BIOLOGICAL CORRELATES OF EXTINCTION: WHAT DOES DIFFERENTIATE SURVIVORS FROM VICTIMS?

José Hidasi-Neto

PhD candidate in Ecology and Evolution, Department of Ecology, Federal University of Goiás – UFG, Goiânia, Goiás, Brasil. (hidasineto@gmail.com)

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ABSTRACT

Since Georges Cuvier introduced the concept of extinction to the scientific community at the end of the 18th century, researchers further studied how, where, and when it tended to occur in nature. Some of these researchers, such as Jean-Baptiste Lamarck and Charles Lyell, speculated whether species with certain biological traits were more prone to extinction than other species lacking these traits (i.e. extinction selectivity). Following the definition of “mass extinction”, first studies on the Cretaceous mass extinction, and the development Conservation Biology field, there has been an increasingly amount of studies on extinction. In addition, several of these studies have been able to identify various biological traits usually found in organisms with high extinction risk (i.e. biological correlates of extinction). In this work, extinction correlates usually found in both past and recent extinctions for several biological groups are reviewed. Also, it is discussed how extinction selectivity can have distinct macroevolutionary effects on biodiversity depending on the extent of environmental disturbances in a specific time period. Moreover, evidences are presented indicating that a new period of mass extinction can begin if conservation actions are not taken properly in the near future. After so many years of development of biological theory on extinction, advantage must be taken of its advances in an objective way in prioritization methods to improve conservation actions while dealing with the reduction of resources for humans and wildlife. This is not only necessary to decrease biodiversity loss, but also to prevent humans from extinction.

KEYWORDS: Extinction selectivity, Mass extinction, Conservation.

EXTINÇÃO SELETIVA: O QUE DIFERENCIA SOBREVIVENTES DE VÍTIMAS?

RESUMO

Georges Cuvier introduziu o conceito de extinção para a comunidade científica ao final do século 18. Desde então, pesquisadores estudam como, onde e quando a extinção tende a ocorrer na natureza. Alguns desses pesquisadores, como Jean-Baptiste Lamarck e Charles Lyell, já especulavam que algumas espécies com determinadas características biológicas eram mais propensas à extinção do que outras que não as possuíam (i.e. extinção seletiva). Após (1) a definição do conceito de “extinção em massa”, (2) os primeiros estudos sobre a extinção em massa do Cretáceo, e (3) o desenvolvimento do campo da Biologia da Conservação, tem havido uma quantidade cada vez maior de estudos sobre extinção. Vários destes estudos identificaram características biológicas normalmente encontradas em

organismos com alto risco de extinção (i.e. correlatos biológicos de extinção). Neste trabalho são revisadas características biológicas normalmente encontradas em espécies extintas no passado e recentemente para vários grupos biológicos. Também é discutido como a extinção seletiva pode ter distintos efeitos macroevolutivos sobre a biodiversidade dependendo da extensão das perturbações ambientais em períodos específicos de tempo. Ainda, são apresentadas evidências que indicam que um novo período de extinção em massa pode começar caso ações conservacionistas não sejam tomadas corretamente no futuro próximo. Após tantos anos de desenvolvimento da teoria biológica sobre extinção, seus avanços devem ser incluídos de maneira objetiva em métodos de priorização para que a efetividade de ações conservacionistas aumente, mesmo que recursos disponíveis para a conservação biológica sejam reduzidos.

PALAVRAS-CHAVE: Correlatos de extinção, Extinção em massa, Conservação.

INTRODUCTION

At the end of the 18th century, Georges Cuvier introduced the concept of species extinction to the scientific community (RUDWICK, 1998; LOCKWOOD, 2008). Since then, geologists, paleontologists and biologists have widely improved the understanding of how and why the individuals of a species can be terminated locally, regionally or globally (i.e. completely extinct) (PURVIS et al., 2000a, 2000b; BAGUETTE et al., 2013). Paleontological records indicate that all species of whole genera, families and orders became extinct throughout geological time (e.g. FEIST & MCNAMARA, 2013). There is also an increasing body of evidence that several species are rapidly going extinct in the following years (WAKE ; VREDENBURG, 2008; BARNOSKY et al., 2011). Despite the development of the research on extinction, there is still a debate whether past and recent extinctions are random or not in respect to which species are more prone to extinction (MCKINNEY, 1997; PURVIS et al., 2000a; HEARD et al., 2007; LOCKWOOD, 2008).

How frequent is extinction in nature? In terms of geological time, it happens all the time (LOCKWOOD, 2008; PIMM et al., 2014). Indeed, most species (about 99.9%) that have ever existed are already extinct (BARNOSKY et al., 2011). Moreover, researchers noted that the amount of extinctions in some specific periods of Earth's history was higher than what would be commonly expected over geological time (i.e. higher than the "background extinction rate"; JABLONSKI, 1991; PROENÇA ; PEREIRA, 2013). As a consequence, paleontologists defined five events of "mass extinction" (Ordovician, Devonian, Permian, Triassic, and Cretaceous events; a.k.a. the "Big Five") as those in which more than 75% of species went extinct in a short time interval (JABLONSKI ; CHALONER, 1994; BARNOSKY et al., 2011). Studies indicate that about 10% of all past species extinctions happened at the "Big Five" (JABLONSKI ; CHALONER, 1994). Therefore, these periods have been targeted as good time intervals to study how and why species go extinct.

The characterization of mass extinction events by NEWELL (1952), the study on the Cretaceous mass extinction event by ALVAREZ et al. (1980), and, probably, the emergence (1980s) and further development (1990s) of the field of Conservation Biology (see MEINE et al., 2006), paved the way to hundreds of studies on species extinctions (BAMBACH, 2006; LOCKWOOD, 2008). This can be observed in the scientific literature with the rapid growth of the percentage of studies with the topic "extinction" since the 1950s (FIGURE 1; also see Figure 1 in LOCKWOOD, 2008). Recently, various of these studies began to indicate that there is a sixth mass

extinction event currently happening due to human activity (BARNOSKY et al., 2011; PIMM et al., 2014). This period is usually referred to as Anthropocene, and it is more precisely defined as the period when human activities started to have impacts as significant or greater than natural processes on ecosystems (DIRZO et al., 2014; CORLETT, 2015). Although the starting date of the Anthropocene is still not defined in the scientific literature, it usually ranges from the Late Pleistocene to the periods of Industrial Revolutions (DIRZO et al., 2014; CORLETT, 2015).

FIGURE 1 – Columns indicate numbers of papers with the topic “extinction” published since 1945 within research areas of Paleontology, Environmental Sciences & Ecology and Evolutionary Biology from the Web of Science repository. The line shows percentages of all articles published within these research areas containing the topic “extinction”. The search was conducted on May 3, 2016.

One must not stick only to extinction patterns, but also to their respective causal processes. In a recent study, FEULNER (2008) proposed a few major extinction drivers related to mass extinction events: (1) comet or asteroid impact, (2) large-scale volcanism, (3) climate forcings (e.g. determined by plate tectonics, solar radiation, and chemical composition of ocean water), (4) gamma-ray burst. However, it is notable that these are highly unpredictable but influential drivers ("grey and black swans"; LOGARES ; NUÑEZ, 2012) associated to some more basic and widely mentioned extinction drivers in conservation studies: (1) habitat loss, (2) habitat fragmentation, (3) habitat degradation, (4) overexploitation, (5) invasive species, and (6) spread of diseases (PRIMACK ; RODRIGUES, 2008). For example, SZABO et al. (2012) found that the introduction of invasive species (mainly on oceanic islands), overexploitation (mainly on continental islands), and agricultural-related habitat loss and degradation (mainly on continents) were responsible for 141 human-related bird species extinctions since the 1500s. They also noted that most of these extinctions (78.7%) happened on oceanic islands, indicating that the restricted range of island species contributed to the high number of historical bird extinctions. Moreover, in an attempt to compare past and recent extinction drivers of the marine biodiversity,

HARNIK et al. (2012) found a higher variety of threats for biodiversity in recent time in comparison to past periods of high extinction rate due to human activity (see Table 1 in HARNIK et al., 2012).

Soon after Cuvier introduced the concept of extinction to the scientific community, researchers such as Jean-Baptiste Lamarck, Charles Lyell, and Charles Darwin, began to speculate whether some taxa were more prone to extinction than others (MCKINNEY, 1997). On the first half of the 19th century, Charles Lyell wrote about the extinction proneness of cold-intolerant plants in colder periods, and about the high extinction proneness of small-ranged species (LYELL, 1832; see MCKINNEY, 1997). Lyell even noted that human activities related to habitat loss and overexploitation were responsible for the extinction of small-ranged endemic species and to the introduction of domesticated species throughout the anthropogenic world (LYELL, 1832; WILKINSON, 2004). Several recent studies have pointed out that species presenting certain biological traits can be more prone to extinction than species lacking such traits. For instance, large body mass, small range size and high habitat and dietary specialization have been widely recognized as important positive correlates of extinction proneness (MCKINNEY, 1997; PURVIS et al., 2000b; DULVY et al., 2003). Despite advances in the subject, it is still necessary to investigate whether these biological correlates of extinction differ among taxa and whether they explain both past and current extinctions (TABLE 1; MCKINNEY, 1997; PURVIS et al., 2000b).

TABLE 1 – Summary of biological correlates of extinction risk and reasons why they are usually thought to predict species' extinction risk.

Extinction correlate	Reason
Geographic range	Species with small geographic range may have narrower niches, being able to use a smaller variety of conditions and resources from the environment (MCKINNEY, 1997). In addition, species with small geographic range commonly have low local abundance at multiple scales, and more fragmented ranges (MCKINNEY, 1997).
Home range	Species with large home range are more vulnerable to extinction drivers such as habitat loss, degradation, and fragmentation (PURVIS et al., 2000b).
Population density	Populations with less individuals are expected to suffer stronger negative effects from demographic stochasticity, slow evolutionary rates, and inbreeding (PURVIS et al., 2000b). Also, species with low population density commonly have small geographic ranges, high trophic position, high habitat specialization and large body size (MCKINNEY, 1997; SHAHABUDDIN & PONTE, 2005).
Trophic level	High-trophic level species are very vulnerable to cumulative negative effects on species at lower trophic levels (PURVIS et al., 2000b).
Dietary specialization	Dietary specialized species are expected to have narrow niches, usually presenting low local abundance and small geographic range (MCKINNEY, 1997).
Dispersal ability	Species with low dispersal ability may have traits related to low capacity to colonize new habitats and to low reproductive ability (SODHI et al., 2008). In addition, dispersal ability is commonly positively correlated to geographic range size (NOGUÉS-BRAVO et al., 2014). Species with low dispersal ability also tend to have highly fragmented, small populations (BAGUETTE et al., 2013).
Habitat specialization	Similarly to dietary specialization, habitat-specialized species are expected to have narrow niches, presenting low local abundance and small geographic range (MCKINNEY, 1997).
Generation time	Long generation time is related to decreased probability to which populations' birth rates will be able to compensate increases in mortality rates (PURVIS et al., 2000b).
Body size	Large species tend to be habitat- and dietary-specialized, and to have low population density, long generation time, high age at maturity, and large home range (MCKINNEY, 1997; PURVIS et al., 2000b). Large species are usually more affected by hunting than smaller ones (PURVIS et al., 2000b).
Island living	Island species tend to have small geographic ranges and small populations. They also tend to be very vulnerable to extinction drivers such as invasive species and overexploitation (MCKINNEY, 1997; PURVIS et al., 2000b; SZABO et al., 2012).
Age at maturity	Similarly to generation time, high age at maturity is related to decreased probability to which populations' birth rate will be able to compensate increases in mortality rates (PURVIS et al., 2000b).
Clutch size	Large clutch size indicates high reproductive ability, and it is found in species with fast life histories (HUANG et al., 2013). Such species can more easily colonize new patches (BROMHAM et al., 2012).

Here are presented differences and similarities between past and recent extinctions in relation to how biological extinction selectivity acts on species with different biological traits. For this, relationships commonly found between several biological extinction correlates and extinction risk in both past and recent extinctions are listed. It is also discussed how distinct environmental scenarios can have different types of extinction selectivity, and how they can promote or not evolutionary changes within clades. Then, evidences suggesting that urgent actions need to be taken against the loss of currently threatened biodiversity are presented. Finally, it is shown the need for studies on background extinction rates, and discussed how studies on extinction (especially extinction selectivity) can enhance our knowledge on the outcomes of conservation planning.

PAST EXTINCTIONS

Pioneer studies on extinction relied on comparisons between fossils and extant organisms. For instance, when “dinosaurs” were described by Richard Owen in the nineteenth century (SPOTILA et al., 1991), it was clear that those giant reptiles were no longer living. However, paleontologists at the 19th and early 20th centuries were mainly focused on taxonomic and phylogenetic relationships rather than on biological traits of dinosaurs (SPOTILA et al., 1991). Moreover, considering that absolute dating techniques were not available by that time, not much could be told about the mechanisms related to the enigmatic extinction of dinosaurs. Much later, Alvarez et al. (1980) published evidences that a large asteroid collided with the Earth at the end of the Cretaceous period (~65 million years ago). Notably, knowledge on the biology (e.g. trophic level) of extinct animals (including dinosaurs) were in accordance with their predictions. For example, the suppression of plant photosynthesis due to the reduction of sunlight might have caused the reduction of populations of several plant species that were essential for herbivorous dinosaurs, which would have caused negative effects on populations of their related predators (ALVAREZ et al., 1980).

Despite the limitations of studying fossils, there are several studies indicating biological correlates of extinction for organisms that lived before the global effects of human activity (TABLE 2; TABLE 3). To study biological correlates in past extinctions, researchers have to make use of various proxies for assessing biological traits of species. For example, using dental morphology, Wilson (2013) found an extinction selectivity against dietary specialist mammals during the late Cretaceous mass extinction event. Also, using information on the distribution of fossils of organisms that lived over the past 500 million years, and information on water depth, substrate and latitude to define habitats of organisms, Harnik et al. (2012) found an extinction selectivity against small-ranged and habitat specialized marine invertebrates. The use of proxies to study biological traits of already extinct species is essential in paleobiological studies. However, researchers always need to be certain of what these proxies really tell them about species, so that wrong conclusions because of poorly defined assumptions are avoided.

TABLE 2 – Summary of biological correlates of extinction risk (based on Table 2 in Purvis et al., 2000b) in past (before 1500 AD) extinctions for several biological groups. The superscript g and l letters indicate if the studies used global (species) or local (population) measures of extinction. Reference numbers (see TABLE 3) and studied time periods of the respective studies are in parentheses.

Extinction correlate	Positive	Negative	No relationship
Geographic range		Terebratulide brachiopods ^g (20, Devonian), Marine invertebrates ^{g&l} (14, 23, Phanerozoic), Scleractinian corals ^{g&l} (28, K/Pg boundary)	
Population density		Marine gastropods ^g (17, Permian-Early Jurassic), Corals ^{g&l} (30, Neogene-Quaternary)	Marine invertebrates ^{g&l} (23, Phanerozoic), Scleractinian corals ^{g&l} (28, K/Pg boundary), Bivalves ^{g&l} (18, 29, K/Pg boundary)
Trophic level	Marine teleosts ^g (16, K/Pg boundary), Neoselachian sharks ^g (19, K/Pg boundary)		
Dietary specialization	Mammals ^l (15, K/Pg boundary), Marine teleosts ^g (16, K/Pg boundary)		
Habitat specialization	Marine invertebrates ^{g&l} (23, Phanerozoic)		
Body size	Mammals ^l (15, K/Pg boundary), Marine teleosts ^g (16, K/Pg boundary), Neoselachian sharks ^g (19, K/Pg boundary), Gastropods ^{g&l} (21, P/Tr boundary), Eutheriodont therapsids ^{g&l} (24, P/Tr boundary), Sea urchins ^g (27, K/Pg boundary)	Scallops ^{g&l} (26, Late Pliocene-Middle Pleistocene)	Foraminiferans ^{g&l} (22, Late Permian-Late Triassic), Bivalves ^g (29, K/Pg boundary)

TABLE 3 – Reference list for tables 2 and 4 (reference numbers according to the tables).

N	Reference
1	PURVIS et al. (2000b)
2	ANDERSON, et al. (2011)
3	DULVY & REYNOLDS (2002)
4	KOH, et al. (2004)
5	ANGERMEIER (1995)
6	COOPER et al. (2008)
7	CARDILLO et al. (2008)
8	GAGE et al. (2004)
9	JONES et al. (2003)
10	COMONT et al. (2014)
11	HUTCHINGS et al. (2012)
12	SODHI et al. (2008)
13	LEHTINEN & RAMANAMANJATO (2006)
14	PAYNE & FINNEGAN (2007)
15	WILSON (2013)
16	FRIEDMAN (2009)
17	PAYNE et al. (2011)
18	LOCKWOOD (2003)
19	KRIWET & BENTON (2004)
20	HARNIK et al. (2014)
21	PAYNE (2005)
22	REGO et al. (2012)
23	HARNIK et al. (2012)
24	HUTTENLOCKER (2014)
25	HERO et al. (2005)
26	SMITH & ROY (2006)
27	SMITH & JEFFERY (1998)
28	KIESSLING & BARON-SZABO (2004)
29	MCCLURE & BOHONAK (1995)
30	JOHNSON et al. (1995)

Body size and geographic range size are two relatively well-studied traits on past species extinctions. These traits are usually based on two pieces of information commonly collected in paleontological studies: the morphology of fossils and the location where they are found. Large organisms are usually seen as highly specialized and with low reproductive rates (MCKINNEY, 1997; CARDILLO et al., 2005), while organisms with narrow distributions are usually considered to have low dispersal ability and to be more susceptible to extinction drivers such as habitat loss, fragmentation and degradation (MCKINNEY, 1997; FRITZ et al., 2009). For instance, PAYNE (2005) found a global extinction selectivity against large gastropods during the Late Permian mass extinction. On the other hand, MCCLURE ; BOHONAK (1995) found no size selectivity for bivalves during the end-Cretaceous mass extinction. Notably, size selectivity should be dependent on both the taxon and time-period studied. Moreover, there is much yet to learn about the life history of organisms and the environmental conditions where they lived before we define general patterns of size selectivity (see MCKINNEY, 1997). Using global data on marine invertebrates, PAYNE ; FINNEGAN (2007) found a selectivity against narrow-ranged organisms over most of the Phanerozoic eon. It is also notable that they found a weaker geographic range selectivity during mass extinctions, which shows that widespread environmental disturbances can reduce our perception of biological correlates of extinction.

RECENT EXTINCTIONS

There are several species reported to have become extinct since the 1500s. According to the International Union for Conservation of Nature (IUCN), there are at least 861 species of animals and plants documented as extinct and 68 species documented as extinct in the wild (IUCN, 2017). Humans have a major role in promoting these extinctions. For instance, Szabo et al. (2012) found that human-related extinction drivers caused most bird extinctions since 1500. Moreover, recent amphibian extinctions have been caused by the widespread of a pathogenic fungus driven by climate change (ALAN POUNDS et al., 2006), which is acknowledged to have a major anthropogenic component (IPCC, 2014).

The scenario is even more problematic when local extinctions are considered. Charles Lyell once noted that some domesticated species were becoming increasingly more common throughout the urbanized world in areas where they were not found before (LYELL, 1832; WILKINSON, 2004). More than a century later, Charles Elton studied how invasions of non-native species could cause the local extinction of native species by modifying both the habitat and the biological interactions within communities (ELTON, 1958). Following this line, McKinney ; Lockwood (1999) suggested that native, usually specialist species are being replaced by non-native, usually generalist species at multiple scales, producing a worldwide biotic homogenization. The authors suggested that some traits such as large size, low fecundity, slow dispersal, and high habitat specialization, are typically found in species that are locally replaced by others with opposing traits.

Biological correlates of recent extinctions are abundant in the scientific literature. For instance, studying the occurrence and the number of generations per year of British ladybird beetles, Comont et al. (2014) found an extinction selectivity against ladybirds with small geographic range and long generation time. Similarly, Hero et al. (2005) found an extinction selectivity against species with small geographic range and small clutch size in their study on the occurrence and number of eggs laid per female of amphibians in Eastern Australia. Dulvy e Reynolds (2002) identified body size as the only biological correlate of local extinctions of the skates (Rajidae, Rajiformes) of the world. Some traits identified as good correlates of past extinctions (some both in mass and background extinctions), such as small geographic range, big body size, and high habitat and dietary specialization, are also commonly identified in recent extinctions (TABLE 3; TABLE 4). These traits are closely related to the probability that demographic changes could lead species to extinction due to a single or multiple extinction drivers.

TABLE 4 – Summary of biological correlates of extinction risk (based on Table 2 in Purvis et al., 2000b) in recent (since 1500 AD) extinctions for several biological groups. The superscript g and l letters indicate if the studies used global (species) or local (population) measures of extinction. Reference numbers (see TABLE 3) of studies are in parentheses.

Extinction correlate	Positive	Negative	No relationship
Geographic range		Primates ^g , Carnivores ^g (1), Birds ^{g&l} (1, 2, 8), Freshwater fishes ^l (2, 5), Tropical butterflies ^l (4), Mammals ^g (7), Bats ^g (9), Ladybird beetles ^l (10), Frogs ^{g&l} (6, 25)	Skates ^l (3)
Home range	Carnivores ^l , Primates ^l (1), Mammals ^g (7)		
Population density		Primates ^g , Carnivores ^g (1), Terrestrial mammals ^g , Birds ^g (2), Mammals ^g (7), Reptiles ^l (1, 13), Frogs ^l (13)	
Trophic level	Primates ^g , Carnivores ^g (1)		Freshwater fishes ^l (5)
Dietary specialization	Hoverflies ^g (1), Freshwater fishes ^l (5)		
Dispersal ability		Insects ^g (1), Birds ^l (2), Bats ^g (9)	
Habitat specialization	Reptiles ^l , Primates ^g (1), Tropical butterflies ^l (4), Freshwater fishes ^l (5), Frogs ^g (6), Birds ^g (1, 8), Angiosperms ^l (12)		Insects ^g , Birds ^g (1), Reptiles ^l , Frogs ^l (13)
Generation time	Carnivores ^g , Birds ^g (1), Ladybird beetles ^l (10)	Birds ^g (1)	Primates ^g , Reptiles ^l , Hoverflies ^g (1)
Body size	Primates ^g , Hoverflies ^g (1), Terrestrial mammals ^{g&l} , Marine mammals ^{g&l} , Marine fishes ^{g&l} , Freshwater fishes ^l (2), Birds ^{g&l} (1, 2, 8), Skates ^l (3), Frogs ^g (6), Mammals ^l , Chondrichthyans ^l (11)	Birds ^{g&l} , Mammals ^g (1), Freshwater fishes ^g (2)	Mammals ^g , Carnivores ^g (1), Tropical butterflies ^l (4), Freshwater fishes ^l (5), Bats ^g (9), Teleosts ^l (11), Reptiles ^l (1, 13), Frogs ^l (13)
Island living	Mammals ^g (1), Bats ^g (9)	Birds ^g (1)	Primates ^g , Carnivores ^g (1)
Age at maturity	Terrestrial mammals ^g , Freshwater fishes ^l , Marine fishes ^l (2), Mammals ^l , Teleosts ^l , Chondrichthyans ^l (11)		Bats ^g (9)
Clutch size		Terrestrial mammals ^g , Birds ^g (2), Bats ^g (9), Mammals ^l (11), Frogs ^{g&l} (6, 25)	Teleosts ^l , Chondrichthyans ^l (11)

PATTERNS OF EXTINCTION SELECTIVITY: RANDOM OR NOT?

Extinction drivers in background and current extinctions are relatively more diverse than those in past mass extinction events (DULVY et al., 2003; PAYNE ; FINNEGAN, 2007; JACKSON, 2008; TURVEY ; FRITZ, 2011; PROENÇA ; PEREIRA, 2013). Mass extinction events presented broad and, in some extent, homogeneous and rapid effects on whole populations of species (PAYNE ; FINNEGAN, 2007; PAYNE ; CLAPHAM, 2012). On the other hand, more local extinction drivers seem to have stronger effects in periods of background extinction, especially when considering the lack of evidence for broad environmental disturbances during these intervals (PAYNE ; FINNEGAN, 2007). In addition, although it seems species are going through a new event of mass extinction (see next section), human activity is not only responsible for regional but also for local processes that can lead species to extinction (PRIMACK ; RODRIGUES, 2008). Therefore, distinct drivers of extinction can act at multiple scales throughout human-modified regions. Notwithstanding, biological correlates of extinction should always be studied in light of which extinction drivers were, are, or probably will be acting at specific spatial (e.g. local, regional or global) and temporal (e.g. the past 500 or the next 100 years) scales being studied.

A way of investigating whether extinctions are random or not at distinct time periods is studying patterns of extinction selectivity in species with certain biological traits. It is commonly accepted that the extinction selectivity that happens in both background and current-time extinctions is not only non-random but also affect evolutionary patterns within clades (JABLONSKI, 2005). In that sense, this selectivity, usually referred to as “constructive extinction selectivity”, would be able to promote or reinforce adaptations, gradually changing species traits through space and time. For instance, Smith e Roy (2006) found a non-random species-level extinction selectivity against small scallops of Plio-Pleistocene California. They also found that surviving species tended to be larger than the median size for their respective genera, which indicates a trend in biological trait evolution of the scallops, revealing the occurrence of a constructive extinction selectivity.

As previously mentioned, environmental disturbances during past mass extinctions were broad and rapid, causing impactful demographic changes in species populations. In addition, only a few species had adaptations or exaptations that allowed them to survive these events (JABLONSKI, 2005). These characteristics of mass extinction events usually make the identification of extinction selectivity patterns harder. Although examples of biological correlates of extinction can be found for mass extinctions (KITCHELL et al., 1986; PAYNE ; FINNEGAN, 2007; WILSON, 2013), some authors claim that the kind of selectivity during these events with broad and rapid environmental impacts was not able to promote or reinforce species adaptations (“not constructive”; RAUP, 1984; JABLONSKI, 2005). This type of non-random selectivity, where species with specific biological traits are more prone to extinction but no adaptation is promoted, is usually referred to as “nonconstructive extinction selectivity” (RAUP, 1984; JABLONSKI, 2005). Furthermore, the most accepted evidence for the occurrence of nonconstructive selectivity during mass extinction events is the commonly observed selectivity against narrow geographic range in taxa higher than the species level (see Table 1 in JABLONSKI, 2005). Moreover, contrarily to periods of background and current extinction, selectivity against traits at several levels (individual, species, and clade levels), such as body size, dietary specialization and species-level geographic range, are not commonly

identified during mass extinction events (Jablonski, 2005). However, there is still much to learn about macroevolutionary processes and patterns in periods of mass extinction, as examples of constructive selectivity during these events can still be found in the scientific literature (e.g. KITCHELL et al., 1986; WILSON, 2013; HUTTENLOCKER, 2014).

Mass extinctions are also thought to promote ecological restructurings of the biota (DINEEN et al., 2014; ABERHAN ; KIESSLING, 2015). Extinctions in these periods would open up vacant niches (LEKEVICIUS, 2009), or ecospace (BENTON, 1995; LOCKWOOD, 2008), allowing dominant species to be replaced by others, and also allowing the diversification of marginal taxa (JABLONSKI, 2005). For example, Silvestro et al. (2015) found that shifts in the origination and extinction rates of plants occurred during mass extinction events. The authors found that the currently dominant seed-bearing plants and angiosperms respectively had decreased extinction and increased origination rates after the Cretaceous mass extinction event (SILVESTRO et al., 2015). Another example from the same mass extinction event is the rise of present-day mammals. Some authors claim that the Cretaceous mass extinction opened up ecospace, allowing the increase of inter- and intra-diversification rates of mammals (MEREDITH et al., 2011). Curiously, other authors argue that the relationship between the Cretaceous event and the rise of mammals was not so direct, presenting evidences that the diversification of mammals gradually increased until reaching a peak much later of the mass extinction event (BININDA-EMONDS et al., 2007). Notably, the occasional extinction of dominant species from geographically broadly distributed taxa in periods of mass extinction appear to be more probable than in periods of background and recent extinctions (PAYNE ; FINNEGAN, 2007). Although more studies should clarify this topic, these latter periods seem to present a disproportional survivorship of dominant species (PAYNE ; FINNEGAN, 2007).

THE SIXTH MASS EXTINCTION: “DAYS OF FUTURE PAST”

Studies are revealing an increasing number of species that will probably face extinction in a few years. According to the IUCN, there are already 24,431 eukaryotes (animals, plants, fungi and chromists) documented as threatened (Vulnerable, Endangered or Critically Endangered category) with extinction (IUCN, 2017). In addition, it is a consensus that human activity has a great contribution to the biodiversity loss that the planet is currently facing (CORLETT, 2015; DIRZO et al., 2014; PIMM et al., 2014). For example, human-induced habitat loss and overexploitation were responsible for the recent decline of several marine species with large body mass, small range size, or high habitat specialization (DULVY et al., 2003). Moreover, it has been shown that the potential loss of threatened species to extinction is not spatially, taxonomically, phylogenetically or ecologically random (PURVIS et al., 2000a; HIDASI-NETO et al., 2013, 2015; PIMM et al., 2014). For instance, Hidasi-Neto et al. (2013) found several cases where threatened birds at multiple spatial scales were phylogenetically and ecologically more similar than expected by chance. This indicates the occurrence of an extinction selectivity against biological traits shared by phylogenetically and ecologically similar species.

Some researchers claim that the extinction intensity we are currently facing may be even higher than commonly accepted. These authors agree that we are in the middle of a big extinction event due to the effects of widespread extinction drivers caused by human activity on terrestrial and marine species populations (BARNOSKY

et al., 2011; CORLETT, 2015; DIRZO et al., 2014; HARNIK et al., 2012; PROENÇA ; PEREIRA, 2013; WAKE ; VREDENBURG, 2008). This event may come to be the sixth mass extinction if conservation measures are not urgently taken (WAKE ; VREDENBURG, 2008; BARNOSKY et al., 2011). For example, over one-third of amphibians are threatened, and this number can increase because most amphibians have small geographic ranges (WAKE ; VREDENBURG, 2008). BARNOSKY et al. (2011) found that if threatened species go extinct in 100 years, and the rate of extinction keeps constant through time, it would take 240 to 540 years for a worldwide loss of 75% species. Therefore, the extinction intensity in the Quaternary can reach a similar level found during the Big Five, and a higher level than those found during other “small” extinction events (FIGURE 2). Furthermore, as it is known that the Anthropocene presents a high species extinction intensity and that this intensity is mostly directed to species sharing similar biological traits, ways should be found to predict and conserve clades that are more prone to go extinct.

FIGURE 2 – Estimated extinction intensity for several extinction events. Information for the Big Five (Ordovician, Devonian, Permian, Triassic, Cretaceous events) was taken from Table 1 in BARNOSKY et al. (2011), while information for the Pliensbachian, Tithonian, Cenomanian and Priabonian events was taken from Table 1 in JABLONSKI (1991). The two Quaternary scenarios are based on results from BARNOSKY et al. (2011). The first scenario refers to the time needed to reach a loss of 75% of vertebrate species if all threatened species become extinct in 100 years and the rate of species loss remain constant through time. The second scenario is similar to the first one, but only Critically Endangered species become extinct in 100 years.

EXTINCTION SELECTIVITY AND CONSERVATION PRIORITIZATION: “THE AGONY OF CHOICE”

It is a consensus among researchers that conservation resources (e.g. money, scientists, time) are not enough to conserve the world’s threatened biodiversity (VANE-WRIGHT et al., 1991). Thus, discussions about where these resources should be directed have vastly increased in the past years (ISAAC et al., 2007; BECKER et al., 2010; HIDASI-NETO et al., 2015). Currently threatened species commonly share traits related to high vulnerability to extinction (e.g. small geographic range, low abundance, and long generation time). For instance, less abundant species have proved to be more prone to extinction independently of their geographic ranges (PIMM ; JENKINS, 2010; PROENÇA ; PEREIRA, 2013). Therefore, widespread but

scarce species such as top predators are usually found to be at high risks of extinction (PIMM ; JENKINS, 2010; PROENÇA ; PEREIRA, 2013; PIMM et al., 2014). In that sense, conservation resources can be directed to species or groups of species (e.g. top predators) sharing traits that increase their risks of extinction. Alternatively, conservation resources can be directed to species or groups of species with traits ecologically relevant (e.g. scavenging) to the communities they live in. Nevertheless, a strategy that increasingly gains attention is to focus on both the endangerment level and the ecological and/or evolutionary relevance of organisms (for information on charismatic and flagship species in conservation practice see Smith et al., 2012).

The concern on prioritizing the conservation of species based on their endangerment level and their ecological, socio-economic, scientific, and existence (among other) values is not new. In 1869, the “Act for the Preservation of Sea-Birds” of the United Kingdom was one of the first modern legislations against the extinction of ecologically important organisms that are disproportionately vulnerable to extinction and have great socio-economic value for humans (BARCLAY-SMITH, 1959). The idea was to prohibit the hunting of seabirds during their breeding season, preventing from the loss of, for example, their valuable scavenging function and their ecological service of pointing out good localities for fishing (BARCLAY-SMITH, 1959). However, it was only after the second half of the 20th century that approaches have been developed and used for prioritizing the conservation of species in an objective manner (ISAAC et al., 2007; BECKER et al., 2010; HIDASI-NETO et al., 2015; IUCN, 2017). For instance, the IUCN uses demographic variables (e.g. population size and generation time) to measure the endangerment level of species (IUCN, 2017). In addition, the EDGE (“Evolutionarily Distinct and Globally Endangered”) initiative, launched by the Zoological Society of London, was developed to allow the conservation prioritization of threatened species that are also very distinct in relation to their evolutionary history (ISAAC et al., 2007). In this approach, a very evolutionarily distinct species can be prioritized over a less evolutionarily distinct one even if it has higher extinction risk. Other approaches, like the EcoEDGE (“Ecologically and Evolutionarily Distinct and Globally Endangered”), which is an expanded version of EDGE, include species traits that are related to valuable ecological functions and services on the prioritization process (HIDASI-NETO et al., 2015). This latter type of approach can be used to help on the conservation of ecological community functioning and the benefits it provides to human well-being.

CONCLUDING REMARKS: LOOKING FOR BACKGROUND ACTORS

Although in the present work it was mostly discussed about extinctions during periods with unusually high rates of extinction (e.g. mass extinctions), there is still much to learn about usual background extinction rates. For example, it is still needed to be able to accurately understand and estimate these rates (see DE VOS et al., 2014) so that more precise answers can be found about whether or not current extinction rates are higher than expected without the effects of human activity on biodiversity (e.g. PIMM et al., 2014). Van Valen proposed that the probability of extinction of any given taxon is independent on how long it has already existed (“Law of Constant Extinction”; see LIOW et al., 2011). Van Valen also proposed the Red Queen hypothesis, stating that, for a given clade, organisms must face a deteriorating environment while constantly evolving to survive in response to co-occurring organisms that are also constantly evolving (LIOW et al., 2011; QUENTAL ; MARSHALL, 2013). In accordance with this hypothesis, Quental e Marshall (2013)

found that high extinction rates can be as important as low origination rates to cause declines of diversity within clades. Although mechanisms responsible for these declines are still unclear (QUENTAL ; MARSHALL, 2013), they are probably hidden within biological traits of species and, thus, at least in part in biological extinction selectivity. In conclusion, researchers should be able to differentiate species extinctions that are naturally expected from those that are driven by humans. Improving the understanding on how extinction works in nature will enable conservation attention to be directed mostly to species directly affected by human activity.

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