Evolution of life history traits and evolutionary paleoecology

Peter D Smits[1]

[1]psmits@uchicago.edu, Committee on Evolutionary Biology, University of Chicago

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1 Theoretical framework

1.1 Evolutionary paleoevology

Evolutionary paleoecology has been defined as the study of the effect of ecological characters expressed at any level on the macroevolutionary process [Kitchell, 1985]. While macroevolution is defined as the long term speciation (p) and extinction (q) dynamics [Jablonski, 2008], this does not remain the sole manner of discussing macroevolutionary dynamics [Kitchell, 1990, 1985]. Instead, macroevolution can be discussed in terms of the dynamics of differential fitness. Here fitness is defined as the expected time till extinction [Cooper, 1984] which can be considered a universal statement of fitness.

Expected time till extinction is defined for descrete time intervals as

$$E[t_{ext}] = \sum_{t=0}^{\infty} p_t t \tag{1}$$

where p is the probability that the subject of interest goes extinct and t is time [Cooper, 1984]. For continuous time, expected time till extinction is defined

$$E[t_{ext}] = \int_0^{\infty} \phi(t) t \mathrm{d}t \tag{2}$$

where $\phi(t)$ is the probability density distribution for the time of extinction [Cooper, 1984].

1.2 Survival analysis

Survival analysis is the statistical field of representing and modeling time till event data, namely the time till failure of an object. For example, this might be the amount of time a part can experience a specific force before experiencing mechanical failure or the amount of time a person survives after contracting a specific disease. In a paleontological context, this can be considered the longevity of a particular taxon from it's first appearance date (FAD) till it's last appearance dat (LAD).

The survival function ($S(t)$), which is a statement of the probability that an individual (i.e. species) will survive longer than some specific amount of time t, is defined

$$S(t) = P(T > t) \tag{3}$$

where T is the survival time and is greater than, or equal to, 0.

Related to $S(t)$ is the hazard function $h(t)$, which is defined as the instantaneous potential for failure given t amount of time. $h(t)$ is defined

$$h(t) = \lim_{\Delta t \to \infty} \frac{P(t \leq T < t + \Delta t | T \geq t)}{\Delta t} \tag{4}$$

Effectively, this is the velocity or first derivative of $S(t)$.

The survival (Eq. 3) and hazard functions (Eq. 4) are directly related, with one being derived from the other. The general form of $S(t)$ is

$$S(t) = \exp \left[- \int_0^t h(u) \mathrm{d}u \right] \tag{5}$$

and the general form of $h(t)$ being

$$h(t) = - \left[\frac{\mathrm{d}S(t)/\mathrm{d}t}{S(t)} \right] \tag{6}$$

The relationship between the survival function

In the context of biology, $\bar{S(t)}$ for some sample is the mean (expected) survival time or fitness [Cooper, 1984]. Additionally, $h(t)$ is the failure rate and can be interpested as the extinction rate.

Because of this survival curves have had a long history of use in paleobiological studies [Foote, 1988, 2001, Kitchell and Hoffman, 1991, Levinton, 1974, Raup, 1975, 1978, Simpson, 1953, Van Valen, 1973]. The Law of Extinction, or Red Queen hypothesis, stems from analysis of survival curves [Van Valen, 1973]. In terms of modeling the hazard function of a survival curve, the Law of Extinction states that the hazard function is a special case of equation 6 and is defined

$$h(t) = \lambda \tag{7}$$

where λ is some constant. Given the hazard function in equation 7, the survival function is easily defined

$$S(t) = \exp^{-\lambda t} \tag{8}$$

This formulation means that extinction rate is (stochastically) constant over the entire duration of a taxon [Van Valen, 1973]. For further discussion, see below. Other theoretical concepts for extinction rate are that younger taxa have a greater extinction rate than older taxa, or vice-versa. These alternative $h(t)$ functions would be better fit but other, non-uniform, distributions.

Assessing the linearity or nonlinearity of the hazard function for a given sample has been the focus of a lot of research [Kitchell and Hoffman, 1991, Raup, 1975, 1978].

1.3 Macroevolution

Macroevolution, as defined above, has broadly been classified into two categories: effect and species selection [Jablonski, 2008].

Effect macroevolution where selection on a trait expressed at the organismal level effects long term patterns in p and q [Jablonski, 2008, Vrba, 1983]. Effect macroevolution is characterized by "upward" causation, because selection at lower levels (organism) effects the structure of the higher levels (genus and up) [Jablonski, 2008]. Jablonski [2008] defines these traits as "aggregate traits" which can be the entire distribution of a trait for a taxon or some summary statistic (e.g. mean) of a trait distribution. An example aggregate trait would be body size.

Species selection is where selection acts upon a trait that cannot be reduced to the organismal level [Jablonski, 2007, 2008]. It is important to note that macroevolution does not only mean species selection [Vrba, 1983] though they have historically been conflated.

1.4 Law of Extinction

The Law of Extinction, known also as the Red Queen Hypothesis, is defined above (Eq. 7 and 8)

Raup [1975] emphasized the importance of the Law of Extinction, what he called Van Valen's Law, because it represented the first step towards a general theory statement in paleobiology of how to interpret the fossil record that wasn't taxon specific nor just an enumeration of events.

2 Effect of life history on survival in Permian brachiopods

How life history characters effect the macroevolutionary processes of different groups is extremely fundamental to the study of evolutionary paleoecology.

Brachiopods are a relatively ecologically homogenous group that represented a major portion of the later Paleozoic marine community. Here, I focus on three particular ecological traits which define and differentiate most brachiopod taxa: substrate affinity, stabilization strategy, and habitat preference. Each of these three traits are expressed at the organism level and are logically fundamental to the survival of an organism and species. Because of uneven geographic preservation and potential taxonomic concerns, for this study I analyzed the brachiopod record of Australia during the Permian. This specific region and time period is well studied and represents a rather continuous geographic sample with consistent taxonomy [Clapham and Bottjer, 2007, Clapham and James, 2008, 2012].

Using expected time till extinction as the definition of fitness [Cooper, 1984], I investigate survival differences between different life history trait combinations. This analysis shares many similarities with taxonomic survivorship analysis [Van Valen, 1973, 1979] and cohort survivorship analysis [Raup, 1978]. Survivorship analysis is the analysis and modeling of time till event data CITATION. While modeling this time till event data, time-constant and time-varying are used to determine the effect of these variables on survivorship CITATION. Additionally, the comparison of different categories can be used to determine if these categories have similar or different survivorship trajectories CITATION.

Historically, one of the principle questions addressed via paleontological survivorship analysis was of the shape of the survivorship curve. Particularity, the emphasis was on determining if the survivorship curve was linear or not [Kitchell and Hoffman, 1991, Pearson, 1992, Raup, 1975, Sepkoski, 1975, Van Valen, 1973]. Effectively, the question was whether the hazard function (Eq. 4 and 6) of the survivorship curve was best modeled as a constant (Eq. 7) or not.

Here, instead I focus on how the survivorship and hazard functions of might vary between different life history trait combinations. Additionally, using a approach inspired by cohort suvivorship analysis [Raup, 1975] I will investigate how fitness changes over the Permian as climate and habitat structure and availability changed over time CITATIONS.

3 Evolution of correlation in life history traits in brachiopods

4 Cosmopolitan versus endemic dynamics in Cenozoic terrestrial mammals

5 UNNAMED CHAPTER

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