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The controversy space on Quaternary megafaunal extinctions

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ABSTRACT

In this work, we analyze the origin and development of the debate on megafaunal extinctions using the Controversy Space Model (CSM). The CSM is composed of a common ground of theoretical agreements and a dialectical dynamic of disputes regarding the causes of extinction, called refocalization, identifying phases of conceptual blockage and unblockage. The hypotheses are clustered in three major groups, according to causes of extinction: anthropic, biotic, and environmental. We argue that the evolution of the controversy space follows a succession of questions relevant to each period, the answers to which need to be settled to allow the debate to move forward. We postulate that nowadays this controversy space is suffering a period of conceptual blockage. This may be because authors are assembled around two major paradigms: environmental versus anthropic causes. Each of these two theoretical positions looks at a portion of reality that may be partially true, but incomplete in terms of a global theory of extinction. We propose that this conceptual blockage could be solved by developing a mathematical model in which each hypothesis plays a role in a mechanistic way. The relative importance of each hypothesis may vary depending on its respective context. It follows from this that it should not matter which cause is favored: the emphasis should be given to all causes acting together in a predictable manner.

1. Introduction

We are all looking for the hidden serial killer.

Resembling the fascination for crime stories, speculations about the causes of terrestrial mammal extinctions in the Quaternary have been at the center of one of the most exciting and unresolved debates in contemporary biology. For over the last two centuries, hundreds of papers have been written on this topic, proposing a range of explanations. There is plenty of literature supporting or attacking these proposed hypotheses, and to this day there is no agreement forthcoming (Koch and Barnosky, 2006; Haynes, 2009). In this paper we introduce a different paradigm that can provide a vantage point from which to encompass the various positions in this debate. This is the model of *controversy spaces* (Nudler, 2011), a heuristic tool for the reconstruction of the process of conceptual change in the history of the scientific debates.

A controversy space has a range of features. Above all, it proposes a unit of epistemic analysis located above the competing theories within the debate, and ranging across various controversies that may seem otherwise unconnected or incommensurable. The controversy space model (CSM) assumes that all controversies take place against a background of shared theoretical agreements: what Nudler (2011) calls the common ground. The Quaternary megafaunal extinctions debate, as we propose in this paper, is a controversy space whose origin and development over time is amenable to analysis from the perspective of the CSM.

The CSM emerged originally from the study of conflicts and adheres to a dialectical conception of knowledge. Controversies, disputes and disagreements are the engines of scientific and philosophical progress. Unlike conflicts, controversies take place on an underlying common ground shared by all the parties in dispute. On

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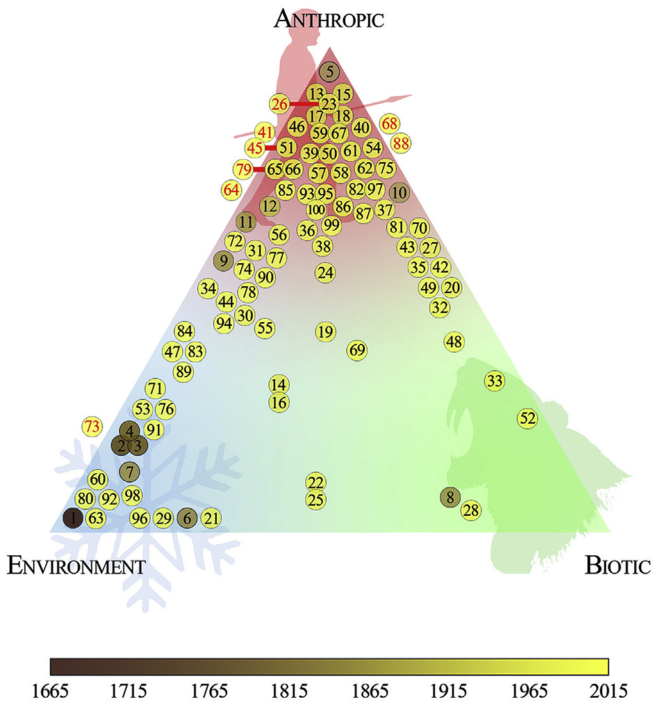

Fig. 1. To construct our CSM and illustrate the philosophical changes in the search for the causes of Quaternary extinctions, we performed an exhaustive search in the related scientific literature. We first selected papers related to the controversy space, and in a second cut, those related with debates regarding the causes of megafaunal extinctions. Finally, we selected about 100 papers as representatives of the foci of the controversy space (see supplementary information 1 for references). After this, we discussed the relative position of each selected work into this figure; the position of each paper is qualitative (and, for visualization purposes, avoids overlapping), reflecting a consensus among the authors. Circles outside the main area of the triangle represent papers that stand in opposition to one side of the debate (or to a specific paper, in the cases where they are connected by a red line), without providing support to alternative extinction explanations.

the surface, controversies consist of a set of disagreements that provide the foci of discussion. Almost no philosophical or scientific controversy is isolated but intersects with other disciplinary disputes that, in turn, may have other foci or objects of disagreement, but which share the same common ground. In other words, a controversy space is a structured set of controversies woven around shared problems (Nudler, 2011).

Controversy spaces are dynamic structures. The foci of discussion may change over time, a process called refocalization. This refocalization can occur for several reasons: a new actor may appear with a new hypothesis, a focus may become part of the common ground (as a result of agreements reached during the discussions), or an assumption or agreement that belonged to the common ground may rise to the surface and become itself the focus of controversy. Refocalization implies the creation of new concepts or the redefinition of the already available ones (Nudler, 2011). Also, new discoveries may create a new conceptual framework in which some concepts can be readapted. Rational dialectical engagement is the main driver of the dynamic of a controversy space. However, no scientific theory is context-free and there are other, non-rational aspects that shape the controversy spaces, which need to be considered in this study.

While we recognize the influence of non-rational elements in the evolution of ideas, we believe that science makes its path in history overcoming obstacles that impede the progress of thought. Given these difficulties, the dialectical evolution of the controversy space has stages of conceptual stagnation or conceptual blockage, and stages of conceptual unblockage in which the controversy space recovers its initial momentum. The aim of this paper is to analyze the historical pattern of conceptual change in the debate on the causes of Quaternary extinctions using the model of controversy spaces.

2. Origin and evolution of the controversy space on megafaunal extinctions

We argue that the evolution of the controversy space follows a succession of questions relevant to each period, the answers to which need to be settled to allow the debate to move forward. Answering these questions implies several things: application of new technologies, creation of new concepts, formation of the common ground and reformulation of new questions; all of which are at the origin of the process of refocalization.

For example, we identified a starting point, perhaps too old, but unequivocally at the beginning of the series of questions that lead us to modernity and our specific topic. The series begins with the dispute over the origin of the fossil material, and from there develops in a cascade of other questions. Following a chronological scheme in dealing with such questions (see Fig. 1), we analyze the difficulties of the framework, the evolution of common ground composition, the refocalization, the conceptual blockages and conceptual unblockages that occurred in the evolution of ideas from 1665 to 2015 (Tables 1 and 2 for summary).

Table 1
Major episodes of the controversy space.

Date	Raise of major questions	Entrances into the common ground	Foci of dispute	Relevant actors	Conceptual blockage	Unblockage/ refocalization
1565	The nature of fossil material	Resemblances with living organisms (drawings of Gessner)	Organic versus inorganic origin	Gessner, Colonna	In situ creation of fossils or "celestial" origin	none
1665–1700	Origin of the controversy space regarding causes of the existence of fossils. Matter, form and placement of fossil materials	Resemblances with living organisms	Origin of fossil matter, biological versus mineral composition, explanations regarding the placement of fossils and the resemblances of the forms	Gessner, Hooke, Stensen	No link between fossils and organic origin, creationist hypotheses have more convincing explanatory power	Evidences of organic origin of fossils in the works of Hooke and Stensen. Links to the extinction of once-living organisms
	Age of fossils	Organic origin of stony fossils	Fossils as remains of recent organisms versus the conception of the old antiquity of fossils	Hooke vs Wallis, also Kircher	Lack of understanding of the process of fossilization. Limited perception of time frame	Fossil antiquity proposed by Hooke, but neglected in his time

Table 1 (*continued*)

Date	Raise of major questions	Entrances into the common ground	Foci of dispute	Relevant actors	Conceptual blockage	Unblockage/ refocalization
1700–1795	Local versus global extinction process	Fossils as remains of death animals	Fossils as remains of animals still alive in unexplored regions versus the conception of global extinctions	Jefferson, Lamarck, Cuvier, also poets as surrogates of the common belief	Global extinctions were not conceivable because the great chain of being would break	Cuvier fossil evidences demonstrated the unlikeliness of finding alive extincted megafauna
1795–1830	Divine or natural process of extinction	Fossils as globally extinct species	Ciclic creacionism versus gradual and linear transformism	Cuvier, Lamarck, Hutton	Lack of alternative conceptual framework against creacionism	Not yet, besides incipient evidences of evolution
	Age of Earth	Megafauna extinction as a global fenomena	Creacionism, short-term catastrophism versus long-term gradualism	Buffon, Cuvier, Hutton, Lyell	Conception of the length of time	Hutton "discovery" of tempo profundo Lyell (1830) uniformitarism
	Speed of the process	Fossils and deposits have the same correlative age	Catastrofism versus gradual uniformitarism	Cuvier, Lyell		
1810–1863	Universality of the process Physical causes of extinction Biological causes of extinction Age of humans	Causes of extinction are due to geological processes Extinction prone-species Antiquity of the Earth and fossils Several ice ages Antiquity of man and coexistence with	Local versus global processes Floddings versus ice age Racial senility versus adaptacionism Earth scientists vs archaeologists regarding antiquity of man	Cuvier, Buckland, Parkinson Cuvier, Agassiz, Lyell Darwin; Lyell Lyell, Boucher de Perthes	Lack of convincing evidences for a global explanation. Strong influence of the ahistorical cycles of geological and biological processes	Aceptance of Agassiz's Ice age Acceptance of adaptacionism. Acceptance of human antiquity (Brixham cave) Acceptance of historical patterns and time's arrow
	Human intervention	Megafauna Uniformitarian-gradualist paradigm	Human overkill versus geological driven causes	Fleming, Lyell, Owen, Wallace		
1863–1950	Search for the global cause	Either abiotic, biotic or antropic are key to extinction	Debate regarding which cause provides better global explanation	Wallace (and see Fig. 1)	Imposibility of establishing exact chronology, lack of paleontological evidences	Libby (1950) radiocarbon technique
1966–2000	Intensity of human overkill	Man influence in extinction, radiocarbon database	Overkill versus climate as a global explanation, blitzkrieg versus stiegkrieg	See section 8 and 9, this paper and Figs. 1 and 2	Univariate and local approaches lacking global explanation	There is no unblockage or agreement forthcoming
2000–2015	Degree of importance of variables	The intervention of several causes in the global explanation	Disputes against weights of variables in the global context		Lack of a global extinction theory	Steps toward a general theory of extinction?

Table 2
Principal hypotheses about megafaunal extinction with reference examples (See Appendix I for references).

	References	Against
1. Physical		
1.1. Climate related		73
1.1.1. Direct (ej: cooling during ice ages, overwarming, megadrought)	2, 7, 11, 28, 30, 34, 60, 91, 92	38
1.1.2. Indirect (ej: area reduction or fragmentation, changes in flora)	21, 22, 25, 29, 44, 47, 53, 55, 69, 71, 76, 77, 78, 80, 83, 84, 89, 90, 94, 96	85
1.2. Geological events		
1.2.1. Direct (catastrophic: volcanism, bolid impacts, sea ingressions)	1, 3, 4, 14, 15, 63	
1.2.2. Indirect (gradual changes, mountain formation, landbridge formation)	6	
1.3. Energy related traits (combination of climate and geology)		
1.3.1. Available energy per unit area (island or continental carrying capacity)	48	
1.3.2. Geographical variation of solar incidence (latitude, elevation)	98	
2. Biological		
2.1. Species level traits		
2.1.1. Body size	49, 69	
2.1.2. Reproductive potential	42	
2.1.3. Island naivety to human presence	49	
2.2. Community level traits		
2.2.1. Competition (GABI, introduced competitors)	8	
2.2.2. Predation (natural overkill, introduced predators)	20	
2.2.3. Diseases	33	
2.3. Ecosystem level traits		
2.3.1. Coevolution disruption (before or after megafaunal extinction)	27, 48	
2.3.2. Ecosystem collapse (before or after megafaunal extinction)	52	

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Table 2 (*continued*)

3.Anthropic	5, 9, 12	
3.1. Direct killing		
3.1.1. Overkill (Blitzkrieg)	13, 15, 17, 18, 20, 23, 32, 39,40, 42, 46, 49, 50, 51, 54, 56, 58, 59, 67, 82, 87, 97	26, 41, 45, 60, 68, 70, 79, 88
3.1.2. Island overkill	10, 36, 37, 57, 65, 66, 82, 85, 97	64, 88
3.1.3. Protracted overkill	38, 43, 55, 61, 62, 69?, 72, 75, 77, 78, 84, 86, 90, 93, 94, 95, 99, 100	
3.2. Indirect killing		
3.2.1. Competition with predators	81	
3.2.2. Niche construction (Sitzkrieg, habitat destruction: from fires to agriculture)	27, 31, 35, 43, 70,	
3.3.3. Coup de grace (partial effect)	11, 19, 30, 34, 44, 47, 71, 74	

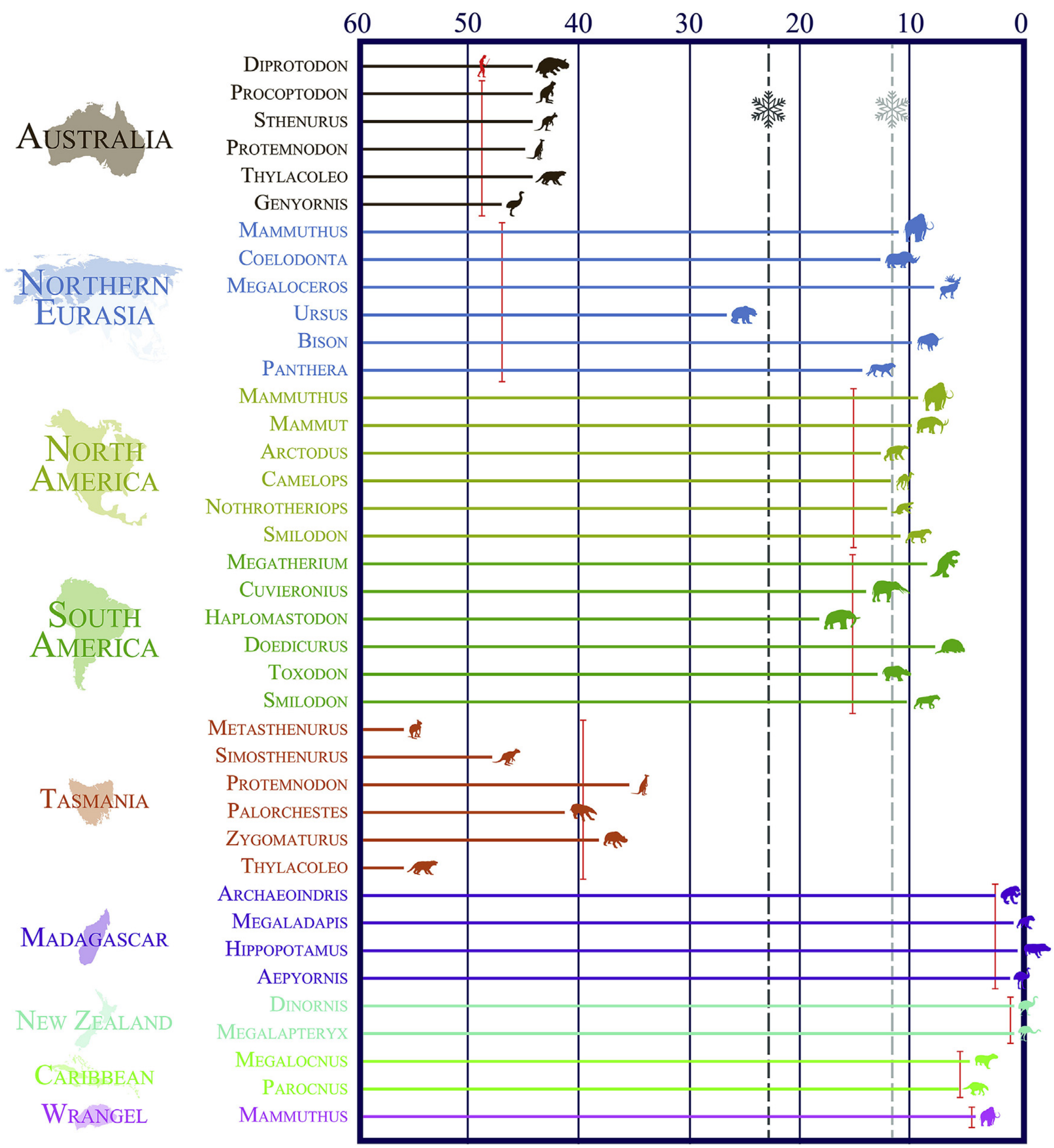

Fig. 2. Extinction times of a few megafauna genera over different landmasses. Human arrival on each landmass is represented by a red line. The last glacial maximum and the Younger Dryas event are represented by dark and light dashed lines, respectively. This representation illustrates some trends regarding Quaternary extinctions literature, like the places where both climate and humans are constantly evoked as a cause (e.g. the Americas), or places where a given cause is primarily defended (e.g. northern Eurasia or the represented islands).

3. What are fossils? the origin of the controversy space

Given that most of the study of the controversy space is a matter of interaction between the building of the common ground and the accumulation of evidence (mostly fossils), we choose to start with the fossil problem because the understanding of fossils played a crucial role in nearly all episodes of the controversy space.

The word fossil has meant different things – being used to describe any dug up material before the nineteenth century (Rudwick, 2008) – which can difficult the tracing of past evidences regarding its conceptual origin (as we understand it today). That way, we focused on the debate regarding whether or not fossils were organic in origin, because the answer drives the controversy space toward causal explanations in which the extinction debate emerged. Such distinction between organic and inorganic was not evident, even when similarities with living organisms were plain, especially given the mineralogical structure of fossilized materials.

Although there were previous authors like Da Vinci, Rudwick (2008) recognizes the work of Gessner (1565) as probably the first reference to the organic origin of fossils. In his detailed drawings comparing fossils with living beings we can identify the first attempt to dissolve the debate about the organic origin of fossils including these works into the common ground.

Other focus intermingled with the problem of the matter of fossils were the explanations regarding the placement in where some fossils were found. For instances, the discovery of marine fossils on hilltops and far from the sea were used to refute the hypotheses of organic origin.

Conceptual unblockage took place 100 years after Gessner's book, when unquestionable evidence of the organic origin of fossils were presented and the link to the extinction of once-living forms were suggested as explanations. For this reason, we choose this event as the first marker given that before it there were no debates concerning the cause of extinctions leading to future foci. The primacy of the interpretation of fossils as beings extinct somewhere in the geological past is attributed either to Niels Stensen (1667) or to Robert Hooke (1665), depending on authors or publication criteria (Inwood, 2003). Stensen dissected a shark and pointed out the similarity between shark teeth and tongue-stones (Glossopetrae), claiming that tongue-stones were actually teeth of very large fossil sharks. He also demonstrated signs of decay in tongue-stones, implying that they were not being formed at the present time but were relics of an earlier period. Before this, Hooke (1665) observed that the micro-structure of some specimens of fossil wood resembled closely that of rotten or charred pieces of ordinary wood. He extended his conclusion to other cases of stony objects with organic resemblances, like ammonites and nautilus, claiming their organic origin. Despite the evidences presented by Stensen and Hooke, the focus of controversy regarding an organic origin didn't immediately dissolve, given that biologists criticized the lack of explanatory power of the fossil phenomena in terms of form, matter and placement in a unified theory (Rudwick, 2008).

4. Are fossils product of local extinctions of species that remain extant somewhere else? or are they globally extinct?

After Hooke's and Stensen's works about the organic origin of fossils were proposed, the step toward the recognition of fossils as extinct once-living organisms still faced a strong conceptual blockage. Even when local extirpations of species were widely accepted, the controversy focus of dispute was the recognition of extinction as a natural, global process. The disappearance of species from the planet was in direct conflict with the notion of a “perfect creation”, that stated that living beings had been created a single time, and were meant to exist forever (Elhrich and Elhrich, 1981). The biological nature of fossils had been accepted, but it was widely believed that those same animals represented in the geological record were still alive in an unexplored region of the Earth. Missing parts were not conceivable in the whole of creation, as denoted by cultural references and metaphors like “the great harmony” or “the great chain of being”, immortalized in Shakespeare's Macbeth or in the poems of Alexander Pope. Trapped in this kind of metaphors, global extinctions were not possible because the whole chain of being would break. Only with the work of Georges Cuvier (1796) the unlikeliness of finding animals like *Megatherium americanum* in South America and other megafauna alive somewhere was demonstrated.

5. What is the age of the earth? how old are fossils? how old are humans? did humans and megafauna ever coexist?

The key problem causing the conceptual blockage in this episode of the controversy space is the conception of the length of time (Rudwick, 2008b, 2014). According to Kant (1881) our perception of reality depends on our intuition of time and space. If the space-time window is too narrow, the knowledge can hardly advance in the understanding of processes that exceed those limits. Heidegger (1962) declares that time is the horizon for any possible understanding, then, our sense of reality depends crucially on our conception of time. Within this framework, an important conceptual blockage that got in the way of the debate's advance was the uncertainty regarding the age of the Earth, spanned around six thousand years (Ussher, 1650), a very short period to easily accommodate any explanation regarding extinctions. In the beginning of the nineteenth century there was already a consensus about the correlation of chronology and stratigraphic position, including the chronological correspondence between fossils and strata in which these were found, making it part of that time's common ground.

Early foci regarding the age of the Earth in the context of our controversy space trace back to works of Hooke and Buffon, that raised doubts about the concept of Earth's antiquity (with the latter even proposing a sudden catastrophic origin for the Earth 75,000 years ago; see Buffon, 1778). The debate between Werner and Hutton regarding the origin of granites (neptunists versus plutonists) also intercepted this controversy space. Werner proposed that all of the Earth's rocks were formed by rapid chemical precipitation from a “world ocean” in catastrophic fashion (Gould, 1991). In his efforts to elucidate the igneous or plutonic origin of granites, Hutton (1788) challenged the planet's antiquity in a scientific context. He considered the center of the Earth as a massive heat source where continuous processes destroy and form rocks, giving rise to continents. Following that framework, Earth would be a steady-state predictable *machina mundi*, continuously being formed by the same forces that we see in present time, with cycling processes like rock formation, sedimentation and erosion taking place very slowly. Such processes imply that Earth would be millions of years old (Gould, 1991; Rudwick, 2014). This refocalization – the discovery of *tempo profundo* Rossi (1984) – is perhaps the most relevant of the whole controversy space. In this new concept, Hooke's ideas about the antiquity of fossils were incorporated to the common ground, linked with the antiquity of the strata containing it.

What still remained unacceptable was the possible antiquity of men, in spite of the fact that there were already evidences of coexistence between humans and megafauna in several geological deposits. This new focus and conceptual blockage remained a convoluted topic between 1800 and 1860, especially among earth scientists and archaeologists. For instance, in 1833, Schmerling found what he took to be human skulls, mammoth teeth, stone

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artifacts and the bones of extinct mammals in a cave in Belgium. His case was rejected by Charles Lyell and other distinguished earth scientists (Rudwick, 2014).

Even when authors like Jacques Boucher de Perthes (1847) proposed the human-megafauna coexistence in the gravel of Somme valley, the creationist-catastrophist framework was still dominant. Such propositions were disregarded with the whole creationist wrapping as pure “rubbish” by Darwin (Grayson, 1984) and also by Lyell. This rejection is a good example of non-rational influences in the dialectic process because neither Darwin nor Lyell recognized evidences of great value inside the “rubbish” of the opposing theory. Human antiquity was not accepted until the excavations of Boucher de Perthes in 1858, at Brixham Cave, Devonshire, England, together with the geologists and paleontologists Hugh Falconer and William Pengelly. They proved the association between bones of extinct elephants, rhinos, hyenas and bears and human lithic artifacts. The Brixham Cave excavation was overseen by Lyell himself and the evidence became irrefutable. Charles Lyell, who at first discredited the idea that humans and megafauna had coexisted, changed his mind (i.e: Lyell, 1863), and together with Boucher de Perthes began to influence the consensus regarding human antiquity, including then in the common ground. This refocalization arises in concurrence with Darwin–Wallace paper presented at the Linnean Society of London on July 1st 1858. The conceptual blockage was overcome, allowing the controversy space to move forward.

Darwin (1859) in “On the Origin of Species” established the missing theoretical framework that would finally allow scientists to acknowledge the arrow of time, a history of unique events in the evolution. Here it is worth to remark that the conceptual blockages of this episode of our controversy space could only be cracked once the concept of *tempo profundo*, along with the idea that Earth itself had a history, had been established in the common ground (Gould, 1991; Rudwick, 2014; see Table 1).

6. What process caused the extinctions? was it an exceptionally fast and catastrophic event or a slow and gradual development/mechanism?

The question about Earth's age brought along another focus of controversy; what processes could have caused the extinctions? The speed of extinction processes should be directly scaled with the age of the planet itself.

It was once again Hooke (1665) that proposed the first causal hypotheses surrounding extinctions, attributing them to physical causes like earthquakes, floods or some other natural catastrophe. Together with already mentioned authors, many eminent scientists like Cuvier (1812), Buckland (1823), and Boucher de Perthes (1847) still shared a creationist-catastrophist view at that point, standing against the conceptions of Hutton and Lyell about the uniformitarianism of geological processes. The link between creationism and catastrophists has its roots in the already discussed conception of time, because they had to fit many processes into the short time scale of the biblical paradigm. The discovery of *tempo profundo* demolished the need of catastrophic explanations; however, the opposite is not true: catastrophes does not need long periods of time to occur. In a perhaps extreme refocalization, the uniformitarianism replaced the catastrophism in an excessive fashion. After the consolidation of an uniformitarianist-gradualist-evolutionist common ground (i.e: Lyell, 1830, 1863; Darwin, 1859) most of the catastrophic hypotheses were undeservedly neglected. Catastrophes do occur on the Earth, can destroy ecosystems and should cause mass extinctions. However, like volcanic activity, hurricanes or asteroid collisions, are frequently local or regional phenomena.

At the end of the 19th century the common ground included the idea that the Earth had a long history of gradual cooling, organisms were gradually adapted to changing environments and species would evolve and disappear throughout time in a linear and progressive manner. The excessive influence of Lyell's gradualism in the new paradigm was pointed out by Eldredge and Gould (1977), though the linear and gradual process may be punctuated occasionally by periods of sudden and violent change, including mass extinctions. It was in the context of this catastrophism versus uniformitarianism debate that the next relevant question to be solved emerged regarding what caused the extinctions.

7. The first controversies in the search for a cause: were the extinctions caused by floods or glaciations?

With the reality of the extinctions established, the new refocalization of the controversy space was regarded their causes (see Table 1 for summary). As mentioned, the first hypotheses to explain the extinctions were associated with biblical catastrophes. In this context, fluvial deposits, some of which containing fossil materials, were attributed to floods called “diluvium” that “proved” the occurrence of a universal deluge (Genesis 7:2; Mateo 24:37–39). Another proposition, still in a catastrophist common ground, included “rapid refrigeration” due to a “Siberian winter” to explain mammoths' extinction in Siberia (Cuvier, 1812).

It was in this framework that, in opposition to biblical-driven “diluvium” hypotheses, a new catastrophic explanation was proposed: the ice age. Louis Agassiz (1837) was the new actor in the controversy space and the first to propose the ice age as an extinction cause in a scientific framework. He acknowledged the previous works of Goethe, which informally proposed ideas about a glacial age. Within the framework of uniformitarianism, the notion of an ice age was initially met with much skepticism. The consensus was that the Earth had been cooling slowly and steadily throughout its long history: it was difficult to adjust to the idea that there had been a sudden cold period and then a return to comparative warmth.

In the following decades, evidences of drastic and global climatic changes were found in Europe (Würm) and North America (Wisconsin), a cycle that we today recognize as the Pleistocene glaciations.

Given its global aspect, the ice age hypothesis was quickly adopted by catastrophists. For Agassiz, the sudden drop of temperature should have been directly responsible for the late Pleistocene extinctions and also a hard evidence to refute the uniformitarianism paradigm as a whole. Charles Lyell came to agree with Agassiz's propositions regarding the glaciations' influences over the extinctions, but attacked the catastrophic paradigm over which these explanations stood, defending instead more gradual extinction processes.

The idea of global ice age gradually gained its consensus, helped with polar explorations. It was accepted that there had not been just one ice age, but a sequence of them, raising the hypothesis about their role in mass extinctions of large mammals, being the mammoths the iconic examples.

8. Were biological effects involved?

Inside this dispute among mainly physical causes for the extinctions, we can identify the participation of some explanations that involve biological factors. It was evident that, whatever the cause, extinct species did not represent the totality of local faunas anywhere they occurred, and that fact demanded some attention. Darwin (1839) was one of the first to introduce the concept of extinction-prone species when he observed that only the smallest representatives of several mammal families survived the Pleistocene extinction event in South America. At that point, he believed in the principle of specific senility, meaning that species, as individuals, were prone to senescence and disappearance due to time, and were replaced by new species, a process that should maintain the number of species on the planet ever balanced. But he soon abandoned these ideas in favor of an adaptive paradigm connected to Lyell's views of extinctions as a result of changing environmental conditions.

Although still away from the hot zones of the controversy space (Fig. 1), the role of biological traits in the demise of the megafauna is discussed until today (Barnosky et al., 2015; Van Valkenburg et al., 2015). For instances, Grayson (2007) argued that each species has his own ecological responses, and therefore, “megafauna” cannot be considered as a homogeneous package. Johnson (2002) considered that rather than body size, life history and ecology are the main determinants of megafauna extinctions during the Quaternary. Whitney-Smith (2004) considers the implications of second-order predation in late Pleistocene mammal extinctions in North America. Dirzo et al. (2104) suggest ongoing patterns of size-differential extinction in Pleistocene mammals.

9. Had humans a role in the extinctions?

The presence of human remains at extinct megafauna sites was known, as already mentioned, since Cuvier. By then, however, the debate was focused on different matters, and suggestions that humans could have played a part in the extinctions, like the one made by Lamarck at the time, were not taken into serious account by the scientific community. Any argument defending anthropological impacts as an important variable in the extinction process had to confirm the fundamental assumption of coexistence between men and megafauna species.

Fleming (1826) was another author to pioneer arguments in favor of anthropic impacts. He studied the historical distribution of birds in England and concluded that many species had vanished from cultivated lands, arguing thus that humans could have caused the large mammals of the Pleistocene to disappear. He also opposed catastrophic ideas to explain the extinctions based on evidences of species' survival until well after the glaciation period. Other scientists, like Lyell and Wallace, that had once defended environmental causes for the extinction, gradually changed their ideas as new evidence was uncovered, accepting that humans could have exerted at least some influence over the extinction event.

The extinctions' controversy space entered the twentieth century with a uniformitarian, gradualist and unilinear-evolutionist common ground, that considered biotic, abiotic and anthropic causes (although with different strengths) as possible causes. From the nineteenth Century until after the Second World War, the debate failed to advance in any significant extent, entering into a phase of conceptual blockage due to the impossibility of fine chronological comparisons between the times of human arrival on the continents, megafauna extinction and climatic shifts. This barrier was only broke in the fifties, when Libby (1952) developed the radiocarbon dating technique, revolutionizing not only Quaternary science, but paleontology and archaeology as a whole. Table 3 summarizes the accepted chronology of events based on radiocarbon data.

Table 3
Summary of human arrival, extinction peaks, and climate change chronologies.

Place	Time of human arrival	Extinction peak range	Area	Climate change influence	Examples
Europa	46800	41000 to 11000	10000	high	Mammuthus, Coelodonta, Megaloceros, Ursus, Bison, Panthera
Asia	47000	30000 to 10000	22000	high	Mammuthus, Coelodonta, Megaloceros, Ursus, Bison, Panthera
Africa	Origin	none[a]		low	Bos primigenius, Camelus, Stephanorhinus, Elephas iolensis, Orycteropus crassidens
Norteamerica	15000	15000 to 9000		high	Mammuthus, Mammut, Arctodus, Camelops, Nothrotheriops, Glossotherium, Smilodon, Euceratherium
Sudamerica	15000	15000 to 8000		high	Milodon, Smilodon, Megatherium, Paleolama, Cuvieronius, Haplomastodon, Doedicurus, Toxodon
Australia	48000	52000 to 44000		debatable high	Diprotodon, Genyornis, Procoptodon, Sthenurus, Thylacoleo, Protemnodon, Simosthenurus
Madagascar	2300	2300 to 150		low	Aepyornis, Megaladapis, Archaeoindris, Geochelone, Hippopotamus
New Zealand	650	1000 to 600		low	Dinornis, Euryapteryx, Megalapteryx, Emeus
Caribean	5500	5500 to 4500		low	Megalocnus, Parocnus
Tasmania	40000	56000 to 35000		debatable high	Macropus, Metasthenurus, Palorchestes, Protemnodon, Thylacoleo, Simosthenurus, Zygomaturus
Wrangel	4300	4000		low	Mammuthus

Summarized from Araujo 2013 and Araujo et al. this issue.
[a] from 30000 to 300.

10. Which is *the* cause of the megafauna extinction?

Although controversies about the cause of late Quaternary extinctions have long been present, it was not until the formalization of Martin's overkill hypothesis (1966, 1967a,b) that a true focus was established, and a strong focus of dispute defined. In the years of 1966 and 1967, through the exchange in Nature with Leakey (Leakey 1966, 1967 versus Martin 1966, 1967a) and the publication of “Pleistocene Extinctions: the search for a cause” (Martin and Wright, 1967), Martin's ideas (Martin, 1967b) of modern human's expansion and overhunting across America (ideas that a few years later were expanded to encompass all continents) were presented to the scientific community worldwide, sparking a debate that would last for decades to come. The ideas and arguments present in this debate were further organized with the publication of “Quaternary Extinctions: a prehistoric revolution” (Martin and Klein, 1984). From thereon, papers defending either side of the climatic-anthropological focus (or any particular position on a climatic-anthropological spectrum, in recent years), became commonplace both in specialized and high-impact (e.g. Nature, Science) scientific journals (see Table 2).

The publication of the overkill hypothesis soon met an array of opponents (Fig. 1), like Graham and Lundelius (1984), Markgraf (1985) and Berger (1991), which refuted the possibility of extensive human hunting as a main cause of extinctions for specific environments and/or species in favor of climatic explanations. Other authors, like Meltzer (1986), criticized specific parts of Martin's hypothesis, without providing support for the opposite side of the debate. There was much discredit regarding the idea that relatively small populations of hunter-gatherers would be capable of bringing to extinction so many species of large animals on continental scales and in such a short period. This discredit was directly attacked by mathematical models that provided support to overkill scenarios (such as Alroy, 2001 and Diniz-Filho, 2004; but see Koch and Barnosky, 2006 Supplemental Material for an extensive list of examples). From this point forward, statistical and modelling frameworks gained more and more space in the literature, gradually pushing argumentative publications to the background of the discussion.

10.1. The advances and focus of dispute of the different hypothesis

Although the main controversy around the extinctions remained on a polarized climatic–anthropic axis for many years (Fig. 1), some sub-focuses of dispute appeared within each side of the focus. Proponents of climatic-driven extinctions, after abandoning early concepts of the hypothesis (such as "deep freeze"; Koch and Barnosky, 2006), argued for either direct or indirect environmental impacts as a cause for the extinction event (Table 2), creating an observable disagreement in the precise mechanism that would lead to the demise of megafaunal species.

In a similar way, along the evolution of the anthropic impacts hypothesis, and the advancement of radiocarbon dating chronology, divergences about the time of coexistence between humans and megafauna on most continents arose, a dispute that appears to be reaching a consensus due to the ever growing dates that point to a longer coexistence (see Johnson, 2006; Barnosky and Lindsey, 2010, Table 3; also, see Lima-Ribeiro and Diniz-Filho, 2013a and 2013b for exceptions regarding South America). Islands remain a slightly different case in which defining coexistence times as short or long become more complicated. That is due to island's geographical and energetic constraints, which limit the growth capabilities of populations and the possibility of finding refuges (Grayson and Meltzer, 2003). Any discussion about a "blitzkrieg" on islands should consider their area (Hansen and Galetti, 2009; Abramson et al., this issue).

10.2. The debate into the new millennium

Based on more careful hypotheses testing, the focus of dispute advanced into the new millennium, producing more literature about the subject than any previous moment in history (Table 2). In a global perspective, several authors kept on defending anthropic causes (although, in most cases, in different pace than Martin's original proposal; like Burney, Flannery, Johnson and others; Fig. 1), while some continued arguing for different forms of environmental impacts (see Grayson, Nogués-Bravo, Wroe and others in Fig. 1). Also, in the second decade of the new century, the first mathematical analyses of the extinctions using data from the whole planet began to arise. These analyses found that either a combination of human impacts and climate changes would be necessary to cause the extinctions, or that the former was the main determinant of megafauna demise (Lima-Ribeiro et al., 2012; Prescott et al., 2012; Araujo, 2013; Sandom et al., 2014).

Different regional trends also emerged in the debate (Fig. 2). Most of the authors involved came to accept anthropogenic explanations for the extinctions in North America and Australia (Koch and Barnosky, 2006); although there were some divergences in the literature regarding these continents (Lorenzen et al., 2011, Wroe et al., 2013; Wroe and Field, 2006). South America and Africa, landmasses that remained "apart" from the bulk of the debate in the previous century, were assessed only in recent years. A recent review of evidences from Africa pointed to climate as a probable cause (Faith, 2014). For South America, synergic causes have been more often defended, but there are divergences regarding the role of humans (Borrero, 2009; Barnosky and Lindsey, 2010; Cione et al., 2009; Lima-Ribeiro and Diniz-Filho, 2013a). Eurasia, probably due to its protracted chronology, remains a strong focus of dispute until present, perhaps with most authors leaning toward climatic explanations (Koch and Barnosky, 2006; Lorenzen et al., 2011; also see Sandom et al., 2014 and Araujo et al. in this issue for results that point to synergistic effects and to a lack of support for either variable, respectively).

In recent years, perhaps due to the ever growing number of papers using mathematical frameworks that allow comparisons between "explanatory weights" of variables, arguments in favor of a synergy between causes became frequent. The idea of human and climate acting together is almost as old as the debate itself, but measuring how much each factor influenced the outcome of extinctions was a tendency that came about in the twenty-first century (Prescott et al., 2012, Sandom et al., 2014; Araujo et al., this issue). Many scientists today seem to believe that it is no longer a matter of finding the ultimate cause of extinctions, but determining the precise way in which each variable influenced the demise of the megafauna.

10.3. The assessment of biological effects

Another important trend that can be observed in both sides of the debate is the attribution of biological effects as an important part of the extinction process. When invoked along with environmental causes for extinctions, these effects take the form of ecological niche modifications due to loss of local diversity or geographical disentanglement of a rich flora supposedly responsible for the maintenance of megafauna richness (e.g. Graham and Lundelius, 1984; Guthrie, 1984). Human-driven extinctions were also often associated with biological factors that were either a consequence of human niche construction (e.g. Laland et al., 2007; Odling-Smee and Laland, 2012), or a life-history or ecological trait that enhanced megafaunal species' vulnerability to hunting (eg. Johnson, 2002; Whitney-Smith, 2004) linked human impacts with second-order predation as biotic effects raising species extinction risk.

10.4. Alternative explanations

Few authors looked for alternative explanations for the late Quaternary extinction event. Perhaps the most noteworthy examples are the hyper-disease hypothesis by MacPhee and Marx (1997) and the extraterrestrial impact hypothesis postulated by Firestone et al. (2007). These works can be understood as sub-hypothesis of the anthropic and climatic hypothesis respectively, given that the former suggests that proposed pathogens would have humans as vectors, and the latter that abrupt environmental changes brought by the bolide impact would be the direct cause of the extinctions. However, even if they received some attention at their respective publication times, it soon became apparent to the scientific community involved in the debate that these hypotheses could not explain extinctions at a broad scale. There was never concrete evidence about the spread of a pathogen, and if there were climatic consequences to a bolide impact, they were likely an issue only in the northern hemisphere. That way, these alternative hypotheses never configured an actual controversy in the Quaternary extinctions controversy space.

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10.5. Multicausal models

Previous focuses of the controversy space were developed regarding the search for *the* cause without coming to a consensus. Moreover, even in some of the most recent multivariate, global approaches, the dispute continues in terms of the relative weight of one or other variable to the explanation without an attempt to resolve the controversy space as a multicausal theory, which is about the same dispute as before in terms of conceptual blockages. Several recent examples are in the form of "the cause is this, *not* the other" (i.e.: Johnson, 2002; Keer, 2003; Sandom et al., 2014; Araujo et al., this issue), or in a sequence of funerals and resurrections (Fiedel and Haynes, 2004 *contra* Grayson and Meltzer, 2003).

11. What is the probability of extinction of a given species in a given time and space? looking for the unblockage of the controversy space

Nowadays, the controversy space on the causes of megafauna extinction is suffering a period of conceptual blockage. This may be because authors are clustered around the two major paradigms (environmental versus anthropic causes, Fig 1) in a sometimes, inflexible disputational fashion. Unlike 19th century authors (e.g.: Lyell, Wallace, Darwin) that changed radically their way of thinking according to the new evidences, modern authors seems to be reluctant to recognize the achievements from the opposite school of thought. This controversy space is one of the most passionate debates of science, resembling fans of soccer teams or pre-election bids between political parties (Levy, 2011). Since 1966 to present, scientific publications have followed a dialectical pattern in which these two opposite positions have been alternately defended and attacked.

If the controversy space remains unresolved for so long and has maintained its cohesion it is partly because all share some reason in their approaches, as each specialist builds their own set of data bounded to a limited window of space and time. Each window looks at a portion of reality that may be true in its partiality, but incomplete in terms of the explanatory power of global patterns and processes. Perhaps, a more inclusive and general theory of extinction should contribute to explain: a) both the causes of extinction and of survival, b) the disparate rates of extinction in biomes, islands and continents, and c) its differences among continents and biomes; in order to produce model of their particular tempo and modes in regional and larger scales.

We suggest that a refocalization of the controversy space may take place through the formalization of the ecological systems under study in the form of mathematical models. Examples of this conceptual approach have recently emerged, such as Prescott et al. (2012), Lima-Ribeiro and Diniz-Filho (2013), Sandom et al. (2014). The value of such an approach is generally recognized from a number of points of view. Indeed, models occupy central stage in the semantic view proposed by Patrick Suppes (Suppes, 1967; van Fraasen, 1980). Their autonomy from theory and their value as critical instruments of scientific endeavor, nevertheless, has more recently been revalued (Morrison and Morgan, 1999) their actual implementation as neither just theory nor just data, but typically involving both, may be the source of their power as scientific instruments. In any case, their role as conceptual links between the semantic content of theory on the one hand and experiment or observation on the other is paramount in the methodology of science (Suppe, 1998). In the spirit of Levins' idealized models (Levins, 1966; Suppe, 2000; Weisberg, 2006), and in agreement and defense of this modern approach (Lanata et al., 2008; Eriksson et al., 2012; Surovell and Grund, 2012) we can contribute to the solution of the conceptual blockage by means of mathematical and simulation models (see Abramson et al., this issue).

While the mathematical formulation is presented in an accompanying paper (Abramson et al., this issue), let us delve here into some of the requirements and implications of our proposal. The relative importance of each piece of the whole "extinction machinery" may vary depending on each scenario. Then, it should not matter which piece is more important: the emphasis should be in the formal framework provided, and especially in the qualitative explicative and predictive power of the model (Levins, 1966). This possibility appeared only recently catalyzed by the big data revolution and the ability to analyze large amounts of data, from which general behaviors, trends, and dynamical properties in general can be inferred.

Mathematical and simulation models should be able to produce new answers on questions:

> If the habitat would have been optimal when humans arrived, would the extinction have happened anyway?
> If humans had not arrived, would the extinction have happened?
> How does the area of the landscape affect the outcome?
> How do other details of the natural history of the fauna (body size, reproduction rate, competitive ability, etc.) affect the outcome?

Today, we cannot "travel to the past" to answer these questions with just our field data. Instead, we have clues that allow us to simulate multiple and plausible scenarios where relevant and numerous variables interact. Besides, mathematical models allow to qualitatively explore the dynamical trajectories of a system starting from proposed initial conditions. This, in turn allows discerning between plausible and forbidden scenarios, helping to settle the dispute by reducing the spectra of valid starting hypothesis. In this work and in Abramson et al. (this issue), we take such a perspective in an attempt to unblock the controversy space.

Let us imagine a system of interacting populations in a finite landscape, comprising the three main dimensions involved in the controversy space: environment, biotic and anthropic, as shown in Fig. 1. In this framework, survival and extinction of each species is the result of a dynamical process throughout space and time (Laguna et al., 2015). For instance, humans invading a new biome and constructing a new ecological niche as exploiting in many ways the newfound fauna, environmental changes affecting the available resources, and species struggling for the available space, are examples of such processes. The relevant question to deal with in such scenarios would be: What is the probability that species i occupies the place x at time t? A mathematical implementation of such an approach is given by the formulation of an adequate function providing the dynamic of the system. As mentioned above, we have initiated such a program as successive approaches of increasing complexity. In the sister paper (Abramson et al., this issue), and making use of results by Araujo (this issue) and the chronology of our Table 3, we attempt a step in this direction as a contribution to the conceptual unblockage of the controversy space.

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