The Currency and Tempo of Extinction

Helen M. Regan,[1,*] Richard Lupia,[2,†] Andrew N. Drinnan,[1,‡] and Mark A. Burgman[1,§]

1. School of Botany, University of Melbourne, Parkville, Victoria 3052, Australia;
2. Sam Noble Oklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, Norman, Oklahoma 73072

ABSTRACT: This study examines estimates of extinction rates for the current purported biotic crisis and from the fossil record. Studies that compare current and geological extinctions sometimes use metrics that confound different sources of error and reflect different features of extinction processes. The per taxon extinction rate is a standard measure in paleontology that avoids some of the pitfalls of alternative approaches. Extinction rates reported in the conservation literature are rarely accompanied by measures of uncertainty, despite many elements of the calculations being subject to considerable error. We quantify some of the most important sources of uncertainty and carry them through the arithmetic of extinction rate calculations using fuzzy numbers. The results emphasize that estimates of current and future rates rely heavily on assumptions about the tempo of extinction and on extrapolations among taxa. Available data are unlikely to be useful in measuring magnitudes or trends in current extinction rates.

Keywords: mass extinction, current extinction, mammals, vascular plants, fuzzy sets, uncertainty.

Estimates of extinction rates are a major cause for public concern about the environment and for the development of priorities for conservation and environmental protection. There have been approximately 490 animal extinctions and 580 plant extinctions recorded globally since 1600 (May et al. 1995). The available data suggest that the frequency of these extinctions has increased dramatically

* To whom correspondence should be addressed. Present address: Applied Biomathematics, 100 North Country Road, Setauket, New York 11733; e-mail: helen@ramas.com.

† E-mail: rlupia@ou.edu.

‡ E-mail: a.drinnan@botany.unimelb.edu.au.

§ E-mail: m.burgman@botany.unimelb.edu.au.

in the past 100 yr (fig. 1), and a likely explanation for most of these extinctions is human impact on the environment. Arguments leading to the conclusion that we are experiencing a mass extinction event are marred by the fact that there is little information provided on the reliability of calculated extinction rates. Instead, point estimates of rates in geological time and in recent time are reported, implying that we know extinction rates without error.

Although it is widely acknowledged that uncertainty exists in all of the constituent parameters in calculations of global extinction rates (Raup 1986) and confidence limits typically are reported in the paleontological literature, only rarely is that uncertainty carried over and incorporated into extinction rates in the conservation literature. The aim of this article is to examine conclusions regarding extinction rate estimates offered in the literature (see Myers 1979; Lovejoy 1980; Ehrlich 1990; May et al. 1995; Pimm et al. 1995) and improve these in a straightforward way. We provide an account of some of the sources of uncertainty in calculations of global extinction rates and propose one method, fuzzy arithmetic, for dealing with some of them. We believe there are three main issues that deserve attention in comparisons of current and background extinction estimates.

The first issue concerns the nature of the available data. The background extinction rate is calculated from data largely obtained from the fossil record, whereas current extinction rates are obtained from modern observational data. Both rates are highly uncertain. The fossil record cannot tell us how many species existed throughout geological time, only how many appear as fossils. We expect that many more species existed, but it is impossible to know how many. The apparent life span of fossil species is usually truncated by preservational sampling biases. The number of extant and (recently) extinct species can be estimated irrespective of a fossil record. However, differences in sampling and recognition prevent error-free estimation of true values. The result is that the uncertainty in our estimates of background and current rates of extinction arise in different ways.

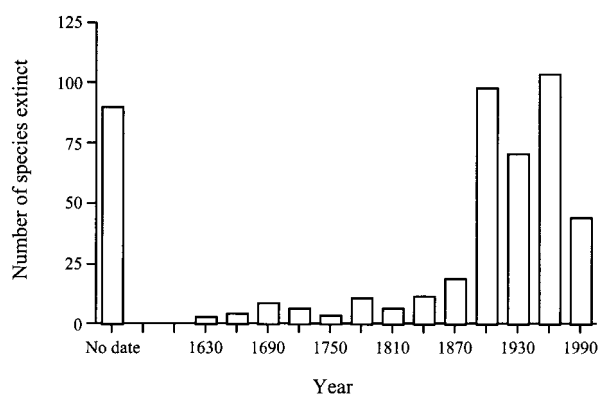The second issue is the selection of an appropriate metric for measuring extinction rates. Estimates of the mag-

Figure 1: Number of recorded animal extinctions in recent history (after Jenkins 1992). The values represent the number of extinctions recorded within the 30-yr period up to the date labeling the class.

nitude of extinction events depend greatly on the metric used. Furthermore, to make fair comparisons of current rates with background rates, it is important to ensure equivalent currencies. We should account for the fact that background extinction rates pertain to the taxa that appear in the fossil record (i.e., the preservable taxa), whereas current extinction rates include all known extinct taxa regardless of their propensity to be preserved.

The third issue is that of disparate temporal scales in comparisons of current and background extinction rates. Despite addressing some of the uncertainty in the calculation of extinction rates and aiming for fairer comparisons, we are still unsure of how current extinction rates, based on a few hundred years of data, relate to background rates, which are calculated over a substantially larger time frame. It is almost certain that a rate based on the last few hundred years will overestimate long-term rates because of the possible front-loading of modern extinctions. Any conclusions regarding mass extinction need to be made with this in mind.

In this article, we deal with the first two issues. The uncertainty in each of the parameters is estimated from sources in the literature and propagated throughout the calculation according to the preferred extinction metric. The methods and rationale behind uncertainty propagation are discussed and examples of calculations of extinction rates are provided for mammals globally, and for angiosperms (flowering plants) in Australia. Finally, we highlight the implications of accounting for uncertainty in extinction rates and discuss the problem of incomparable temporal scales.

Sources of Uncertainty

To model successfully the uncertainty in extinction rate calculations, it is important to identify the main sources

of uncertainty in the component parameters and calculations. Some of the major sources of uncertainty include the following (see May et al. 1995 and references therein for further discussion). First, extinction rate calculations usually assume that extinction events are independent. The loss of one species may have ramifications for some other taxonomically unrelated species (Walker 1991; Lawton and Brown 1994; Hulbert 1997). Second, the number of currently extant species is unknown—the current total number of species may lie between 3 million and 30 million (May 1990; Erwin 1991; Gaston 1991). Third, the process of certification of extinction in most countries ensures a considerable time lag between the extinction of a species and its certification (Smith et al. 1993*b*). Fourth, reported extinction rates reflect the effort expended to detect extinctions and availability of monitoring information, not necessarily true rates (Smith et al. 1993*b*; May et al. 1995). Fifth, species concepts vary markedly among both taxonomic groups and researchers. Sixth, application of background rates based on averages over all groups or based on related but nonidentical taxa is extremely tenuous because of the variation of extinction rates within and between taxa. Seventh, variation in preservation rate means that observed extinctions in the fossil record fundamentally are not equivalent to observed extinctions in the modern biota.

To combine all of the different types of uncertainty into one calculation is a formidable (and perhaps impossible) task. What is required is a reduction of the overall problem to manageable tasks in which the most significant contributors to the overall uncertainty are identified and dealt with appropriately.

Measuring Extinction Rates

In order for comparisons of current and background extinction rates to be valid, an appropriate metric of the current extinction rate needs to be employed. The background rate must also be chosen carefully, and the rates should be standardized to a common currency.

There are multiple metrics for measuring extinction rates in the fossil record, each incorporating various potential kinds of errors (e.g., Gilinsky 1991; Foote 1994; Jablonski 1995). It is important that modern rates be calculated using paleontological metrics (or vice versa) to ensure comparability. We investigate four different paleontological metrics below. In order to highlight the differences among background rates between taxa (noted above), we compare results using the background rate both for fossil marine invertebrates (for which there is arguably the best record of speciation and extinction) and for fossil mammals, specifically. Table 1 lists parameters frequently cited in the literature relevant to the calculation of current

Table 1: Data on current mammal extinction, extant diversity, and background extinction rates

	Data
Number of recent mammal extinctions	60
Number of observation years	400
Number of extant mammal species	4,327
Number of extant species (recorded)	1,400,000
Number of extant species (estimated)	10,000,000
May et al. (1995) "fossil" background rate	1 species/yr
Fossil marine invertebrate background rate	.25 extinctions/species million years[a]
Fossil mammal background rate	.40 extinctions/species million years

Note: See May 1990; Hammond 1992; May et al. 1995; Raup 1991; Foote and Raup 1996.

[a] "Extinctions per species million years" implies that, on average, 25% of marine invertebrate species in any million-year period become extinct in the following million years.

mammalian extinction rates. These parameters are used in the following calculations. The calculations assume that extinction rates are constant through time.

The percentage of extant mammals that have become extinct in recent times is

$$\frac{\text{number of mammal extinctions}}{\text{number of mammal species}} \times 100$$

$$= \frac{60 \times 100}{4,327} = 1.4\% \text{ extinction.} \quad (1)$$

The expected number of mammal extinctions (in 400 yr, using invertebrate background rate and observed extant diversity) is calculated as

$$\frac{\text{number of mammal species}}{\text{number of species (recorded)}}$$

$$\times \text{ background extinction rate}$$

$$\times \text{ number of observation years}$$

$$= \frac{4,327}{1.4 \times 10^6} \times 1 \times 400 \quad (2)$$

$$= 1.2 \text{ mammal species extinctions}$$

$$\text{expected in 400 yr.}$$

The expected number of mammal extinctions (in 400 yr, using invertebrate background rate and estimated extant diversity) is

$$\frac{\text{number of mammal species}}{\text{number of species (estimated)}}$$

$$\times \text{ background extinction rate}$$

$$\times \text{ number of observation years}$$

$$= \frac{4,327}{10 \times 10^6} \times 1 \times 400 \quad (3)$$

$$= 0.17 \text{ mammal species extinctions}$$

$$\text{expected in 400 yr.}$$

The total rate of extinction (per million years), that is, the total number of mammal species extinctions we could expect in the next million years, assuming the current rate continues, is

$$\frac{\text{number of mammal extinctions}}{\text{number of observation years}}$$

$$\times 10^6 = \frac{60 \times 10^6}{400} \quad (4)$$

$$= 150,000 \text{ mammal species}/10^6 \text{ yr.}$$

The per taxon rate of extinction (per million species years), that is, the number of mammal species expected to go extinct in 1 million years given the available number of species with the potential to go extinct, is calculated as

$$\frac{\text{number of mammal extinctions}}{\text{number of mammal species}}$$

$$\times \frac{10^6}{\text{number of observation years}} \quad (5)$$

$$= \frac{60}{4,327} \times \frac{10^6}{400} = 34.7 \text{ species}/10^6 \text{ yr.}$$

It is apparent from the examples in table 2 and from the metrics above that the calculated magnitude of the current extinction event can vary widely given the same set of data. This range of magnitudes, all of which are based on metrics that are biologically justifiable at some level, lends itself to broad interpretations.

Choosing the Appropriate "Currency" for Extinction Rate Calculations

In light of the uncertainties discussed above, we can evaluate the most appropriate metric of extinction. Metric (1) (percentage extinction = 1.4%) is low compared to the magnitude of extinction postulated at the Cretaceous-Tertiary boundary (K/T) event for both invertebrates (70%) or mammals (66%) (see table 2) because it does not take the time frame over which the events occurred into account. The current crisis and the K/T event might or might not have occurred on comparable timescales.

Metrics (2) and (3) (for which the expected numbers of extinctions in 400 yr are 1.2 and 0.17, respectively) yield higher relative magnitudes of current extinction than metric (1) (50 and 353 × background, respectively; table 2) given observed mammalian extinctions. However, they use a background estimate of extinction rate based on an average across fossil marine invertebrates (for which we have the best record), not the mammals.

Metric (4) (the total rate of extinction) and metric (5) (the per taxon rate of extinction) are essentially identical. The total rate of extinction does not account for the number of relevant taxa (i.e., mammals in this example). Because the per taxon rate of extinction (metric [5]) accounts

for both the time over which the extinctions are measured, and the number of relevant taxa, this metric is intuitively appealing (Gilinsky 1991; Jablonski 1995). Foote (1994) has shown that this metric can be highly biased by interval length (duration of time over which extinctions and diversity are tallied). Nevertheless, other methods less biased by interval length are biased by differences in standing diversity. The best metric (but still not unbiased) in simulations was what Foote (1994) termed "Van Valen's metric" (Van Valen 1985), but this metric requires estimates of species origination, for which we have no reliable information for extant species, as well as species extinction within the interval under question. We postulate then that the per taxon rate of extinction is the most appropriate for the purpose of comparison with background rates, particularly because many of the paleontological estimates are presented in these units.

Finally, even with a taxon-specific background extinction rate and an appropriate metric for extinction calculations, the data we wish to analyze are still not in comparable currencies. As mentioned above, modern species might be discriminated on the basis of morphology (both hard and soft anatomy), genetics, color, song, or breeding habits. In the fossil record, paleontologists likewise use available features but, more often than not, that means morphology alone. Furthermore, paleontologists observe extinctions in the fossil record if and only if the taxon has been preserved and recovered somewhere at least once. Both of these factors must be accommodated in translating data on extant species and recent extinctions into comparable currencies.

Table 2: Calculations of the extinction rates resulting from metrics (1)–(5) compared to rates based on the fossil record

Metric	Calculated value	Versus "fossil" background rate	Versus mammal background rate
(1)	1.4% extinction	1.4/70 × 100 = 2.0% of marine invertebrate extinction at K/T[a]	1.4/66 × 100 = 2.1% of mammal extinction at K/T[b]
(2)	1.2 species extinctions expected in 400 yr	60/1.2 = 50 × BR in fossil record[c]	
(3)	.17 species extinctions expected in 400 yr	60/.17 = 353 × BR in fossil record[c]	
(4)	150,000 species extinctions expected in 10^6 yr	150,000/1,082 = 139 × marine invertebrate BR	150,000/1,731 = 87 × mammal BR
(5)	34.7 extinctions per species million years	34.7/.25 = 139 × marine invertebrate BR	34.7/.4 = 87 × mammal BR

Note: Data from table 1; BR = background rate.

[a] Approximately 70% of marine invertebrate species became extinct at Cretaceous/Tertiary Boundary (Jablonski 1995).

[b] Approximately 66% of mammal species became extinct at Cretaceous/Tertiary Boundary (Alroy 1999).

[c] Metrics (2) and (3) are based on the May et al. (1995) estimate of background rate in fossil record and fraction of extant fauna that are mammals; thus, there is no distinction between marine invertebrate and mammal background rates.

Setting Bounds on Extinction Rates

The method chosen to set bounds on uncertain parameters is via fuzzy sets. Fuzzy sets are tools that were devised to deal with vagueness. A concept is vague if it permits borderline cases; that is, there is no clear demarcation of a concept and its complement (Sorensen 1989; Williamson 1994). For instance, the word "tall" is vague because a person of 1.8 m in height is neither clearly tall nor clearly not tall. No amount of analysis or empirical investigation can determine whether a 1.8-m person is tall (Sorensen 1997).

In classical set theory, objects are assigned a membership value (0 or 1) dependent on whether they are members of a particular set. If the membership function takes the value $\mu_A(x) = 1$, then x is an element of the set A, otherwise it is not. In fuzzy set theory, on the other hand, the membership function, $\mu_A(x)$, takes values from the interval [0, 1] (Zadeh 1965). In this way, an element, x, can have partial membership in a set, A, if its corresponding membership value is strictly between 0 and 1.

Fuzzy numbers are special cases of fuzzy sets in which all the elements are numbers and the corresponding membership function is convex (local minima) and normal (maximum membership value of 1). The simplest general examples of fuzzy numbers are triangular and trapezoidal, examples of which are provided in figures 2 and 3, respectively.

Although fuzzy sets were introduced to deal with vagueness, more recently they have been employed to handle the uncertainty that arises because of measurement error, ignorance, and so forth. There are a number of ways in
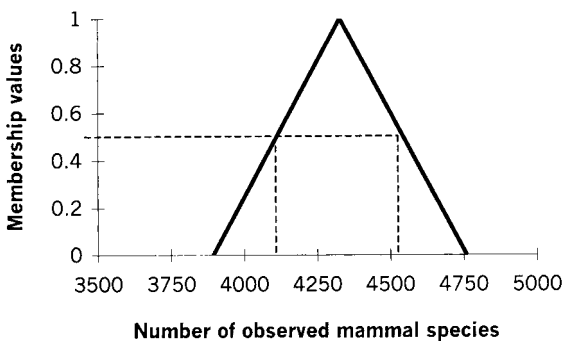

Figure 2: Number of observed mammal species represented as the triangular fuzzy number [3,894, 4,327, 4,760]. The value 4,327 is the best estimate and the plausible lower and upper bounds are 3,894 and 4,760, respectively. The horizontal dashed line indicates a cross section of the membership function at 0.5. The vertical dashed lines indicates the interval corresponding to a membership value of 0.5. Fuzzy arithmetic is performed across all such interval cross sections of the relevant fuzzy numbers.
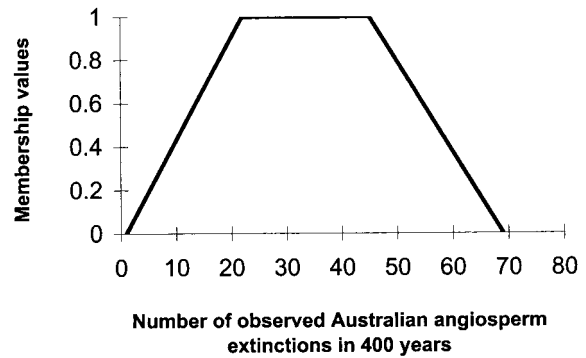

Figure 3: Number of observed Australian angiosperm extinctions in the past 400 yr represented as the trapezoidal fuzzy number [1, 22, 45, 69].

which fuzzy sets can be employed to harness this type of uncertainty. For instance, a measurement (the best estimate) can be regarded as "close to" the true value of the quantity of interest. By constructing a fuzzy number around the best estimate and within plausible bounds, we can address the vagueness in the term "close to" and use this to account for uncertainty in our measurement.

Fuzzy numbers produced in this way can be combined via arithmetic operations to result in an estimate of an uncertain quantity (see Kaufmann and Gupta 1985 and examples below). This is the strategy we employ to incorporate uncertainty into the calculation of extinction rates. For convenience, we choose to represent parameter uncertainty with triangular and trapezoidal fuzzy numbers throughout. Fuzzy numbers are convenient for the purposes of this study because they enable the incorporation of uncertainty into calculations when data are limited. They can be interpreted as extensions of intervals that allow specification of a best estimate in addition to upper and lower bounds.

Fuzzy arithmetic has advantages over well-known alternative methods for uncertainty propagation, for instance, confidence limits approaches and Monte Carlo methods. Arithmetic performed on confidence intervals (CI) throughout would require more data than is available. Furthermore, there is no known method of calculating the confidence level of the result of interval arithmetic applied to confidence intervals unless, of course, the confidence levels are all 100% or 0% (see Moore 1966 for details of interval analysis). With such a result, the effort and assumptions involved in meticulously assigning confidence limits is lost in the calculation.

Monte Carlo methods are even more problematic than confidence limits approaches for the purposes of this study because they require knowledge of the type of probability distribution for each parameter, in addition to information

regarding correlation coefficients and dependencies between parameters (see Ferson and Burgman 1995; Ferson 1996 for a discussion on the limitations of Monte Carlo simulations). The operations involved in fuzzy arithmetic ensure that uncertainty is propagated in a way that honors the fact that we have unknown dependencies and distribution shapes. The result is a best estimate and bounds that would contain the range of values produced using Monte Carlo or confidence limits approaches if we had the information to perform these types of analyses.

Examples: Extinction Rates of Mammals and Angiosperms

Mammals are one of the most intensively studied groups of animals on Earth today. Moreover, the fossil record of mammals is well documented, well resolved, and extinction rate estimates over the past 65 million years have been published recently (Foote and Raup 1996; Foote 1997; Alroy 1998). Consequently, mammals are one of the best examples for comparing modern versus background extinction rates.

From table 2, we note that the calculations, without considering uncertainty, yield a point estimate of 34.7 extinctions per species million years—nearly 100 times greater than the average extinction rate over the past 65 million years from the fossil record. The question now is, Allowing uncertainties in the data we are using, what is the most likely range of extinction rates consistent with current data?

First, we accept that the number of mammal species is 4,327 (±10% as estimated in WCMC 1992) and that the number of observed extinctions equals 60 (±10%). Thus, the fuzzy number of observed mammal species is [3,894, 4,327, 4,760] ([lower bound, best estimate, upper bound]; fig. 2) and the fuzzy number of observed extinctions is [54, 60, 66].

In order to achieve fair comparisons of current data with that obtained from the fossil record, we assume that the uncertainty in the number of current species and the number of species in the geological past arise in similar ways. Hence, we do not attempt to estimate the number of as yet unidentified extant species because we cannot estimate the corresponding total number of species in the geological past from the fossil record, only those that appear as fossils. Similarly, we do not provide estimates for the true number of recent extinctions (e.g., estimates that include unidentified extinct species) because there are fossil extinctions that we are likely to have missed. We assume then, that the error in the observed number of extant species and current extinctions is primarily a function of uncertainty in whether a species would be recognizable in the fossil record based on morphology alone. In this way,

we attempt to achieve comparable recent and background rates of extinction.

The fossil record is not a random sample of the species that have ever existed on Earth but is biased in favor of some species, some habitats, some regions, and some time intervals. Although paleontologists cannot specify which particular species will be preserved, recovered, and identified, studies of the preservation potential of different modern species in different habitats has led to an understanding of the relative probability of preservation for species with particular traits. For the discussion here, and with due recognition that there is uncertainty in these generalities as well, we limit ourselves to consideration of geographic range size and to overall preservation potential.

In terms of geographic range, the probability that a species will enter the fossil record is proportional to the size of its geographic range. Although there are exceptions, the fossil record of island faunas is sampled particularly poorly. For the sake of this exercise, we regard only islands versus nonislands (e.g., Australia is not considered to be an island but New Zealand is), and consider a range of alternatives: from assuming there is 0 probability of island species appearing as fossils, to assuming all island species may be found as fossils. Of the 60 observed extinct species (WCMC 1992), 34 species were restricted to small islands, and we would suspect that these species would be most likely, but not certainly, to be missing from the fossil record, all else being equal. The fuzzy number of observed mammal extinctions restricted to islands is [0, 34, 37]—from 37 (34 + 10%, if known species underestimate morphological species; following WCMC 1992) to 34 (best estimate) to 0 (because there is a chance of finding all of them). This range of values allows us to include alternative assumptions regarding preservation potential simultaneously in the extinction rate calculation. The bounds on the resultant extinction rate will be determined, in part, by including all island extinctions in the total number of mammal extinctions, for one bound, and excluding them from the total, for the other bound, with intermediate assumptions in between. In this way, the sensitivity of our assumptions is represented in the width of the resultant range of values.

Overall preservation potential of a species depends on the proportion of individuals of the species that are likely to be preserved and implicitly incorporates differential destruction, transport, sorting, identification, and all of the other processes that degrade the record. However, because it is analyzed only for those areas for which we have a fossil record, it is appropriate that we adjust for the absence of island species before we apply this correction. Foote (1997) calculated the preservation potential of mammals based on J. Alroy's database of fossil mammals as 67% (approximate 99% CI: 65%–70%). We can multiply the above fuzzy number of observed mammal extinctions, mi-

nus the fuzzy number on islands that might not be found, by the preservation potential to give the following numerator for our calculation

$$([54, 60, 66] - [0, 34, 37]) \times [0.65, 0.67, 0.70]. \quad (6)$$

The number of observed mammal species in the denominator has to be corrected in the same manner. The number of mammal species that would fail to be preserved in the fossil record because they are endemic to a single island is 475 (WCMC 1992). This does not account for the number that are endemic to two islands or to islands that are part of a larger country (e.g., Hawaiian Islands). It is anticipated, however, that the entire range of selected values will include this scenario. An intuitive upper bound is the total number of endemic mammal species in the world, currently estimated at 1,593. So we could create the fuzzy number of mammal species unlikely to be preserved by taking the range from 0 (all found) to 1,593 + 10% (morphological species; following WCMC 1992) with the best estimate being 475. This would yield the denominator:

$$([3,894, 4,327, 4,760] - [0, 475, 1,753])$$
$$\times \ [0.65, 0.67, 0.70]. \quad (7)$$

Note that the preservation potential appears in both the denominator and the numerator in this calculation. Instead of canceling the preservation potential term from the equation, we have retained it in an attempt to simulate the possibility of unequal preservation rates across islands and mammals. However, in the uncertainty propagation, the variability in preservation potential would be accounted for twice, resulting in a suboptimal range of values for the overall extinction rate. In order to include the uncertainty in preservation potential only once, we have chosen to reduce the preservation potential in the numerator to the point estimate 0.67 while retaining the bounds in the denominator. This assumption could be further improved by splitting categories into finer ecologically significant divisions and assigning specific preservation probabilities to each.

Finally, to what should we compare the calculated extinction rate range? To be fair, our calculated range should be compared to the range of estimates based on the published literature, not any single point estimate. Estimates of background mammalian extinction rates per species million years vary but generally fall within the range of 0.21 (strictly for lineages rather than species but represents a conservative estimate; Alroy 1998) to 0.46 (Foote 1997). Thus, the final form of our estimate of the current ob-

served extinction rate among mammals, relative to background, is

$$\frac{([54, 60, 66] - [0, 34, 37]) \times 0.67}{([3,894, 4,327, 4,760] - [0, 475, 1,753]) \times [0.65, 0.67, 0.70]}$$
$$\times \frac{10^6}{400} \times \frac{1}{[0.21, 0.46]} . \quad (8)$$

The arithmetic needed to perform this calculation can be broken down into a series of interval calculations for each membership value from 0 to 1 (see fig. 2). Fuzzy arithmetic ensures that each uncertain parameter is combined to achieve lower and upper bounds on the extinction rate within which we can be certain the true value lies, given certainty in the input data (see Kaufmann and Gupta 1985; Mareš 1994; Ferson et al. 1999 for details). Based on our calculations, the current rate of mammalian extinction lies between 17 and 377 times the background extinction rate measured over the past 65 million years (fig. 4). The best estimate of the current rate, however, falls between 36 and 78 times the background rate.

Global extinction rates are not easily calculated for the world's flora: the total number of species and the imprecise knowledge of taxonomy and distribution for many of them make a global treatment unreliable, if not impossible. It is, however, feasible to perform the analysis on a regional basis if the flora is sufficiently well known, is isolated from other regions (i.e., independent of other floras), and the region is of sufficient size or character that it could reasonably be expected to have the same characteristics of the world's flora (i.e., it is a large enough subset that it encompasses all the variation of the entire set). The flora of the Australian continent could be considered to meet these criteria.
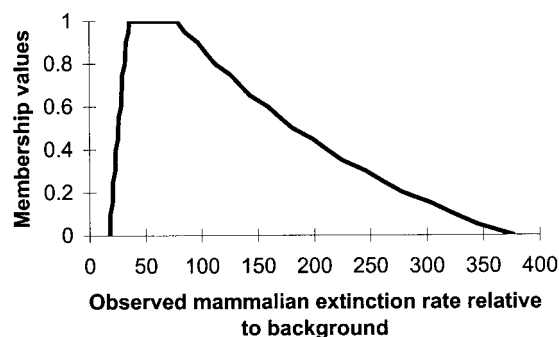

Figure 4: Fuzzy number for the estimate of the current observed extinction rate among mammals, relative to the background rate. The current mammalian extinction rate lies between 17 and 377 times the background rate measured over the past 65 million years. The best estimate of the current rate is around 36–78 times the background rate.

One way to gauge the errors in an estimate is to examine relative changes in the status of endangered and extinct taxa through time (Smith et al. 1993*a*). Most of the changes in status do not represent real changes in conservation status; rather, they are the result of taxonomic revisions and the collection of new observations. Information on extinct and endangered Australian plants has been collated and published in several editions of "Rare or Threatened Australian Plants" (ROTAP) over the past 20 yr (Leigh et al. 1981; Briggs and Leigh 1988, 1996). These can be used to estimate the number of species considered extinct and to generate estimates of the confidence in their status. Leigh et al. (1981) listed 109 species as extinct. Briggs and Leigh (1996) considered only 22 of those species still to be extinct; 30 had been revised to "status unknown." A total of 57, or slightly over 50%, had been either rediscovered or were considered, following later taxonomic revision, to be synonymous with other taxa. Briggs and Leigh (1996) listed 69 species as extinct (22 from 1981 and 47 additional species). Given that systematic and field studies between 1981 and 1996 resulted in the discovery of about 50% of the species considered extinct in 1996; we might expect the same proportion of the additional 47 species to be reclassified eventually. Thus, while the number of true extinctions may be as high as 69, it is most likely between 22 and 45. The number of angiosperm species described in the Australian flora is 15,638 (Australian National Botanic Gardens Web page: http://155.187.10.12/anbg/), but the actual number may be as much as 10% greater, that is, 17,202.

We can make some attempt to reconcile these extinct and extant figures with how they might be observed in the fossil record. The fossil record of vascular plants is heavily biased toward deciduous, woody plants that grow in lowland areas near lakes and watercourses where sediments are deposited. Herbaceous plants are rarely fossilized; their leaves tend to wither on the plant. Arid and upland regions lack conducive depositional environments. Often there are insufficient morphological features in commonly preserved organs such as leaves and pollen to distinguish species. Compounding this is the fact that very few of the plant remains that are fossilized are ever discovered. These factors always result in the fossil record underestimating the actual diversity of a flora. Species that may be considered reliably preservable include those with the following characteristics: deciduous, preferring relatively mesic environments, with hard woody leaves, having discernible pollen. Of the 69 possibly extinct taxa, very few have these characteristics. Several presumed extinct species are Western Australian woody shrubs/trees in Acacia and Myrtaceae, but it is unlikely that they would be preserved because the environment they inhabit is too dry to produce depositional

sediments. Perhaps the only species that could confidently be expected to be fossilized is a species of Musa from Queensland. Much of Australia's extant flora is arid, semiarid, upland, and/or herbaceous, and of course very little of it is deciduous. As little as 20% (~3,000) are potentially fossilizable. This information transfers to a trapezoidal fuzzy number characterized as [1, 22, 45, 69] (see fig. 3) for the uncertain number of Australian angiosperm extinctions in the past 400 yr and a triangular fuzzy number characterized as [3,000, 15,638, 17,202] for the uncertain total number of fossilizable Australian angiosperms. The absolute (as opposed to the relative figures calculated for mammals above) per taxon extinction rate was calculated using fuzzy arithmetic as between 0.14 and 57.5 extinctions per species million years, with a best estimate of around 3.4 to 7.0 extinctions per species million years. The resultant membership function appears in figure 5.

Discussion

There is little doubt that species are going extinct extremely rapidly and that we are in the midst of a major extinction interval. The way in which this extinction interval compares quantitatively with the fossil record, however, is largely undocumented. The exercise in interpreting modern data in a way that makes comparisons with the fossil record valid (or at least less invalid), points out the need to evaluate parameters in terms of common currencies. We attempted to make the attributes of the data equivalent between the modern data set, about which we have more complete information, and the fossil data set, about which we have limited information. The chief advantage of attempting to propagate uncertainty throughout a calcula-
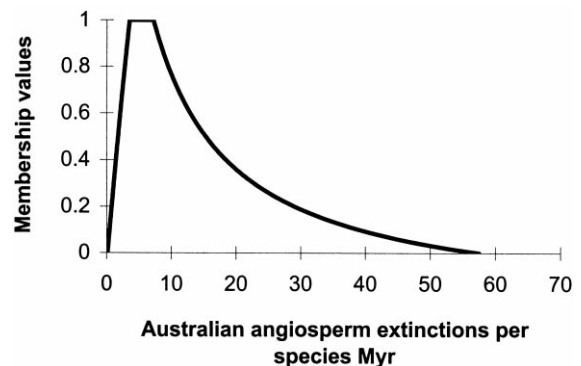

Figure 5: Fuzzy number for the current per taxon extinction rate for Australian angiosperms. The current per taxon extinction rate is around 3.6–7.1 extinctions per species million years and within the bounds of 0.14–57.5 extinctions per species million years.

tion is that it forces us to examine and quantify the magnitude of uncertainties in the estimates of each parameter.

Predictions about the likely fate of the current biota rest on the assumption that the current rate in groups such as mammals is representative of the rates in other taxa, and that rates are closely tied to land clearance and the geographic expansion of intensive human land use (Myers 1979; Lovejoy 1980; Raven 1988; Reid 1992). There is little doubt that if estimates of current extinction rates are roughly correct, then they are not sustainable simply because if they are to continue, Earth will lose most of its biota within a few decades (Pimm et al. 1995). Recognition that species may be differentially susceptible to human activities raises the possibility that the current extinction rate might not be sustained for long because only the most susceptible species will be eliminated (Balmford 1996).

Whether or not the observed extinction rate is comparable to the largest mammalian extinctions at the end-Eocene and Miocene-Pliocene (discounting the end-Pleistocene, which might have had a human component) cannot yet be evaluated because of the problem of scaling rates based on 400 yr to a million years. The possibility that extinction events are clustered in time because species are differentially susceptible to human activities is plausible and may result in overestimation of projected extinction rates. Many other elements of uncertainty outlined above may result in underestimation.

While our calculations include many assumptions and suffer many omissions, they do emphasize the impact of an appropriate metric, equivalent currencies and the consideration of uncertainty on global extinction rates. The results of this analysis highlight the paucity of data and reinforce the importance of collecting better information on species extirpations and extinctions from a much broader taxonomic spectrum.

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