

The Clade Replacement Theory: A framework to study Age-dependent extinction

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Abstract

There is no scientific consensus about whether and how species' evolutionary age, or the elapsed time since their origination, might affect their probability of going extinct. Different age-dependent extinction (ADE) patterns have been proposed in theoretical and empirical studies, while the existence of a consistent and universal pattern across the tree of life remains debated. If evolutionary age predicts species extinction probability, then the study of ADE should comprise the elapsed time and the ecological process acting on species from their origin to their extinction, or to the present for extant species. Additionally, given that closely related species share traits associated with fitness, evolutionary proximity could generate similar ADE patterns. Considering the historical context and extinction selectivity based on evolutionary relatedness, we build on previous theoretical work to formalize the Clade Replacement Theory (CRT) as a framework that considers the ecological and evolutionary aspects of species age and extinction probability to produce testable predictions on ADE patterns. CRT's domain is the diversification dynamics of two or more clades competing for environmental space throughout time; and its propositions or derived hypotheses are: i) incumbency effects by an early arriving clade that limit the colonization and the diversification of a younger clade leading to a negative ADE scenario (younger species more prone to extinction than older ones), and, ii) an ecological shift triggered by an environmental change that imposes a new selective regime over the environmental space and leads to a positive ADE scenario (extinction probability increasing with age). From these propositions, we developed the prediction that the ADE scenario would be defined by whether an ecological shift happens or not. We discuss how the CRT could be tested with empirical data and provide examples where it could be applied. We hope this paper will provide a common ground to unify results from different fields and foster new empirical tests of the mechanisms derived here while providing insights into CRT theoretical structuration.

Key words: Extinction, Competition, Ecology, Evolution, Theoretical structuration.

Introduction

Age-dependent extinction (ADE), or the relationship between the species' age (elapsed time since its origination) and its extinction probability, has macroevolutionary importance because resolving whether such a relationship exists can help us understand the extinction dynamics of living and extinct clades (Doran et al. 2006; Slik et al. 2015; Benton 2016). Yet, there is no consensus on ADE overall direction, specifically whether extinction is age-independent or if younger or older species are more prone to extinction (see Januario and Quental 2021). Empirical evidence has supported contrasting patterns depending on the biological group, taxonomic and spatial scale, whether the lineage is extinct or extant, or whether the study is based on extinct or modern species (Silvestro et al. 2020; Tanentzap et al. 2020; Hagen et al. 2018). Theoretical expectations may justify both positive and negative age-dependent extinction, or neutral effects — i.e., age-independent extinction (Pearson 1995; Balmford 1996; Van Valen 1973). For example, stronger competitive performance of older species could hamper the ability of new species to establish in a region, leading to a higher extinction probability on younger species— i.e., a negative ADE (Balmford 1996). Alternatively, environmental changes could make older species that originated in a different environment more prone to extinction than younger species, thus leading to a positive ADE scenario (Pearson 1995). Finally, extinction rates could be driven by multiple intrinsic and environmental factors that do not correlate with age, effectively resulting in age-independent extinction (Van Valen 1973).

Contrasting patterns in ADE might not necessarily imply a lack of effect of species age on extinction probability but perhaps a dependence on the context of the system. Understanding such context requires considering the elapsed time and the environment the species has occupied from its origin to the present or its demise (Žliobaitė et al. 2017; Fortelius et al. 2014). Thus, ADE patterns should be interpreted within a historical context accounting for the legacy of the processes that determine when species thrive or go extinct (Svenning et al. 2015; Ezard et al. 2011; Vellend 2010).

Likewise, shared evolutionary history can deterministically affect species' extinction vulnerability given that closely related species are more likely to share traits affecting their fitness (Purvis 2008; Jablonski 1994). For example, large body size (Jablonski 1996; Cooper and Purvis 2010), long generation time, slow development (Purvis et al. 2000), and limited dispersal ability (Kotiaho et al. 2005) are often interpreted as traits associated with higher extinction rate while also being phylogenetically conserved. Accordingly, evolutionary relatedness could affect ADE scenarios (Marshall 2017; Russell et al. 1998).

Here we propose the Clade Replacement Theory (CRT) based on long-debated processes and patterns documented in the literature (e.g., Benton 1987; Simpson 1953) and formalize it as a plausible framework to make testable predictions on ADE patterns emerging from the evolutionary context and history of a biological system. We first enumerate the theories and evidence supporting different ADE patterns, and describe the differences in how the relationship between species age and extinction probability is estimated based on living or extinct species. Secondly, we describe the CRT following the theoretical structure proposed by Scheiner and Willig (2013), which sets a hierarchical system for organizing and systematizing theories in ecology. The theoretical structure starts at the highest level with the domain, which establishes the temporal and spatial scope of the theory, then descends to propositions, which are concepts used as causal links between process and pattern, and finally, at the lowest hierarchical level, we find the models, which are a representation of the natural world where predictions are made and hypotheses are tested. Then, we explain how different ADE scenarios may derive from CRT's propositions, or statements about the relationship between processes and patterns. We address the CRT theoretical problems and limitations, and how implementing other propositions within the CRT structure should help solving them. Finally, we discuss the methodologies and empirical datasets on which the CRT could be implemented and spur future research avenues.

Glossary

Age-and-Area hypothesis: It postulates that older species would have had more time to disperse and attain larger geographical ranges, and, thus, reducing their extinction vulnerability (Willis 1922).

Demographic drift: Random changes in populations' relative abundances (Vellend 2010; Hubbell 2001).

Ecological opportunity: Underexploited or recently emerged resources and habitats (Schluter 2015; Stroud and Losos 2016).

Ecological shift: A new ecological context imposed by environmental fluctuations or geological events (Barnosky 2001; Benton 2009).

Evolutionary constraints hypothesis: It postulates, in the ADE context, that older species, due to genotypic or phenotypic constraints, exhibit a lack of change during millions of years and may not be able to adapt to new biotic or abiotic pressures (Hansen and Houle 2004; Eldredge et al. 2005; Futuyma 2010), thus becoming increasingly vulnerable to extinction risks.

Exaptation: A trait not shaped by natural selection or evolved for a function unrelated to its current use (Gould and Vrba 1982).

Extinction filter hypothesis: It posits that older species have endured past extinction events and may have developed traits that confer resilience to new abiotic and biotic threats (Balmford 1996).

Extinction probability: The probability of a species going extinct.

Extinction rate: The expected number of extinction events per lineage per unit of time.

Hard selection: A selective regime not based on intraspecific competition and caused by extreme conditions on fragmented and peripheral populations at range margins (Wallace 1975).

Incumbency effects: An early radiating clade preempts the available environmental space, inhibiting the diversification and colonization of other clades (Rosenzweig and McCord 1991; Reijenga et al. 2021).

Incumbent clade: An early arriving clade that preempts through diversification the available environmental space (Valkenburgh 1999; Benton 1991).

Key innovation: Emergent traits that enable a clade to interact with the environment in a novel way (Jablonski 2017; Rabosky 2014).

Environmental space: The global environmental conditions of a region (Fukami 2015; Tanentzap et al. 2015).

Red Queen hypothesis: It postulates that biotic interactions cause species to evolve in a context where an advantage gained by one species implies environmental deterioration for the other interacting species (Van Valen 1973).

Soft selection: A selective regime where extreme trait values, through competition, confer advantage or disadvantage independent of their absolute values (Wallace 1975).

Surrogate clade: A latter-arriving clade that is inhibited to diversify and become dominant by the incumbent clade (Benton 1991; Valkenburgh 1999).

Stabilizing selection: A form of natural selection characterized by favoring average phenotypes and excluding extreme variants (Lieberman and Dudgeon 1996; Hansen 1997).

Time-and-specialization hypothesis: It postulates that older species are more specialized because they have had more time to match their environments (Pearson 1995; Raia et al. 2016).

Existing ADE hypotheses

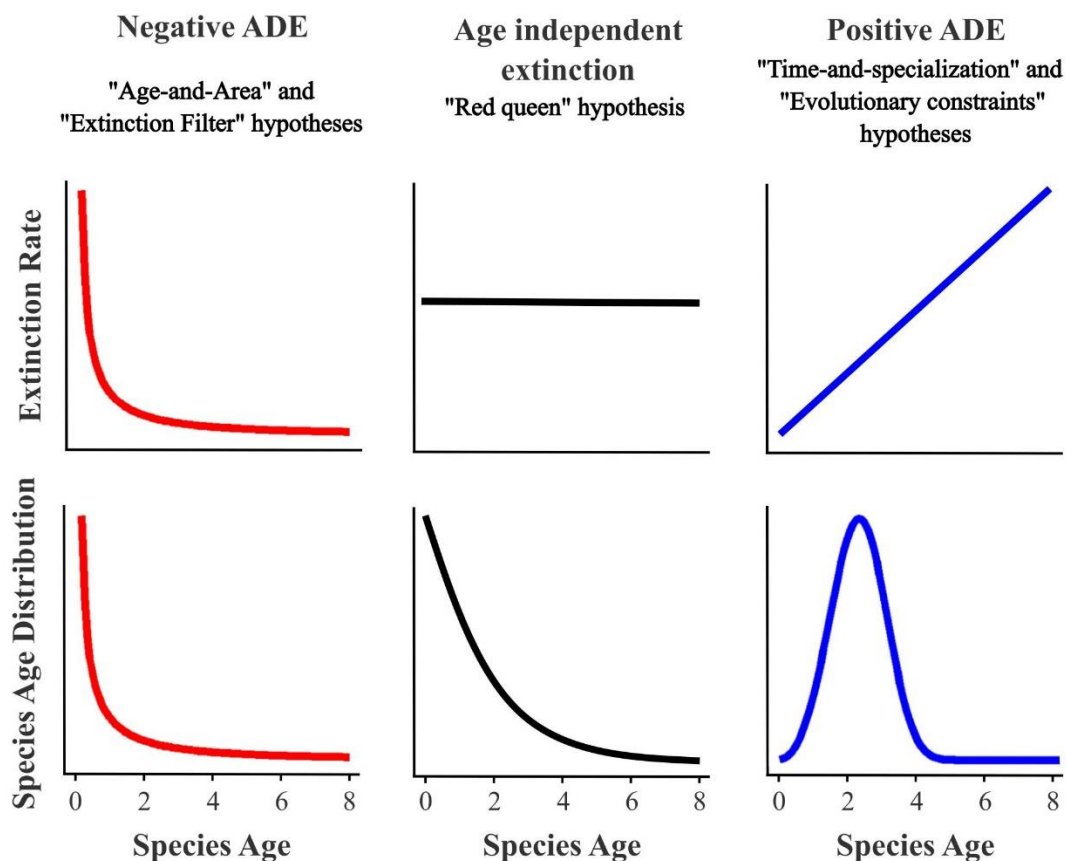
The age-independent hypothesis predicts that the net effect of all biotic interactions and abiotic factors translates into a random process of extinction, in which species age effectively does not predict extinction probability (Van Valen 1973). In contrast, the ADE hypotheses predict a relationship between species' age and biological properties which define the species' fitness within its environment and, thus its survival probability (Box 1; Hagen et al. 2018). These properties may include life history traits, biotic interactions, population size, and geographic range (Jablonski 1994).

The “Red Queen hypothesis” postulates that biotic interactions cause species to evolve in an evolutionary race where an advantage gained by one species implies environmental deterioration for the other interacting species (Van Valen 1973). Thus, species have to keep the evolutionary pace or become extinct (Barnosky 2001; Strotz et al. 2018; Voje et al. 2015). This results in a pattern of age-independent extinction, where all lower taxa (e.g., genera or species) within a higher taxon (order or family) share a constant extinction probability (Hagen et al. 2018). In other words, the Red Queen hypothesis provides a mechanistic explanation for the null ADE pattern (Liow et al. 2011; Brockhurst et al. 2014; Vrba 1993).

The “Age-and-Area hypothesis” postulates that older species should have had more time to disperse and thus attain larger geographical ranges by local adaptation (Willis 1922). A greater spatial distribution is correlated with a greater niche breadth and larger population sizes, which would reduce the vulnerability of such species to local environmental variability and demographic drifts (Slatyer et al. 2013; Gaston 1998). Thus, this hypothesis predicts a negative ADE. A similar pattern is predicted by the “Extinction filter hypothesis”, which postulates that older species have survived through past extinction events and, therefore, may have developed resilience to new threats and changes in selective regimes, thus also leading to negative ADE (Balmford 1996).

In contrast, the “Time-and-specialization hypothesis” (Pearson 1995; Clavel et al. 2011; Poisot et al. 2011) posits that specialization is higher in older taxa because they had more time to evolve specific ecological characteristics to match their environments. Under biotic or abiotic changes, specialized older species may be more vulnerable than recent and generalist taxa, thus leading to positive ADE. A similar ADE pattern can alternatively be explained by an “Evolutionary constraints hypothesis”, which, in the ADE context, posits that older taxa may become less able to compete against new emerging lineages or to adapt to new biotic or abiotic pressures due to phenotypic and genotypic constraints (Hansen and Houle 2004; Eldredge et al. 2005; Futuyma 2010).

Box 1. Different extinction processes, their hypotheses, Age-Dependent Extinction (ADE) direction, and expected species age (elapsed time between origination and extinction) distribution, as predicted by a stochastic extinction process with ADE *sensu* Hagen et al. (2018). Negative ADE scenarios result in Weibull-distributed species ages with shape parameter <1 . In a Null ADE scenario, the species age distribution follows an exponential distribution, as predicted by a standard birth-death process. Positive ADE scenarios result in Weibull-distributed species ages, with shape parameters >1 (Hagen et al. 2015).



ADE empirical evidence

Empirical evidence has been sought from paleobiological data. ADE has been estimated in the fossil record using different statistical, probabilistic, or machine learning approaches (Silvestro et al. 2020 and references therein) that are generally based on an estimation of taxon longevities from the stratigraphic duration and a comparison with their expected distribution under different ADE scenarios (Box 1). In this context, Leigh Van Valen (1973) showed an age-independent effect for 2500 lineages within major plant, invertebrate, and vertebrate groups, which he used as the basis for his law of constant extinction. More recently, evidence for a positive ADE has emerged from studies in planktonic foraminifera (Doran et al. 2006; Ezard et al. 2011), trilobites, conodonts, and graptolites (Pearson 1995), whereas evidence for a negative ADE effect has been found for Phanerozoic marine animals (Finnegan, Payne, and Wang 2008), Ordovician graptolites (Crampton et al. 2016), Cenozoic terrestrial Carnivora (Hagen et al. 2018), marine invertebrate clades (Silvestro et al. 2020), and ruminant mammals (Januario and Quental 2021). Macroevolutionary signatures of age-dependent extinction have also been investigated on dated phylogenetic trees of extant species, where extinction rates can be inferred using reconstructed birth-death models (Alexander et al. 2016; Stadler 2013).

Recently, there have been several attempts to study ADE patterns in extant species based on phylogenetic data. Some studies have evaluated the relationship between the species extinction risk compiled in the Red List by the International Union for the Conservation of Nature (IUCN 2016) and the species ages inferred from the branch lengths of time-calibrated phylogenies (Davies et al. 2011; Gaston and Blackburn 1997; Johnson et al. 2002; Tanentzap et al. 2020; Verde Arregoitia et al. 2013). Although these studies do not explicitly define or assess ADE, the hypotheses and mechanisms employed in macroevolutionary research that are potentially relevant to understand the relationship between current extinction risk and evolutionary age, and both fields could benefit from an integrated theoretical framework. However, while using extant species may help us understand

extinction dynamics, the current approach has some conceptual and methodological limitations when compared to the paleontological approach. We note, for example, that the extinction risk, defined by the Red List conservation status, for extant taxa is not the same as an extinction event in the fossil record, which, alongside the species origination, establishes the species duration in geological time and can be incorporated into the ADE distributions previously described (Box 1). Moreover, estimating species' age from the branch lengths of phylogenies can lead to under or over estimations because phylogenies do not explicitly assign a species label to their branches, and therefore we cannot directly use them to establish species age. Finally, compared to the paleontological approach, species' extinction probability in studies of extant species is to a large extent driven by anthropogenic pressures (Barnosky et al. 2011; Cowie et al. 2022), which almost certainly deviate from pre-human extinction dynamics (e.g., Andermann et al. 2020). Indeed, important current drivers of extinction risks such as habitat loss or direct exploitation (Pyron and Pennell 2022; Otto 2018), are not directly a function of species age, even though indirect associations might lead to ADE patterns. Despite these possible discrepancies, empirical studies of living taxa have speculated on both negative and positive ADE risk. For example, a positive ADE emerged from studies in birds (Gaston and Blackburn 1997; Alexander et al. 2016), reef fishes (Jennings et al. 1999), Bornean mammals (Meijaard et al. 2008), primates (Redding et al. 2010), marsupials (Johnson et al. 2002), and conifers (Tanentzap et al. 2020); whereas a negative ADE was found for South African plants and across several plant clades (Davies et al. 2011; Tanentzap et al. 2020). Also, age-independent extinction risk emerged from terrestrial mammals (Verde Arregoitia et al. 2013).

The contrasting evidence for ADE found across datasets and clades suggests that there is no universal rule imposing a homogeneous trend between species age and extinction rate and that we should aim to develop a theoretical framework able to account for the multiple expressions of ADE. Here we propose the Clade Replacement Theory (CRT) as such a framework to develop testable hypotheses to study ADE.

Clade Replacement Theory

The clade replacement concept emerges from a common and well-documented event in the fossil record: the temporal association between the demise of an ecologically dominant clade and the rise to dominance of a new clade (Sepkoski 1996; Benton 1987). Multiple examples of this phenomenon are found in the fossil record such as the replacement of brachiopods by bivalves (e.g., Liow et al. 2015; Sepkoski 1996), dinosaurs by mammals (e.g., Benton 1987), and gymnosperms by angiosperms (e.g., Carvalho et al. 2021; Condamine et al. 2020; Lupia et al. 1999; Niklas et al. 1983). Several hypotheses on the plausible mechanisms leading to clade replacement exist (e.g., Benton 1987; Rosenzweig and McCord 1991; Sepkoski 1996; Van Valkenburgh 1999). There are a series of terms and concepts in the clade replacement literature that imply different theoretical components, such as “evolutionary relay,” “incumbent replacement hypothesis,” “ecological displacement model,” “double-wedge pattern,” “active displacement model,” “passive replacement model,” “progressive process,” “competitive extinction hypothesis,”; showing heterogeneity in the terminology used to refer to related concepts. Here we propose the Clade Replacement Theory (CRT) as a framework to study ADE following the hierarchical system for organizing and systematizing theories in ecology proposed by Scheiner and Willig (2013). Adopting this structure facilitates the integration of hypotheses and models, such as the previously stated terms, and paves the way for a comprehensive theory to be developed in the future.

First, we establish the CRT domain, or the scope of the theory, which is the diversification dynamics of two clades competing for environmental space and resources throughout time (Benton 1991; Gilinsky and Bambach 1987). Here, we define environmental space as the global environmental conditions within a region (Fukami 2015; Tanentzap et al. 2015). Thus, CRT’s spatial scale can range from regional to global. An example at a regional scale is the replacement dynamics among three subfamilies within the dog family Canidae that occurred in North America (Silvestro et al. 2015). An

example at a global scale is the replacement of dinosaurs by mammals (Benton 1987). In terms of temporal scale, the CRT should span the necessary time for the diversification process of the two or more involved clades, ranging from thousands to millions of years. Nevertheless, the exact temporal scale should be contingent on each clade replacement case and will be affected by the rapidity of environmental changes involved. This point is further developed on the second proposition subsection. The CRT's assumptions are: i) an ecological similarity between two or more clades or groups of taxa, and ii) different colonization or origination times. Both assumptions create the context for two historical contingencies, which we define as CRT's propositions.

First proposition

The first historical contingency is the incumbency effects over environmental space by an early-arriving clade (hereafter called incumbent clade), which limits colonization and diversification of later-arriving clades (hereafter called surrogate clades) (Fukami 2015; Jablonski 2008; Van Valkenburgh 1999). The dispersal process defines the colonization sequence, which depends on taxa dispersal abilities, distance, geographical barriers, and environmental conditions (Eiserhardt et al. 2013; Holyoak et al. 2005). For incumbency effects to happen, the incumbent clade must diversify filling the environmental space with taxa before the arrival of the surrogate clades (Rosenzweig and McCord 1991; Silvertown et al. 2005). The filling of the environmental space by the incumbent clade reduces the number of resources and habitats available for the surrogate clades, especially those habitats that have the most common biotic and abiotic conditions in the environmental space (Gehrke and Linder 2011; Urban and de Meester 2009). This generates two patterns in the allocation of environmental space between clades: i) species from the incumbent clade would occupy regions with environmental conditions that are more frequently available in the accessible geographical space — and therefore closer to the average conditions —, while ii) species from the surrogate

clades would occupy habitats with rare environmental conditions and far from the mean values (hereafter referred to as environmental periphery, Figure 1).

The environmental space periphery would cause higher turnover rates on the surrogate clade via two non-exclusive processes. Habitats that deviate from a region's average conditions may be subject, but not necessarily, to greater environmental instability, such as the quaternary climatic fluctuation effects on tropical forest (Carnaval et al. 2009) or the tree line variability in Alpine systems (Nicolussi et al. 2005; Gehrig-Fasel et al. 2007), which would impose a hard selection regime (*sensu* Wallace 1975) that periodically erases part of the local community (Bell et al. 2021; Cutter and Gray 2016). Likewise, the environmental space periphery, by definition, would have a smaller spatial extent than the environmental space center. This would imply small ranges and populations for the surrogate clades, and thus, their species would be more vulnerable to stochastic extinction due to environmental perturbations (e.g., fires and extreme weather), ecological drift, fixation of deleterious mutations, and hybridization (Thuiller et al. 2007; Vellend 2010; Kyriazis et al. 2021). Accordingly, high extinction rates in the environmental periphery would produce resource underutilization and habitat availability, enabling the surrogate clades to recolonize, exploit and diversify, enhancing the speciation rates, and thus, producing high turnover rates (Stroud and Losos 2016; Agrawal 2001; Kawecki 2008).

In contrast, species from the incumbent clade, occupying the environmental average conditions, would probably be subject to stabilizing selection (Lieberman and Dudgeon 1996), producing low turnover rates due to a more stable environment. These different forms of selection, which promote higher speciation and extinction rates in the environmental periphery, would generate a phylogenetic footprint of incumbency effects, where the overall age of species would increase toward the center of the environmental space (Leopold et al. 2015). That is, species from the incumbent clade would be on average older than species from the surrogate clades.

Figure 1. Representation of a two-dimensional environmental space and the occupation patterns caused by incumbency effects. The species from the incumbent clade (blue polygons) occupy an area in the environmental space center, at the margin of which, the species from the surrogate clades (orange patches) are found (environmental periphery).

Second proposition

An ecological shift caused by environmental fluctuations or geological events is the second historical contingency (Barnosky 2001; Benton 2009). The shift establishes a new ecological context, producing a change in selection pressures. The species of the incumbent clade, which until then had maintained dominance over the region, are selected against and affected negatively in their fitness and diversification rates (Erwin 2015; Chen and Benton 2012). The temporal and spatial scales of the changes in the environmental space produced by the ecological shift should be of a magnitude sufficient to affect macroevolutionary processes (thousands to millions of years and regional to global), such as a cooling climate negatively affecting lamniform sharks (Condamine et al. 2019b) or the reef habitat decline triggering the pycnodontiformes demise (Cawley et al. 2021). The loss of fitness by the incumbent clade would offer the surrogate clades access to an ecological opportunity only if one or more of the latter had an adaptation to endure and compete effectively in this new ecological context (Wellborn and Langerhans 2015; Betancur et al. 2012). As an example, let us assume that the environmental space periphery is represented by colder conditions than the environmental space center, and one of the surrogate clades is adapted to this cold climate. If an ecological shift, such as a glaciation, leads to low temperature of the environmental space, this surrogate clade would have higher probability of being better adapted in this new selective regime than the incumbent clade. In addition, the emergence of a key innovation by the surrogate clade could also help it to replace the incumbent clade after an ecological shift. Key innovations are traits that enable a clade to interact with the environment in a novel way (Jablonski 2017; Rabosky 2014). Well-known examples of key innovations are the evolution of flowers and pollination syndromes in

angiosperms (e.g., Chanderbali et al. 2016; Fenster et al. 2004), or the pharyngeal jaw development by African cichlids (e.g., Mabuchi et al. 2007; Seehausen 2006). However, the fossil record shows, in some cases, a macroevolutionary lag between the rise of a key innovation and the diversification of a clade (Strömberg 2005; Jablonski and Bottjer 1990). Thus, key innovations may have an exaptation condition, by which it would enable the surrogate clade to take advantage of a new selective regime not present yet (Wellborn and Langerhans 2015; Gould and Vrba 1982). As suggested by Simpson (1953), a clade must have geographic, evolutionary, and ecological access for radiation to occur. After the second historical contingency, the surrogate clade finds itself in the region (geographic access), is adapted to the conditions (evolutionary access), and the loss of fitness by the incumbent clade would confer it ecological access. Under the new environmental conditions which impose changes in selective pressures, the surrogate clade would outcompete, radiate, and replace the incumbent clade (Pires et al. 2017; Friedman 2010).

The magnitude of the ecological shift may impose the temporal and taxonomic scale of clade replacement. The asteroid impact at the end of the Cretaceous (K/Pg event) imposed a drastic ecological shift in Neotropical rainforest, that might have led to the replacement of Gymnosperms by Angiosperms, in a relatively short time (Carvalho et al. 2021). In contrast a more gradual ecological shift, such as the expansion of grasslands in North America at the expense of close forest habitats in the late Miocene (Andermann et al. 2022; Strömberg 2011), may have caused the replacement of Borophaginae by other carnivore clades (Caninae and Felidae), over several million years (Silvestro et al. 2015). Thus, CRT's taxonomic and temporal scales may be contingent of the nature of the ecological shift.

ADE and the ecological shift

ADE would present two possible outcomes depending on whether the second historical contingency happens or not (Figure 2). If an ecological shift has not occurred recently in a system, and the environment presents a legacy of stability, where the species in the incumbent clade are expected to be dominant (Betancur et al. 2012; Silvertown et al. 2005; Reijenga et al. 2021). Species from the surrogate clade, limited in resources and habitat availability, would be restricted to the environmental space periphery, where the turnover rates are expected to be higher (Gehrke and Linder 2011; Tanentzap et al. 2015). Indeed, if the center of the environmental space (occupied by the incumbent clade) is stable, and the periphery (occupied by the surrogate clades) is unstable, we hypothesize that the surrogate clade species (expected to be more recent) would present higher extinction rates than species from the incumbent clade due to higher turnover, producing a negative relationship between species age and extinction. In terms of niche space occupancy, we would expect species of the incumbent clade to occupy niche positions in proximity to the mean niche space's environmental conditions, whereas species of the surrogate clade would occupy the peripheric niche positions (Gaston and Blackburn 1997; Venier and Fahrig 1996; Rinnan and Lawler 2019). Similarly, it could be expected an overall effect of niche position increasing centrality (proximity to the mean) with increasing species age. We thus expect lower extinction and speciation rates in the incumbent clade, whereas the surrogate clade should present the opposite, given the high turnover of the environmental space periphery (Table 1; Rosenblum et al. 2012; Cutter and Gray 2016; Pinto-Ledezma et al. 2017; Pyron 2014).

In contrast, if an ecological shift occurs establishing a new selective regime, species from the incumbent and surrogate clade might present maladaptation to the new environment (Brusatte et al. 2008; Rosenzweig and McCord 1991; Van Valkenburgh 1999). However, if the surrogate clade or some of its species possess an adaptation to the new environment, its species will have the capacity to outcompete and replace the incumbent clade across the environmental space and over time

(Losos 2010; Pires et al. 2017; Stroud and Losos 2016). Therefore, species from the incumbent clade, which would be on average older, would be more prone to extinction than members from the surrogate clade in this changing environment scenario, producing a positive relationship between species age and extinction. Under these conditions, the incumbent clade is expected to present higher extinction rates, while the surrogate clade would have higher speciation rates due to the change in the selective regime (Silvestro et al. 2015; Condamine et al. 2020). As for environmental space occupancy, we expect incumbent clade species to progressively move toward the periphery of the new environment, while the surrogate clade species will occupy increasingly central niche positions (Table 1). Both signals would reflect a clade replacement process over the environmental space.

Figure 2. The effect of an ecological shift on the relationship of species longevity and extinction. (A) If the ecological shift does not happen and the environmental space center is stable, ADE would have a negative direction (older taxa would be less extinction prone). (B) Whereas, if the shift happens, and produces a replacement of the incumbent clade by one of the surrogate clades, ADE would have a positive direction (younger taxa would be less extinction prone).

Table 1. Given the two Clade Replacement theory propositions (Incumbency effects and Ecological shift), a priori predictions about key properties (Age-dependent extinction, Diversification rates, Richness, Niche position) for the Incumbent and Surrogate clades.

	Proposition 1: <i>Incumbency effects</i>		Proposition 2: <i>Ecological shift</i>	
	Incumbent Clade	Surrogate Clade	Incumbent Clade	Surrogate Clade
Age-dependent extinction	Overall negative		Overall positive	
Diversification Rates	Slightly positive and constant	High turnover rates	High extinction rates and almost no speciation	High speciation rates
Richness	High but constant	Low but with high turnover	Rapidly declining	Rapidly augmenting
Niche position	Central	Peripheric	Towards the periphery	Towards the center

CRT operationalization

Populations-based explicit mechanistic eco-evolutionary models (MEEMs, Hagen 2023) could be used to test the CRT's propositions and predictions described on Table 1. This is due to CRT spatio-temporal complexity and the possibility that MEEMs confer to experiment different interconnected hypotheses about emergent biodiversity patterns (Skeels et al. 2023; Rangel et al. 2018). Another advantage of MEEMs is that they do not model species as individual entities, but include their intra-specific variation over space and time (Duchen et al. 2021; Millstein 2009). Thus, implementing a CRT simulation in a MEEM could reveal how population dynamics scale up to the macroevolutionary patterns described here (Hagen et al. 2021).

Empirical analyses of clade competition have paved the way to operationalize CRT and test empirically the proposed predictions (Condamine et al. 2019b; Condamine et al. 2020; Liow et al. 2015; Pires et al. 2017; Silvestro et al. 2015; Van Valkenburg 1999). The implications of CRT on ADE patterns should be tested with fossil datasets, which provide the most direct evidence of species longevity, despite their inherent sampling biases (Hagen et al. 2018). The identification of a CRT study case, i.e., the recognition of likely incumbent and surrogate clades, can follow two interdependent paths. First, this could be done studying clades or groups that participated in major biological invasions such as the one triggered by the Great American Biotic Interchange (Carrillo et al. 2020) and Indo-Australian interchanges (Lohman et al. 2011; Skeels et al. 2023). Second, there are also cases of well-documented sequential replacement in the fossil record (Sepkoski and Sheehan, 1983), especially on ecological similar and evolutionarily related clades, such as terrestrial mammal carnivores (Pires et al. 2017) and sharks (Condamine et al. 2019b). The probability and intensity of clade competition could be tested using quantitative methods that evaluate the effect of biotic interactions on diversification dynamics, such as the Multiple Clade Diversity Dependence model (Silvestro et al. 2015, 2017), which extends diversity-dependent speciation and extinction

within and among clades. Alternatively, the similarities among clades' morphospaces could be used as proxies of competition intensity (Cawley et al. 2021).

To detect an ecological shift, we suggest two alternatives. First, an ecological shift should happen after a major climatic or geological events such as the ones that drove the mass extinctions (Bond and Grasby 2017). Second, diversification slowdowns evaluated through environmental-dependent phylogenetic models can offer an insight about an ecological shift (Condamine et al. 2019a; Kergoat et al. 2018), mainly when contrasted with paleoenvironmental data. After identifying a clade competition event, correlated with an ecological shift, it would be possible to test the proposed ADE predictions through quantitative methods to estimate species longevity from fossil occurrences (Silvestro et al. 2020).

CRT underlying assumptions, limitations and future directions

The Clade Replacement Theory is based on some underlying assumptions, which enable us to focus on the ADE scenarios (Scheiner and Willig 2013). Nevertheless, acknowledging and exploring these assumptions further, both in empirical research and theoretical formalization, can help to organize and unify the CRT, to the extent that better understanding and more concrete predictions about ADE scenarios and other patterns would come from its theoretical structure (Scheiner and Willig 2008). For instance, we assumed that species within clades reflect the average properties of the meta-populations they are composed (Wiley and Mayden 2000), particularly when affected by the different forms of selection here proposed. Therefore, in its current form, CRT is not suitable to evaluate differences in local adaptations of species' populations. However, we see the potential to scale down the CRT to explain community turnover, i.e., relaxing the assumption of clade's common descent. Thus, CRT's propositions could apply, at smaller temporal and spatial scales, to an incumbent and surrogate communities disputing for environmental space. Regarding CRT propositions, incumbency effects assume the existence of ecological limits to diversification due to environmental space pre-emption by the incumbent clade, which inhibits the colonization and

diversification of the surrogate clade (Rabosky 2013; Rabosky and Hurlbert 2015). Likewise, incumbency effects by the incumbent clade over the surrogate clade assume a degree of functional redundancy between the competing clades (Loreau 2004; Rosenfeld 2002). In the second proposition, we assume that the ecological shift that would negatively affect the incumbent clade and benefit the surrogate clade. However, it is possible that the ecological shift could set different extinction regimes, and even, a general evolutionary turnover which can cause an extinction independent of species age (Crampton et al. 2016). Likewise, it is not entirely clear how the assumption that a local competition between ecologically similar members of two different clades would have macroevolutionary consequences, given that even a simple two species-model of competition presents several possible equilibrium solutions (Jablonski 2008; Holt 2011).

We think that CRT has some theoretical connections with other macroevolutionary theories and patterns. For example, if we assume that the environmental space center is represented by low latitudes and the periphery by high latitudes, CRT is consistent with the predictions of the Tropical Niche Conservatism hypothesis for explaining the Latitudinal Diversity Gradient (Wiens and Donoghue 2004; Stevens 2011). Likewise, it would help to explain, given the proposed high turnover on the environmental space periphery, the higher speciation and extinction rates for different taxa outside the tropics (Pyron 2014; Rabosky et al. 2018; Igea and Tanentzap 2020; Morales-Barbero et al. 2021).

The CRT first proposition, incumbency effects, could offer a mechanistic support to the age-dependent speciation phylogenetic model (Hagen et al. 2015), which produces the imbalance, or the difference between the daughter clades' sizes, seen in empirical phylogenies. Indeed younger species in the environmental space periphery are linked to a higher turnover and available ecological opportunities (Cutter and Gray 2016), with higher speciation rates compared to the older species in the environmental space center.

Conclusions

We discussed the lack of theoretical and empirical consensus on the age-extinction relationship and we reviewed the main points related to the debate of ADE. We formalized and proposed clade replacement processes and patterns as a theoretical framework towards improving our understanding of the species age effect on extinction probability. We structured the clade replacement theory on two propositions that encompass the historical context of ecological processes operating over the diversification dynamics of two or more ecologically similar clades. The propositions are i) incumbency effects by an incumbent clade inhibit the surrogate clade diversification, and ii) ecological shifts triggered by an environmental fluctuation or geological event, impose a different selective regime over the environmental space. The two propositions lead to opposite expectations in terms of ADE whereby, if the environment is stable, we expect a negative ADE — i.e., a higher extinction probability for species from the surrogate clade —, while an ecological shift can lead to a positive ADE — i.e., a higher extinction probability for species from the incumbent clade. In addition, the intensity and frequency of the ecological shift could set a general evolutionary turnover which can lead to no relationship between age and extinction probability. Finally, we discussed the assumptions and limitations of the clade replacement theory, and proposed how it could be tested with quantitative methods to study ADE on the fossil record. We hope these expectations can be used to formulate testable hypotheses in analyses of empirical datasets of extinct and extant clades.

Conflicts of interest

We declare no conflicts of interest.

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Author's contributions

CC: Conceptualization (lead); Writing-original draft (lead); Writing-review & editing (equal). FV: Conceptualization (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). RD: Conceptualization (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). JC: Writing-original draft (supporting); Writing-review & editing (equal). DS: Writing-original draft (supporting); Writing-review & editing (equal). BV: Conceptualization (lead); Writing-original draft (supporting); Writing-review & editing (supporting).

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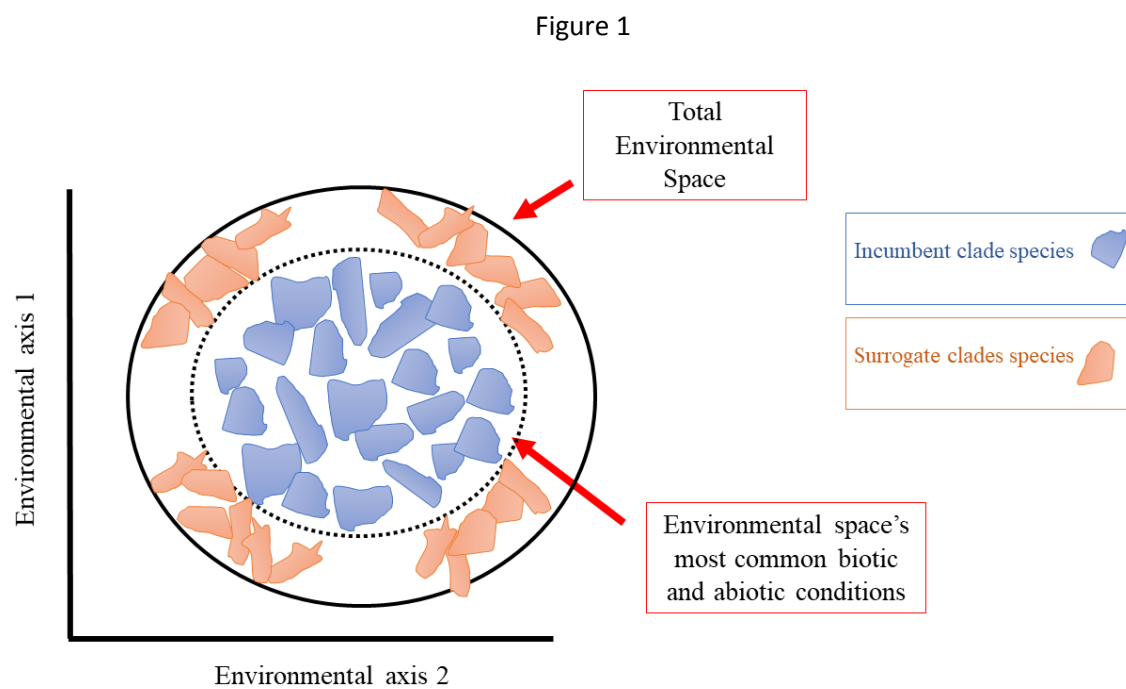
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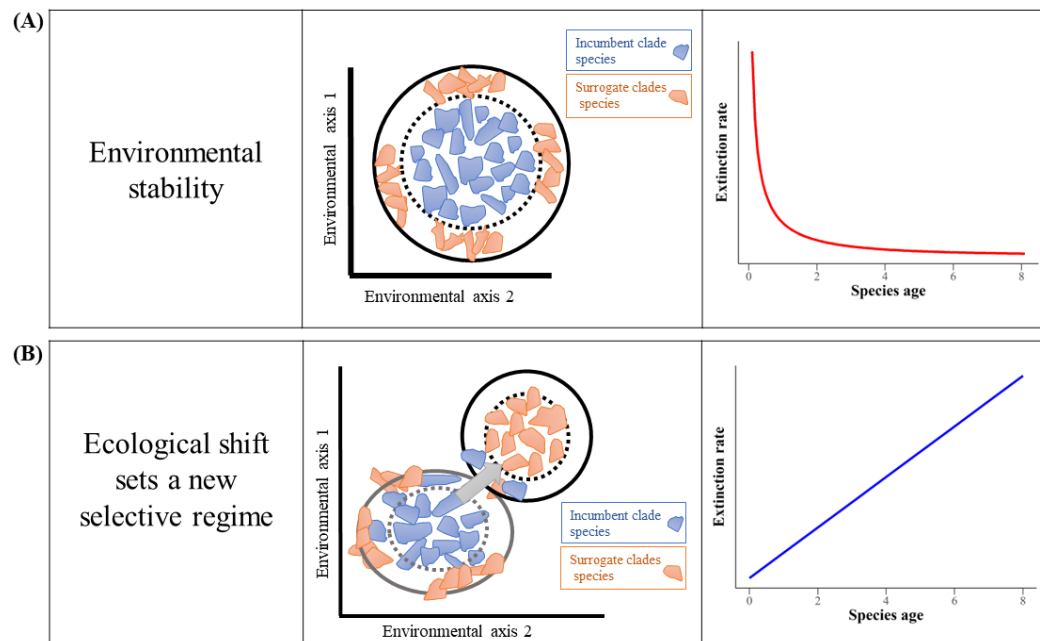
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Figure 2



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