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WHY PALEOBIOLOGICAL INSIGHTS MATTER FOR CONSERVATION BIOLOGISTS

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ABSTRACT. — Paleobiology and conservation biology seem to be very distant disciplines. The first deals with extinct organisms in the distant past and the latter with extant organisms undergoing changes due to large anthropogenic influences. However, it is increasingly being recognised that paleobiological insights are relevant in many branches of biology, especially in conservation and organismal biology. Here, I describe an empirically driven paleobiological model that has important implications for conservation questions. The model states that species rise to their characteristic maximal geographic spread over a very long time and also decline to final extinction over a similarly long time, on the order of hundreds of thousands of years on average. I discuss the implications of this finding for conservation biology, which tends to work with data and processes that occur over decadal time scales.

KEY WORDS. — conservation biology, conservation paleobiology, extirpations, macroevolution, fossil record

Navjot Sodhi, to whom this volume of the Raffles Bulletin of Zoology is dedicated to, like most biologists and naturalists, was very concerned about extinctions of the current day. He devoted much of his life to understanding why population declines, and why extirpations and extinctions occur (Brook et al., 2003; Koh et al., 2004a; Sodhi et al., 2004; Brook et al., 2008), using mainly current day data (Castelletta et al., 2000; Liow et al., 2001; Koh et al., 2004b).

The contemporary extinction crisis is often referred to as the sixth mass extinction (Wake & Vredenburg, 2008; Dunn et al., 2009; Barnosky et al., 2011), referencing the "big five" mass extinctions known from the fossil record of the Phanerozoic (Raup & Sepkoski, 1982). The fossil record not only allows us to compare current extinctions with past extinctions in the near-time and deep-time realms (Dietl & Flessa, 2011) but also serves as a base-line for pre-human intervened communities (Jackson & Johnson, 2000). Despite a widespread awareness of the existence of the fossil record, crucial paleobiological insights are exceedingly seldom considered by conservation ecologists and other biologists researching on extant organisms. When the paleobiological literature is cited in the neotological literature, it tends to be only superficially referenced in broad comparisons. This is unsurprising as the data and tools used in paleontological and neontological studies have historically been quite distinct. I argue, using a single recent paleobiological insight as an illustrative example, why the lack of depth in the consideration of paleobiological insights should change in organismal biology, and in particular for conservation biology.

It is commonly assumed that species geographic ranges are *relatively* stable over longer time scales, such that species can be said to have characteristic ranges (Fitzpatrick & Turelli, 2006; Krug et al., 2008). Although it is recognised that geographic ranges of many species have contracted dramatically in recent times due to anthropogenic environmental change, ranges prior to human impacts are implicitly assumed to have been relatively stable (Wake & Vredenburg, 2008; Pompa et al., 2011). This stability is inherent until some factor, such as climate change (Harte et al., 2004), habitat loss (Myers et al., 2000), and biotic invaders (Mack et al., 2000) negatively impact the populations involved. The IUCN Red List (IUCN = International Union for Conservation of Nature) classifies species according to their risk of global extinction (IUCN, 2011), using a combination of criteria involving occupancy and abundance. Many species that have had assessments by the IUCN have had their IUCN extinction risk categories changed, mostly for the worse, within decades (Hoffmann et al., 2011), indicating that global declines can occur extremely rapidly in the face of anthropogenic change. Given that an average species has a duration of a few million years (Coyne & Orr, 2004; Foote & Miller, 2007), these recent declines and extinctions happen so quickly that they would appear as instantaneous disappearance in the time scale of the geological record. In other words, geographic ranges or spatial occupancy (referred to as geographic spread thereafter)

should in theory fluctuate around some characteristic average value for any given species and rapidly decline close to the extinction of the species (Fig. 1A).

But can temporal duration, geographic ranges and spatial occupancy be estimated from the geological record, given the notorious patchy nature of fossil preservation? The answer is yes, albeit only for organisms that have high preservations rates, such as bivalves, brachiopods, and bryozoans, and even for mammals, especially those that can be recognised by their teeth. Although the data available for reconstructing occurrences of fossilised organisms maybe somewhat sparser than those potentially available for extant organisms, the fossil record represents a temporal component that is intractable studying only current day or even historical data.

A recent finding involving molluscs, mammals, and phytoplankton, among other organisms, made independently by different teams, debunks the assumption that geographic spread for a given species is temporally relatively stable: species increase in their geographic ranges and spatial occupancy *gradually* through geologic time, stay at their characteristic maximum for a relatively short period of time, and *gradually* decline to final extinction (Foote, 2007; Foote et al., 2007; Liow & Stenseth, 2007; Liow et al., 2010; see Fig. 1B). Note that the time scale in question here is on the order of hundreds of thousands years, not decades or centuries. This is on a timescale that is also longer than paleoecological data commonly used in studies of Quaternary changes (Willis et al., 2010). A single peak in geographic spread, rather than multiple peaks and troughs, is the best model for the bulk of the data examined (Jernvall & Fortelius, 2004; Foote et al., 2007; Liow et al., 2010). This model of temporal rise and fall in occurrence of species has been named the "hat" model (Liow et al., 2010) and has general implications for evolutionary studies (Liow & Stenseth, 2007; Gaston, 2008; Losos, 2011). Here, I expand on the implication of the hat model for conservation biology.

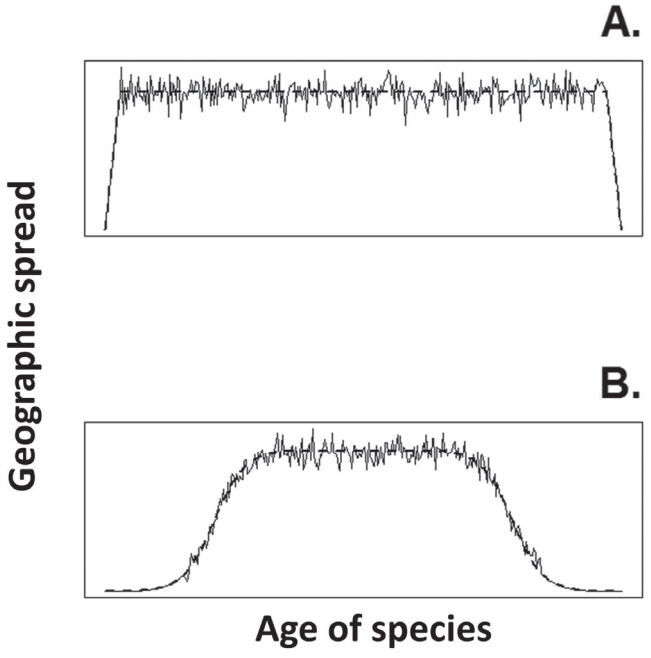

Fig. 1. Geographic spread over time. (A) Shows a plot of the geographic spread (as measured by geographic range or spatial occupancy) of a species over its lifetime. A species rises very quickly to its characteristic geographic spread, be it very large in a widespread species or small in endemic species. Its geographic spread then fluctuates due to varying population growth and migration rates. At the end of its life, the geographic spread of the species then contracts very rapidly, on the order of less than hundreds of years, to zero. (B) Shows the "hat" model of temporal geographic spread over the life of a species. This is different from (A) in that the rise of the geographic spread of the species is slow, occurring over tens of thousands of years. Similarly, the decline of the species occurs over a very long time.

First, one of the main lines of conservation research is estimating how species distributions will shift, given high rates of contemporary environmental change (Hughes, 2000; Araujo & Rahbek, 2006). It is often implicitly assumed that species distributions prior to anthropogenic change are static and/or at their optimum when modelling range shifts (e.g., Lawler et al., 2006). However, as explained above, the fossil record shows us that geographic spread are not static, but in fact may have a characteristic hat trajectory, overlaid by effectively stochastic variations ultimately caused by a multitude of factors that influence population growth rates and immigration (Fig. 1B). This implies that knowing whether the species in question is on the up-swing, peak, or down-swing part of its life may be crucial in modelling distributions, no matter what the imposed environmental change may be. This knowledge of where a species is in its life should perhaps also influence conservation decisions, as a species nearing its natural end may be give less priority than one that is at its peak (Willis et al., 2007), given the limitations of funding.

Second, which traits render species more prone to extinction, are hotly debated in the literature. Geographic ranges, modes of dispersal, degree of ecological specialisation, body size, and generation times are among the most discussed traits (Koh et al., 2004b; Cardillo et al., 2005). However, extinction proneness may be more directly related to where in the hat trajectory a species is. Species at the start and the end of the hat trajectory may be more prone to extinction (Fig. 2A). Those which have slower rates of spread may also be more prone to extinction for a longer period of time during the early phases of its life (Fig. 2B). Currently widespread species may be at the "peak" part of the hat trajectory and hence more buffered from global declines. Certainly, hat trajectories can have different forms. Not only do species have different realised durations (such that some hats are shorter than others), hats can also differ in heights. Fig. 3A shows trajectories that are otherwise similar, but have different maximum spreads. Hence the grey species is at any one time more extinction-prone than the black species, all things being equal, even though its realised duration is the same. Species may also take longer or shorter periods of time to rise to their maximum spread (Fig. 3B) such that they also have different extinction risks (see Fig. 2B). Lastly, rise and fall rates may be highly asymmetrical (Fig. 3C). These characteristic shapes may well reflect biological traits such as dispersal mechanisms, reproductive modes, and ecological flexibility.

Third, the hat model stresses that accounting for detectability is important in conservation studies. The shape of the hat trajectory implies that a species at the end of its life is increasingly difficult to observe or detect. In other words, the observed shape of the hat trajectory is likely a combination of biological processes (varying population growth rates and migration rates at different times in the life of a species) and detection processes (a species may appear rarer than it actually is at certain times during its life). Although an increasing number of studies monitoring endangered species do carefully model detection probabilities (Martin et al., 2009; Karanth et al., 2010; Karanth et al., 2011) there are also many others that use simple counts and other measures that do not explicitly account for detection probabilities. This is not to say that species thought to be on the decline may not be on the decline at all, but a warning that we may draw the wrong conclusions in importance instances, for example where we need to prioritise spending on conservation efforts.

Paleobiological data provide other relevant and crucial insights for conservation biology. Data series involving extant organisms are a few hundred years long at best, but many ecological and evolutionary processes exceed these time scales (Willis et al., 2010) . Species distribution models can predict where species will migrate given projected climates changes and their current distribution and ecological preferences. However, preferences are ecologically flexible and evolutionarily labile to some extent and the fossil record can give clues as to how flexible they are for a given species (Dietl & Flessa, 2011).

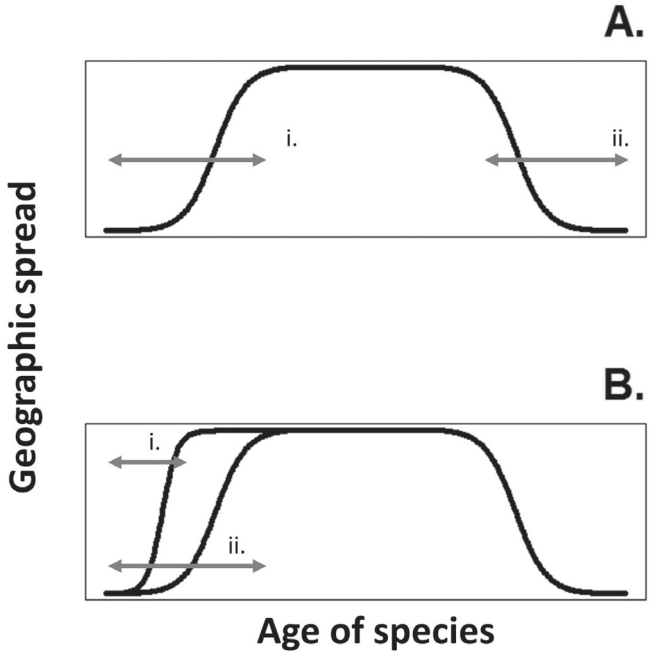

Fig. 2. Changing extinction risks. How prone a species is to extinction depends on its ecology and the interaction thereof with its changing environment. But in addition, it will also depend on where it is in relation to its life. (A) All other things being equal, a species is more prone to extinction during the early phases of its life when its geographic spread is still increasing (i) and also during the late phases of its life when its geographic spread is decreasing significantly (ii). (B) The shape of the temporal change in geographic spread also contributes to differences in extinction risk. The rise trajectory of species (i) is steeper than that of (ii), indicating a quicker rise to its maximum spread, such that it has a relatively shorter phase of being less widespread. Hence the species (i) is at greater risk of extinction for a shorter period of time, relative to its projected life.

Biological processes know no boundary in time, just like organisms whether invasive, endangered or otherwise, know no country boundaries. Biological processes are continuous and the artificial divide between neontology and paleontology hinders our efforts in conserving organisms and processes on our planet. Trying to understand an elephant from only its trunk is a frustrating exercise. It is much better to have a glimpse of its tail and ears, even if those do not represent the elephant in its entirety. Navjot would certainly have supported a multi-pronged approach to conservation biology, even though he has not personally delved into the paleontological realm during a lifetime of highly productive research.

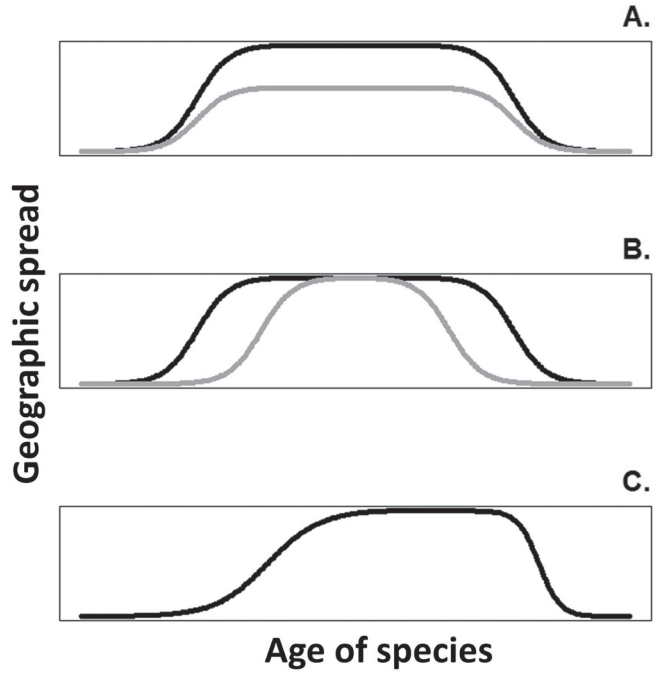

Fig. 3. Different geographic spread trajectories over time. Although paleobiological data suggest that species have hat shaped trajectories over geologic time, these can varying extensively from species to species. For example, some species may have higher maximum spread (A), others may stay at their maximum spread for a shorter period of time (B) and rates of rise and fall may be highly asymmetrical (C). These different shapes may reflect underlying differences in ecology (see text).

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