The *Cronus* hypothesis – extinction as a necessary and dynamic balance to evolutionary diversification

Corey J. A. Bradshaw[1,2] and Barry W. Brook[1]

[1]The Environment Institute and School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia 5005, Australia
[2]South Australian Research and Development Institute, P.O. Box 120, Henley Beach, South Australia 5022, Australia
corey.bradshaw@adelaide.edu.au; barry.brook@adelaide.edu.au

Abstract The incredible diversity of life on Earth veils the tumultuous history of biodiversity loss over deep time. Six mass extinction events since the Cambrian species explosion (including the current *Anthropocene*), and many smaller extinction spasms, have terminated 99 % of all species that have ever existed. Evolution and extinction, as universal processes, have been unified previously under James Lovelock's *Gaia* hypothesis, and most recently, under Peter Ward's *Medea* hypothesis. *Gaia* (the Greek Earth mother) posits that life on Earth functions like a single, self-regulating organism, whereas *Medea* (siblicidal wife of Jason of the Argonauts) describes instead a self-destructive feedback where life 'seeks' to destroy itself. We argue that these contrasting views are actually extremes of a scale-invariant stability-entropy spectrum of speciation and extinction for all life on Earth, much as the abundance and stability of a metapopulation of an individual species is the emergent property of births, deaths and migration. In this context, we propose a new metaphor called the *Cronus* hypothesis (patricidal son of *Gaia*) to explain how these processes can be quantified with existing mathematical tools and so be used to describe the ebb and flow of life on Earth along a thermodynamic spectrum. We also argue that *Cronus* provides a broader framework with which to link the natural history research domains of evolutionary, ecological and extinction biology.

Key Words: Extinction; Speciation; *Gaia*; *Medea*; Biodiversity; Panspermia; Thermodynamics; Entropy

"For an evolutionary biologist to ignore extinction is probably as foolhardy as for a demographer to ignore mortality." – David M. Raup (1994)

1. Introduction

The Earth's incredible diversity of life (e.g., conservative estimates of extant [living] species richness: > 4 million protists, 16600 protozoa, 75000-300000 helminth parasites, 1.5 million fungi, 320000 plants, 4-6 million arthropods, > 6500 amphibians, 10000 birds and > 5000 mammals – Adl et al. 2007; AmphiWeb 2009; Dobson et al. 2008; Fenchel & Finlay 2006; Frost 2009; Gill 2002; Hawksworth 1991; Novotny et al. 2002; Prance 2001; Wilson & Reeder 2005) has experienced at least five mass extinction events since the Cambrian period (i.e., during the Ordovician [490–443 million years ago (mya)], Devonian [417–354 mya], Permian [299–250 mya], Triassic [251–200 mya], and Cretaceous [146–64 mya] – Sodhi et al. 2009), with up to 95 % of species disappearing in the Permian extinction event alone (Benton 2003), and 50 to 80 % in the other events. Just as evolution has driven the evolutionary diversification of millions of species over billions of years of Earth's history, extinction has kept remarkable pace: more than 99 % of all species that have ever existed on the planet are now forever consigned to the geological vaults (Raup 1986, 1994).

Although the 'background' extinction rate suggests that an average species' life span is approximately 1 – 10 million years (Frankham et al. 2002; Raup 1986), the pattern of deep-time extinctions is anything but constant. Mass extinction events have a variety of ultimate causes, from bolide impact to volcanism, and from marine anoxia to rapid climate change, some of which might have been the result of amplifying feedbacks arising from external catastrophic triggers – such as an asteroid strike causing immediate mortality, short-term cooling from dimming atmospheric dust, and long-term warming from the carbon dioxide released from vast amounts of vaporised limestone (Alvarez 2003; Bambach 2006; Benton 2003; Conway-Morris 1997; Courtillot 1999; Erwin 2006; Gomez et al. 2007; Hallam 2005; Hallam & Wignall 1997; Hoffman 1989; Ward 1994). Despite early flirtations with the idea of regular return times (Raup & Sepkoski 1986), subsequent work has failed to confirm any detectable periodicity in extinction events (Benton 1995), and even species recovery post-event differs markedly (Conway-Morris 1998; Erwin 1998, 2001; Erwin 2006; Jablonski 1989; Raup 1991).

There is general consensus that we have now entered the sixth mass extinction event (recently reviewed in Sodhi *et al.* 2009), which has been dubbed the *Anthropocene* (Crutzen 2002) because its primary driver is human over-consumption, over-population, and associated degradation of the biosphere. This current biodiversity crisis (Ehrlich & Pringle 2008) is characterized by extinction rates exceeding the deep-time average background rate by 100- to 10000-fold (Pimm & Raven 2000), even though total species loss is still less than that during the largest deep-time mass extinctions (Gaston 2000;

Pimm et al. 1995; Singh 2002; Smith et al. 1993). Although we have a growing comprehension of the principal drivers of extinction and their synergies (Bradshaw et al. 2008; Brook et al. 2008; Field et al. 2009; Purvis et al. 2000; Sodhi et al. 2008a; Sodhi et al. 2009; Sodhi et al. 2008b), our appreciation of its complexities is still rudimentary (Brook et al. 2008; Fagan & Holmes 2006; Melbourne & Hastings 2008).

Anyone not familiar with the intricacies of biotic extinction might perceive it to be a relatively direct and rapid process whereby all individuals making up the populations of a defined species are 'removed' from the Earth by either direct exploitation, the sudden appearance of an alien predator, or the broad-scale destruction of habitats. However, the reality is that species disappear for a host of complex and interactive reasons (Brook *et al.* 2008; Melbourne & Hastings 2008), and the ultimate hammer driving the nail into a species' coffin is often not the same mechanism that caused it to decline in the first place (Brook et al. 2006; Caughley 1994). Some good examples of this mechanistic disconnect include the heath hen *Tympanuchus cupido cupido* (decline by over-harvesting; extinction from inbreeding depression, fire and predation – Gross 1931; Johnson & Dunn 2006) and the great auk *Pinguinus impennis* (decline from hunting; extinction of the last remaining population by volcanic eruption – Halliday 1978). Even the generally well-accepted idea that particular evolved traits heighten a species' extinction 'proneness' are somewhat naïve because they ignore the circumstances under which these evolved via natural selection in the first place (Brook *et al.* 2008). Instead, it is the pace and character of environmental change (Brook *et al.* 2008; Sodhi *et al.* 2009) that leads to non-random rates and patterns of extinction among taxa (Jablonski 1989; Purvis *et al.* 2000).

Given this context, we argue here that extinction is as integral a part of the history of life as speciation, and the two dynamic and interacting forces have traded blows over vast spans of time. This consistent interaction suggests to us a new way of contextualizing and modelling extinction within a broader biophysical framework. We term this new extinction-speciation trade-off the '*Cronus* hypothesis', which we describe in more detail below, and contrast it with existing concepts of global biodiversity patterns illustrated by the *Gaia* (Lovelock 2006), *Medea* (Ward 2009a, b) and entropy (Whitfield 2007) hypotheses.

2. The *Gaia* Hypothesis

In the 1960s, James Lovelock conceived the novel concept of *Gaia* – an ecological hypothesis positing that life on Earth functions like a single, self-regulating organism (Lovelock 1965; Lovelock 1972; Lovelock & Margulis 1974). He also coined the now-common term 'Earth systems science' to describe the study of planetary-scale biotic-geophysical interactions. Named after the Greek legend of the goddess of the Earth, the *Gaia* (*Γαῖα* – Atsma 2009) hypothesis (and all its modern variants – summarized in Ward 2009a) suggested that the planet's biodiversity is comprised of a complex array of ecological feedbacks that promote homeostasis (Barlow & Volk 1992) – a 'goal' leading to conditions favourable to terrestrial life (Volk 2006). In other words, *Gaia* explained life itself as an aggregate that interacts with the physical environment to maintain conditions favourable for life (Ward 2009a). In the original papers (Lovelock 1965; Lovelock 1972; Lovelock & Margulis 1974), Lovelock suggested that the Earth's ecosystems seek an "optimum" state – a notion that was critiqued heavily based on evolutionary arguments (Dawkins 1982; Doolittle 1981; Ehrlich 1991; Wilson & Sober 1989). However, Lovelock has recently downplayed the notion of optimality (Watson 2009). His latest treatises of the *Gaia* hypothesis (Lovelock 2006; Lovelock 2009), which he has upgraded to a "theory" (Volk 2006), instead focus on non-linear 'tipping points' and eventual collapse of the Earth's life-support system, with apocalyptic implications for the planet's human carrying capacity (Watson 2009). As such, the "revenge of *Gaia*" (Lovelock 2006) is a poetic metaphor for the imminent loss of Earth's regulatory system, implying that chaos will ensue.

3. A new metaphor: the *Cronus* Hypothesis

But what if the diversity of life operated not like a single, self-regulating organism, but is instead akin to an interacting and competing 'population', with species representing its individuals? Under such a model (Fig. 1), speciation and extinction are analogous to the demographic processes of birth and death that underpin the local or regional growth rate of a biological population – for as death necessarily

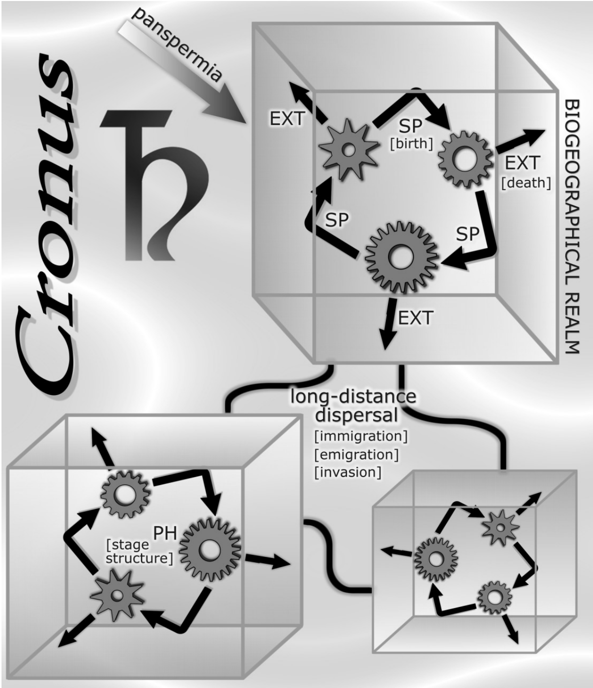

Figure 1. The *Cronus* (♄) metaphor for the diversity of all planetary life, operating as an interacting and competing population of organisms. Cogs represent species assemblages (**SA**) of different composition and magnitude (e.g., number and type of species represented by variability in the number and shape of a cog's teeth). The organization of assemblages is similar to the stage structure of populations. Rates of speciation (**SP**) are analogous to [**birth**] in population models. Extinction of species (**EXT**) occurs within assemblages (or entire assemblages can disappear during mass extinction events) – a process operating like mortality [**death**] of individuals in a population. Groups of species assemblages can interact within a single biogeographical realm as a sub-population within the global metapopulation, with different community composition (diversity, biomass, etc.) among realms (equivalent to sub-populations occupying areas of differing habitat suitability within a landscape). Realms are connected by dispersal and invasion operating over short (e.g., human-mediated invasion) or longer (e.g., continental plate tectonics; island colonization) time scales, processes analogous to [**immigration & emigration**] among sub-populations. Panspermia represents the hypothesized seeding of a primitive Earth by extraterrestrial microorganisms, potentially deriving from its own planetary metapopulation of organisms.

terminates life, extinction is an inevitable part of evolution. In this framework, phylogeny is akin to the internal age or stage structure of the population, and biogeography captures the complexities of its habitat use and density distribution across local space, including historical refugia, competitive exclusion and connectivity. In this macro view, biogeographical realms are equivalent to local populations of the global biota, with immigration and emigration occurring across the planetary 'metapopulation' (*sensu* Hanski 1999) of species. If credence is given to the somewhat radical idea of 'panspermia' (Joseph 2009a) – the seeding of a primitive Earth by extraterrestrial microorganisms (Hoyle and Wickramasinghe 2000; Joseph 2009a,b; Napier 2004) – then even the planet itself might be just one subpopulation within a widely dispersed interstellar metapopulation (Joseph 2009b).

We have chosen to call this framework, describing the global biota as a planetary population, the *Cronus* hypothesis. *Cronus* (*Κρόνος* – symbolized as ♄) was the patricidal (or patri-emasculating) youngest son of *Gaia*, the Earth mother. *Cronus* was also the leader of the first generation of Titans, the giant descendants of *Gaia* and *Uranus*, the sky father. *Cronus* was incited by his mother to kill *Uranus* for perceived crimes against *Gaia*'s other descendants, and *Cronus* himself was overthrown by his own son, *Zeus*, and banished to Hades (Atsma 2009). Given the tumultuous and competitive life-and-death history of *Cronus*, we believe this metaphor better captures the processes of inter-species competition and mutualisms that our population analogy of speciation and extinction embodies. Under the *Gaia* model, self-regulation works to avoid extinction because it is akin to the loss of a body part (function is reduced), whereas under *Cronus*, extinction is part of the process of natural selection (providing restoration of function through subsequent diversification).

We argue that the concept of *Cronus* has merit on two fronts. First, the notion of a community of species as a population of selfish individuals (Dawkins 1989) retains the Darwinian view of contestation, without the necessity of cooperation that the organismal *Gaia* concept implies. Self-regulation in *Cronus* occurs naturally as a result of extinction modifying the course of future evolution and opening up new opportunities for diversification to fill empty niches. Second, by regarding macroevolutionary forces as equivalent to population processes, deeper analogies emerge which are useful for scientific interpretation of observed phenomena, and are amenable to mathematical manipulation using models developed for ecological lines of inquiry (Fig. 2). For instance, the causes of extinction can be thought of as equivalent to the different processes that lead to individual deaths within a population, be it from accidents (e.g., catastrophic extinctions from bolide strikes, volcanism, intense storms, wildfire; or chance demographic failure at low population size – Melbourne & Hastings 2008), senescence (e.g., higher extinction probability in older phylogenetic lineages – Johnson 1998; Lawton & May 1995; Nee & May 1997), conflict, starvation and disease (e.g., invasion of new competitors or predators [including humans], species-area effects following the biotic interchanges caused by continental drift, or fragmentation of habitats – McKinney 1998), poison (e.g., oceanic hypoxia and acidification, increased atmospheric CO_2), and even congenital defects (e.g., habitat specialization or large body size, leading to higher susceptibility of species to particular stressors – Brook *et al.* 2008). Moreover, the differential mortality rates that are characteristic of the alternative life stages of many organisms can be compared to clades with low or high evolutionary turnover (Jablonski 1989).

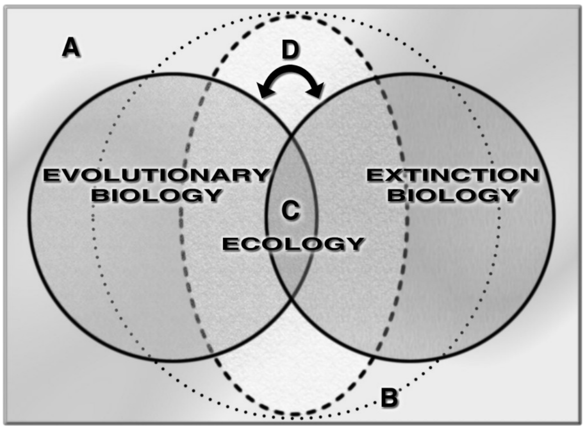

Figure 2. The macro-domains of natural history. Under the *Cronus* metaphor for the dynamic ebb and flow of life on Earth as analogous to a population of organisms, evolutionary biology is the study of the 'birth' rates and carrying capacity (selection balance) of species, and extinction biology is phylogenetic 'death'. Ecology envelopes the processes linking the temporal and spatial flux of biodiversity within the total physical environment (A). These major spheres contribute to, and acquire knowledge from, other fields of natural and environmental sciences such as molecular biology, chemistry and physical geography (B). Applied and theoretical disciplines such as conservation biology, paleontology, systematics and biogeography emerge from the nexus of these major fields (C), and exploit additional information from the broad realms of socio-economics, history and mathematics. Extinction both modifies, and is an outcome of, evolutionary processes (D). This schematic of the interrelationship of and interaction between research fields illustrates our major point that when the biology of extinction is perceived in the context of *Cronus*, it emerges quite naturally as a distinct and fundamental field of scientific inquiry which complements other major domains. To illustrate with a medical analogy, when a person dies, immediate interest focuses on what that individual loss has costs us (e.g., emotional impact, life insurance, loss of services they provided, etc.). This is akin to the applied discipline of conservation biology, which is concerned with preventing the loss of species on both intrinsic and utilitarian grounds (e.g., loss of ecosystem services). Yet when cancer or obesity death rates increase in a society, there is a need to understand and reduce broader causes through evidence-based epidemiological research. *Cronus* is the analytical framework that encapsulates equivalent lines of inquiry in extinction biology.

4. The *Medea* Hypothesis

We are not first to suggest an entirely new framework and metaphor for life on Earth since *Gaia*. Peter Ward (Ward 2009a, b) recently outlined a rather different perspective to *Gaia* and *Cronus* – the *Medea* hypothesis. To extend the Greek mythology metaphor, the sorceress *Medea* (*Μήδεια*) was the granddaughter of *Helios* the sun god and wife to Jason of the Argonauts who later killed her own sons as revenge for Jason's unfaithfulness (Atsma 2009). Instead of the self-regulating super-organism *Gaia*, Ward describes the Earth's mass extinctions as *Medean* events – large biodiversity loss driven by life itself (Ward 2009a). Arguing that the *Gaia* hypothesis cannot account for large shifts in the Earth's temperature over geological time, *Medea* describes how the massive flux of atmospheric carbon dioxide and methane by the processes of plant, microbial and animal respiration was the very cause of such volatile conditions which lead to (at least some) mass extinctions (Ward 2009a, b). In essence, the *Medean* perspective describes a self-destructive, or anti-order component where life 'seeks' to destroy itself, and it can do so on a massive scale due to amplifying feedbacks under certain circumstances (Ward 2009a, b). Modern human society might eventually merit the *Medean* soubriquet.

5. Entropy

The ideas of order and chaos alluded to above have spawned another way of looking at life (and death) on Earth. A concept gaining traction amongst evolutionary ecologists is the application of thermodynamic laws to models of evolution and extinction (Whitfield 2007). Directionality theory quantifies the rules governing the flow of metabolic energy between populations of competing individuals and environmental resources (Demetrius 2000). Thermodynamic models describe rules of heat energy transfer between aggregates of matter, so the family of parameters defining thermodynamics can be related formally to biotic patterns. Here, evolutionary entropy, a measure of heterogeneity in the age of reproducing individuals, is predicted to increase as a system evolves from one stationary state to the next, just as thermodynamic entropy increases for irreversible processes (Demetrius 2000). Entropy determines the rate of decay of fluctuations in abundance due to inherent demographic variability and increases in bounded populations over generations. Thus, extinction of species within a community can be considered a systematic loss of entropy, which results in reduced efficiency of energy flow and so leads to a decline in ecosystem stability (Whitfield 2007). Although such mathematical analogies currently have little direct empirical support, the application of physical laws to extinction dynamics demands more attention, because it could provide a theoretical framework for predicting extinction patterns in the future.

6. Dynamic stationarity

We can extend the population analogy by considering constant the amount of non-living ‘energy’ on the Earth that is available for incorporation into biomass (an evolutionary ‘carrying capacity’); thus, speciation itself must elicit extinction, and extinction gives rise to further speciation (Raup 1986) – in effect an evolutionary zero-sum game described by the Red Queen model (Benton 2009). This process begat the concept of ‘constant extinction rate’ (Van Valen 1973), which states that for any group of related organisms there is a constant probability of extinction of any taxon (Stenseth 1979; Van Valen 1973). Just as most of a species’ individuals that have ever lived are now dead (e.g., only 9 % of all humans that have ever been born are living today despite the post-industrial surge in population; Westing 1981) – so too most species that have ever existed are extinct (Raup 1986, 1994). At least over the last few geological epochs (Pleistocene onwards), there has been remarkable constancy in total biomass and species diversity despite rapid shifts in community composition via extinctions and colonisation events (Barnosky 2008; Brown et al. 2001). Even though periodic and broad-scale changes in productivity can invoke large shifts in diversity and biomass, re-equilibration via speciation and colonisation will tend to smooth biomass and diversity fluctuations when examined over sufficient geological time scales. Even the famous Sepkoski curve, describing the logistic increase in marine species diversity over time (Sepkoski et al. 1981), is at least partially a sampling and taphonomic artefact, with recent bias-corrected curves suggesting relative stability in species diversity throughout the past 530 million years of visible life (Phanerozoic Aeon; Benton 2009).

What does this evolutionary zero-sum game of living matter portend for humanity? Most species on the planet today are rare in the sense that they are comprised of few individuals (Gaston 2008). Put another way, the state of commonness is unusual, and those few species that dominate total biomass do not tend to do so over the entire course of their evolutionary lifespan. In the current *Anthropocene* extinction event, even once-common species, such as the American bison (*Bison bison*) and passenger pigeon (*Ectopistes migratorius*), can decline to rarity or extinction (Gaston 2008; Gaston & Fuller 2008). What the future holds for the Earth’s currently most common species, such as humans and their commensals, is uncertain, but the ideas of extinction and biomass-diversity constancy suggest that our time in the limelight of numerical dominance is limited (see Matheny 2007).

7. Conclusion

Comparing these four ways of viewing life on Earth and beyond, and the opposing forces of speciation and extinction, our *Cronus* hypothesis and the thermodynamic framework of entropy loss are most similar and comprehensive – both approaches allow for mathematical description of evolutionary forces, offset by extrinsic and intrinsic causes of species loss. In contrast, Lovelock's *Gaia* and Ward's *Medea* can be best viewed as extremes of a continuum between cooperation and self-destruction (i.e., *Gaia* versus anti -*Gaia*, or *Gaia* and her "evil twin" – Ward 2009a), which ultimately require some intermediary process. As such, we posit that the background processes of natural history mostly operate closer to the centre of these extreme views (Fig. 3) – that this is in fact the equilibrium – and as such we argue that *Cronus* provides a better framework for explaining the patterns we observe in global biodiversity throughout most of the span of deep time (and space).

Analogous to Lovelock's parable of *Daisyworld* for applying a mathematical framework to the *Gaia* hypothesis (Lenton & Lovelock 2000; Watson & Lovelock 1983), a *Cronus* view of evolutionary and extinction dynamics could be modelled by modifying existing metapopulation tools (Hanski 1998, 1999). For example, species as individuals with particular 'mortality' (extinction) rates, and lineages with particular 'birth' (speciation) rates, could interact and disperse among 'habitats' (biogeographical realms). 'Density' feedback could represent anything from competitive exclusion to parasitic, mutualistic or commensal symbiosis. As a 'population' (species) declines, perverse feedbacks such as inbreeding depression can induce Allee effects (Courchamp et al. 2008) that further exacerbate extinction risk – this is one *Medean*-like phase of the population analogy represented by *Cronus*. In contrast, stochastic fluctuation around a 'carrying capacity' (niche saturation; energy limitation) achieved through compensatory population dynamics arising when environmental conditions are relatively stable becomes the *Gaia*-like equilibrium embedded with *Cronus*. The *Cronus* model also has the advantage of being scale-invariant – it could be applied to the turnover of microbial diversity inhabiting a single macro-organism through to inter-planetary exchange

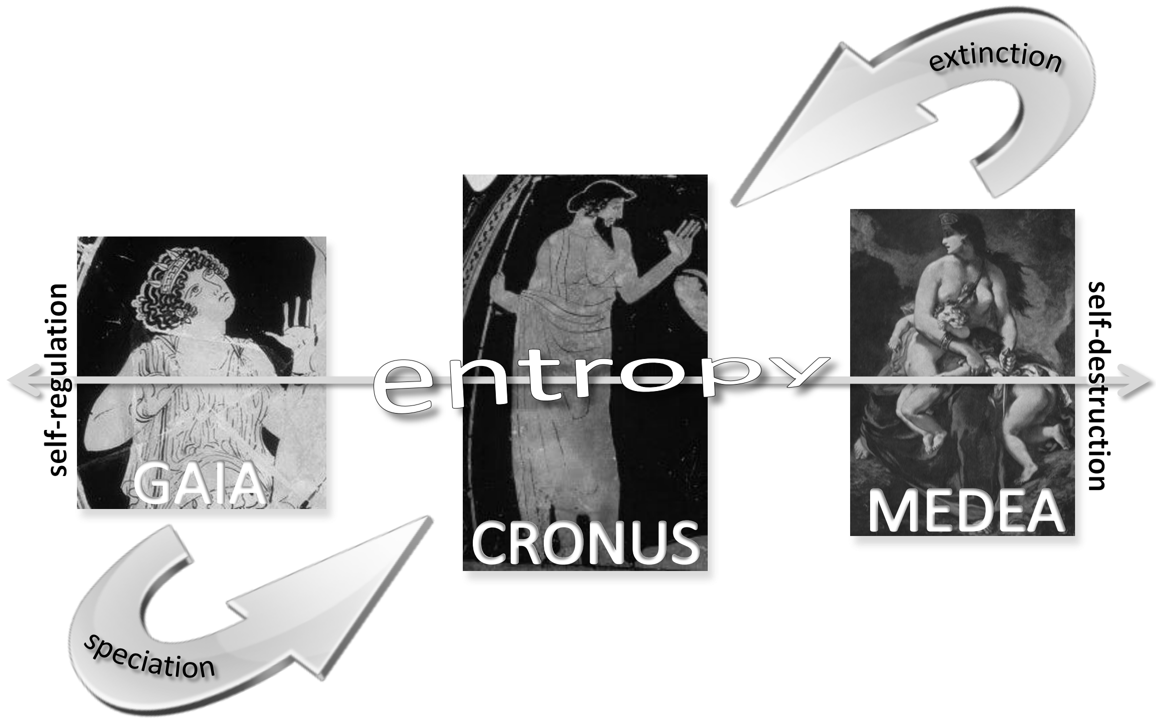

Figure 3. Three metaphors for the evolution, extinction and maintenance of life on Earth, named after figures from Greek mythology. *Gaia* represents order and self-regulation, whereas *Medea* is self-induced entropy loss. Our concept of *Cronus* bridges these extremes by considering the play-off between speciation (birth) and extinction (death) as a balanced product of these opposing tendencies. *Gaia* image from Attic Red Figure by Aristophanes ca. 410-400 BC (housed in Antiken-museen, Berlin, Germany – Berlin F2531, BAN: 220533; source: www.theoi.com). *Cronus* image from Attic Red Figure by the Nausicaa Painter ca. 475-425 BC (housed in Metropolitan Museum, New York, USA – New York 06.1021.144, BAN: 214648; source www.theoi.com). *Medea* image from oil on canvas by Eugène Ferdinand Victor Delacroix 1862 (housed in Musée des Beaux-Arts, Lille, France; source www.wikipedia.com).

of life. When combined with more theoretical development (and, ideally, experimental or numerical testing) of the thermodynamic model of biological entropy, *Cronus* mathematics can be used by evolutionary ecologists, palaeontologists and exobiologists to pose and test novel hypotheses regarding the ever-changing patterns of life on Earth.

References

Adl, S. M., Leander, B. S., Simpson, A. G. B., Archibald, J. M., Anderson, O. R., Bass, D., Bowser, S. S., Brugerolle, G., Farmer, M. A., Karpov, S., Kolisko, M., Lane, C. E., Lodge, D. J., Mann, D. G., Meisterfeld, R., Mendoza, L., Moestrup, O., Mozley-Standridge, S. E., Smirnov, A. V., Spiegel, F. (2007). Diversity, nomenclature, and taxonomy of protists. Systematic Biology, 56, 684-689.

Alvarez, W. (2003). Comparing the evidence relevant to impact and flood basalt at times of major mass extinctions. Astrobiology, 3, 153-161.

AmphiWeb (2009). AmphibiaWeb: Information on amphibian biology and conservation. University of California, Berkeley, California. http://amphibiaweb.org/.

Atsma, A. J. (2009). The Theoi Project, Greek Mythology. Auckland, New Zealand. http://www.theoi.com.

Bambach, R. K. (2006). Phanerozoic biodiversity mass extinctions. Annual Review of Earth and Planetary Sciences, 34, 127-155.

Barlow, C. & Volk, T. (1992). Gaia and evolutionary biology. Bioscience, 42, 686-693.

Barnosky, A. D. (2008). Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. Proceedings of the National Academy of Sciences of the USA, 105, 11543-11548.

Benton, M. J. (1995). Diversification and extinction in the history of life. Science, 268, 52-58.

Benton, M. J. (2003). When Life Nearly Died: The Greatest Mass Extinction of All Time. Thames & Hudson, London.

Benton, M. J. (2009). The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. Science, 323, 728-732.

Bradshaw, C. J. A., Giam, X., Tan, H. T. W., Brook, B. W., Sodhi, N. S. (2008). Threat or invasive status in legumes is related to opposite extremes of the same ecological and life history attributes. Journal of Ecology, 96, 869-883.

Brook, B. W., Sodhi, N. S., Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. Trends in Ecology and Evolution, 25, 453-460.

Brook, B. W., Traill, L. W., Bradshaw, C. J. A. (2006). Minimum viable population size and global extinction risk are unrelated. Ecology Letters, 9, 375-382.

Brown, J. H., Ernest, S. K. M., Parody, J. M., Haskell, J. P. (2001). Regulation of diversity: maintenance of species richness in changing environments. Oecologia, 126, 321-332.

Caughley, G. (1994). Directions in conservation biology. Journal of Animal Ecology, 63, 215-244.

Conway-Morris, S. (1997). Palaeontology: Grasping the opportunities in the science of the twenty-first century. Geobios, 30, 895-904.

Conway-Morris, S. (1998). The evolution of diversity in ancient ecosystems: a review. Philosophical Transactions of the Royal Society of London B, 353, 327-345.

Courchamp, F., Ludik, B., Gascoigne, B. (2008). Allee Effects in Ecology and Conservation. Oxford University Press, Oxford, United Kingdom.

Courtillot, V. (1999). Evolutionary Catastrophes: The Science of Mass Extinction. Cambridge University Press, Cambridge, UK.

Crutzen, P. J. (2002). Geology of mankind: the Anthropocene. Nature, 415, 23.

Dawkins, R. (1982). The Extended Phenotype. W. H. Freeman, New York, NY.

Dawkins, R. (1989). The Selfish Gene. Second Edition edn. Oxford University Press, Oxford.

Demetrius, L. (2000). Thermodynamics and evolution. Journal of Theoretical Biology, 206, 1-6.

Dobson, A., Lafferty, K. D., Kuris, A. M., Hechinger, R. F., Jetz, W. (2008). Homage to Linnaeus: How many parasites? How many hosts? Proceedings of the National Academy of Sciences of the USA, 105, 11482-11489.

Doolittle, W. F. (1981). Is nature really motherly? CoEvolution Quarterly, 29, 58-65.

Ehrlich, P. (1991). Coevolution and its applicability to the Gaia hypothesis. In Scientists on Gaia (eds Schneider, S. H. & Boston, P. E.), pp. 19-22. MIT Press, Cambridge, MA.

Ehrlich, P. R. & Pringle, R. M. (2008). Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions. Proceedings of the National Academy of Sciences of the USA, 105, 11579-11586.

Erwin, D. H. (1998). The end and the beginning: recoveries from mass extinctions. Trends in Ecology and Evolution, 13, 344-349.

Erwin, D. H. (2001). Lessons from the past: biotic recoveries from mass extinctions. Proceedings of the National Academy of Sciences of the USA, 98, 5399-5403.

Erwin, D. H. (2006). Extinction: How Life on Earth Nearly Ended 250 Million Years Ago. Princeton University Press, Princeton, NJ.

Fagan, W. F. & Holmes, E. E. (2006). Quantifying the extinction vortex. Ecology Letters, 9, 51-60.

Fenchel, T. & Finlay, B. J. (2006). The diversity of microbes: resurgence of the phenotype. Philosophical Transactions of the Royal Society of London B, 361, 1965-1973.

Field, I. C., Meekan, M. G., Buckworth, R. C., Bradshaw, C. J. A. (2009). Susceptibility of sharks, rays and chimaeras to global extinction. Advances in Marine Biology, 56, doi:10.1016/S0065-2881(09)56004-X.

Frankham, R., Ballou, J. D., Briscoe, D. A. (2002). Introduction to Conservation Genetics. Cambridge University Press, Cambridge, UK.

Frost, D. R. (2009). Amphibian Species of the World: an Online Reference Version 5.3. American Museum of Natural History, New York. http://research.amnh.org/herpetology/amphibia/.
Gaston, K. J. (2000). Global patterns in biodiversity. Nature, 405, 220-227.
Gaston, K. J. (2008). Biodiversity and extinction: the importance of being common. Progress in Physical Geography, 32, 73-79.
Gaston, K. J. & Fuller, R. A. (2008). Commonness, population depletion and conservation biology. Trends in Ecology and Evolution, 23, 14-19.
Gill, F. (2002). Birds of the World: Recommended English Names. Princeton University Press, Princeton, NJ.
Gomez, J. J., Goy, A., Barron, E. (2007). Events around the Triassic-Jurassic boundary in northern and eastern Spain: A review. Palaeogeography Palaeoclimatology Palaeoecology, 244, 89-110.
Gross, A. O. (1931). Banding the last heath hen. Bird Banding, 2, 99-105.
Hallam, A. (2005). Catastrophes and Lesser Calamities: The Causes of Mass Extinctions. Oxford University Press, New York.
Hallam, A. & Wignall, P. B. (1997). Mass Extinctions and Their Aftermath. Oxford University Press, Oxford, UK.
Halliday, T. (1978). Vanishing Birds: Their Natural History and Conservation. 1st edn. Holt, Rinehart and Winston, New York.
Hanski, I. (1998). Metapopulation dynamics. Nature, 396, 41-49.
Hanski, I. (1999). Metapopulation Ecology. Oxford University Press, Oxford, UK.
Hawksworth, D. L. (1991). The fungal dimension of biodiversity: magnitude, significance, and conservation. Mycological Research, 95, 641-655.
Hoffman, A. (1989). What, if anything, are mass extinctions. Philosophical Transactions of the Royal Society of London B, 325, 263-261.
Hoyle, F. and Wickramasinghe, N.C. (2000) Astronomical Origins of Life: Steps towards Panspermia (Kluwer Academic Press, USA).
Jablonski, D. (1989). The biology of mass extinction: a palaeontological view. Philosophical Transactions of the Royal Society of London B, 325, 357-368.
Johnson, C. N. (1998). Species extinction and the relationship between distribution and abundance. Nature, 394, 272-274.
Johnson, J. & Dunn, P. (2006). Low genetic variation in the heath hen prior to extinction and implications for the conservation of prairie-chicken populations. Conservation Genetics, 7, 37-48.
Joseph, R. (2009a). Life on Earth came from other planets. Journal of Cosmology, 1, 1-56.
Joseph, R. (2009b). The evolution of Life from other planets. Journal of Cosmology, 1, 100-200.
Lawton, J. H. & May, R. M., eds. (1995). Extinction Rates. Oxford University Press, Oxford, UK.
Lenton, T. M. & Lovelock, J. E. (2000). Daisyworld is Darwinian: constraints on Adaptation are important for planetary self-regulation. Journal of Theoretical Biology, 206, 109-114.
Lovelock, J. (2006). The Revenge of Gaia. Penguin Books, London.
Lovelock, J. (2009). The Vanishing Face of Gaia: A Final Warning. Basic Books, New York, NY.
Lovelock, J. E. (1965). A physical basis for life detection experiments. Nature, 20, 568-570.
Lovelock, J. E. (1972). Gaia as seen through the atmosphere. Atmospheric Environment, 6, 579-580.
Lovelock, J. E. & Margulis, L. (1974). Atmospheric homeostasis by and for the biosphere - the Gaia hypothesis. Tellus, 26, 2-10.
Matheny, J. G. (2007). Reducing the risk of human extinction. Risk Analysis, 27, 1335-1344.
McKinney, M. L. (1998). On predicting biotic homogenization: species-area patterns in marine biota. Global Ecology and Biogeography Letters, 7, 297-301.
Melbourne, B. A. & Hastings, A. (2008). Extinction risk depends strongly on factors contributing to stochasticity. Nature, 454, 100-103.
Napier, W. M. (2004). A mechanism for interstellar panspermia. Monthly Notices of the Royal Astronomical Society, 348, 46-51.
Nee, S. & May, R. M. (1997). Extinction and the Loss of Evolutionary History. Science, 278, 692-694.
Novotny, V., Basset, Y., Miller, S. E., Weiblen, G. D., Bremer, B., Cizek, L., Drozd, P. (2002). Low host specificity of herbivorous insects in a tropical forest. Nature, 416, 841-844.
Pimm, S. L. & Raven, P. (2000). Extinction by numbers. Nature, 403, 843-845.
Pimm, S. L., Russell, G. J., Gittleman, J. L., Brooks, T. M. (1995). The future of biodiversity. Science, 269, 347-350.
Prance, G. T. (2001). Discovering the plant world. Taxon, 50, 345-359.
Purvis, A., Jones, K. E., Mace, G. M. (2000). Extinction. BioEssays, 22, 1123-1133.
Raup, D. M. (1986). Biological extinction in Earth history. Science, 231, 1528-1533.
Raup, D. M. (1991). Extinction: Bad Genes or Bad luck? W.W. Norton, New York.
Raup, D. M. (1994). The role of extinction in evolution. Proceedings of the National Academy of Sciences of the USA, 91, 6758-6763.
Raup, D. M. & Sepkoski, J. J., Jr. (1986). Periodic extinction of families and genera. Science, 231, 833-836.
Sepkoski, J. J., Bambach, R. K., Raup, D. M., Valentine, J. W. (1981). Phanerozoic marine diversity and the fossil record. Nature, 293, 435-437.
Singh, J. S. (2002). The biodiversity crisis: a multifaceted review. Current Science, 82, 638-647.
Smith, F. D. M., May, R. M., Pellew, R., Johnson, T. H., Walter, K. R. (1993). How much do we know about the current extinction rate. Trends in Ecology and Evolution, 8, 375-378.
Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H., Bradshaw, C. J. A. (2008a). Measuring the meltdown: drivers of global amphibian extinction and decline. PLoS ONE, 3, e1636.
Sodhi, N. S., Brook, B. W., Bradshaw, C. J. A. (2009). Causes and consequences of species extinctions. In The

Princeton Guide to Ecology (ed Levin, S. A.), pp. 514-520. Princeton University Press, Princeton, New Jersey.
Sodhi, N. S., Koh, L. P., Peh, K. S.-H., Tan, H. T. W., Chazdon, R. L., Corlett, R. T., Lee, T. M., Colwell, R. K., Brook, B. W., Sekercioglu, C. H., Bradshaw, C. J. A. (2008b). Correlates of extinction proneness in tropical angiosperms. Diversity and Distributions, 14, 1-10.
Stenseth, N. C. (1979). Where have all the species gone? On the nature of extinction and the Red Queen Hypothesis. Oikos, 33, 196-227.
Van Valen, L. (1973). A new evolutionary law. Evolutionary Theory, 1, 1-30.
Volk, T. (2006). Real concerns, false gods. Nature, 440, 869 -870.
Ward, P. (2009a). Gaia's evil twin. New Scientist, 202, 28-31.
Ward, P. (2009b). The Medea Hypothesis: Is Life on Earth Ultimately Self-Destructive? Princeton University Press, Princeton, NJ.
Ward, P. D. (1994). The End of Evolution: On Mass Extinctions and the Preservation of Biodiversity. Bantam, New York.
Watson, A. (2009). Final warning from a sceptical prophet. Nature, 458, 970-971.
Watson, A. J. & Lovelock, J. E. (1983). Biological homeostasis of the global environment: the parable of Daisyworld. Tellus, 35, 284-289.
Westing, A. H. (1981). A note on how many humans that have ever lived. Bioscience, 31, 523-524.
Whitfield, J. (2007). Survival of the likeliest? PLoS Biology, 5, e142 doi:10.1371/journal.pbio.0050142.
Wilson, D. E. & Reeder, D. M., eds. (2005). Mammal Species of the World: A Taxonomic and Geographic Reference, pp 2142. Johns Hopkins University Press, Baltimore, Maryland.
Wilson, D. S. & Sober, E. (1989). Reviving the superorganism. Journal of Theoretical Biology, 136, 337 -356.