0
9460 cfss(class) = (class*.1)-.1
9470 FOR taxa = 1 TO n%
9480    IF fsss(taxa)*10 >= class -1 AND fsss(taxa)*10< class THEN
9490        failures = failures + 1
9500        totals = totals+1
9510    ELSE
9520        failures = failures
9530        totals = totals
9540    END IF
9550 NEXT taxa
9560 fssf(class) = failures
9570 ltf(class) = (n%-totals)+failures
9580 IF (n%-totals)+failures = 0 THEN
9590    rate = 0
9600 ELSE
9610    rate = failures/((n%-totals)+failures)
```

```
9620 END IF
9630    rfss (class) = rate
9640 NEXT class
9650 PRINT"ESS lifetable completed"
9655 PRINT
9660 END SUB

9670 REM epstein’s test for ESS data
9680 SUB epsteinfss STATIC
9685 PRINT "calculating Epstein’s Test (ESS)"
9690 SHARED n%,epf
9700 unsort = 0
9710 FOR i = 1 TO (n%-1)
9720    x = fep(i)
9730    y = fep (i+1)
9740        IF y<x THEN
9750            fep(i+1) =x
9760            fep(i) = y
9770        END IF
9780 NEXT i
9790 FOR i = 1 TO (n%-1)
9800    x = fep(n%-i)
9810    y = fep(n%+1-i)
9820        IF y<x THEN
9830            fep(n%+1-i) = x
9840            fep(n%-i) = y
9850            unsort = unsort+1
9860        END IF
9870 NEXT i
9880 IF unsort >0 THEN
9890    GOTO 9700
9900 END IF
9910 FOR ep = 1 TO n%
9920    IF (ep) = 1 THEN
9930        sum = n%*fep(1)
9940    END IF
9950    IF (ep) = 2 THEN
9960        sum = fep(1)+(n%-1)*fep(2)
9970    END IF
9980    IF (ep) >2 THEN
9990        dsum = 0
10000        FOR j = 1 TO ep-1
10010            dsum = dsum + fep(j)
10020        NEXT j
10030            term = dsum + (n%-ep+1)*fep(ep)
10040    END IF
10050    total = total+term
10060 NEXT ep
10070 sum = total-term
10080 epf (1) = sum
10090 mean = ((n%-1)*term/2)
10100 epf(4) = mean
10110 sd = SQR(((n%-1)*(term^2))/12)
10120 epf (5) = sd
10130 con = 1.96*sd
```

```
10140 epf (6) = con
10150 ucl = mean+con
10160 epf (3) = ucl
10170 lcl = mean - con
10180 epf (2) = lcl
10190 PRINT "Epstein’s Test (ESS) completed"
10195 PRINT
10200 END SUB

10300 SUB adetest STATIC
10310 SHARED ade$,n%,csq
10315 PRINT "calculating A-D extinction test"
10320 FOR taxa = 1 TO n%
10330 value = 0
10340 an = ancestor (taxa)
10350   IF an = 0 THEN
10360       valid = valid
10370       ade$(taxa)  = "I"
10380   ELSE
10390       value = lod(taxa)-lod(an)
10400   END IF
10410   IF value <> 0 THEN
10420       valid = valid +1
10430   ELSEIF value = 0 AND an>0 THEN
10440       i = i +1
10450       ade$(taxa) = "E"
10460   END IF
10470   IF value > 0 THEN
10480       a = a +1
10490     ade$(taxa)  = "A"
10500   END IF
10510   IF value < 0 THEN
10520        d = d +1
10530        ade$(taxa) = "D"
10540    END IF
10550 NEXT taxa
10560 REM chi squared routine
10570 ex = valid/2
10580 csq = ((a-ex)^2)/ex + ((d-ex)^2)/ex
10590 chi(1) = a
10600 chi(2) = d
10610 chi(3) = csq
10620 PRINT "A-D extinction test completed"
10625 PRINT
10630 END SUB

10700 REM creates random dataset
10710 SUB random STATIC
10715 PRINT "assigning random ancestors"
10720 SHARED n%, comp
10730 FOR rand = 1 TO n%
10735 comp = 0
10740 fad = fad (rand)
10750 an = ancestor(rand)
10760    IF an = 0 THEN
```

```
10770            ran (rand) = 0
10780           GOTO 10900
10790    ELSEIF anc >0 THEN
10800        RANDOMIZE TIMER
10810        comp  = INT (RND*(n%-1)+.5)+1
10820    END IF
10830    IF comp = rand AND an > 0 THEN
10840        GOTO 10800
10850    ELSEIF fad(comp)>= fad AND fad >=lod(comp) THEN
10860        ran(rand) = comp
10870    ELSE
10880        GOTO 10800
10890    END IF
10900 NEXT rand
10910 PRINT "operation completed"
10915 PRINT
10920 END SUB

11000 REM PERFORMS A-D EXTINCTION TEST ON RANDOM DATA
11110 SUB adertest STATIC
11115 PRINT "calculating survivorship control test"
11120 SHARED ader$,n%,csq
11130 FOR taxa = 1 TO n%
11140 value = 0
11150 rand = ran (taxa)
11160    IF rand = 0 THEN
11170        valid = valid
11180        ader$(taxa)  = "I"
11190    ELSE
11200       value = lod(taxa)-lod(rand)
11210   END IF
11220    IF value <> 0 THEN
11230        valid = valid +1
11240    ELSEIF value = 0 AND rand>0 THEN
11250        i = i +1
11260        ader$ (taxa) = "E"
11270   END IF
11280   IF value > 0 THEN
11290        a = a +1
11300        ader$(taxa)  = "A"
11310   END IF
11320   IF value < 0 THEN
11330        d = d +1
11440        ader$ (taxa) = "D"
11450   END IF
11470 NEXT taxa
11480 REM chi squared
11490 ex = valid/2
11500 csq = ((a-ex)^2)/ex + ((d-ex)^2)/ex
11510 chi(4) = a
11520 chi(5) =d
11530 chi(6) = csq
11540 PRINT "survivorship control test completed"
11545 PRINT
11550 END SUB
```

```
11600 REM perfroms A-D speciation test
11610 SUB adstest STATIC
11615 PRINT "calculating A-D speciation test"
11620 SHARED n%,ads$,csq
11630 FOR taxon = 1 TO n%
11640 fad = fad(taxon)
11650 anc = ancestor(taxon)
11660 aanc = ancestor(anc)
11670 c=0
11680     FOR taxa =1 TO n%
11690        IF anc =ancestor(taxa) AND anc>0 THEN
11700            c =c+1
11710        END IF
11720    NEXT taxa
11730 REM defines A-D status
11740     IF anc = 0 THEN
11750        i = i+1
11760        ads$(taxon) = "I"
11770    END IF
11780    IF c = 1 THEN
11790    IF aanc>0 THEN
11800        d=d+1
11810        valid = valid+1
11820        ads$ (taxon)= "D"
11830    ELSEIF aanc = 0 THEN
11840        i=i+1
11850        ads$(taxon)= "I"
11860    END IF
11870 END IF
11880 IF c>1 THEN
11890 comp = 0
11900 high = 0
11910    FOR tax = 1 TO n%
11920        IF fad(tax)>=comp THEN
11930            IF anc = ancestor(tax) AND anc>0 THEN
11940                 comp = fad(tax)
11950                 high = tax
11960            END IF
11970         END IF
11980    NEXT tax
11990    IF comp>fad THEN
12000         a=a+1
12010         valid = valid+1
12020         ads$(taxon) = "A"
12030    END IF
12040    IF comp = fad AND taxon < high THEN
12050        a=a+1
12060        valid = valid +1
12070        ads$(taxon) = "A"
12080        ELSEIF comp = fad AND taxon = high THEN
12090            IF aanc > 0 THEN
12100                d=d+1
12110                valid = valid +1
12120                ads$(taxon) = "D"
```

```
12130             ELSEIF aanc = 0 THEN
12140                i=i+1
12150                ads$(taxon) = "I"
12160            END IF
12170        END IF
12180 END IF
12190 NEXT taxon
12200 REM chi squared
12210 ex = valid/2
12220 csq = ((a-ex)^2)/ex + ((d - ex)^2)/ex
12230 chi(7) = a
12240 chi(8) = d
12250 chi (9) =csq
12260 PRINT "A-D speciation test completed"
12265 PRINT
12270 END SUB

13000 REM A-D speciation test (restricted)
13010 SUB adsrtest STATIC
13015 PRINT "calculating A-D speciation test (restricted)"
13020 SHARED n%, adsr$,csq
13030 FOR taxon = 1 TO n%
13040 num = number (taxon)
13050 fad =fad (taxon)
13060 anc = ancestor (taxon)
13070 aanc = ancestor (anc)
13080 c = 0
13090    FOR taxa = 1 TO n%
13100        IF anc = ancestor (taxa) AND anc>0 THEN
13110            c= c+1
13120        END IF
13130    NEXT taxa
13140 REM define relationships
13150    IF anc = 0 THEN
13160        i = i+1
13170        adsr$ (taxon) = "I"
13180    END IF
13190    IF c = 1 THEN
13200        IF lod (anc)>fad OR lod(aanc)>fad THEN
13210            i = i +1
13220           adsr$(taxon) = "IE"
13230        END IF
13240        IF lod (anc)=< fad AND lod (aanc) =< fad THEN
13250            IF  aanc>0 THEN
13260               valid =valid+1
13270               d = d+1
13280               adsr$(taxon)= "D"
13290            END IF
13300        END IF
13310        IF lod(anc)=<fad AND lod (aanc)=< fad THEN
13320            IF  aanc = 0 THEN
13330                i = i +1
13340                adsr$ (taxon)= "I"
13350             END IF
13360        END IF
```

```
13370    END IF
13380    IF c>1 THEN
13390    pot = 0
13400    panc = 0
13410    difft = 1
13420    high =0
13430    comp = 0
13440        FOR ta = 1 TO n%
13450            IF anc =ancestor(ta) AND anc>0 THEN
13460                IF fad(ta)>=fad AND ta<>num THEN
13470                    pot = pot+1
13480                    diff = fad - fad(ta)
13490                        IF diff < difft AND diff <> 0 THEN
13500                            difft=diff
13510                        ELSEIF diff = 0 THEN
13520                            difft = 0
13530                        END IF
13540                END IF
13550            END IF
13560        NEXT ta
13570        IF pot = 0 THEN
13580            panc = 0
13590        END IF
13600        IF pot = 1 AND difft < 0 THEN
13610            FOR z = 1 TO n%
13620                gap = fad-fad(z)
13630                IF gap = difft THEN
13640                    IF ancestor(z) = anc AND anc>0 THEN
13650                        panc = z
13660                     END IF
13670                 END IF
13680            NEXT z
13690        END IF
14700    IF pot =1 AND difft = 0 THEN
14710        FOR y  = 1 TO n%
14720            IF ancestor(y) = anc AND anc>0 THEN
14730                gap = fad-fad(y)
14740            END IF
14750            IF gap = difft THEN
14760                IF y>num THEN
14770                    panc = y
14780                 ELSEIF y=< num THEN
14790                    panc = 0
14800                END IF
14810            END IF
14820        NEXT y
14830    END IF
14840    IF pot > 1 AND difft < 0 THEN
14850        small =difft
14860            FOR p  = 1 TO n%
14870               IF ancestor(p)=anc AND anc>0 THEN
14880                    gap = fad-fad(p)
14890                END IF
14900                    IF gap > small AND gap < 0 THEN
14910                    small=gap
```

```
14920                END IF
14930           NEXT p
14940           FOR ps = 1 TO n%
14950               IF fad-fad(ps) = small THEN
14960                   panc = ps
14970               END IF
14980           NEXT ps
14990    END IF
15000    IF pot >1 AND difft = 0 THEN
15010        FOR q = 1 TO n%
15020            IF fad(q) = fad THEN
15030                IF q>num THEN
15040                    IF ancestor(q)=anc AND anc>0 THEN
15050                        top = q
15060                    END IF
15070                 END IF
15080             END IF
15090        NEXT q
15060    IF num < top THEN
15070        panc = top
15080     ELSE
15090         hit = 0
15100         FOR e = 1 TO n%
15110             IF anc =ancestor(e) AND anc>0 THEN
15120                 IF fad(e)>fad THEN
15130                      hit =hit+1
15140                      dif = fad - fad(e)
15150                          IF dif < dift THEN
15160                              dift=dif
15170                           END IF
15180                  END IF
15190              END IF
15200           NEXT e
15210     IF hit = 0 THEN
15220          panc = 0
15230     ELSE
15240        small =dift
15250            FOR p  = 1 TO n%
15260                IF ancestor(p) = anc AND anc>0 THEN
15270                    gap = fad-fad(p)
15280                 END IF
15290                IF gap > small AND gap < 0 THEN
15300                    small=gap
15310                 END IF
15320             NEXT p
15330             FOR ps = 1 TO n%
15340                 IF fad-fad(ps) = small THEN
15350                     IF ancestor(ps) = anc AND ancestor>0 THEN
15360                       panc = ps
15370                     END IF
15380                 END IF
15390              NEXT ps
15400            END IF
15410         END IF
15420    END IF
```

```
15430    FOR tax = 1 TO n%
15440        IF fad(tax)>=comp THEN
15450            IF anc = ancestor (tax) AND anc>0 THEN
15460                comp = fad(tax)
15470                high =tax
15480            END IF
15490        END IF
15450    NEXT tax
15460    IF comp>fad THEN
15470         IF lod (anc) >fad OR lod (panc)>fad THEN
15480            i= i+1
15490            adsr$(taxon) = "IE"
15500        ELSEIF lod(anc)=<fad AND lod (panc)=<fad THEN
15510            valid =valid+1
15520            a=a+1
15530            adsr$(taxon)= "A"
15540        END IF
15550    END IF
15560    IF comp = fad AND taxon<high THEN
15570        IF lod (anc) >fad OR lod (panc)>fad THEN
15580            i= i+1
15590            adsr$(taxon) = "IE"
15600        ELSEIF lod (anc)=<fad AND lod(panc)=<fad THEN
15610            valid=valid+1
15620            a = a+1
15630            adsr$ (taxon) = "A"
15640        END IF
15650    END IF
15660    IF comp=fad AND taxon = high THEN
15670        IF aanc = 0 THEN
15680             i = i+1
15690             adsr$ (taxon) = "I"
16000        END IF
16010        IF aanc>0 THEN
16020            IF lod (anc)=<fad AND lod(aanc)=<fad THEN
16030               valid=valid+1
16040               d = d+1
16050               adsr$ (taxon) = "D"
16060             ELSEIF lod (anc) > fad OR lod(aanc)> fad THEN
16070                i = i +1
16080                adsr$ (taxon) = "IE"
16090            END IF
16000         END IF
16010       END IF
16020     END IF
16030 NEXT taxon
16040 REM chi square
16050 ex = valid/2
16060 csq = ((a-ex)^2)/ex+((d-ex)^2)/ex
16070 chi (10) = a
16080 chi (11) = d
16090 chi(12) = csq
16100 PRINT "A-D speciation test (restricted) completed"
16110 END SUB
1
```

APPENDIX II

LISTING OF THE TREE GROWTH PROGRAM CODE

This code should be copied into a QuickBasic program file and run from there.

```
CLS
backcolor 273
forecolor 38
TEXTFONT 8
TEXTSIZE 50
MOVETO 0,50
PRINT "TREE GROWTH"
TEXTSIZE 20
PRINT "This program grows random trees of specified size for export into
ADAPTS."
try=0: PRINT
INPUT "input maximum size of tree that is acceptable:", size
INPUT "input minimum size of tree that is acceptable:", min
5 DIM  info(size, 3)
ext=0
try=try+1
counter=1
time=1
info(1,1) =1
10 IF counter-ext<>0 THEN GOTO 100
FOR p = 1 TO counter
 info(p,1)=time-info(p,1)
 info(p,2)=time-info(p,2)
NEXT p
IF counter>=min THEN
    OPEN "clip:" FOR OUTPUT AS #1
    FOR q = 1 TO counter
        WRITE#1, q, info(q,1)/10, info(q,2)/10, info(q,1)/10-info(q,2)/10,
info(q,3)
   NEXT q
   CLOSE #1
ELSEIF counter<min THEN
ERASE info
GOTO 5
END IF
PRINT:PRINT:PRINT "Tree number";try;"became extinct with";counter;"species
after";time/10"time increments":PRINT "and was accepted."
PRINT
PRINT "Now quit TREE GROWTH and paste the data into a spreadsheet"
END
100 FOR y= 1 TO counter
IF info(y,1)>0 AND info(y,2)>0 THEN
    GOTO 200
END IF
IF info(y,1)>0 AND info(y,2)=0 THEN
RANDOMIZE TIMER
    IF RND*100>99 THEN
         counter=counter+1
         IF counter > size THEN
```

```
         ERASE info
         GOTO 5
         END IF
         info(counter,1)=time
         info(counter,3)=y
    END IF
END IF
IF info(y,1)>0 AND info(y,2)=0 THEN
    IF RND*100>99 THEN
        info(y,2)=time
        ext=ext+1
    END IF
END IF
200 NEXT y
time=time+1
MOVETO 0,250
PRINT "attempt no."; try, "diversity"; counter-ext, "size so far"; counter;"
"
GOTO 10
1
2
```

Figure 1. This shows a simple example of diversity, with a calculation interval of one.

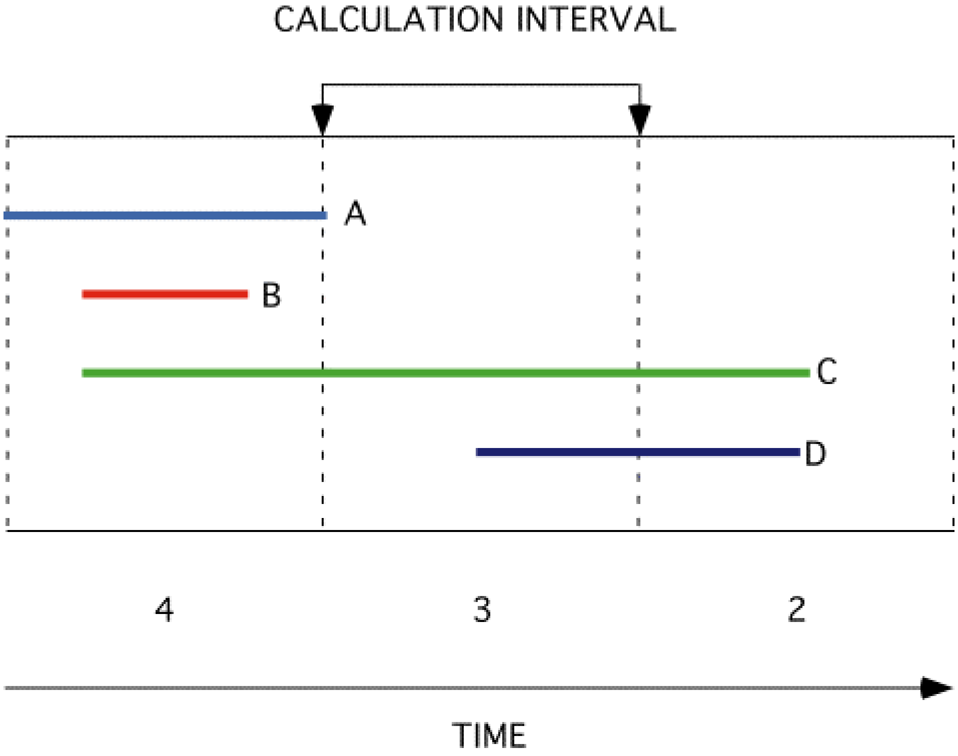

Figure 2. Diagram to help to explain the procedure for calculation of the EISS.

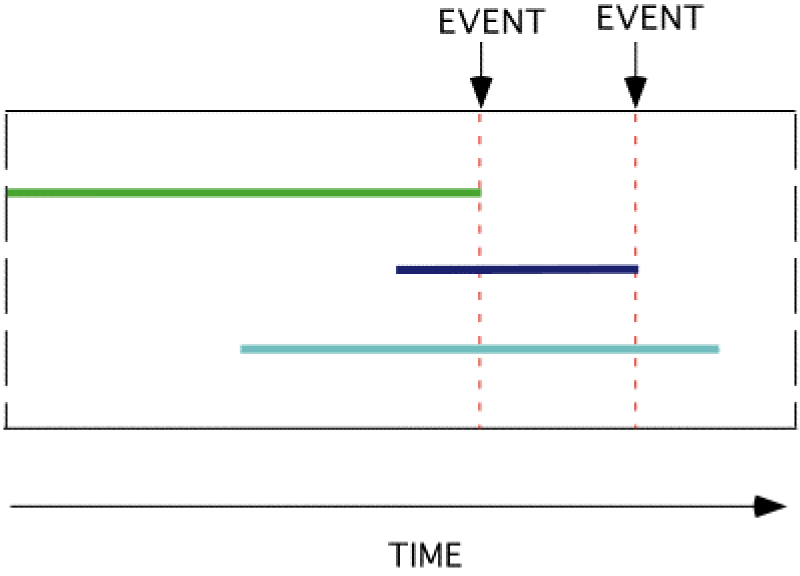

Figure 3. Diagram to help explain the EISS procedure for multiple extinctions.

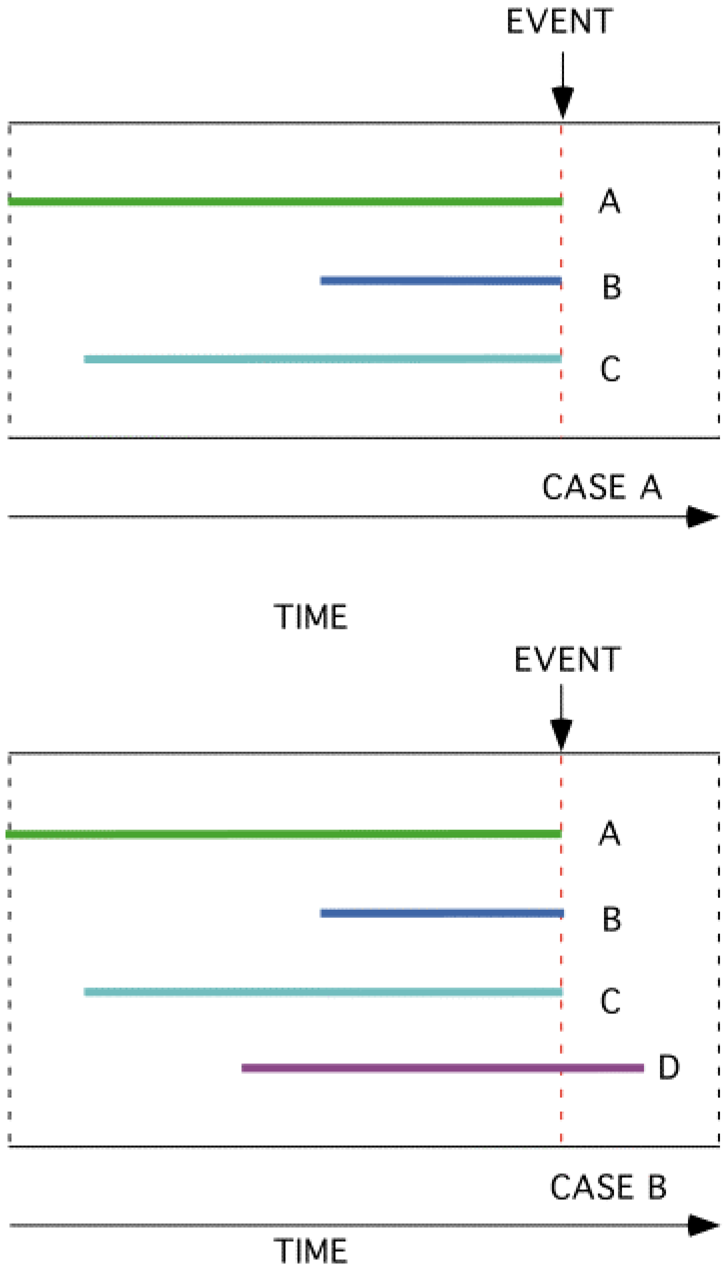

Figure 4. The two "valid" cases for the A-D extinction test. Case 1 shows the ancestor outliving the descendant, Case 2 shows the descendant outliving the ancestor. In this and all following diagrams, taxa with an arrow survive and taxa with a circle have become extinct. Ancestral taxa are shown in blue, descendants in red.

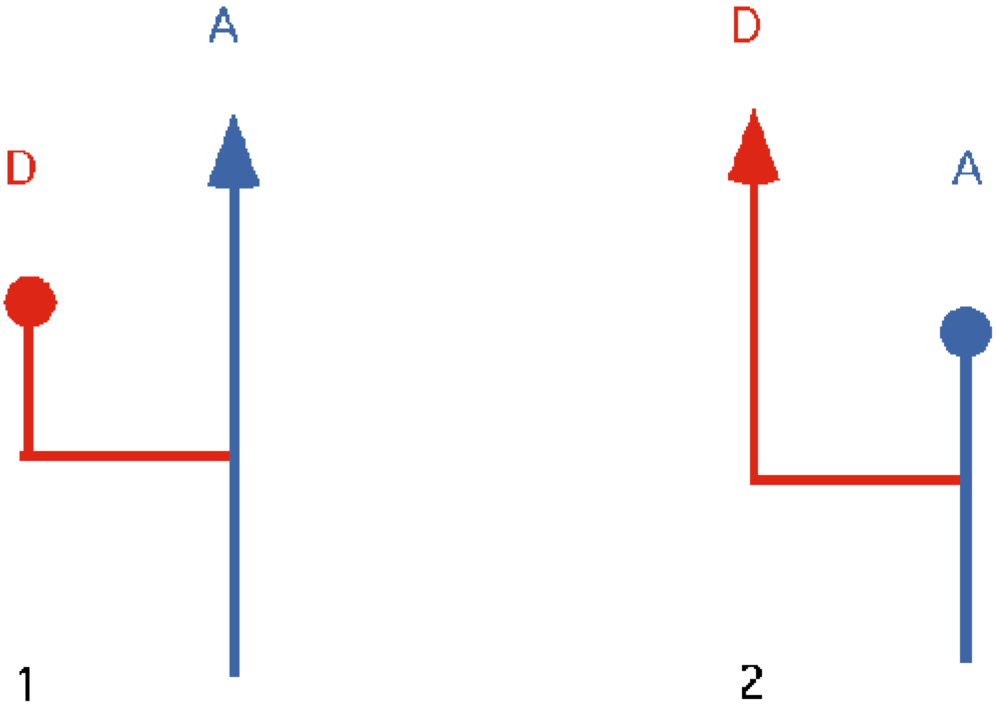

Figure 5. Topologies relating to the A-D speciation and A-D speciation (restricted) test.

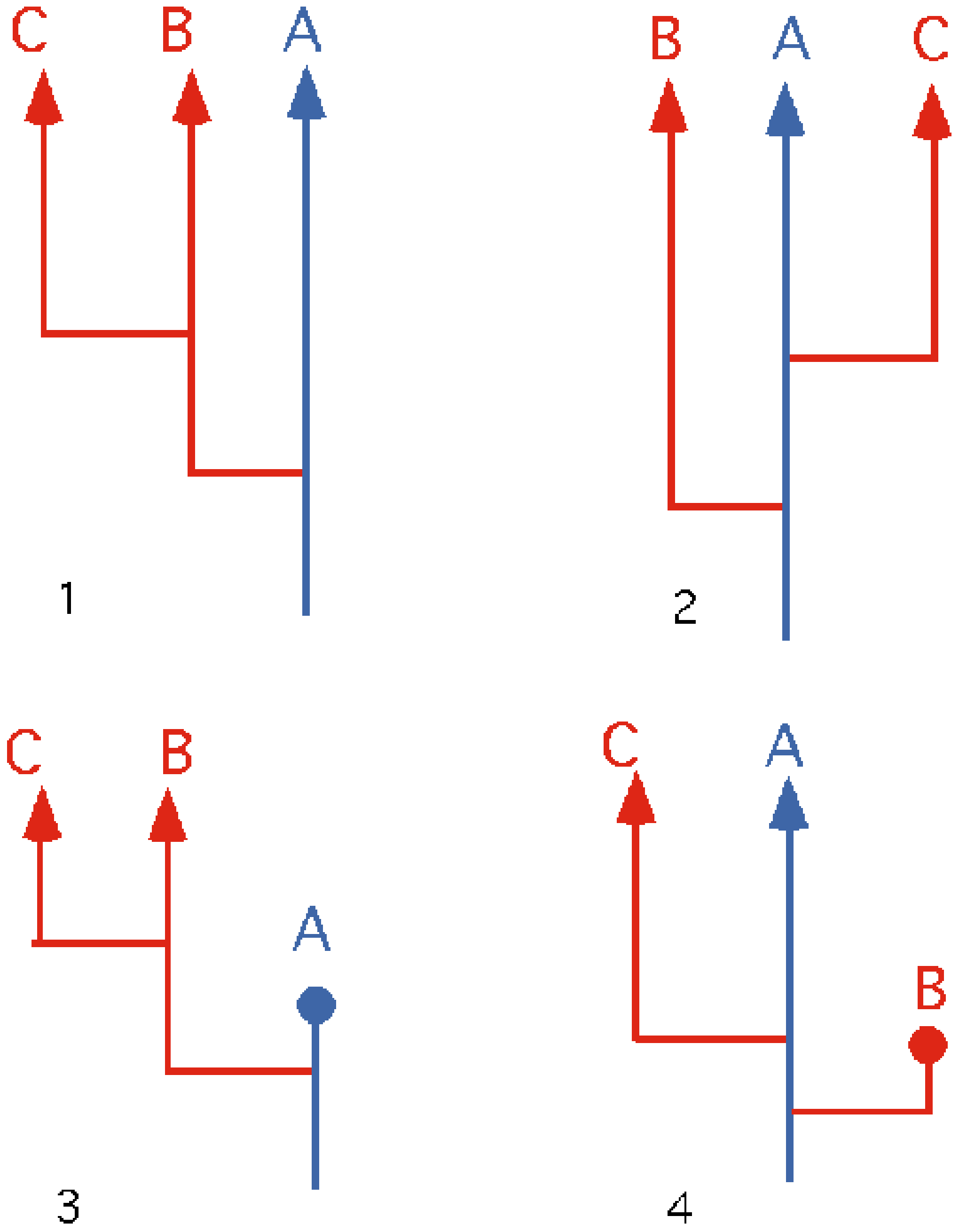

Figure 6. Diversity of the random phylogeny generated by TREE GROWTH across simulation time.

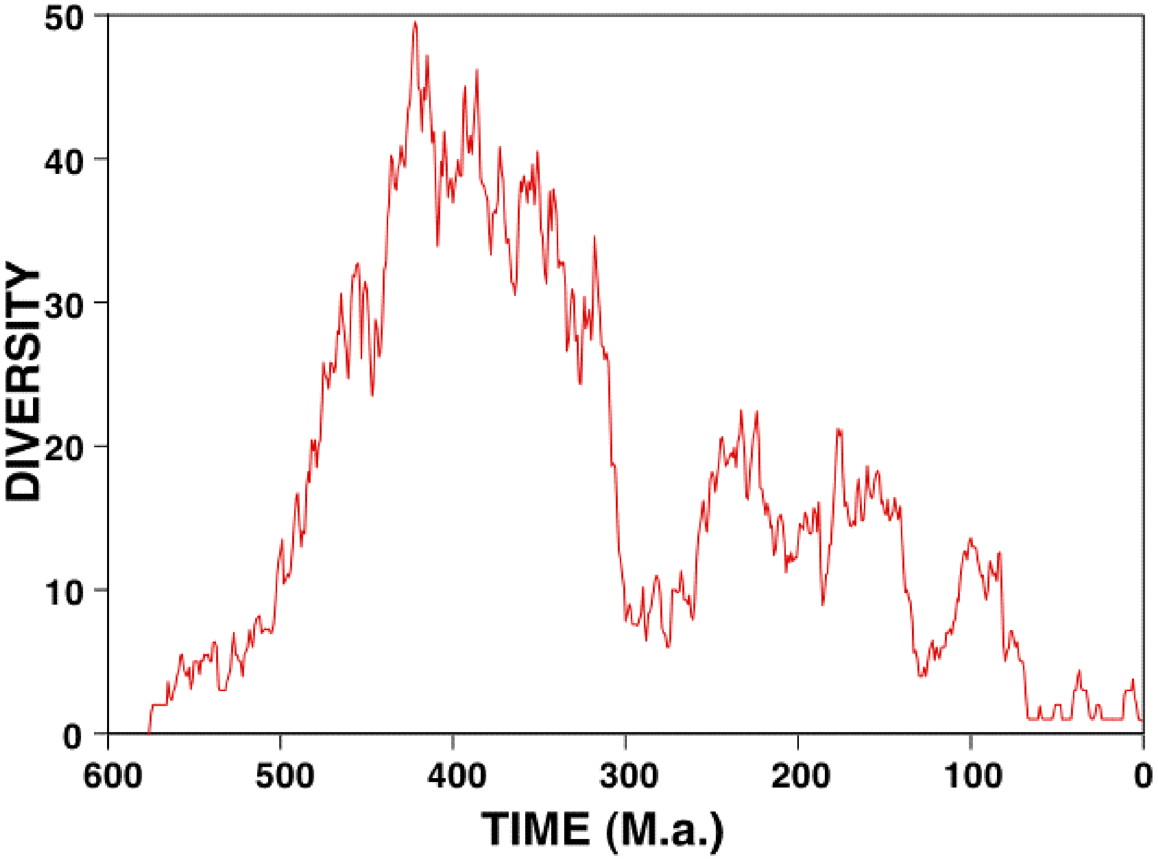

Figure 7. Dynamic survivorship and CSS curves for the TREE GROWTH data.

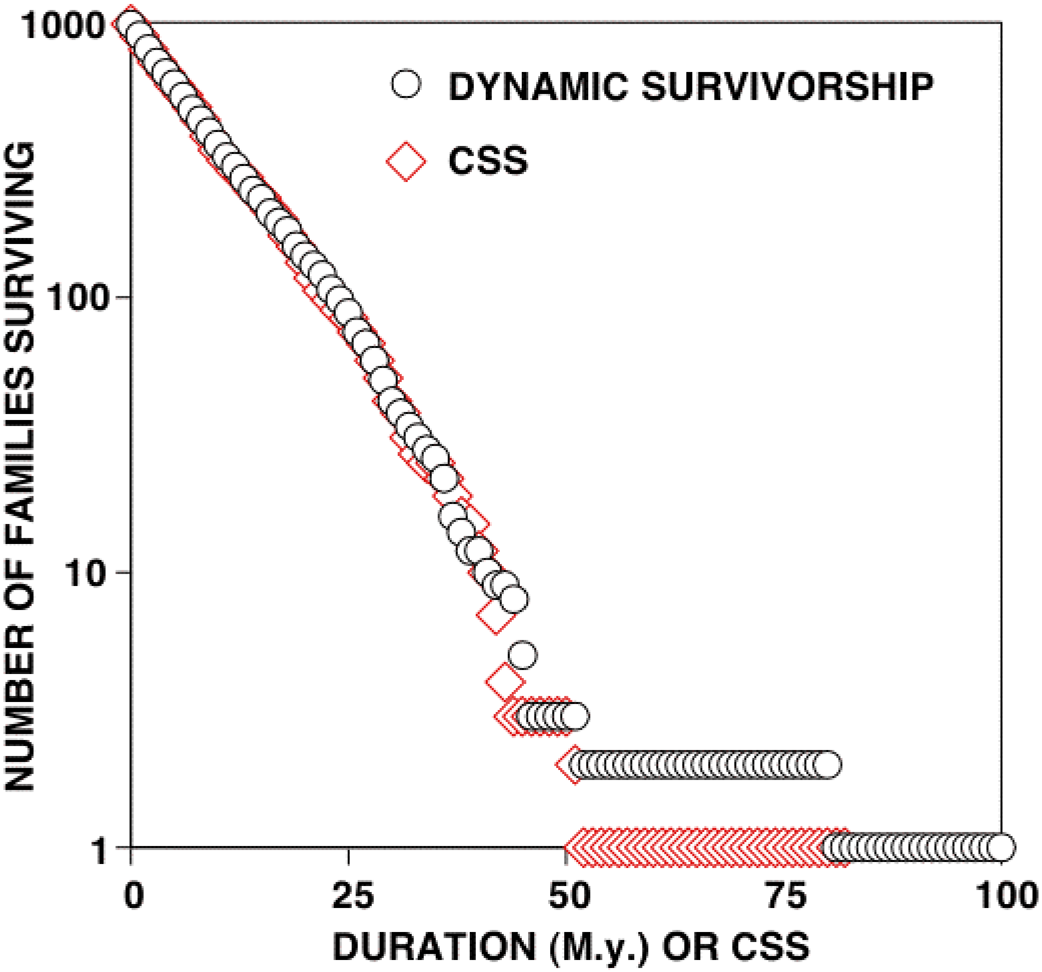

Figure 8. EISS plot for the TREE GROWTH data.