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Idade evolutiva e probabilidade de extinção

Salvador, setembro de 2023

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Idade evolutiva e probabilidade de extinção

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Orientador: Dr. Bruno Vilela

Co-orientador: Dr. Ricardo Dobrovolski

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“Vou aprender a ler pra ensinar meus camaradas”.

Capinan/Roberto Mendes

"There is no science without fancy, and no art without facts."

Vladimir Nabokov

**“... the great Tree of Life, which fills with its dead and broken branches the
crust of the Earth, and covers the surface with its ever branching and
beautiful ramifications.”**

Charles Darwin

*A mi papá, quien eligió creer que los alemanes y suizos disputaban esta tesis, y a mi
abuelo Amílcar, quien me legó su amor por Brasil sin haberlo visitado nunca.*



PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA: TEORIA, APLICAÇÃO E VALORES

Rua Barão de Jeremoabo, s/n. Ondina – Salvador – Bahia – CEP. 40.170-000 UNIVERSIDADE
FEDERAL DA BAHIA – INSTITUTO DE BIOLOGIA



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Título da Tese: “Idade evolutiva e probabilidade de extinção”

Doutorando: Carlos Roberto Calderón del Cid

Orientador: Bruno Vilela de Moraes e Silva

De acordo com o regimento geral da UFBA e com o regimento interno deste programa de pós-graduação, foram iniciados os trabalhos da Comissão Examinadora, composta pelo professor Dr. Bruno Vilela (Presidente), Dr. Tiago Quental, Dra. Levi Carina Terribile, Dr. Henrique Batalha-Filho e o Dr. Mário Trindade Dantas, às 14:00h do dia 15 de setembro de 2023. O doutorando fez a apresentação oral da dissertação durante 50 minutos. Após o encerramento das arguições, às 17:00 horas, a Comissão Examinadora pronunciou-se pela sua Aprovação, conforme parecer em anexo. Esta Ata será assinada pelos membros da Comissão Examinadora e deste Colegiado de curso, para compor o processo de emissão do diploma.

Salvador, 15 de setembro de 2023.

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**PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA:
TEORIA, APLICAÇÃO E VALORES**



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Introdução

Revisão Bibliográfica

Metodologia

Resultados Obtidos

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Prof. Dr. Bruno Vilela de Moraes e Silva
Orientador

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La frontera austral

Carlos Calderón del Cid

En las florestas de lo que hoy sería África Oriental, hace 5 millones de años, entre las copas de los árboles y sobre el suelo siempre húmedo, vivía una gran población de chimpancés. Poseían una estructura social compleja donde los machos cuidaban del territorio y encontraban alimento y las hembras resguardaban a las crías y fortalecían las alianzas de poder. Se alimentaban principalmente de frutas, la favorita era el gigía un fruto parecido a la actual guayaba, pero ocasionalmente también cazaban pequeños primates y venados. Al compartir los alimentos, especialmente la carne, se constataba la jerarquía social. Los chimpancés nacían, copulaban y morían dentro del drama de su grupo: complots, cambios de régimen, exilios, enemistades; y nada parecía más importante. Su tumultuosa armonía se vio alterada cuando una mañana, después de una lluvia torrencial, encontraron que dos de sus patrulleros, los que vigilaban la frontera austral de su territorio, fueron ejecutados. Es decir, sus cuerpos sin vida fueron dejados ahí, sin ser devorados. Los machos más fuertes fueron a explorar los confines del sur y descubrieron que una población de homínideos, más bípedos que ellos y por ende torpes para escalar los árboles, se habían asentado en un claro de la floresta, comiendo gigía casi descompuesta. Los chimpancés ponderaron sus propios números y los del enemigo, y decidieron atacar sin llamar refuerzos. Mataron cuatro invasores y ahuyentaron al resto. Pensaron que habían resuelto el problema, que los invasores se habían marchado de vez, sin embargo, eventualmente aparecían en la frontera oriental o austral, casi siempre cuando los árboles de gigía florecían. Los chimpancés reforzaron el patrullaje en los confines, lanzando comitivas de 5 hasta 10 machos férreos, siempre exitosas. Una, dos, veinte generaciones de chimpancés pasaron así, sin que los invasores fueran una verdadera amenaza, apenas algo que había que ahuyentar; hasta que el clima comenzó a cambiar. Sintieron que llovía menos y las madrugadas eran más frías. Las ranas y sapos ya no cantaban por las noches y las aves lo hacían menos por las mañanas, porque muchas se habían marchado. Contemplaron aterrorizados cómo los árboles de gigía se secaban y caían estriptosos en la floresta, abriendo grandes claros. Ya no había fruta de ningún tipo y tuvieron que volcarse completamente a la caza. Pero ya no habían monos ni pequeños venados. Habían comenzado a aparecer, pastando en los claros cada vez más extensos, enormes bisontes y venados. Los chimpancés intentaron cazar, pero los animales eran demasiado poderosos para ser sometidos. Diezmados, comenzó a haber casos de canibalismo. Lo que antes había sido una floresta imponente se convirtió en una llanura interminable y monótona. El último chimpancé vio, dejándose morir a un costado de las raíces secas de un árbol de gigía, a los invasores lanzándole piedras a un venado enorme.

Resumo

Resolver se a idade das espécies está associada à probabilidade de extinção tem o potencial de ajudar nosso entendimento sobre as dinâmicas de extinção nos clados vivos ou extintos. O estudo deste padrão é conhecido como extinção dependente da idade (ADE, siglas em inglês), e não há consenso teórico ou empírico sobre o sentido da relação. Nesta tese propomos, como primeiro capítulo, a teoria de substituição de clados (CRT, siglas em inglês) como uma estrutura teórica que considera aspectos ecológicos e evolutivos dos clados para gerar previsões testáveis sobre o ADE. Durante o estudo de ADE percebemos que há uma diferença conceitual entre a idade definida pela paleontologia e pela neontologia. Além disso, esta última, já que é estimada por meio do comprimento dos ramos das filogenias, possui fontes de incerteza. Por conseguinte, como segundo capítulo, através de simulações, avaliamos as taxas de erro na estimação das idades filogenéticas associadas com modos de especiação e distintos cenários de extinção. Propomos também uma abordagem para corrigir as estimativas de idade sob a presunção de uma especiação bifurcativa. Formalizamos o CRT com duas proposições. A primeira é efeito de incumbência por parte um clado antigo sobre o espaço de nicho, o que limita a diversificação e dominância dos clados novos. Devido à colonização e subsequente rápida diversificação do clado antigo sobre o espaço de nicho, particionando ele, nos hipotetizamos que essa trajetória de ocupação de nicho geraria uma tendência das espécies mais antigas a ocupar as posições de nicho mais centrais. Como terceiro capítulo, exploramos dita hipótese no contexto dos tetrápodes neotropicais. Encontramos, que para esses grupos, não há generalidade nesta relação, porém os grupos significativos, apoiaram nossa expectativa. A segunda proposição do CRT é uma mudança ecológica que afeta o fitness do clado antigo oferecendo uma oportunidade para o clado novo diversificar e virar dominante. A partir dessas duas proposições, nos hipotetizamos que o sentido do ADE estará definido pela mudança ecológica. Se esta não acontecer, o ADE será negativo, i.e., espécies mais antigas possuirão menor probabilidade de extinção. Se esta acontecer, o ADE será positivo, i.e., espécies mais novas possuirão menor probabilidade de extinção.

Palavras-chave: Competição, Estruturação Teórica, História evolutiva, Filogenia.

Abstract

Resolving whether species age is associated with extinction probability can help us understand the extinction dynamics of living and extinct clades. This pattern is called Age-dependent extinction (ADE), and there is no theoretical nor empirical consensus about its direction. In this thesis, as the first chapter, we propose the Clade Replacement Theory (CRT) as a framework that considers clades' evolutionary and ecological aspects for generating testable predictions on ADE patterns. During the ADE study, we realized a conceptual difference in species age definition between paleontology and neontology. Besides, because the branch lengths of phylogenies estimate it, the latter has substantial uncertainty sources. Therefore, in the second chapter, we evaluated the error rates of phylogenetic ages associated with speciation modes and different extinction scenarios through simulations. Complementarily, we proposed an approach to correct age estimates under the assumption of bifurcating speciation. We formalized CRT with two propositions. The first one is incumbency effects by the old clade over the niche space, limiting the diversification and dominance of new clades. Due to the colonization and subsequent rapid diversification of the old clade, we hypothesize that this niche occupation trajectory would generate a pattern of older species occupying central niche positions. In the third chapter, we explore this hypothesis in the context of Neotropical tetrapods. We found no generality in the relationship between species age and niche position for these groups. However, the relationships that were significant supported our expectations. The CRT's second proposition is an ecological shift that would select against the old clade, opening up an opportunity for the new clade to diversify and rise to dominance. From CRT's propositions, we developed the prediction that the ADE scenario would be defined by whether an ecological shift happens or not. If it does not happen, we expect a negative ADE; i.e., older species would be less extinction prone. On the other hand, if it does happen, we expect a positive ADE; i.e., younger species would be less extinction prone.

Keywords: Competition, Evolutionary History, Phylogeny, Theoretical structuration.

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Estrutura da Tese

A presente tese está estruturada em três capítulos como segue:

Capítulo I – *The Clade Replacement Theory: A framework to study Age-dependent extinction*

Neste capítulo descrevemos a falta de consenso teórico e empírico ao respeito da relação entre a idade das espécies e a probabilidade de extinção (ADE, siglas em inglês). Argumentamos que é necessária uma estrutura teórica capaz de elaborar previsões, a partir do contexto histórico do sistema, que contemplem efeitos positivos e negativos de ADE. Propomos a teoria de substituição de clados (CRT, siglas em inglês) como dita estrutura e formalizamos CRT a partir de um conhecido sistema hierárquico para organizar e sistematizar teorias em ecologia e evolução. A partir das proposições do CRT, sugerimos previsões concernentes ao sentido de ADE e outros padrões macroevolutivos.

Capítulo II – *Approximating species age from phylogenies under different speciation modes and extinction*

Identificamos que na literatura recente, particularmente em macroecologia, tem sido utilizado o comprimento dos ramos de filogenias calibradas como equivalentes à idade evolutiva das espécies. Porém, as filogenias não contém informação sobre os modos de especiação e as taxas de extinção. Devido a isso, por meio de simulações, avaliamos as taxas de erro associadas com a estimação filogenética de idades em diferentes cenários de extinção e modos de especiação. Concluimos que as taxas de erro são mais altas para especiação por brotamento e anagenética independentemente do cenário de extinção. Complementarmente, propomos uma abordagem baseada no *birth-death process* sob a pressuposição de especiação bifurcativa para corrigir idades estimadas na filogenia.

Capítulo III – *Species age and niche position: An exploratory analysis*

A trajetória no preenchimento de nicho é avaliada tradicionalmente por meio das taxas de diversificação e a acumulação de espécies dos clados avaliados. Porém, qual é o impacto dessa trajetória nas espécies do presente, em termos de ocupação e partição de nicho, é um quesito pouco explorado. Devido à colonização e subsequente rápida diversificação das radiações adaptativas, nos hipotetizamos que haverá uma tendência das espécies mais antigas de uma clado a ocupar posições de nicho mais centrais. Neste estudo exploramos dita hipótese no contexto dos tetrápodes neotropicais. Encontramos que não há generalidade nesta relação, porém, os grupos que foram significativos, apoiaram nossa expectativa na relação entre idade e posição de nicho. Perante essa falta de generalidade, propomos diferentes vias teóricas e práticas para continuar explorando a trajetória da ocupação de nicho nos clados.

Introdução geral

Devido a que a introdução geral da tese seria uma mera tradução do primeiro capítulo e que cada capítulo se sustenta por contra própria, eu me permitirei narrar a história, em termos acadêmicos e, portanto, humanos, da sua elaboração. Contar a história da tese, é dizer o surgimento, os erros, o amadurecimento, é uma maneira também de honrar como a ciência foi se abrindo passo na minha vida durante esses quase cinco anos de doutorado.

A ideia que motivou a minha tese pode ser resumida da seguinte forma, “Será que as espécies mais antigas correm menor ou maior risco de extinção?”, e foi um legado do terceiro capítulo da própria tese do meu orientador, Bruno Vilela. Nesse capítulo, “*Biogeography underlies the effects of evolutionary history on current extinction risks in the Iberian flora*”, os autores avaliam a relação entre a vulnerabilidade à extinção e a história evolutiva das plantas da Península Ibérica (Vilela, 2016). O estudo conclui que os clados mais antigos e mais distintos evolutivamente possuem maior risco de extinção, condizendo com o padrão de outros trabalhos citados (Gaston and Blackburn, 1997; Johnson et al., 2002; Meijaard et al., 2008). Inclusive, a Figura 5 de dito capítulo virou o modelo da minha tese e agora uma reformulação desta constitui a Figura 2 do meu primeiro capítulo. Porém, apesar do norteamento inicial, o projeto virou meu e eu precisava pensar em como generalizar a pergunta, é dizer, não me limitar unicamente às plantas da Península ibérica.

No primeiro levantamento bibliográfico, além das referências citadas na tese de Bruno, eu percebi que existia uma ampla literatura na paleontologia concernente à extinção dependente da idade (ADE, pelas siglas em inglês; Doran et al. 2006; Hagen et al. 2018; Pearson 1995; Silvestro et al. 2020). Não fui consciente da distinção conceptual entre o risco de extinção de espécies vivas e os eventos de extinção em espécies fossilizadas, assim como, a diferença entre a idade das espécies vivas mensurada por meio do comprimento do ramo das filogenias e a duração de uma espécie fóssil, definida pelo lapso entre a origem e a extinção (Foote, 1996). Não obstante, eu percebi que ambos padrões, ADE e a relação entre idade-vulnerabilidade de extinção para espécies vivas (também chamarei de ADE doravante), eram explicados ou incorporados aos mesmos mecanismos e hipóteses. Por exemplo, a Rainha Vermelha, postula que as interações bióticas causam que as espécies evoluam numa carreira

armamentística onde uma vantagem ganha por uma espécie implica um deterioro ambiental para as outras (Van Valen, 1973). Este processo geraria que as espécies ou gêneros dentro de um clado possuam uma probabilidade de extinção constante; é dizer, uma extinção-independente da idade (Brockhurst et al., 2014; Liow et al., 2011; Quental and Marshall, 2013). Para um ADE negativo, ou o padrão onde as espécies mais antigas têm menor risco de extinção, a hipótese de Idade e Área (Willis, 1922), entre outras, é utilizada como mecanismo. Dita hipótese postula que as espécies mais antigas tiveram mais tempo para expandir as distribuições espaciais e, portanto, possuem uma vulnerabilidade menor às mudanças climáticas e derivas demográficas (Gaston, 1998; Slatyer et al., 2013). Em contraste, a hipótese de Idade e especialização (Pearson, 1995; Raia et al., 2016), a qual estabelece que as espécies mais antigas são mais especialistas e, conseqüentemente, se encontram mais vulneráveis às mudanças bióticas e abióticas (Clavel et al., 2011; Poisot et al., 2011), é utilizada para explicar um ADE positivo, onde as espécies mais jovens tem menor risco de extinção. Bruno, na tese dele, aborda a última hipótese na discussão e também descreve outras hipóteses numa tabela no material suplementar, porém, não faz o vínculo entre as evidências neontológicas e a vasta tradição na paleontologia.

Essa falta de integração entre neontologia e paleontologia é interessante, pois, embora ambas estivessem avaliando o mesmo processo macroevolutivo por meio do mesmo arcabouço teórico, não existia um diálogo explícito entre as áreas (Silvestro et al., 2018). Inclusive, as hipóteses, com exceção da Rainha Vermelha, associam a idade com um atributo que confere fitness, ex., distribuição espacial, especialização num eixo do nicho, etc., e, portanto, tem o potencial de incorporar aspectos ecológicos vinculados com a seleção natural (Vellend, 2010). Avaliando ambas literaturas tive a sensação de que as hipóteses de ADE, embora funcionassem como hipóteses alternativas, eram utilizadas a posteriori (mas veja Tanentzap et al. 2020), é dizer, ajudavam a explicar o sentido de ADE mas de certo modo não eram utilizadas de forma preditiva. Também percebi que não há consenso empírico no sentido do ADE, tanto nos estudos paleontológicos como neontológicos (Davies et al., 2011; Ezard et al., 2011; Januario, 2021; Verde Arregoitia et al., 2013). Portanto, depois de insistir nas hipóteses tradicionais citadas anteriormente nas primeiras versões do manuscrito, resolvi procurar uma teoria que pudesse, a partir de cenários que afetassem o fitness das espécies por

meio de processos eco evolutivos, predizer ambos sentidos de ADE. Devido a isso comecei a me aprofundar na literatura de paleontologia.

Enviesado pelo que queria encontrar, depois da leitura fundamental dos trabalhos de Benton e Rosenzweig, vi no conceito de substituição de clados (CRT pelas siglas em inglês) uma possibilidade para obter ambas direções de ADE como um padrão emergente. O conceito de CRT é um evento com ampla documentação no registro fóssil e pode ser definido da seguinte forma: o intervalo entre a queda de um clado ecologicamente dominante e o surgimento e dominância de um clado novo (Benton, 1991; Rosenzweig and McCord, 1991). Entre os exemplos mais famosos se encontram a substituição dos braquiópodes pelos bivalves (Sepkoski, 1996), dinossauros pelos mamíferos (Benton, 1987) e gimnospermas pelas angiospermas (Condamine et al., 2020). A CRT tem dois modelos fundamentais (Benton and Storrs, 1992; Silvestro et al., 2015). O modelo ativo postula que a substituição do clado antigo acontece por mera vantagem competitiva por parte do clado mais recente. Complementarmente, o modelo passivo define que o clado antigo inibe inicialmente a diversificação e dominância do clado mais novo e que a substituição só acontece depois que um fator externo, como uma mudança climática, afeta negativamente o primeiro, permitindo ao clado novo uma oportunidade ecológica para diversificar e dominar (Benton, 2009). As evidências apontam que o modelo passivo é o mecanismo mais comum de substituição (Brusatte et al., 2008; Pires et al., 2017; Valkenburgh, 1999) e também nele vislumbrei o maior potencial teórico para predizer e explicar ADE. Porém, apesar de ser chamados de modelos, não há uma elaboração formal da teoria a partir da qual seriam derivados. É dizer, o CRT, ao menos ao meu entender, não tinha o status de teoria.

Naquela época, simultaneamente às minhas primeiras explorações bibliográficas, cursei a disciplina de História e Filosofia da Ecologia. Nela aprendi a importância da filosofia na ciência, particularmente na construção das teorias (Pickett et al., 2010). A disciplina me aproximou ao livro “*The Theory of Ecology*” de Scheiner e Willig (2013); o qual foi fundamental na minha formação e na elaboração desta tese. Inclusive durante a pandemia criamos junto com colegas de diferentes programas um clube de estudo sobre o livro. No primeiro capítulo é descrita uma estrutura hierárquica a partir da qual se organizam e sistematizam as teorias. Os seguintes capítulos, ecólogos destacados, utilizam dita estrutura para organizar as diferentes teorias ecológicas. Então, dado que percebi a falta de organização

no conceito de CRT, a estrutura proposta por Scheiner e Willig foi minha ferramenta lógica para formalizar a teoria e implementar os sentidos do ADE como hipóteses derivadas dos mecanismos propostos.

O primeiro capítulo da tese, então, versa sobre a falta de consenso no ADE, tanto empírico como teórico, e a implementação do CRT, após a sua formalização, para produzir previsões testáveis sobre os padrões do ADE. Propomos que o CRT possui duas proposições. A primeira é efeito de incumbência do clado antigo sobre o clado recente (Jablonski, 2008). A incumbência limita a diversificação e dominância do clado recente já que as espécies do clado antigo ocupam a maior parte do espaço de nicho (Reijenga et al., 2021). Então, devido a essa ocupação maior por parte do clado antigo, os recursos e habitats para os membros do clado recente estarão limitados e serão aqueles que possuam os valores mais distantes das condições bióticas e abióticas médias do espaço de nicho (Gehrke and Linder, 2011; Urban and De Meester, 2009). É dizer, os membros do clado recente ocuparão a periferia do espaço de nicho. Dita periferia produzirá altas taxas de extinção sobre o clado novo causados por instabilidades climáticas e eventos estocásticos (Carnaval et al., 2009; Kyriazis et al., 2021). Altas taxas de extinção na periferia produzirão subutilização dos recursos e espaço de nicho disponível, permitindo que o clado recente recolonize e diversifique, aumentando as taxas de especiação (Agrawal, 2001; Stroud and Losos, 2016).

Então, já que o clado antigo ocupa o centro do espaço de nicho, caracterizado pelas condições médias, este estará sujeito a seleção estabilizante e, portanto, a um baixo turnover (Cutter and Gray, 2016). A diferença na ocupação do espaço de nicho por parte dos clados gera um ADE negativo, já que o clado antigo possuirá menor probabilidade de extinção quando comparado ao clado recente (Silvestro et al., 2020). Como é possível observar, a primeira proposição do CRT, efeitos de incumbência, também gera outros padrões de importância eco evolutiva além do ADE negativo. Um deles é o padrão de ocupação do espaço de nicho por parte dos clados, o qual, em conceito, viraria o terceiro capítulo da tese, mas abordarei essa temática mais na frente.

A segunda proposição do CRT é uma mudança ecológica causada por flutuações ambientais ou eventos geológicos (Barnosky, 2001). A mudança gera um novo contexto ecológico, onde as espécies do clado antigo, que até aquele momento dominavam o espaço de nicho, são selecionadas contra, sendo afetadas negativamente no fitness e nas taxas de diversificação

(Chen and Benton, 2012; Erwin, 2015). A perda da dominância por parte do clado antigo oferece uma oportunidade ecológica ao clado novo se este possuir uma adaptação ao novo contexto ecológico (Betancur R. et al., 2012; Wellborn and Langerhans, 2015). Nesse novo cenário, o clado novo superaria competitivamente ao clado antigo, substituindo-o no espaço de nicho (Friedman, 2010; Pires et al., 2017). Durante esse processo, o ADE seria positivo, já que as espécies mais velhas pertencentes ao clado antigo se encontrariam mais vulneráveis à extinção.

Quando concluímos a primeira versão do manuscrito, percebemos que o caminho mais natural seria testar as proposições do CRT, e sua capacidade para predizer o sentido do ADE, numa simulação. Com Bruno planejamos implementar as nossas premissas no motor de simulações Gen3sis (Hagen et al., 2021). Porém, sentimos que deveríamos aproveitar a oportunidade da bolsa do sanduíche, CAPES-Print, para cumprir dito objetivo, inclusive tentando trabalhar com o próprio criador do Gen3sis, Oskar Hagen. Enquanto preparava as documentações para concorrer a uma vaga do sanduíche, decidimos iniciar o segundo capítulo (em realidade agora é o terceiro) concernente ao efeito de incumbência sobre a relação entre idade e posição de nicho das espécies. Nossa expectativa é que em climas estáveis como os trópicos encontraríamos que as espécies mais antigas de diferentes grupos biológicos ocupariam, em média, posições de nicho mais centrais (Igea and Tanentzap, 2020; Terribile et al., 2012). Complementarmente, esperaríamos que em climas instáveis como as regiões temperadas o padrão fosse ao contrário, é dizer, as espécies mais novas ocupariam, em média, posições de nicho mais centrais. Começamos nossas análises exploratórias na família de aves Furnariidea nos diferentes biomas dos Neotrópicos. Por meio do pacote CENFA (Rinnan and Lawler, 2019), conseguimos mensurar a marginalidade (a distância entre o centroide do nicho da espécie e o centroide do espaço de nicho) e a especialização (relação entre a variação do espaço de nicho e a largura do nicho da espécie) das espécies. Mensuramos a idade das espécies por meio dos comprimentos dos ramos das filogenias calibradas. Não obstante, em nossas avaliações iniciais não encontramos nenhum padrão. Pensamos que talvez estivéssemos muito limitados na nossa escala biológica, então, já que tínhamos pronto os scripts, decidimos estender as análises para os tetrápodes neotropicais. Me encontrava fazendo as primeiras análises quando a oportunidade do sanduíche, depois de um sem-fim de burocracias que valeram a pena, me levou para Friburgo, Suíça.

A ideia inicial do sanduíche era fazer com Oskar Hagen para trabalhar as simulações do CRT no Gen3sis. Porém, tanto na literatura de ADE (Silvestro et al., 2020) como na de CRT (Silvestro et al., 2017, 2015) aparecia repetidas vezes as contribuições de Daniele Silvestro. Os artigos dele me pareciam elegantes, tanto nos métodos bayesianos e de redes neurais que implementava em dados fósseis (Silvestro et al., 2014, 2011) como na escrita clara e compreensível (Silvestro et al., 2018). Então, escrevi para ambos um e-mail e tomaria uma decisão a partir das suas respostas. Daniele respondeu primeiro e me ofereceu todo o apoio para completar as documentações e me vincular com a UniFribourg. Oskar, por sua parte, ficou contente que tenha entrado em contato, mas ele, quem estava começando um postdoc em IDiv-Leipzig, não podia me hospedar, já que não tinha o status de investigador principal. Na verdade, lembrando as sensações, eu estava cheio de incertezas, me sentia reticente a deixar o Brasil depois da pandemia, não sabia o que fazer com o apartamento onde morava, e apostar no sanduíche, quase no final do doutorado, era como andar a escuras, pois não tinha nenhuma referência de como funcionava o laboratório de Daniele, nem como ele seria como supervisor. O denominador comum de muitas histórias de colegas no sanduíche é que eles só tiveram uma ou duas reuniões com o supervisor ou supervisora durante os seis ou doze meses de estágio. Não obstante, no meu caso, trabalhar sob a orientação de Daniele Silvestro, foi um antes e um depois na minha formação como cientista.

Cheguei em Friburgo em agosto de 2022 com mais medo do que vontade. Era minha primeira vez fora das Américas e o custo da vida em Suíça me assustou, embora minha bolsa foi ajustada a esses padrões. Nas primeiras semanas sofri a solidão e a quietude de Friburgo, eu tão acostumado ao frenesi soteropolitano. Também, desde o começo senti a demanda do laboratório quando na segunda semana Daniele marcou a apresentação geral da minha tese frente ao laboratório cujos membros estavam voltando das férias de verão. Era também minha primeira vez que apresentaria minha tese em inglês, língua que aprendi na Guatemala onde a maioria dos meus professores foram belizenses ou migrantes deportados. Lembro de me sentir nervoso, mas emocionado por apresentar meus projetos ao Daniele. Meu plano foi apresentar o capítulo do CRT, os resultados preliminares dos tetrápodes neotropicais e discorrer sobre o objetivo de implementar a simulação no Gen3sis e elaborar outro capítulo testando empiricamente as proposições do CRT num conjunto de dados fósseis. Não obstante, fui interrompido pelos postdocs do laboratório, Torsten Hauffe e Juan Carrillo,

quando apresentei os resultados dos tetrápodes, particularmente quando descrevi a estimação da idade evolutiva das espécies por meio do comprimento dos ramos de filogenias calibradas. Falaram que essas estimações estavam cheias de incertezas, pois as filogenias, mesmo calibradas, não continham informações fundamentais para determinar a idade das espécies. Eu escutei com atenção, me sentindo um pouco mal, pois ao final eu tinha trabalhado na geração desses dados por mais de dois anos. O que fez a galera refletir, e nesse silêncio expectante comecei a entender as dimensões da brecha entre paleontólogos e neontólogos, foi quando eu mostrei, citando vários artigos, que eu não tinha inventado esse método de estimar as idades por meio de filogenias, e sim, que era uma prática prevalecente nas publicações de macroecologia (Johnson et al., 2002; Tanentzap et al., 2020; Verde Arregoitia et al., 2013).

Nesse primeiro mês em Friburgo a minha tese mudou de estrutura. Para concorrer ao edital do sanduiche eu tinha elaborado um plano de trabalho no qual estabeleci que faria dois capítulos da tese no exterior, a simulação do CRT e uma exploração empírica da segunda proposição do CRT. Porém, Daniele e Juan, na primeira reunião após a minha apresentação, sentiram que não eram objetivos viáveis para 6 meses, além das inconsistências que perceberam nos meus dois primeiros capítulos. Discutimos sobre possíveis caminhos, inclusive fazer uma simulação mais simples, porém não chegamos a nada concreto. Saí um pouco abatido dessa reunião, inclusive com a sensação de não estar dando conta do desafio. Enviei o capítulo teórico do CRT (primeiro capítulo da tese) a Juan e Daniele, e ao cabo de uma semana, numa sexta-feira, recebi de volta um documento totalmente vermelho de tanta correção. Também, nesse mesmo dia pela manhã, encontrei o livro “Writing Science” de Joshua Schimel (2012) deixado por Juan na minha área de trabalho. Naquele momento eu tive que tomar uma decisão respeito a minha atitude perante ao que estava acontecendo. Por um lado, podia me paralisar, permitindo que as emoções de incompetência tomassem conta de mim, ou pelo outro, podia trabalhar a partir dessas críticas e melhorar meus projetos. Foi um final de semana difícil, no qual coloquei minha vida em perspectiva, os meus propósitos e minhas limitações. No domingo decidi que tinha que consequente com o próprio caminho que tinha desejado, pela oportunidade que o Brasil tinha me oferecido para me formar como cientista. Ao final a ciência é uma atividade coletiva que precisa da revisão rigorosa dos colegas e para crescer não podia esperar que passassem pano em mim. Voltei na segunda-

feira com vontade de trabalhar e participar mais das dinâmicas do laboratório. Uma delas, talvez a mais importante, era o café após almoço no jardim botânico do campus. Bebendo café de uma cafeteira italiana gigantesca, com os primeiros ventos frios do começo de outono, e olhando o trabalho dos botânicos no jardim, Torsten comentou que depois da minha apresentação tinha ficado curioso sobre a estimação da idade das espécies a partir da filogenia, fez um levantamento bibliográfico rápido, e descobriu que de fato era uma abordagem comum, inclusive em publicações recentes (Pie and Caron, 2023; Sonne et al., 2022) e ninguém falava sobre as informações faltantes na filogenia que comprometiam a acurácia da idade (mas veja Swenson 2019). Voltamos ao laboratório e num quadro branco Daniele e Torsten definiram um protocolo para abordar essas questões. Basicamente o objetivo desse protocolo era demonstrar por meio de simulações de filogenias (Stadler, 2019) e taxonomias (Barido-Sottani et al., 2019) as taxas de erro, influenciadas pelos modos de especiação e diferentes cenários de extinção, entre a idade verdadeira das espécies e a idade mensurada através do comprimento dos ramos da filogenia. Também, além de apontar o erro, o segundo objetivo era desenvolver algum método para corrigir a estimação filogenética da idade. Daniele incorporou Juan e Torsten no projeto, e sugeriu deixar em suspense o segundo capítulo, já que possivelmente pudéssemos corrigir as idades das espécies com os resultados do projeto. Por conseguinte, desistimos de qualquer tipo de simulação, e o protocolo de Friburgo se converteu no segundo capítulo da minha tese, “*Approximating species age under different speciation modes and extinction*”, e o segundo capítulo original, “*Species age and niche position: an exploratory analysis*”, se transformaria no terceiro, depois da concordância com Bruno.

Considero que uns dos hábitos mais valiosos que aprendi durante o sanduíche foi a organização das tarefas dentro de um marco temporal. Sim, fazer cronogramas. Eu até tinha feito alguns para concorrer ao doutorado e ao sanduíche. Porém, em Friburgo aprendi a ser mais realista respeito à relação atividade-tempo e a desmembrar os objetivos grandes, como escrever um capítulo, em objetivos menores e específicos, como rodar uma análise a partir de filogenias simuladas em um cenário de extinção baixo, que se adequassem ao lapso de uma semana. São *soft skills* que parecem banais, mas que a longo prazo podem definir uma defesa de mestrado ou doutorado bem sucedida. Daniele pede para os orientados definir ditos objetivos semanais no aplicativo Slack. Esses objetivos, junto com dúvidas e problemas, são

comentados e resolvidos nas reuniões semanais, *weeklies*, que ele mantém com os alunos em privado. Nessas *weeklies* discutíamos os avanços do meu projeto junto com os postdocs. Sendo sincero, no começo, as discussões ficavam um pouco elevadas para mim, ao ponto que eu acompanhava meramente anotando. Não obstante, conforme transcorria o tempo e eu me apropriava melhor dos conceitos, consegui ficar na altura das discussões, propondo inclusive formas de apresentar os resultados e as implicações sobre a literatura. A questão mais complexa foi desenvolver uma abordagem para corrigir as estimativas da idade. Nossa primeira tentativa foi treinar modelos. Tentamos modelos neurais, GAM e modelos lineares, porém, nenhum aprendeu nada para corrigir as idades. Isso foi uma revelação importante, pois implicava que a informação faltante, principalmente os modos de especiação, é fundamental para mensurar a idade verdadeira das espécies. Nossa segunda tentativa foi por meio de uma abordagem baseada na função geométrica, sob a pressuposição de especiação por brotamento (*budding speciation*), mas também não melhorava as taxas de erro entre as idades. Finalmente, Daniele e Torsten pensaram numa função baseada no processo de *birth-death* sob a pressuposição de especiação por bifurcação o qual de fato melhorou a acurácia da idade corrigida. Porém, sendo críticos, a especiação por bifurcação é o modo que representa a menor taxa de erro ao respeito à estimação filogenética da idade, e, portanto, não corrige consideravelmente o problema. Considero que a intuição mais notória que tive desenvolvendo esse trabalho é que apesar de que em princípio é uma crítica sobre a estimação da idade a partir de filogenias, também me permitiu refletir muito sobre a evolução das espécies e a maneira em que a representação das filogenias influencia nosso pensamento (Caetano and Quental, 2022).

Voltei ao Brasil no janeiro do 2023, com o primeiro capítulo quase pronto, depois de correções substanciais na escrita e o refinamento conceitual nas partes paleontológicas do ADE, e com quase todos os resultados do segundo capítulo. Em abril submetemos o primeiro capítulo ao *Journal de Evolutionary Biology* o qual foi devolvido na última semana de julho com uma major review. A principal crítica foi a falta da declaração explícita de escalas espaciais e temporais. Assim como uma operacionalização mais direta das hipóteses derivadas do CRT. Estamos trabalhando nisso enquanto termino de escrever esta tese. Em maio terminei a primeira versão do segundo capítulo. Já passou quatro rodadas de revisões

por parte de Juan, Torsten e Daniele. Só estamos esperando uma *friendly review* de Rachel Warnock, quem fez umas recomendações no começo do estudo.

A partir de maio me dediquei por completo ao terceiro capítulo, “*Species age and niche position: an exploratory analysis*”. Recuperei com dificuldade os scripts e dados que tinha abandonado por quase um ano, assim como o manuscrito inicial. A ideia continuava sendo avaliar a relação entre idade das espécies e a posição de nicho. E nossa expectativa, num ambiente estável como os Neotrópicos, seria que as espécies mais antigas ocupassem o centro do espaço de nicho (Gehrke and Linder, 2011; Rosenzweig, 1995). Houve uma modificação conceitual considerável nos fundamentos do artigo. A relação entre idade e posição de nicho era, na primeira versão do manuscrito, um padrão emergente do efeito de incumbência gerado por um clado mais antigo sobre o espaço de nicho, afetando a colonização e diversificação de clados mais recentes. Porém, em discussões com Bruno percebemos que esse padrão não precisava do efeito de incumbência ou de dois ou mais clados para emergir. Precisava de um único clado, e poderia se dar após uma radiação adaptativa (Mittelbach and Schemske, 2015; Schluter, 2015). O particionamento do espaço de nicho entre as espécies de um clado para se diferenciar ecologicamente lhes assignaria diferentes posições de nicho (Losos, 2010; Rundell and Price, 2009). Assumimos, a partir de uma extrapolação da hipótese *abundant niche-centroid* (Maguire, 1973; Osorio-Olvera et al., 2020), que no começo da radiação adaptativa a linhagem colonizaria o centro do espaço de nicho e a partir daí se diversificaria para a periferia. Por conseguinte, essa trajetória do particionamento do espaço de nicho geraria que as espécies mais recentes ocupem posições de nicho mais periféricas em comparação com as espécies mais antigas.

Nas primeiras análises descobri que não havia padrão discernível para as quatro classes de tetrápodes. Os modelos não explicavam nada dos dados. Comecei a me preocupar e contemplei a ideia de desistir desse capítulo e defender somente com os primeiros dois. Porém, Bruno me pediu para eu insistir nos dados que com tanto esforço tínhamos gerado durante a pandemia. Ele me sugeriu ler o artigo de Graham et al. (2018) sobre escala filogenética. Fabrício Villalobos também tinha me recomendado, após minha qualificação no 2021, explorar as classificações taxonômicas; é dizer, não limitar as minhas análises só as classes de vertebrados, mas abordar também as famílias e gêneros. Então, a

operacionalização do estudo virou uma exploração das classificações taxonômicas dos tetrápodes neotropicais respeito a relação entre idade e posição de nicho.

Esse foi o sucinto diário desses quase cinco anos. Embora esteja em termos acadêmicos, acredito que os outros componentes da minha vida estão discretamente presentes no texto. Sempre é injusto avaliar em retrospectiva o que poderia ser feito diferente. Houve erros e desídia, também muita tribulação respeito a minha identidade como cientista. Porém, hoje posso me sentir orgulhoso e agradecido pela perseverança, a disciplina e as infrequentes mas fundamentais intuições científicas que eu mostrei. O meu caminho foi inaugurado pela tese do meu orientador e eu humildemente espero que a minha deixe sendas abertas para outros percorrerm.

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

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 current status. Additionally, given that closely related species share traits associated with fitness, evolutionary proximity could generate 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 latter-arriving 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 risk 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; Michael Benton 2016). Yet, empirical evidence suggests that ADE is contingent: being absent or expressing in different directions depending on the biological group, spatial scale, whether the lineage is extinct or extant, or whether the study comes from paleobiology or modern species (Silvestro et al. 2020; Tanentzap et al. 2020; Hagen et al. 2018; Januario and Quental 2021). Likewise, 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 eco-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 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 obtain 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 stasis hypothesis: It postulates that older species, due to genotypic or phenotypic lack of change during millions of years, may not be able to adapt to new biotic or abiotic pressures (Eldredge et al. 2005).

Exaptation: A trait not shaped by natural selection or shaped 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 to going extinct.

Extinction rate: The number of extinction events 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 (Hansen 2006; Lieberman and Dudgeon 1996).

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).

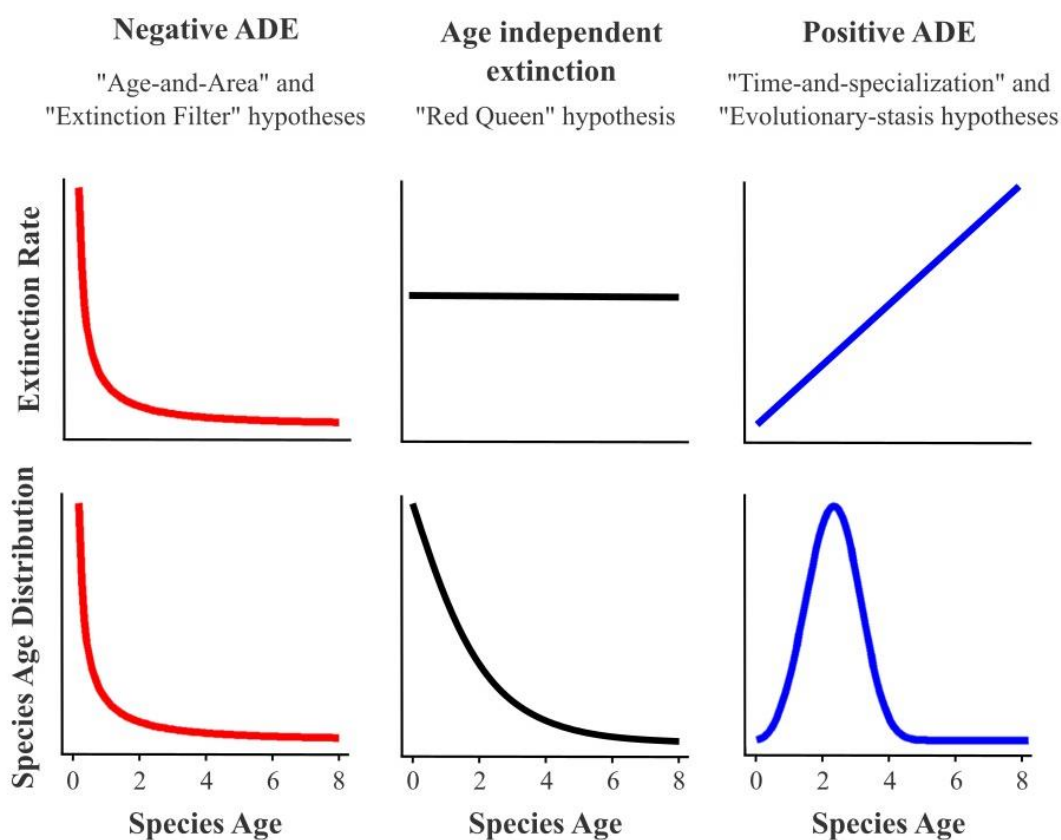
The “Red Queen hypothesis” postulates that biotic interactions cause species to evolve in an evolutionary race where an advantage gained by one species implies environmental deterioration for the other interacting species (Van Valen 1973). Thus, species have to keep the evolutionary pace or become extinct (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 (Brockhurst et al. 2014; Liow et al. 2011; 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 (Gaston 1998; Slatyer et al. 2013). 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 the “Evolutionary stasis hypothesis”, which posits that older taxa may not be able to compete against new emerging lineages nor adapt to new biotic or abiotic pressures due to phenotypic and genotypic stasis in their populations (Eldredge et al. 2005).

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 relationship 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,” etc; 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 selection forms, 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

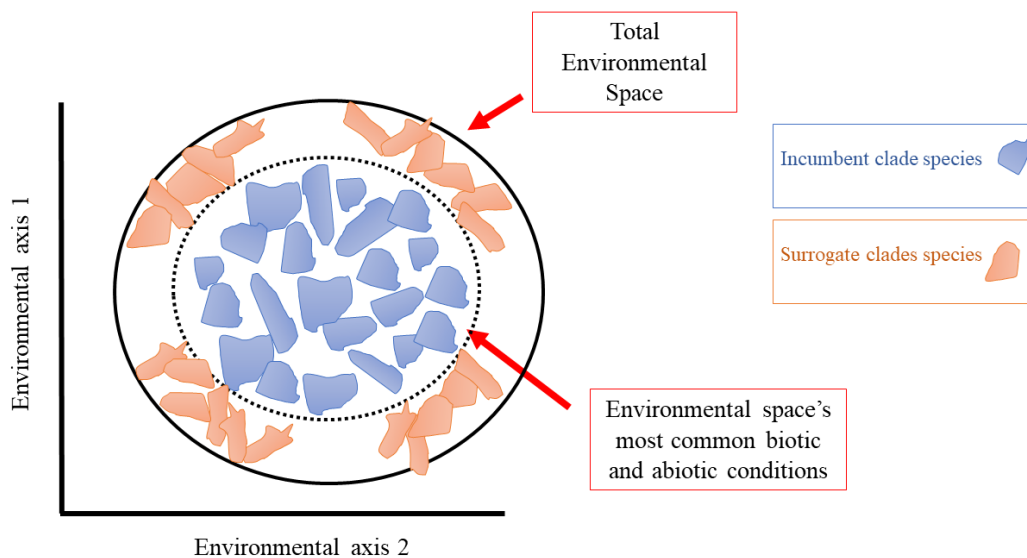


Figure 1. Representation of a two-dimensional environmental space and the occupation patterns caused by incumbency effects. The species from the incumbent clade (blue polygons) occupy an area in the environmental space center, at the margin of which, the species from the surrogate clades (orange patches)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

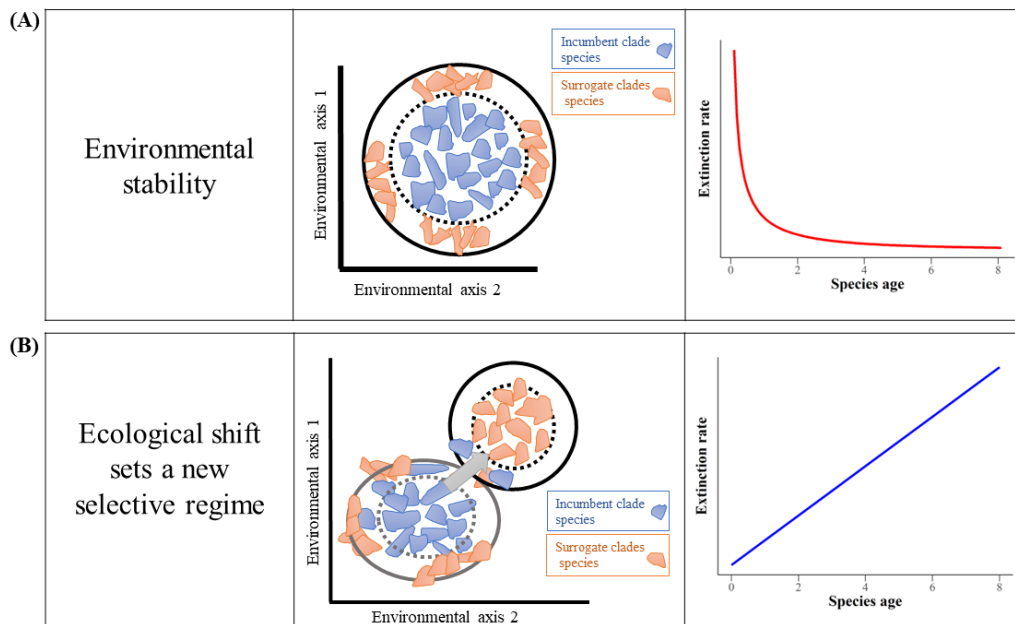


Figure 2. The possible effect of an ecological shift on the relationship of species longevity and extinction. (A) If the ecological shift does not happen and the environmental space center is stable, ADE would have a negative direction (older taxa would be less extinction prone). (B) Whereas, if the 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). 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 longevities 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 (Igea and Tanentzap 2020; Pylon 2014; Morales-Barbero et al. 2021; Rabosky et al. 2018).

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.

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**Approximating species age from phylogenies under different speciation modes
and extinction**

Approximating species age from phylogenies under different speciation modes and extinction

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Abstract

Species age (the elapsed time since origination) can give an insight into how species longevity might influence eco-evolutionary dynamics. Traditionally, species ages have been measured in the fossil record; however, recently, researchers have estimated the ages of extant species from the branch lengths of time-calibrated phylogenies. This approach poses problems because phylogenetic trees typically do not contain direct information about species identity along the branches beyond the tips. When phylogenies do not include all extinct and extant lineages, the branch lengths of the sampled extant species are likely to appear longer than they truly are. Additionally, different speciation modes (e.g., bifurcating, budding, or anagenetic) cause different topological representations of phylogeny and, thus, affect the relationship between branch lengths and species age. Here we evaluate through simulations the effect of extinction, incomplete sampling, and speciation mode on the accuracy of phylogenetic ages as proxies for the true ages of extant species and we quantify the consequences on eco evolutionary inferences. We show that taxon sampling, extinction, and different assumptions about speciation modes greatly influence the accuracy of phylogenetic ages. The error is substantially higher under the assumption of budding than bifurcating speciation and further increased in the presence of incomplete sampling of extant species and with higher extinction. We found that this mismatch would affect eco-evolutionary analyses often performed with phylogenetic ages, for instance, the comparison of species ages and the assessment of extinction risk. For bifurcating speciation, which is most often assumed in these analyses, we develop a probabilistic approach to improve the estimation of species ages, based on the properties of a birth-death process and under the assumption of a fully sampled phylogeny. We find that our model can reduce the error by one order of magnitude under cases of high extinction. Our results indicate that we should be cautious when inferences are made from the relationship between phylogenetic ages and eco-evolutionary variables, and that, under some assumptions, it is possible to obtain good approximations of species age by combining branch lengths with the expectations of a birth-death process.

Key words: Evolutionary history, Extinction rates, Incomplete sampling, Simulations, Speciation modes, Phylogeny.

Introduction

The estimation of species age, or the elapsed time since species origin, is important to evaluate mechanisms that link species longevity with eco-evolutionary processes (Benton, 2013; Swenson, 2019). For instance, age-dependent extinction hypotheses test the relationship between species age and extinction probability, assessing whether extinction rates differ between young and old species (Balmford, 1996; Eldredge et al., 2005; Pearson, 1995). Likewise, species age could be a measure of colonization time, especially in island systems (Tanentzap *et al.* 2015) or during biotic invasions triggered by geological events, such as the formation of the Central American Isthmus for the Great American Interchange (Carrillo *et al.* 2015, 2020). Species age is measured in the fossil record through different statistical and probabilistic approaches based mostly on taxa's stratigraphic duration (Foote, 1996; Foote & Raup, 1996). Several of these approaches consider the differences in fossil sampling and temporal resolution (Alroy et al., 2001; Silvestro et al., 2019). Species ages estimated from paleobiological data offer a reliable measure of species' temporal duration which can be used in macroevolutionary studies (Benton, 2016; Silvestro et al., 2020; Van Valen, 1973). More recently, several studies have used the length of terminal branches in time-calibrated phylogenies as a proxy for the age of extant species (Davies et al., 2011; Gaston & Blackburn, 1997; Johnson et al., 2002; Pie & Caron, 2023; Sonne et al., 2022; Tanentzap et al., 2020; Verde Arregoitia et al., 2013). However, this approximation, which we hereafter refer to as “phylogenetic age”, can lead to over- or underestimations due to three non-exclusive shortfalls.

First, incomplete sampling of extant species, either because no material is available or a species is still unknown to science, can bias phylogenetic age estimation by augmenting terminal branch lengths (Heath et al., 2008; Mynard et al., 2023). Second, extinction events will mask branching events in phylogenetic trees of extant species (Harvey et al., 1994; Nee & May, 1997). Even in phylogenetic trees that include extinct taxa, the incompleteness of the fossil record will inevitably lead to missing lineages and incorrect topologies. Unsampled

extant and extinct species from the phylogeny results in an inflation of the length of terminal branches leading to sampled species (i.e., the tips of the tree), thus altering phylogenetic species ages. For instance, if the extinct species of the *Homo* genus are not included in a phylogeny, the phylogenetic age of *Homo sapiens* is approximately 10 million years, i.e., the age of the last common ancestor with its sister species, the chimpanzee (Rivas-González et al. 2023). This estimate exceeds the age of the oldest known fossil of modern humans by two orders of magnitude (Figure 1; Callaway 2017). The third, and perhaps most challenging shortfall in phylogenetic species ages, is that the tree alone does not contain information about the underlying speciation mode and does not include species labels across its branches, such that only the tips can be unequivocally assigned to a named species (Losos & Glor, 2003). Alternative speciation modes have been discussed in the literature reflecting different biological processes and species concepts, including bifurcating, budding, and anagenetic speciation (Foote, 1996; Silvestro et al., 2018). These modes define the relationship between the ancestral species and its descendants, thus contributing to determining species ages (Rosenblum et al., 2012; Wagner, Erwin, & Anstey, 1995) (Figure 2). Most phylogenetic trees are depicted in the rectangular shape where the two descending lineages split symmetrically from an ancestral lineage, thus suggesting a bifurcating speciation mode where two new species replace the ancestral lineage (Baum et al., 2005; Caetano & Quental, 2022). However, the often-unstated assumption of all birth-death processes commonly used to model phylogenetic branching times, is that speciation occurs as a budding process (sometimes referred to as asymmetric), with a speciation event leading to a single new species and the survival of the parent species, even though we cannot determine which descendant branch is the new species (Gernhard, 2008; Nee et al., 1994; Stadler, 2013). Anagenetic speciation, in contrast, does not lead to a branching event and is therefore not visible on a phylogenetic tree.

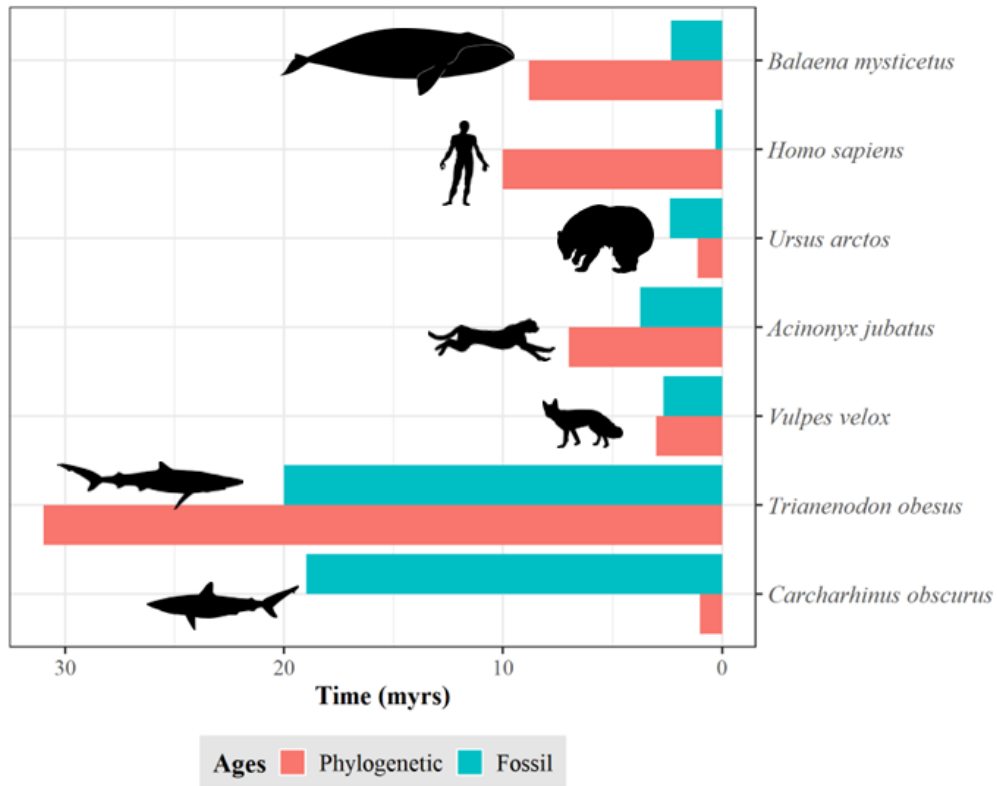


Figure 1. Discrepancy between species ages. Estimations based on the length of the terminal branch in a time-calibrated phylogeny (red) and the first appearance in the fossil record (green). Shark data (*Trianenodon obesus* and *Carcharhinus obscurus*) obtained from Brée et al. (2022). Mammals' phylogenetic data (except *Homo sapiens*) obtained from Upham et al. (2019). Mammals' fossil data (except *Homo sapiens*) obtained from Silvestro et al. (2018). *Homo sapiens* fossil and phylogenetic data obtained from Callaway (2017) and Rivas-González et al. (2023), respectively.

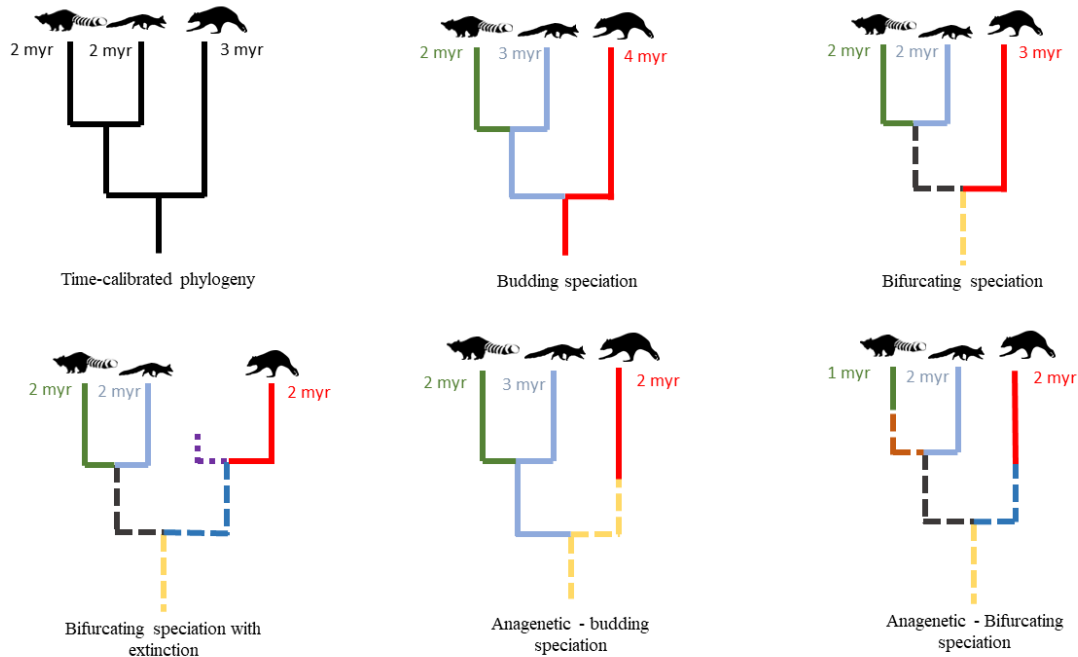


Figure 2. Impact of speciation mode and extinction on species age. For the same hypothetical time-calibrated phylogeny of extant species, the continuation of the same color indicates the same species, solid and dashed lines represent extant and extinct species, respectively, under different speciation modes and extinction scenarios. Numbers display the resulting age of the respective species in million years (myr).

All speciation modes may reflect plausible biological processes, and evidence for each mode has been found in the fossil record (Foote, 1996; Simpson, 1984) and in extant species (Skeels & Cardillo, 2019). Bifurcating speciation can be linked with vicariance or allopatric speciation (Willmann & Meier, 2000), and the Hennigian species concept considers all speciation events as bifurcating (Henning, 1999). Under this speciation mode, phylogenetic ages equal species ages when there is no extinction, and all species are sampled. Budding speciation can be interpreted as the result of parapatric, peripatric, and founder-event speciation (Anacker & Strauss, 2014; Caetano & Quental, 2022) and is related to the evolutionary species concept, which considers any species as descendant of an ancestral lineage with its own evolutionary identity (Simpson 1951, but see Simpson 1961). A phylogenetic tree typically lacks information about which of the two descendent branches is the new species after a speciation event (but see Aze *et al.* 2011). Thus, in the absence of

extinction, the phylogenetic age of one sister species will equal its species age while the other will be older but without the possibility to identify which one is which. Anagenetic speciation is not associated with a branching event but can be used to describe different species or morphospecies (Emerson & Patiño, 2018) delimited by substantial phenotypic change occurring along a lineage (Roopnarine et al., 1999) and will cause a higher phylogenetic age than the genuine species age.

Several studies used phylogenetic age at face value for species age (e.g., Johnson et al. 2002; Tanentzap et al. 2020; Verde Arregoitia et al. 2013), but the potential deviation from the true species ages due to the combined shortfalls outlined above remains unclear. Here we use simulations to quantify the predictability of species age from phylogenetic trees of extant taxa, under different diversification scenarios. Specifically, we performed simulations where we know the true age of species to: 1) quantify the error in phylogenetic ages under various scenarios combining different speciation modes with a range of speciation and extinction rates and incomplete sampling; 2) examine whether this error affects our ability to make qualitative decisions on the order of species ages; 3) explore whether the signal of labeled age-correlated extinction risk is preserved in the phylogenetic age of species. Finally, we propose a new method to estimate species age more accurately under the assumption of bifurcating speciation, which is the most widely used assumption in evolutionary studies (e.g., Tanentzap et al. 2020), and assess its ability to improve our interpretation of age-dependent extinction risks.

Methods

Simulating species ages

We generated complete phylogenies of extant and extinct species under a stochastic birth-death process using the package TreeSim 2.4 (Stadler, 2010) for the R 4.3.0 statistical programming environment (R Core Team 2023). Then we mapped species on the complete phylogenies using the R package FossilSim 2.3.1 (Barido-Sottani et al., 2019) under different speciation modes, thus assigning species labels across all branches of the tree. We used the labels assigned to terminal extant taxa to determine the true species ages. We then dropped all extinct species from the tree and obtained the length of terminal branches, to quantify the phylogenetic age of extant species. Finally, we rescaled all phylogenetic trees to a root age of one, which ensures that the absolute errors in species ages are comparable in plots, and compared the relative true and phylogenetic ages among different simulation scenarios.

Error in equating phylogenetic and species age

To explore whether there is a consistent over- or underestimation of species ages and to quantify error in approximating species ages with phylogenetic ages, we simulated a range of datasets with different speciation modes and diversification rates. First, we simulated 3 sets of 100 phylogenetic trees with 100 extant species based on birth rates equal to 0.1, 0.5, and 1, combined with 100 death rates ranging from 0 to 0.99 in equal increments (Beaulieu & O'Meara, 2016). Second, on each of these phylogenies, was then mapped species according to different scenarios of speciation: (1) budding speciation, (2) bifurcating speciation, (3) a combination of budding speciation and anagenetic speciation with the rate of anagenesis set to half of the birth rate, and (4) bifurcating speciation combined with anagenetic speciation with the rate of anagenesis set to half of the birth rate.

Across all trees, we obtained in total 120,000 extant species, 30,000 for each speciation scenario. For each speciation mode and extinction fraction rate (defined as death/birth Beaulieu & O'Meara, 2016), we calculated the mean absolute percentage error (MAPE) across all species for each tree as measure of the deviation between the phylogenetic ages from the true age.

$$\text{MAPE} = \frac{100}{n} \sum_{i=1}^n \left| \frac{\text{Trueage}_i - \text{Phylogeneticage}_i}{\text{Trueage}_i} \right|$$

Next, for each speciation mode, we plotted the MAPE against the simulated extinction fraction.

Impact of age error in comparing species ages

To explore whether the error introduced by approximating species age with phylogenetic age impacts our ability to make qualitative judgements such as which of two extant species is the younger one, we simulated 1,000 phylogenetic trees with values of extinction fractions of 0.9, 0.5, and 0, combined with a fixed speciation rate of 1 (3000 trees). Second, on each of these phylogenies, we mapped species according to budding and bifurcating speciation. Thus, we simulated 300,000 extant species for each speciation mode. Next, we calculated the proportion of cases where the younger of two species, according to its phylogenetic age, is, in fact, the older one given the true age of the two species. We performed this comparison from the perspective of an empirical research that can only obtain the phylogenetic ages. We made two types of comparisons for each phylogeny: (1) between the youngest and oldest species in the phylogeny, and (2) between two randomly selected species.

Error in the phylogenetic age due to uniform incomplete sampling

We used the intermediate extinction scenario with an extinction fraction of 0.5 to explore the error in equating phylogenetic and true age that is introduced by uniform incomplete sampling under the scenarios of bifurcating and budding speciation. We specified a fully sampled phylogeny and 25% and 50% of incomplete sampling. We simulated trees such that they included sampled 100 tips, i.e., after dropping the unsampled ones. We calculated the MAPE for each tree and compared the incomplete sampling scenarios for each speciation mode.

A probabilistic method to infer species age

Under the assumption of bifurcating speciation, the phylogenetic age represents the upper boundary of plausible species ages and corresponds to the true age in the absence of extinction. However, the true age could be younger if extinction led to the disappearance of recent cladogenetic events from the phylogeny of extant species. Given a phylogenetic age v_i

the probability that the true species age s_i is exactly ν_i is conditional on no other speciation or extinction event having occurred between ν_i and the present. We approximate the probability of no speciation or extinction for an arbitrary small time bin t based on the probability that a lineage results in a single descendant, which is (Kendall, 1946):

$$p_1(t, \lambda, \mu) = \frac{(\lambda - \mu)^2 e^{-(\lambda - \mu)t}}{(\lambda - \mu \times e^{-(\lambda - \mu)t})^2}$$

based on a birth-death process with time-homogenous speciation rate λ and extinction rate μ . The probability that no event occurs over a time window ν , *i.e.*, until the age of the observed node i , is approximated as:

$$p_{\text{no event}}(\nu, \lambda, \mu) = p_1(t, \lambda, \mu)^{\nu/t}$$

In the absence of extinction ($\mu = 0$), the probability of the true species age s_i to be equal to ν_i is 1, because any speciation event following the node ν_i would be observed in the tree of extant species. Thus, we calculate the normalized probability of the speciation event to occur at time ν_i as:

$$P(s_i = \nu_i) = \frac{p_{\text{no event}}(\nu_i, \lambda, \mu)}{p_{\text{no event}}(\nu_i, \lambda, 0)} \quad (1)$$

We then compute the probability of a speciation time for any given time τ as:

$$P(s_i = \tau) = \frac{p_{\text{no event}}(\tau, \lambda, \mu)}{\int_0^{\nu_i} p_{\text{no event}}(u, \lambda, \mu) du} (1 - P(s_i = \nu_i)) \text{ with } \tau \in \{\nu_i, 0\} \quad (2)$$

where the first term quantifies the probability of the species age along a vector of times, while the second term normalizes it after accounting for the probability that speciation occurred exactly at the node. We use equations (1) and (2) to approximate a density describing the probability of a species origination at the observed phylogenetic age and along the branch connecting the node with tip. As point estimates of the species age, we tested whether the mean or the median of the distribution better approximate the true species age.

To evaluate the accuracy of our probabilistic species age estimator, we simulated 1,000 phylogenetic trees with extinction rates of 0.25, 0.15, and 0.05, and a fixed speciation rate of 0.3. Using these phylogenies as inputs, we mapped species on each tree based on a bifurcating speciation process. Then, we calculated the MAPE for each tree as measure of the deviation between the function's estimated and the phylogenetic ages from the true age.

Imprint of extinction risk on phylogenetic ages

To evaluate the impact of the erroneous estimation of species age due to the extinction shortfall on macroevolutionary analyses, we explored whether the assumed relationship between species age and contemporary extinction risk (e.g., Johnson et al. 2002; Tanentzap et al. 2020; Verde Arregoitia et al. 2013) is preserved in the phylogenetic ages. For this, we binned the same number of extant species according to their age in five categories reflecting the increase in extinction risk with age encapsulated by the IUCN categories: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR; International Union for the Conservation of Nature 2016). With this, we generated a positive effect with older species being at higher extinction risk regarding the IUCN categories, assuming bifurcating speciation.

Then, we quantified the share of the 1000 datasets where the order of the mean age per IUCN category did not match with the simulated monotonic increase when utilizing (a) phylogenetic ages, and (b) the probabilistic species age estimator. We also evaluated the effect of nonrandom incomplete sampling on the evaluation of species age-correlated extinction risks.

Results

Error in equating phylogenetic and species age

Under the assumption of bifurcating speciation and with no extinction events, phylogenetic ages matched the true age of extant species (Figure 3). At low extinction fraction (< 0.25), 96% of the phylogenetic age estimations were congruent with the true age. At high extinction fraction (> 0.75), this was also the case for most species (73%). However, age overestimation increased with extinction fraction and in some cases the phylogenetic age erroneously suggested that the species is as old as the root age. While under bifurcating speciation, the phylogenetic age never underestimated the true species age, over- and underestimation occurred in the case of budding speciation. Moreover, the proportion of cases where the phylogenetic ages equal the species age was lower than in the bifurcating scenario (Figure 3). Overestimated ages were more frequent with high extinction while

underestimations occurred with low extinction but in principle both happened under the complete range of extinction rates (Figure 3). Even at low extinction fraction, ~50% of phylogenetic ages did not match the true ages.

In datasets simulated under a mixture of anagenetic and bifurcating speciation, phylogenetic ages deviated more strongly from the true ages than under a pure bifurcating process, given that anagenetic events are unobserved in the phylogeny (Figure SM1). With a low extinction fraction, phylogenetic ages were congruent with the true species ages in 78% of the cases instead of 96%, and with high extinction the share decreases from 73% to 62%. Datasets with mixed anagenetic and budding speciation, phylogenetic ages also deviated more than under a pure budding process; with a low extinction fraction, phylogenetic ages were congruent 40% instead of 50%, and with high extinction the accuracy decreased to 34%.

While a budding speciation mode led to a higher baseline error than bifurcation, the latter showed a stronger increase with extinction (Figure 4). Under both modes of speciation, speciation rates did not have a substantial impact on error in age. For strictly bifurcating speciation, there was no error in the absence of extinction, but the MAPE increased to up to 150% with extinction fractions exceeding 0.75. In contrast, under budding speciation the MAPE was around 25% in the absence of extinction, increasing to 30-120% with extinction fractions exceeding 0.75. In datasets that included anagenetic speciation, the MAPE reached as high as 500% in some simulations (Figure SM2).

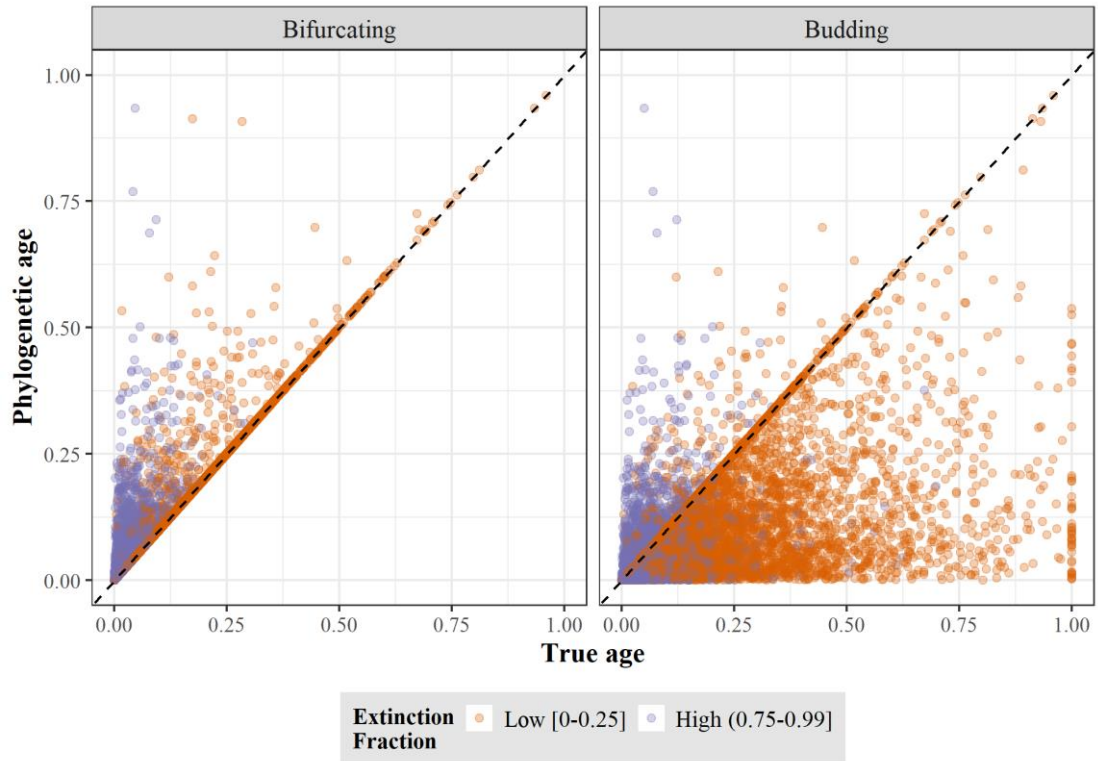


Figure 3. True age versus phylogenetic age at low and high extinction fraction for bifurcating (left) and budding (right) speciation. Each point represents a species and both ages, true and phylogenetic, are scaled to the root age of the correspondent phylogenetic tree.

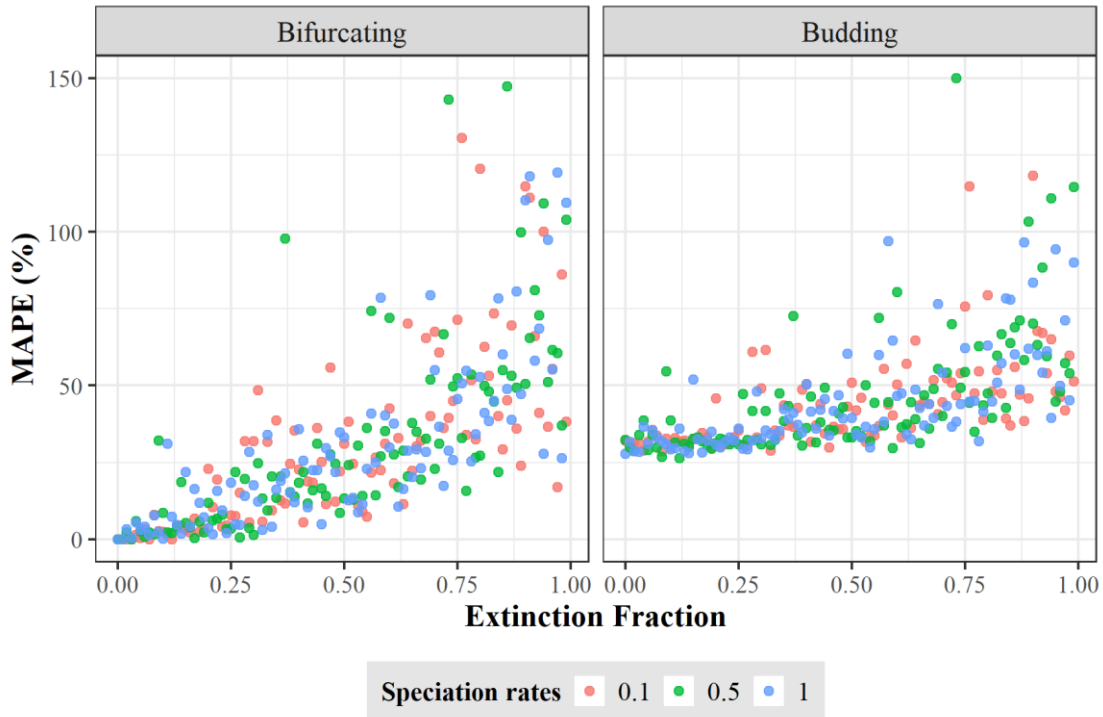


Figure 4. Error in equating phylogenetic age with speciation age. The error was quantified as mean absolute percentage error (MAPE) between the true and phylogenetic ages across all species for each tree simulated under bifurcating (left) and budding speciation (right). Each dot represents one replicate of the 300 trees for each speciation mode using different rates of speciation and extinction fraction.

Impact of age error on comparing species ages

For the combination of strictly bifurcating speciation and all extinction scenarios, selecting the phylogenetically youngest and oldest species never resulted in a case where the presumed older species has been in fact the younger of the two species according to their simulated age (Figure SM3a). Thus, for this speciation mode, there is no risk of a qualitative error when comparing species at the extremes of the age range of a time-calibrated phylogeny. In contrast, for budding speciation, the age rank of the oldest and youngest species was erroneously determined in 2.2% of the simulations in the absence of extinction, increasing to 7.5% and 12.2% for intermediate and high extinction, respectively (Figure SM3b).

Under bifurcating speciation, the age ranking of two randomly selected was incorrect in 6% and 8%, for intermediate and high extinction, respectively (Figure SM4a). Under budding speciation, the error exceeded 25%, irrespectively of the extinction level (Figure SM4b).

Error on equating phylogenetic and species age given uniform incomplete sampling

Under bifurcating speciation, the MAPE for completely sampled trees was $25 \pm 20\%$; for trees missing 25% of the extant species the error increased by 15 orders of magnitude; and for trees missing 50% of the extant species the error increased by 85 orders of magnitude (Figure 5a). Under budding speciation, the MAPE for completely sampled trees was $42 \pm 15\%$; for trees missing 25% of the extant species the error increased by 5 orders of magnitude; and for trees missing 50% of the extant species the error increased by 22 orders of magnitude (Figure 5b).

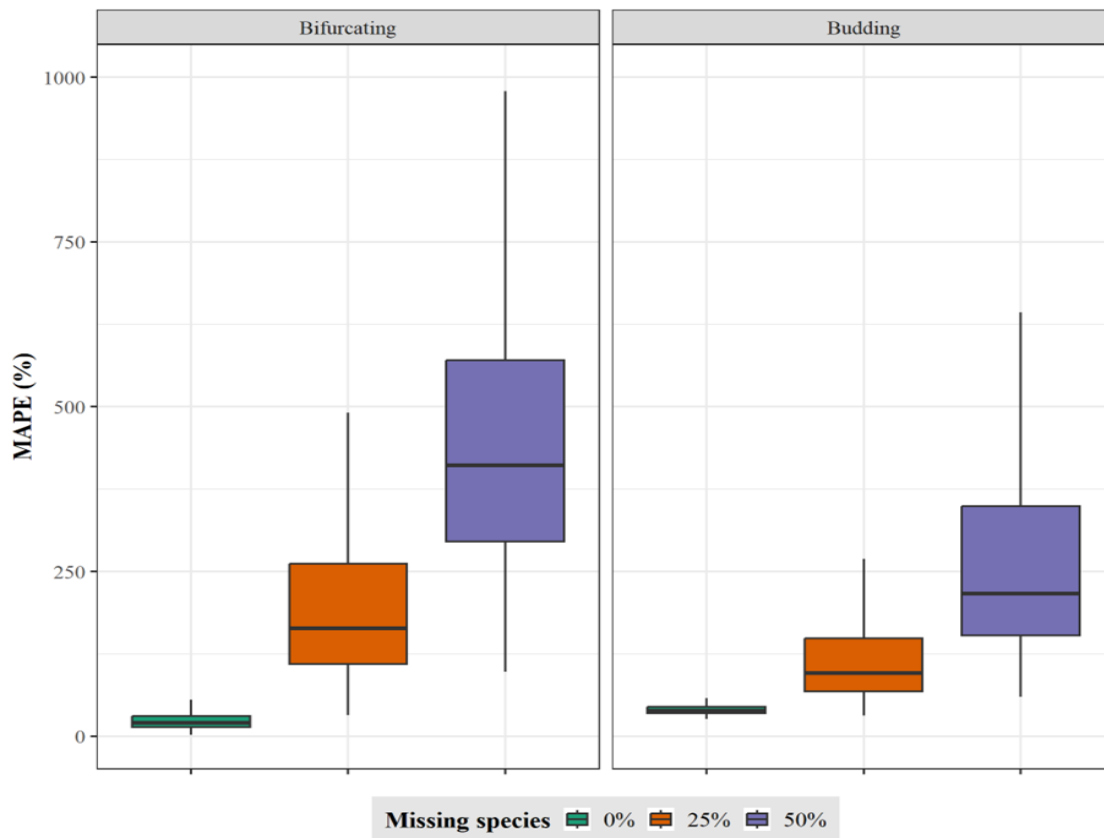


Figure 5. Error in equating the phylogenetic age with true species age for three levels of uniform incomplete sampling (0%, 25%, and 50% missing extant species; from left to right) with an intermediate extinction rate. The error was quantified as mean absolute percentage

error (MAPE) between the true phylogenetic ages across 100 species for each of 1000 trees for each missing species scenario simulated under bifurcating (left) and budding (right) speciation.

Probabilistic species age estimation

With increasing extinction, our probabilistic estimation of species ages resulted in an increasingly lower deviation from the true species age than when the phylogenetic age would have been used (Figure 6). Under low extinction the MAPE was slightly worse compared to the use of phylogenetic ages ($\Delta\text{MAPE} = 2.83 \pm 3.9\%$ when using the mean of the estimated ages and $2.1 \pm 1.3\%$ for the median across estimates). In contrast, with higher extinction, the probabilistic estimation reduced the error associated with phylogenetic age by ~ 2 orders of magnitude ($\Delta\text{MAPE} = -27 \pm 26\%$ for the mean estimated ages and $-32 \pm 28\%$ for the median across estimates). However, our probabilistic function to estimate species ages still resulted in a mean deviation from the true age of up to 30% (Figure SM5).

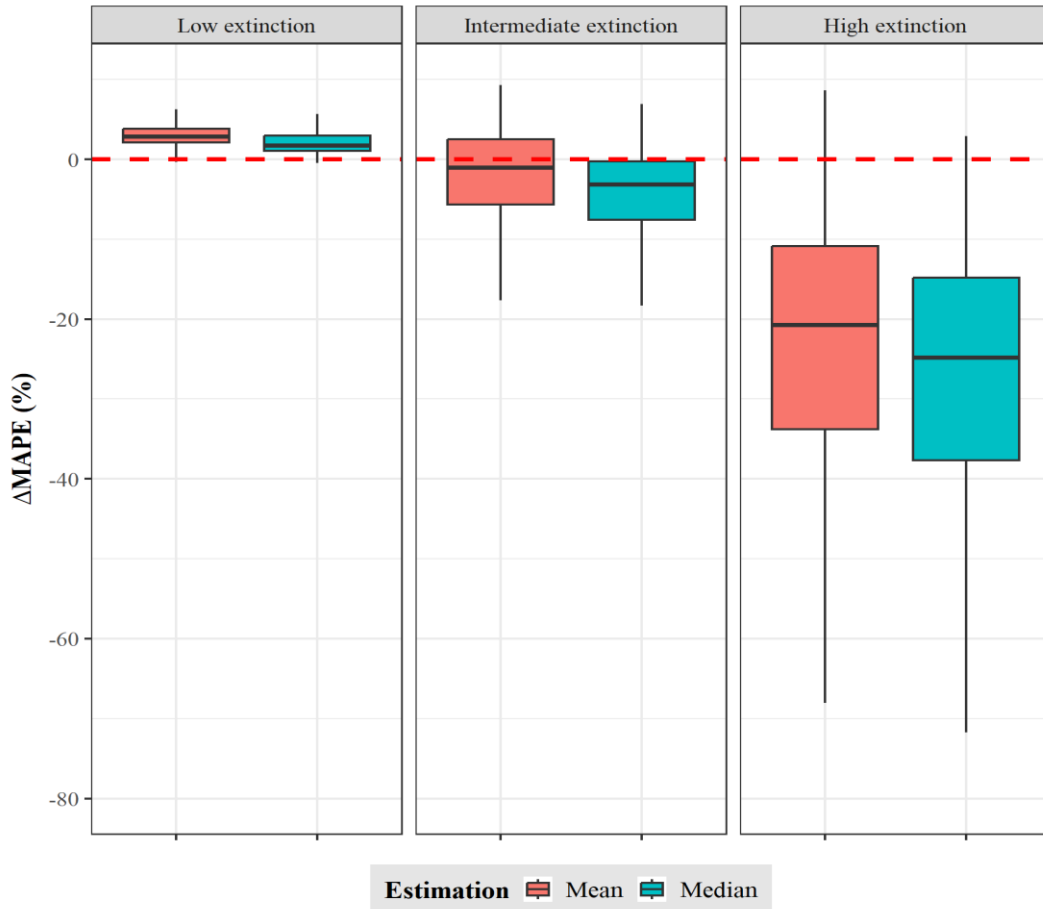


Figure 6. Performance of the probabilistic age estimator. Δ MAPE for the three extinction scenarios (low, intermediate, and high; from left to right) was quantified as the difference of the mean absolute percentage error (MAPE) of the probability estimator point estimates (mean and median) and the MAPE of the phylogenetic age. The MAPE was quantified as the difference between the true and point estimates (mean and median) or phylogenetic ages across 100 species for each of 1000 trees for each extinction scenario simulated under bifurcating speciation. The red dashed line represents no difference between the compared MAPEs.

Detecting age-dependent extinction risk

The use of phylogenetic age as an approximation of species age led to error rates of 1.3, 7.2, and 18.6 % in detecting the correlation between species ages and extinction risk for scenarios with low, intermediate and high extinction rates, respectively (Figure 7). Thus, even under intermediate extinction the true relationship between age and extinction risk was wrongly estimated in a significant fraction of the simulations, and higher extinction rates led to a further substantial drop in the reliability of this approach. In contrast, estimating species ages based on our probabilistic method led to much lower error rates (3 to 4-fold) that dropped to 1.3% and 4% with intermediate and high extinction, respectively.

Under incomplete taxon sampling where the probability of an extant species to be not included in the phylogeny was positive age-dependent the correlation between phylogenetic ages and extinction risk categories showed error rates of 6.2%, 12.8%, and 49.5% for scenarios with fully sampled phylogenies, and 25%, and 50% of missing extant species, respectively (Figure SM6).

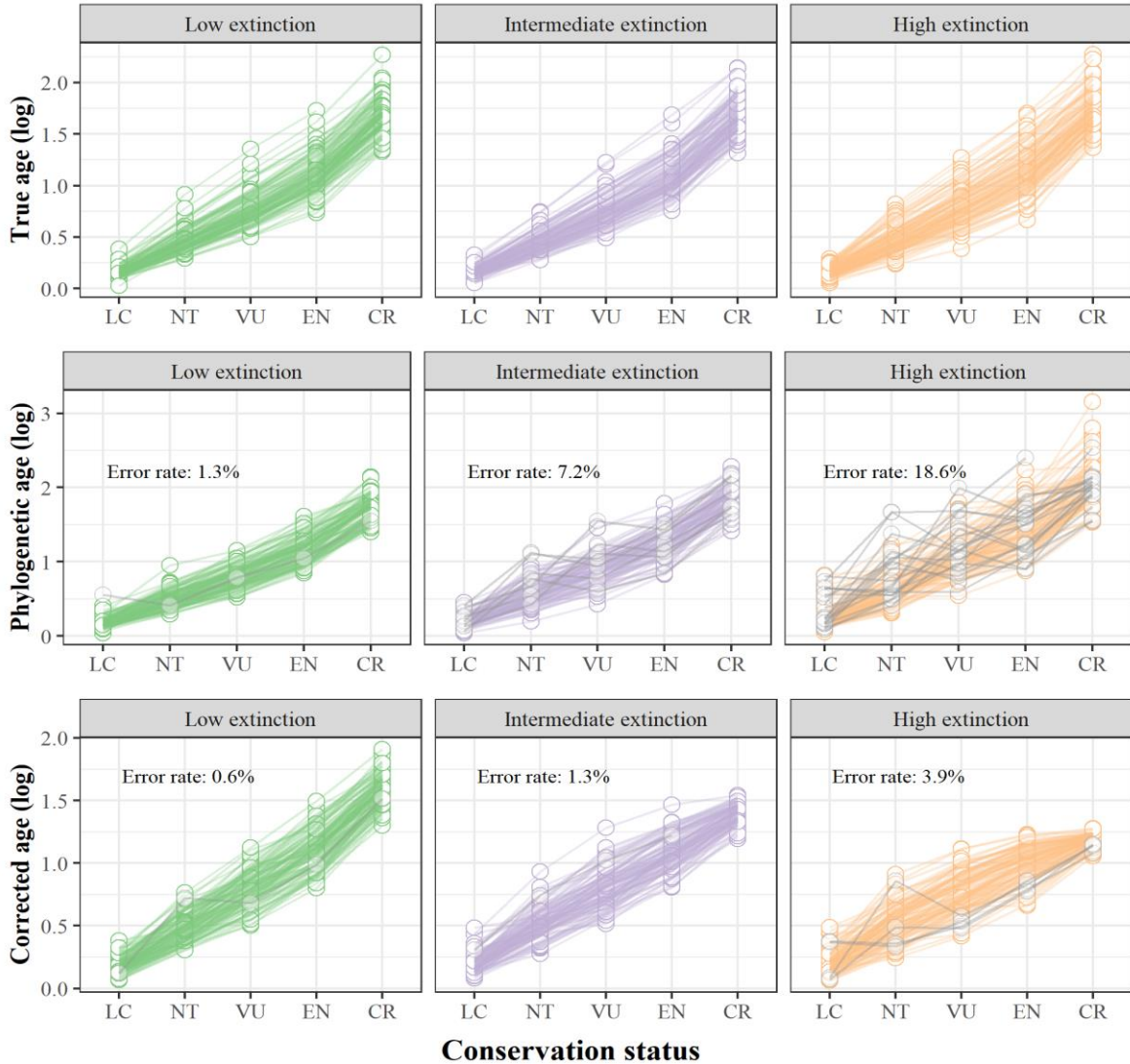


Figure 7. Power to recover an age extinction-risk relationship. Simulated species ages under three extinction scenarios and assuming bifurcating speciation were binned into conservation status categories, which represents an increase in extinction risk by age (LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered). We used the phylogenetic age and the mean age obtained from our probabilistic corrective function to calculate the mean age per conservation status category and assess if every mean age increases over the one of the previous category with lower extinction risk. The error rate is the percentage across all 1000 phylogenies where the relationship between the mean ages and the conservation status categories is not always increasing (shown by grey lines).

Discussion

Our results shows that the three shortfalls, missed extinction events, not knowing the speciation mode, and incomplete sampling of extant species, greatly influence the error that we make when equating the phylogenetic age with the true species age. Moreover, the error patterns are different regarding the combination of the three shortfalls. As expected, a phylogeny whose species mapping was derived under a bifurcating speciation process presents no or low mismatch between true and phylogenetic age due to the dichotomous depiction of phylogenies and that terminal branch lengths are used to quantify phylogenetic ages (Meier & Willmann, 2000). Our study has also shown that under budding speciation phylogenetic age shows a high error even without extinction (Figure 4). Likewise, anagenetic speciation, combined with budding or bifurcating speciation, resulted in high errors. This error is not further increased by extinction, suggesting that if a clade experiences a certain degree of anagenesis, it should be discouraged to estimate ages from phylogenies. However, anagenetic speciation is virtually impossible to quantify as it is difficult to detect, even from fossil time series, resulting in a general debate on the use of the term in evolutionary biology (Vaux et al., 2015) and biogeography (Emerson & Patiño, 2018; Meiri et al., 2018). Incomplete taxon sampling caused the highest error among all shortfalls due to the lengthened terminal branches. Although missing extinction events have in principle the same effect on branch lengths, their influence on error in species ages was lower. Our probability age estimator performed well when compared with phylogenetic age, especially in high extinction scenarios. However, it should be used when there is evidence that the clade under study had speciated by bifurcating speciation.

For bifurcating speciation, the mean error between true and phylogenetic age was the lowest when compared with the other speciation modes. This is because taking the most recent ancestral node as phylogenetic age results in sister species to be identical in age, the same as implied by bifurcating speciation. Due to only introducing bias by extinction, there was a low risk of confusing the oldest with the youngest species (Figure SM3) but a considerable risk to jumble the order of two random species (Figure SM4). Therefore, under a bifurcating speciation scenario, the phylogenetic age indeed captures most of the signal of the true species age. For budding speciation, there is a high discrepancy in ages, even in no-extinction scenarios. However, the already overall high error does not increase further with

augmenting extinction rates. This is due to half of the phylogenetic age estimations in no-extinction scenarios already underestimate the true age as one of the sister lineages is the older, ancestral one. When extinction rates increase, overestimation of ages start and increase until it balances the inherent underestimation at high extinction scenarios. This happens due to the phylogenetic assumption of sister species being identical in age, which is (a) wrong for budding speciation, and (b) under no extinction, only correctly estimates the youngest species of any bifurcation event. Due to these misinterpretation patterns, the qualitative error is high and increases considerably with extinction rates in the example of the oldest vs. youngest species (Figure SM3). Thus, for clades diversifying predominantly through budding speciation, the phylogenetic age is not equal to the true age for half of the species, and some of these mismatches would be large regarding the difference between phylogenetic and true age.

Given the large inaccuracy in phylogenetic age, especially for taxa originating under budding speciation, the question is whether this affects the inferences made from the relationship between species age and eco-evolutionary variables, such as extinction risk, range size, or environmental variables (Gaston & Blackburn 1997, Johnson *et al.* 2002, Tanentzap *et al.* 2015, Pie & Caron 2023). If phylogenetic ages capture at least the relative differences in species ages, it could be argued that it is a valuable measure of species longevity. Some authors acknowledge the problems associated with measuring species age from phylogenies (Swenson, 2019), and have proposed approaches to account for them. For example, Sonne *et al.* (2022) determined young and old Andean hummingbirds by assessing the sensitivity of their results to incomplete taxon sampling, the first shortfall in species age, by generating 1000 trees with randomly missing species. Pie & Caron (2023) accounted for taxonomic incompleteness by pruning an additional 1 – 5% of species and evaluated if their conclusions changed. Although incomplete taxon sampling caused the highest error rates in our evaluation of age-dependent extinction risk (Figure 5), neither strategy acknowledges the other two problems of age uncertainty: the unknown amount of extinction, which for most groups is probably high (Pimm *et al.*, 2014), and the speciation modes. Our evaluation of the imprint of species ages on extinction risk on makes this point clear because it showed that the number of incorrect inferences is considerable high (around 18%) for high extinction

scenarios (Figure 7), even with the simulated strong extinction signal and the assumption of bifurcating speciation, which presents the lowest mismatch regarding true age.

The incomplete sampling of extant species can be caused by (a) named species that are not included in a phylogeny due to, for instance, no available DNA sequence data, or (b) species unknown to science that have yet to be collected and described. The latter refers to the Linnean shortfall, one of the seven key shortfalls of biodiversity (Diniz Filho et al., 2023; Hortal et al., 2015). The overall Linnean shortfall magnitude is unknown, but probably enormous, as indicated by the ever-increasing pace in species descriptions. Obtaining a precise estimate of the number of undescribed extant species is challenging (Caley et al. 2014) and varies based on the taxonomic group and the geographical region under consideration (Hopkins 2007; Vilela et al. 2014). Moreover, the nature of the Linnean shortfall probably is nonrandom, given that is more severe for species with small body sizes, spatial distributions, and niche widths (Riddle et al. 2011).

Our results point out the errors associated with budding and bifurcating speciation; however, how do we know which is the predominant speciation mode of a clade? There is some debate on whether this is possible in first place (Losos & Glor, 2003). However, Anacker and Strauss (2014) proposed that budding speciation leaves its signatures on sister species: they should have overlapping or adjacent ranges, their range sizes should be asymmetrical, and specific ecological traits should differ between them. These signatures are associated with sympatric and peripatric speciation (Barraclough et al., 1998) and were used to estimate speciation modes (Skeels & Cardillo, 2018). Bifurcating speciation can be associated with allopatric speciation and the signatures it leaves on the range of sister species: ranges should not be overlapping or adjacent, range sizes should not necessarily be asymmetrical, and ecological traits should not necessarily differ between them (Barraclough & Vogler, 2000; Fitzpatrick & Turelli, 2006). Although extinction has a lower leverage on the error of species ages than incomplete taxon sampling and the unknown mode of speciation, extinction rates could be estimated from the phylogeny, the fossil record, or a combination of both (Brée, et al., 2022; López-Martínez et al., 2023; Rabosky, 2010; Silvestro et al., 2014). Thus, assessing a clade's speciation mode (through spatial dynamics) and extinction rates before performing species age analyses could help to approximate the error of phylogenetic ages.

For instance, let us suppose that the approaches described in the previous paragraph, suggest that the studied clade speciated predominantly under bifurcating speciation and that we can reliably estimate speciation and extinction rates. In this case, we advise to use our probabilistic age estimator to correct phylogenetic ages. When compared with phylogenetic age, this estimator improved the overall accuracy of age estimation across species in a phylogenetic tree, particularly under a high extinction scenario. Additionally, the function enhanced the power to capture the proper relationship between species age and extinction risk (Figure 7). Therefore, it can be used to test more robustly how species age influence eco-evolutionary dynamics.

Conclusion

This study aimed to estimate the potential deviations between true and phylogenetic age due to incomplete taxon sampling, extinction, and unknown speciation modes. Using simulations, we identified that mostly missing species and budding and anagenetic speciation cause a high mismatch between phylogenetic age and true species age. By contrast, only when a clade is fully sampled, speciated under bifurcating speciation, and possesses a low extinction rate phylogenetic age is a good proxy of species age. Thus, inferences made with phylogenetic age should be taken with caution. Besides pointing out these shortfalls, we derived a probabilistic age estimator to correct species age under the assumption of bifurcating speciation and a completely sampled tree. We showed that the probabilistic estimator has a good performance, particularly in high extinction scenarios, both in the overall age accuracy and when species ages are used in eco-evolutionary analyses. Thus, we advise its implementation when the assumptions are met. We hope this paper will stimulate discussions about the species age information in phylogenetic trees and a critical evaluation of the robustness of correlating with species traits or ecological variables.

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SUPPLEMENTARY MATERIAL

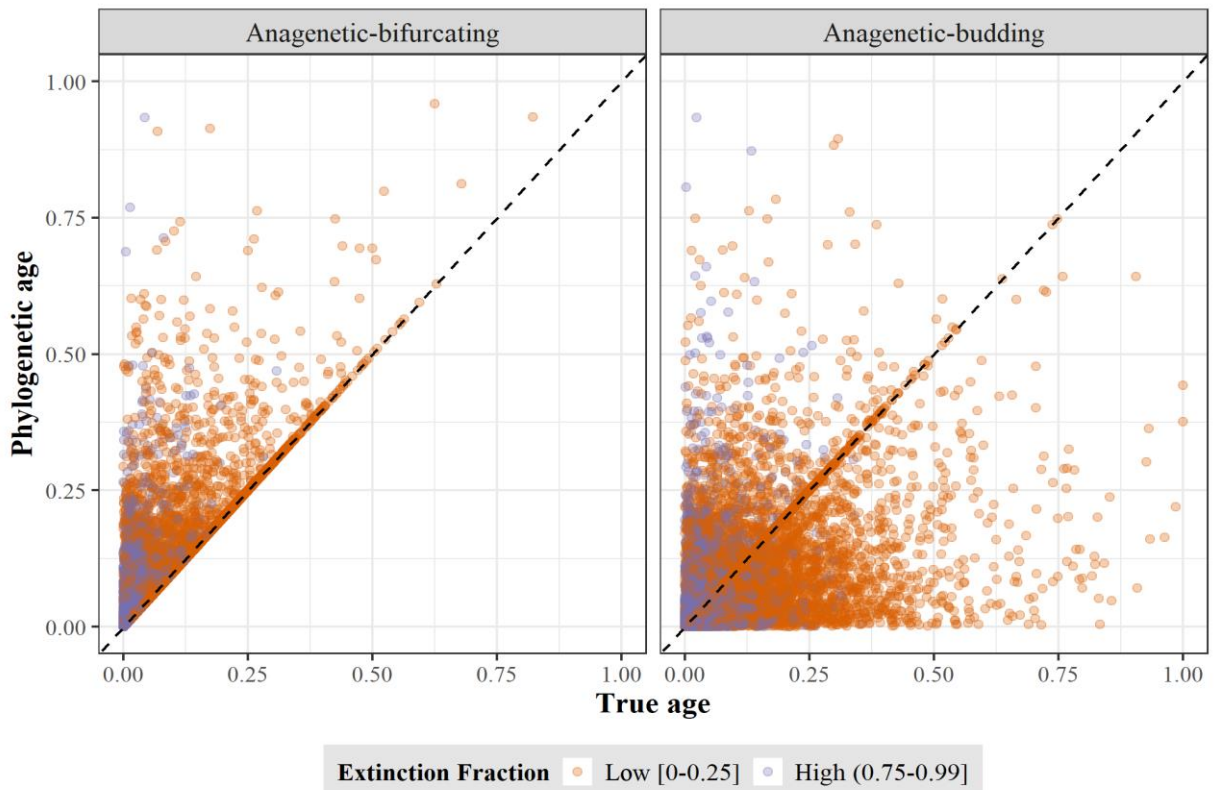


Figure SM1. True age versus phylogenetic age at low and high extinction fraction for Anagenetic-bifurcating (left) and Anagenetic-budding (right) speciation. Each point represents a species. True and phylogenetic ages are scaled to the root age of the correspondent phylogenetic tree.

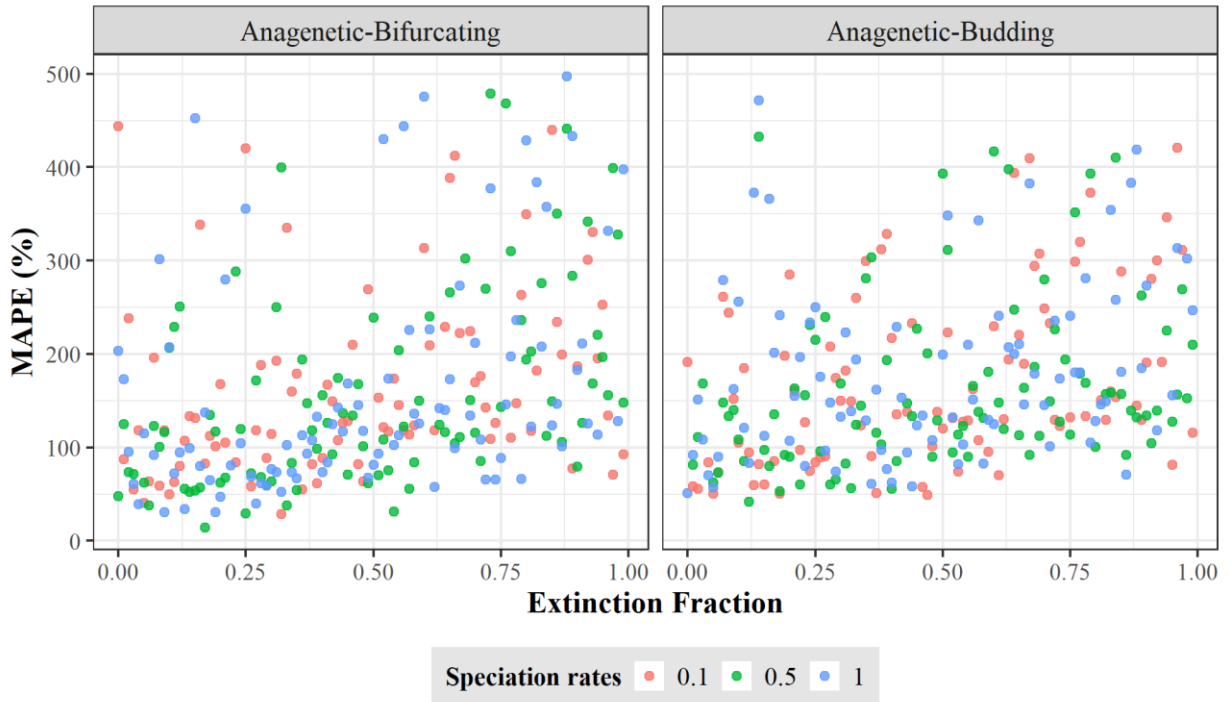


Figure SM2. Error in equating phylogenetic age with speciation age. The error was quantified as mean absolute percentage error (MAPE) between the true and phylogenetic ages across all species for each tree simulated under Anagenetic-bifurcating (left) and Anagenetic-budding speciation (right). Each dot represents one replicate of the 300 trees for each speciation mode using different rates of speciation and extinction fraction.

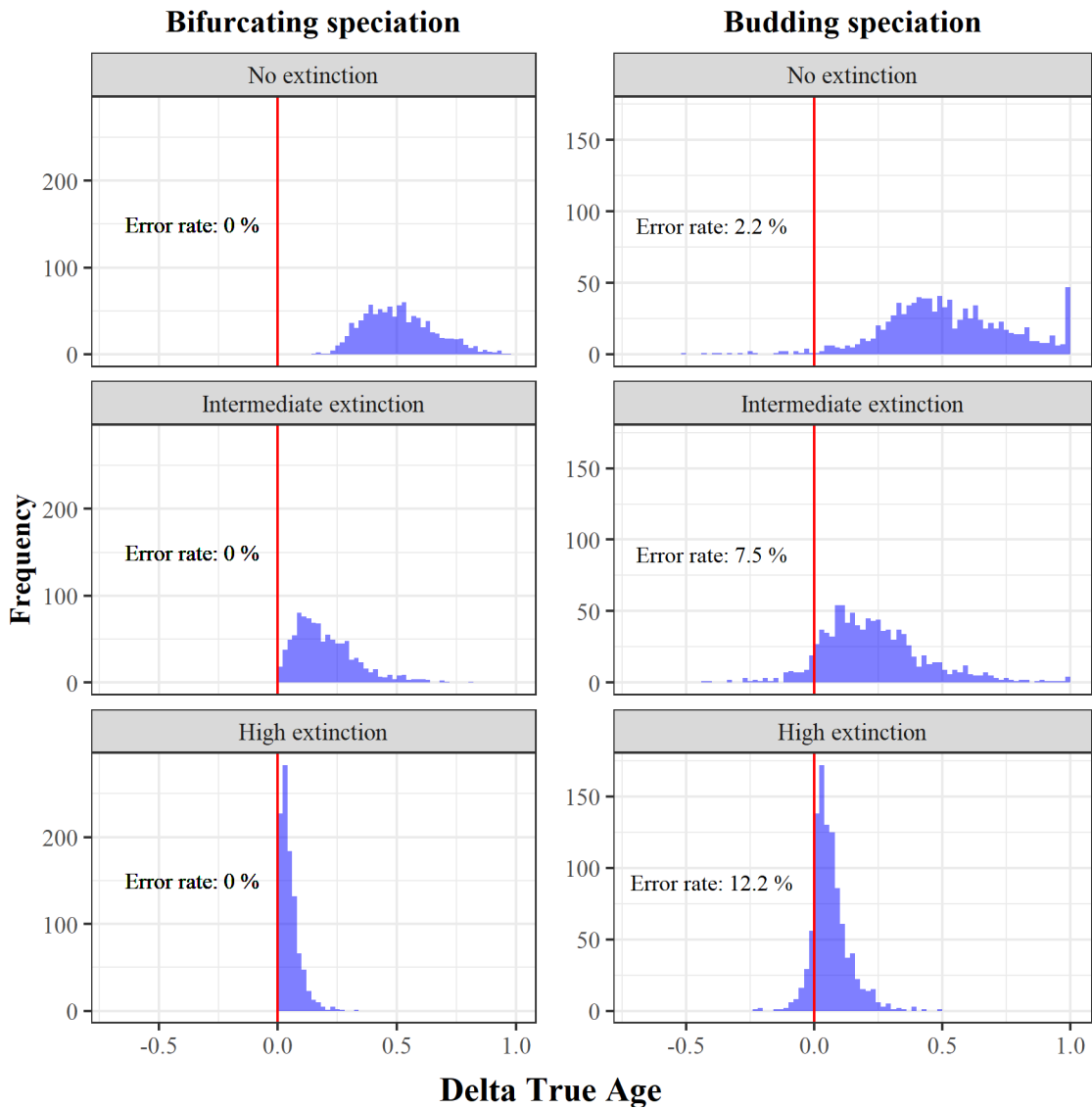


Figure SM3. Error in estimating the relative age of species. For each of the 1000 simulations under bifurcating (left) and budding (right) speciation, combined with three different extinction levels, we selected the oldest and youngest species according to the phylogenetic ages, and calculated the difference in their true ages (Δ True age). A Δ True age smaller than 0 indicates that the phylogenetic oldest species was estimated to be in fact younger than the phylogenetic youngest species, and therefore, the comparison of phylogenetic ages is qualitatively wrong.

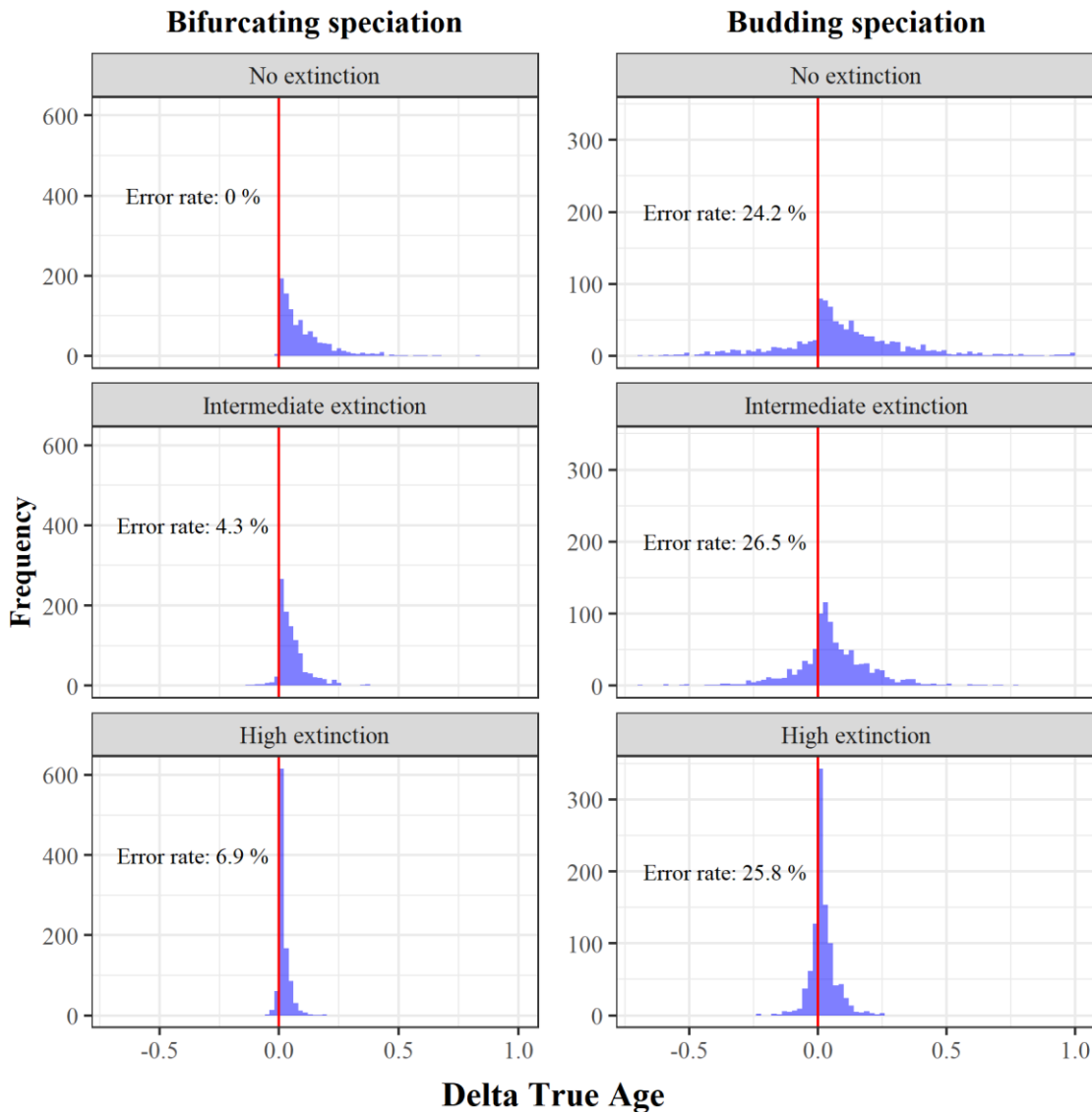


Figure SM4. Risk to confuse older with younger random species. For each of the 1000 simulations under bifurcating (left) and budding (right) speciation, combined with three different extinction levels, we selected two random species and defined which was the older and younger according to the phylogenetic ages, and calculated the difference in their true ages (Δ True age). A Δ True age smaller than 0 indicates that the phylogenetic older species was in fact younger than the phylogenetic younger species, and therefore, the comparison of phylogenetic ages is qualitatively wrong.

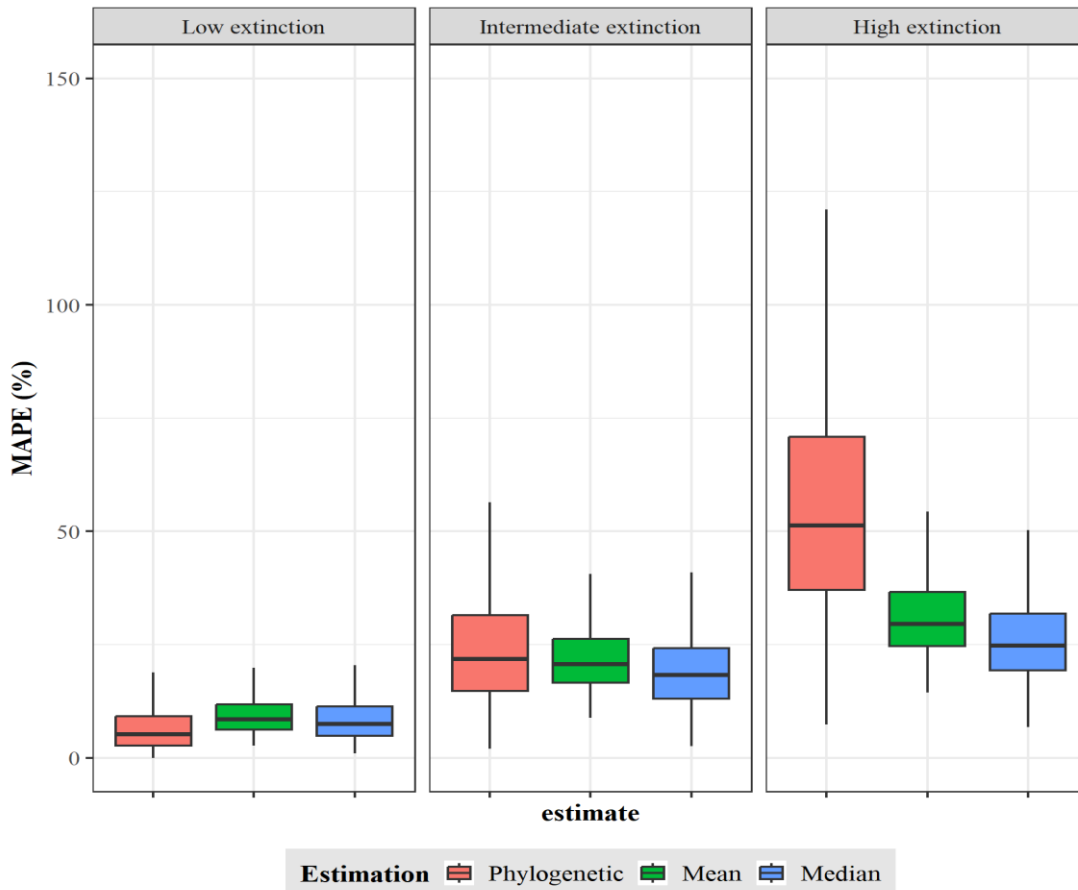


Figure SM5. Performance of a probabilistic age estimator. Error in equating the phylogenetic age and the probability estimator point estimates (mean and median) with the true species age for three extinction scenarios (low, intermediate, and high; from left to right). The error was quantified as mean absolute percentage error (MAPE) between the true and point estimates or phylogenetic ages across 100 species for each of 1000 trees for each extinction scenario simulated under bifurcating speciation.

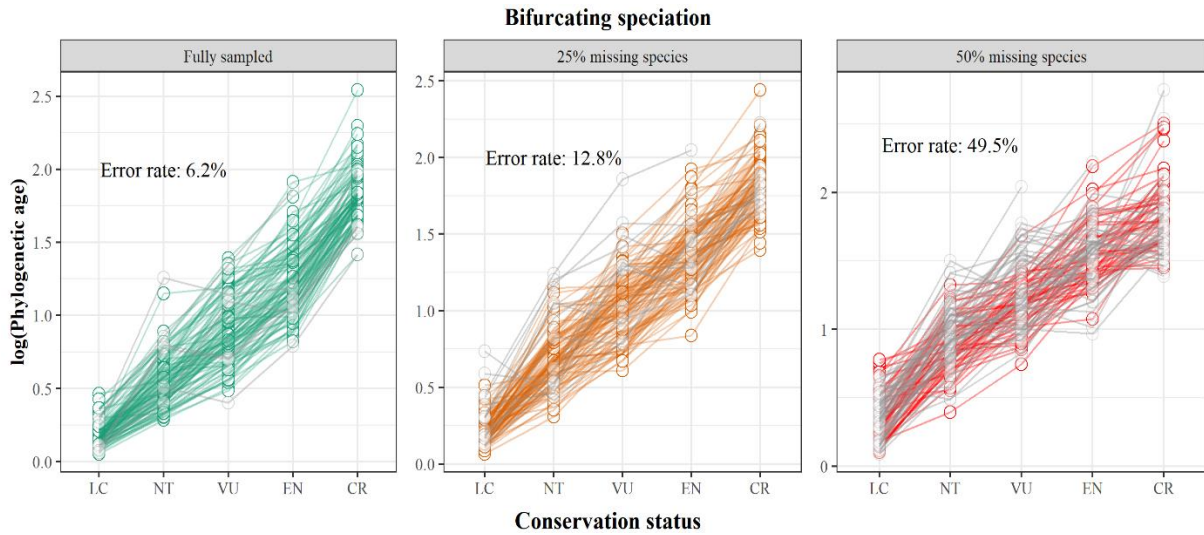


Figure SM6. Impact of incomplete taxon sampling on detecting an age extinction-risk relationship. Simulated species ages under an intermediate extinction scenario and assuming bifurcating speciation were binned into conservation status categories, which represents an increase in extinction risk by true age (LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered). We used the phylogenetic age from fully sampled phylogenies (green), and two incomplete taxon sampling levels 25% (orange) and 50% (red) of missing extant species, to calculate the mean age per conservation status category and assess if every mean age increases over the one of the previous category with lower extinction risk. The error rate is the percentage across all 1000 phylogenies where the relationship between the mean ages and the conservation status categories is not always increasing (shown by grey lines).

Species age and niche position: An exploratory analysis

Species age and niche position: An exploratory analysis

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Abstract

Exploring niche-filling trajectories often focuses on clades' diversification rates and species accumulation. Yet, the impact of niche-filling on extant species, concerning niche space occupation and partitioning, remains relatively unexplored. Here, we propose that the relationship between species age and niche position can reveal a historical imprint of the niche space occupation, particularly in the context of adaptive radiation. In the beginning, the lineage would occupy the niche space center. As diversification proceeds and niche partitioning occurs, the new descendants would occupy habitats and resources progressively far from the niche space mean values. Consequently, this trajectory would increase niche position centrality as species age. In our study, we tested this expectation on Neotropical tetrapods. We considered Neotropical biomes as niche space units, calculating species niche position and specialization from climatic information and species spatial range through the CENFA package. We measured the species' ages from phylogenies and corrected species ages by an approach based on the birth-death process. While the species age-niche position lacked generality, the small subset of significant groups (2.5% of models) did have a negative effect, i.e., older species have central niche positions, supporting our expectation. Complementarily, there was also a lack of evidence regarding species age specialization, with a small significant subset (1.8% of models) showing a negative effect, i.e., older species are more climatic generalists. Despite the uncertainties of the variables used and the small portion of significant groups, the prevailing pattern of older species occupying central niche positions provides evidence of how various clades, spanning different taxonomic levels and ecological roles, have occupied and divided the niche space. We consider this study exploratory because it opens up multiple research venues—for instance, the incorporation of phylogenetic information to reconstruct the niche-filling trajectory explicitly or the theoretical underpinning of the niche space definition. While we couldn't provide evidence for a macroevolutionary-macroecological law – perhaps such a law doesn't exist – our search for generality has prompted potential directions for future studies and a hint of the imprint of niche-filling trajectory on extant species.

Key words: Adaptive Radiation, Marginality, Phylogeny, Specialization.

Introduction

A cross-cutting question between macroecology and macroevolution is how the relative rates of colonization versus speciation influence niche filling and packing (McGill *et al.* 2019). These two processes do not necessarily have to be competing forces over the niche space, here defined as the global environmental conditions of a region (Fukami 2015, Tanentzap *et al.* 2015). Still, the interplay of both and, most importantly, their order and timing can shape the niche-filling trajectory. Paleobiologists have explored this trajectory in the fossil record via the waxing and waning of lineages through geological time (Quental & Marshall 2013, Raia *et al.* 2016a, Silvestro *et al.* 2017). Similarly, recent approaches combining fossil and phylogenetic information, simulations, and geographical analysis have been implemented to test for niche-filling patterns in extant taxa (Ricklefs & Jønsson 2014, Condamine *et al.* 2020, Skeels *et al.* 2023). Both research lines primarily measure niche filling and packing in terms of taxa richness and diversification rates. But the present-day consequences of how species have occupied and partitioned the niche space through time is a question that, to our knowledge, has yet to be directly explored.

Niche position is a species property related to the niche space, defined as the distance between the mean species' niche to the mean niche space conditions (Gaston *et al.* 1997). In ecology, niche position is proposed as a predictor of species' local abundance and occupancy, both determinants of species survivance, usually a competing mechanism against niche breadth or the range of environmental conditions and resources a species uses (Rocha *et al.* 2018, Vela Díaz *et al.* 2020). Rinnan and Lawler (2019) developed the marginality and specialization metrics in their framework for assessing climate change vulnerability. Marginality is equivalent to niche position, with the only difference being that the former is quantifiable; low marginality implies central niche positions, and high marginality refers to peripheric niche positions (Guisan *et al.* 2017). Specialization is defined as the ratio of the niche space variance to that of the species' niche breadth; thereby, it gives a value of how much niche space is encompassed by the species (Hirzel *et al.* 2002). Thus, niche position, measured by marginality and specialization, or the amount of niche space filled by the species, can help us describe how niche space is allocated and preempted among species from a clade, but how do we measure the trajectory, that is, the historical imprint of the niche space occupation?

Species age, or the elapsed time since species origin, expresses the evolutionary history of the species and the clade it belongs to and has important implications for macroevolution, particularly extinction dynamics (Benton 2016, Hagen *et al.* 2018). Traditionally, species age is measured in the fossil record using different approaches based on the taxa's stratigraphic duration (Foote 1996, Foote & Raup 1996). Latterly, some studies have used the branch lengths of time-calibrated phylogenies to measure extant species age (Gaston & Blackburn 1997, Johnson *et al.* 2002, Davies *et al.* 2011, Verde Arregoitia *et al.* 2013, Tanentzap *et al.* 2020, Sonne *et al.* 2022, Pie & Caron 2023); this approach is controversial (Cid *et al.* 2023; second chapter) because it doesn't deal with missing information in the phylogenies, such as extinctions and speciation modes, which produces under and overestimations of the species ages. However, species age in the fossil record has been related to species properties subject to extinction selectivity, such as population and geographical range size, ecological traits, and genetic mechanisms (McKinney 1997, Doran *et al.* 2006, Finnegan *et al.* 2008, Pigot *et al.* 2012), so it is likely that ages in extant species, despite the phylogenetic shortfalls, would keep an extent of this signal. Therefore, its implementation as a proxy for evolutionary history can assess, alongside niche position and specialization, the trajectory of niche space occupation by species within a clade.

To put in context how species age and niche position would operate in the niche space occupation, let's assume an adaptive diversification scenario. The process of adaptive radiations is described as a single lineage having geographical access to an empty niche space and rapidly diverging into species with distinct ecological forms, i.e., occupying different habitats and resources (Schluter 2000, Stroud & Losos 2016). Thus, adaptive radiation assumes that the competitive interactions among species partition the niche space, and thereby, this process assigns different niche positions for the descendants from the diversifying clade. At the beginning of the adaptive radiation, we assume that the lineage would occupy the most common biotic and abiotic conditions in the niche space — and, therefore, closer to the niche space center (Urban & De Meester 2009, Gehrke & Linder 2011). This assumption is a macroevolutionary extrapolation of the abundant niche-centroid hypothesis, which post that species abundances peak at the niche space center and decline towards its periphery (Maguire 1973, Martínez-Meyer *et al.* 2013, Osorio-Olvera *et al.* 2020). Thus, proceeding with the extrapolation, the assumption expects that the ancestral lineage

will colonize the niche space center, where suitability is highest, and the conditions toward the edge of the niche space will be increasingly unfavorable. As diversification goes by and the partition of niche space happens, the new descendants would be occupying habitats and resources progressively far from the mean values— and therefore having more peripheral niche positions. Consequently, this trajectory of niche space occupation would leave an overall effect of niche position increasing centrality with species age.

We are interested in one particular scenario that, in our opinion, would leave clear imprints of niche space occupation: a filled niche space. According to the diversity-dependent hypothesis, a region with filled niche space would present high species richness and a general decline in the diversification rates of its clades (Pigot & Tobias 2013, Rabosky 2013). The Neotropics seems a good candidate, given their higher species richness and lower diversification rates than temperate regions (Pyron & Burbrink 2013, Rabosky *et al.* 2018, Igea & Tanentzap 2020, Morales-Barbero *et al.* 2021). Furthermore, the Neotropics have been the scenario of multiple biotic radiations (Claramunt 2010, Monteiro & Nogueira 2011, Fine *et al.* 2014, Pincheira-Donoso *et al.* 2015, Maestri *et al.* 2017). Here we test how species ages are related to niche position and specialization in the Neotropical tetrapods as a pragmatic way to understand the trajectory of niche space occupation (Travassos-Britto *et al.* 2021). First, we considered the biomes within Neotropics provided by WWF as proper niche spaces. Second, we used the biomes and climatic data to estimate niche position and specialization from each species distribution model through the CENFA package (Rinnan & Lawler 2019). Third, we measured the species' ages from calibrated phylogenies and implemented an approach based on the birth-death process to correct the estimation of species ages in background and high extinction scenarios (Cid *et al.*, 2023, second chapter). To account for and dissect the phylogenetic scale dependencies in the trajectory of niche space, we performed our statistical analysis by downgrading the taxonomic rank, from class to family, to genus (Graham *et al.* 2018). Our general expectation is that marginality decreases with species age, implying that older species would occupy centric niche positions. Regarding specialization, we don't expect any relationship with species age due to the niche space partitioning during adaptive radiations.

Materials and methods

Spatial data and manipulation

We used three different spatial datasets for calculating marginality and specialization. First, we obtained biomes within the Neotropics from the World Wildlife Fund Simplified Biogeographical Realms (Olson *et al.* 2001). We considered neotropical biomes as our unit of analysis because the areas in each realm share macroevolutionary history (Mucina 2019). We measured the species marginality and specialization in the following biomes:

- Tropical & subtropical moist broadleaf forests
- Tropical & subtropical grasslands savannas and shrublands
- Tropical & subtropical dry broadleaf forests
- Tropical & subtropical coniferous forests
- Temperate grasslands savannas and shrublands
- Temperate broadleaf & mixed forests
- Montane grasslands and shrublands
- Mediterranean forests woodlands and scrub
- Mangroves
- Flooded grasslands and savannas
- Deserts and xeric shrublands

Secondly, we obtained Bioclimatic spatial variables from WorldClim (Fick & Hijmans 2017). Third, we extracted species distribution spatial models (DSM) from the International Union for Conservation of Nature (<https://www.iucnredlist.org/>) (IUCN 2016) and BirdLife (<http://www.birdlife.org/>) . We only regarded the polygons with the presence category “extant” and the origin category “native.”

DSM and the bioclimatic variables were clipped against the extent of each biome. With the clipped spatial datasets, we ran the ENFA function (Rinnan DS, 2021), which generated values of marginality and specialization for each species regarding its position in the niche space (biome). Because the distribution of several species expanded to more than one biome, we also calculated weighted values of marginality and specialization by using the amount of area occupied in each biome as an element of the numerical vector weights.

Phylogenetic data and manipulation

We obtained the phylogenetic hypotheses of mammals, amphibians, squamates, and birds in VertLife (<https://data.vertlife.org/>) and Birdtree (<https://birdtree.org/subsets/>). For mammals, we used 100 random trees from the Mammals birth-death tip-dated DNA-only distribution (Upham *et al.* 2019). For the amphibians, we extracted 100 random trees from the Amphibians Posterior All Species distribution (Jetz & Pyron 2018). For squamates, we used 100 random trees from the Squamate Posterior All Species distribution (Tonini *et al.* 2016). For birds, we utilized 100 random trees from the Hackett All species distribution (Jetz *et al.* 2012). Then, we calculated the average (hereafter called phylogenetic age) and standard deviation across the 100 ages generated for each species in our datasets.

Posteriorly, due to the phylogenetic shortfalls in estimating species age described in the introduction, we implemented Cid *et al.* (2023; under review, second chapter) function to improve age estimations. This function is based on the properties of the birth-death process, works under the assumption of bifurcating speciation, and as input, it takes the age estimated by the branch lengths and the clade's speciation and extinction rates. It generates, for each species, a vector of probable ages and their corresponding probabilities. We calculated, from the branch length age, two age types, one with the speciation and extinction rates estimated from the phylogenetic tree (hereafter called “background extinction”) and the other with a high extinction fraction (hereafter called “high extinction”), or the extinction rate as 90% of the speciation rate estimated from the tree. We calculated the weighted mean from the background and the high extinction ages.

All phylogenetic manipulations were done with the *ape* (Paradis E & Schliep K, 2019) and *phytools* (Revell L., 2012) R packages.

Statistical analysis

First, we performed an ANOVA to compare the marginality and specialization values on the classes of Neotropical tetrapods; then, we implemented a Tukey's HSD Test for multiple comparisons. To test the trajectory of niche space occupancy, we related marginality and specialization to species ages in each Neotropical biome. The age was log-transformed to account for normality. We used linear models, considering species age (phylogenetic, background extinction, and high extinction) as predictor variable and marginality and

specialization as dependent and separate variables. We performed our statistical analysis by downgrading the taxonomic rank, from class to family, to genus, because we wanted to evaluate the importance that the trajectory of niche space occupation had over different phylogenetic scales (Graham *et al.* 2018). To perform the analyses, we only admitted the groups that had more than nine species. The residuals of each model were utilized to test for phylogenetic signal, Pagel's lambda and Bloomberg's K (Revell 2010). When any of the phylogenetic signal parameters from the residuals of a specific model was equal to or greater than one, we ran a PGLS with the variables of this model and the corresponding phylogenetic tree. To account for multiple testing, we implemented the false discovery rate (FDR) considering the multiple comparisons made in the same biome, class, and taxonomic rank (e.g., Mangroves-Mammals-Family; Pike (2011)); and considered significant models with an adjusted p-value equal to or greater than 0.1 and an adjusted R squared greater than 0.1. To present graphically our results, and for scaling the regression coefficients for comparison, we used the standardized Beta, which was produced scaling each linear model (Bring 1994), and plotted all the models that had a p-value equal to or lower than 0.05 and an adjusted R squared (or pseudo-R squared for PGLS models) greater than 0.1. We presented the tables in the results/data/processed folder of the GitHub repository.

We repeated the below described analyses with the weighted marginality and specialization to perform an overall assessment of the Neotropics. To perform FDR, we considered as groups the number of taxa (families or genera) inside each tetrapod class. We only presented the models (Supplementary material) with an adjusted p-value equal to or greater than 0.1 and an adjusted R squared greater than 0.1.

Data manipulation, graphics, statistical analysis were performed in R-program version 4.2.3 (Wickham 2011, R Core Team 2019, R Studio Team 2020) and we provide the R scripts, the raw and processed data, and the final tables in the following GitHub repository: https://github.com/caldecid/age_position_redlist

Results

We processed the CENFA metrics (marginality and specialization) for 1175 Mammals, 1826 Squamates, 1435 Amphibians, and 3001 Aves. When performing the taxonomic rank and given that we only admitted groups with more than nine species, our analyses encompassed, Mammals, 23 families, and 28 genera; Squamates, 23 families and 37 genera; amphibians, 21 families and 33 genera; and Aves, 49 families and 60 genera.

Mammals (mean marginality = 2.19 (95% confidence interval (CI) = 2.13, 2.26)) and Aves (2.24 (CI = 2.19, 2.28)) presented a lower marginality than Squamates (2.57 (CI = 2.51, 2.62)) or Amphibians (2.85 (CI = 2.79, 2.91); Figure 1A). Tukey HSD test found that all pairwise comparisons for marginality were significantly different ($p < 0.001$), except between Mammals and Aves ($p = 0.7$). Squamates (mean specialization = 12.5 (CI = 11.65, 13.27)) and Amphibians (12.1 (CI = 11.18, 13.0)) presented a higher specialization than Mammals (8.77 (CI = 7.76, 9.78)) or Aves (6.03 (CI = 5.40, 6.66); Figure 1B). Tukey HSD test found that all pairwise comparisons for specialization were significantly different ($p < 0.001$), except between Squamates and Amphibians ($p = 0.93$).

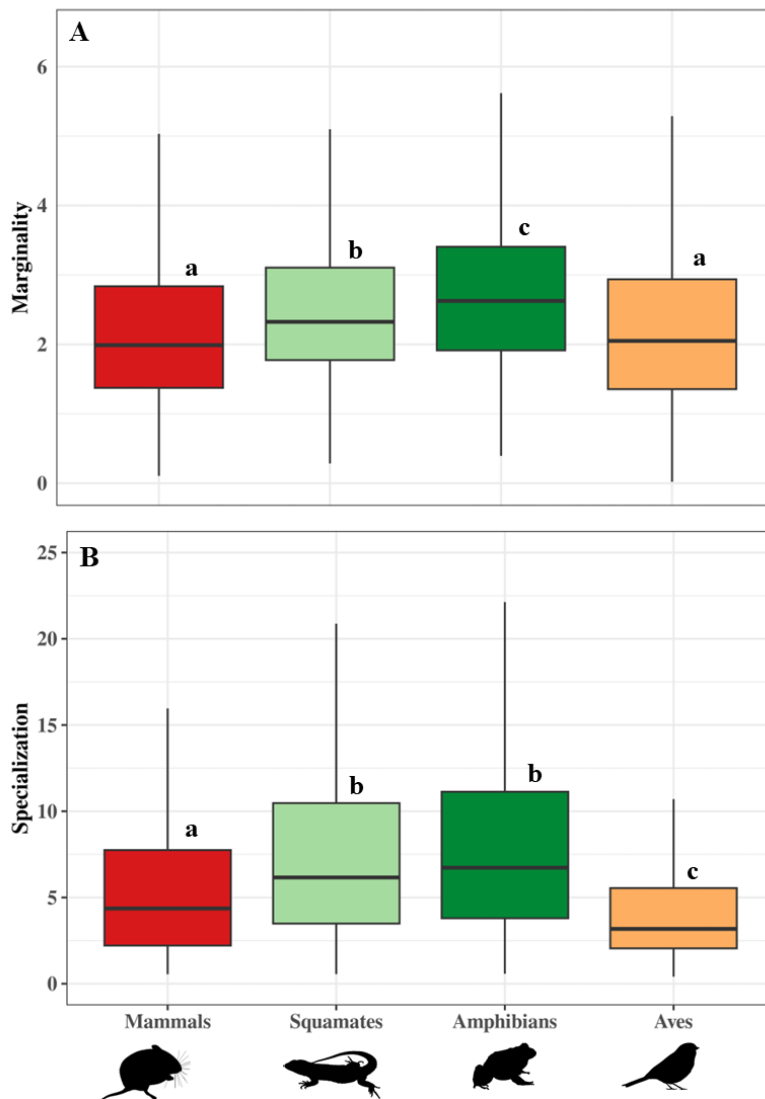


Figure 1. The marginality and specialization metrics of Neotropical Mammals (red), Squamates (light green), Amphibians (green), and Aves (orange). The boxes represent the median, the first and third quartile of the CENFA metrics for all Neotropical species in each class. (A) Marginality is defined as the distance between the centroid of the species climatic niche and the centroid of the global niche space. (B) Specialization represents the ratio of the niche space variance to that of the species' niche breadth. Different low case letters (“a”, “b”, “c”) indicate significant differences among groups. The outliers are not shown.

Neotropical biomes

Age vs. Marginality

For “Tropical & subtropical moist broadleaf forests”, we evaluated 210 (5 significant (3 passed the FDR test); Figure 2A) vertebrate families and 276 (7 (1 passed the FDR test) significant) genera. For “Tropical & subtropical grasslands savannas and shrublands”, we evaluated 138 (3 (0); Figure 2B) families and 86 (3 (2 FDR)) genera. For “Tropical & subtropical dry broadleaf forests”, we evaluated 164 (4 (1 FDR); Figure 2C) families and 140 (4 (0)) genera. For “Tropical & subtropical coniferous forests”, we evaluated 90 (2 (0); Figure 2D) families and 34 (1 FDR) genera. For “Temperate grasslands savannas and shrublands”, we evaluated 12 (1 (0)) families and 6 (1 FDR) genera. For “Temperate broadleaf & mixed forests”, we evaluated 2 (0) families and 2 (0) genera. For “Montane grasslands and shrublands”, we evaluated 88 (1 FDR) families and 42 (2 (1 FDR)) genera. For “Mediterranean forests woodlands and scrub”, we evaluated 2 (1(0)) families and 2 (1(0)) genera. For “Mangroves”, we evaluated 134 (0) families and 72 (2 (0)) genera. For “Flooded grasslands and savannas”, we evaluated 76 (1(0)) families and 20 (0) genera. For “Deserts and xeric shrublands”, we evaluated 124 (4 (0); Figure 2E) families and 58 (1 (0)) genera. From the 22 significant families, 15 presented a negative effect (68%; Figure 2F). From the 22 significant genera, 17 presented a negative effect (77%; FigureSM1).

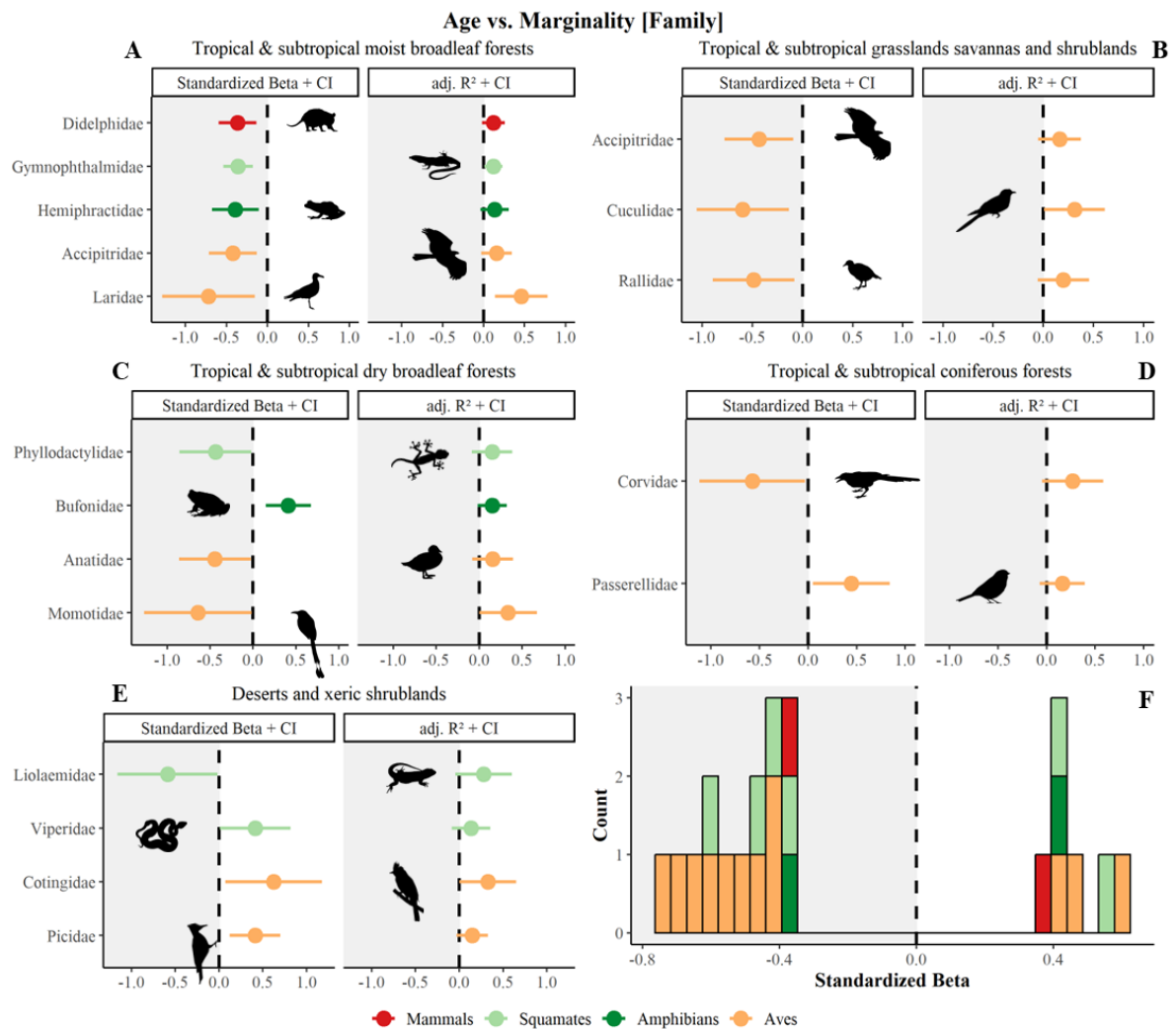


Figure 2. Relationship between species age and marginality for each Neotropical biome at family level. The significant groups are dots colored according to the class they belong: Mammals (red), Squamates (light green), Amphibians (green), and Aves (orange). The x-axis represents the parameter values and the y-axis shows the family names. Left panels in each biome stand for the standardized Beta and the correspondent confidence interval (CI) of each significant model. Right panels in each biome stand for the adjusted R² and the correspondent CI of each significant model. The dashed black line intersects the zero on the x-axis to separate the gray panel (negative values) from the white panel (positive values). A) Tropical & subtropical moist broadleaf forests; B) Tropical & subtropical grasslands savannas and shrublands; C) Tropical & subtropical dry broadleaf forests; D) Tropical & subtropical coniferous forests; E) Deserts and xeric shrublands; and F) Standardized Beta histogram; x-axis represents the Beta values and y-axis the count.

Age vs. Specialization

For “Tropical & subtropical moist broadleaf forests”, we evaluated 210 (2 (0 passed the FDR test) significant; Figure 3A) vertebrate families and 276 (4 (1 passed the FDR test) significant) genera. For “Tropical & subtropical grasslands savannas and shrublands”, we evaluated 138 (4 (2 FDR); Figure 3B) families and 86 (5 (1 FDR) genera. For “Tropical & subtropical dry broadleaf forests”, we evaluated 164 (1 (0 FDR)) families and 140 (0) genera. For “Tropical & subtropical coniferous forests”, we evaluated 90 (2 (1 FDR); Figure 3C) families and 34 (1 (0 FDR)) genera. For “Temperate broadleaf & mixed forests”, we evaluated 2 (1(0 FDR) families and 2 (1(0 FDR)) genera. For “Temperate grasslands savannas and shrublands”, we evaluated 12 (0) families and 6 (0) genera. For “Montane grasslands and shrublands”, we evaluated 88 (3 (1 FDR); Figure 3D) families and 42 (2 (1 FDR)) genera. For “Mediterranean forests woodlands and scrub”, we evaluated 2 (1 (0 FDR)) families and 2 (1 (0 FDR)) genera. For “Mangroves”, we evaluated 134 (2 FDR; Figure 3E) families and 72 (0) genera. For “Flooded grasslands and savannas”, we evaluated 76 (0) families and 20 (1 FDR) genera. For “Deserts and xeric shrublands”, we evaluated 124 (2 (0 FDR); Figure 3F) families and 58 (1 FDR) genera. From the 17 significant families, 10 presented a negative effect (~59%; Figure 3G). From the 15 significant genera, 8 presented a negative effect (~53%; FigureSM2).

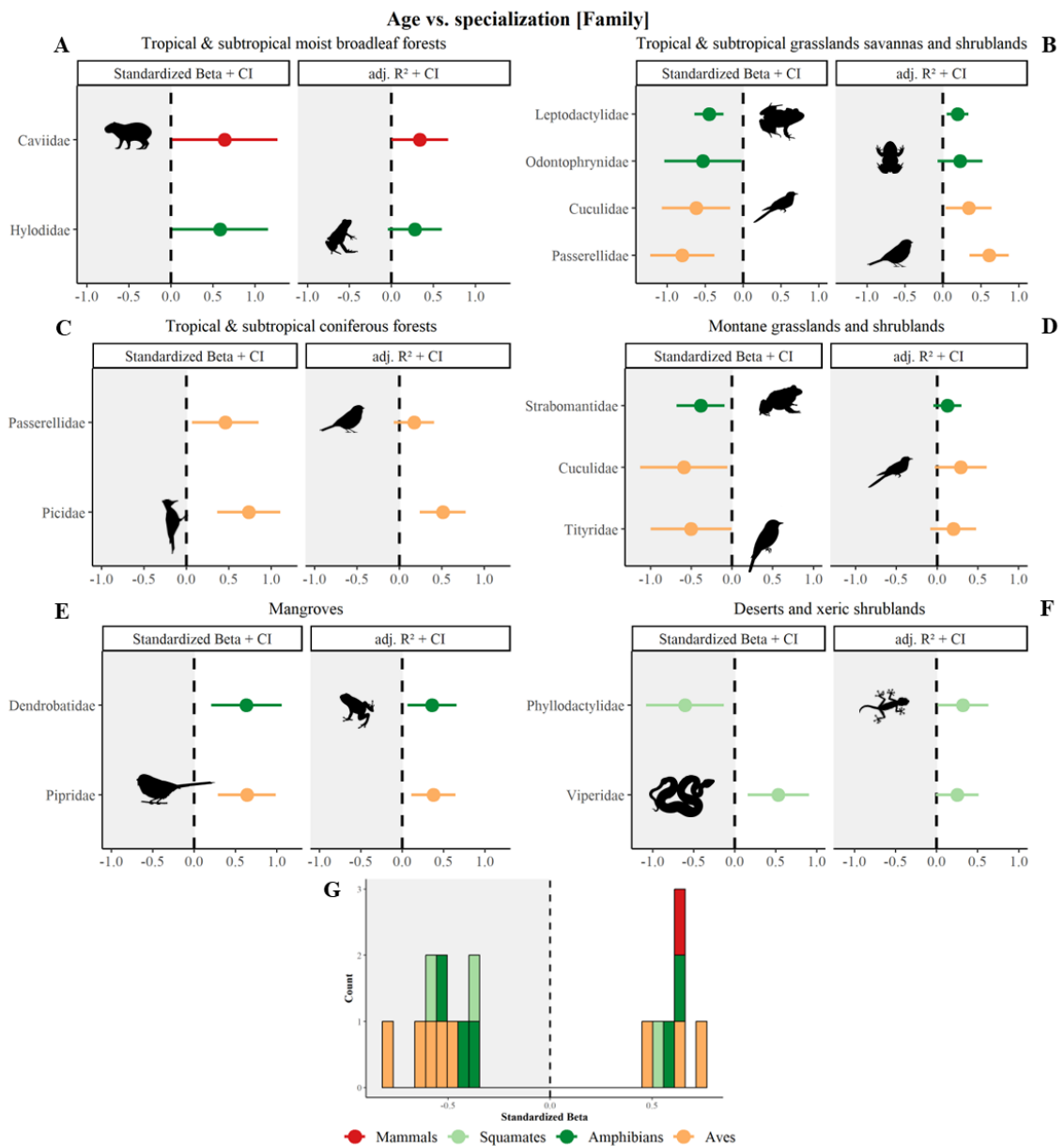


Figure 3. Relationship between species age and specialization for each Neotropical biome at family level. The significant groups are dots colored according to the class they belong: Mammals (red), Squamates (light green), Amphibians (green), and Aves (orange). The x-axis represents the parameter values and the y-axis shows the family names. Left panels in each biome stand for the standardized Beta and the correspondent confidence interval (CI) of each significant model. Right panels in each biome stand for the adjusted R² and the correspondent CI of each significant model. The dashed black line intersects the zero on the x-axis to separate the gray side (negative values) from the white side (positive values). A) Tropical & subtropical moist broadleaf forests; B) Tropical & subtropical grasslands savannas and shrublands; C) Tropical & subtropical coniferous forests; D) Montane grasslands and shrublands; E) Mangroves; F) Deserts and xeric shrublands; and G) Standardized Beta histogram; x-axis represents the Beta values and y-axis the count.

Weighted ENFA

Age vs. Marginality

For Mammals, two families (9% of Mammals' families), Cervidae ($p < 0.001$; Figure 4A) and Didelphidae ($p < 0.01$; Figure 4B) presented a negative age-marginality relationship. For Squamates, one family (4%), Gymnophthalmidae ($p < 0.001$; Figure 4C) presented a negative age-marginality relationship. For Aves, one family (2%), Accipitridae ($p = 0.005$; Figure 4D), presented a negative age-marginality relationship. All models passed the FDR test and were supported by the background and high extinction model (Table SM1).

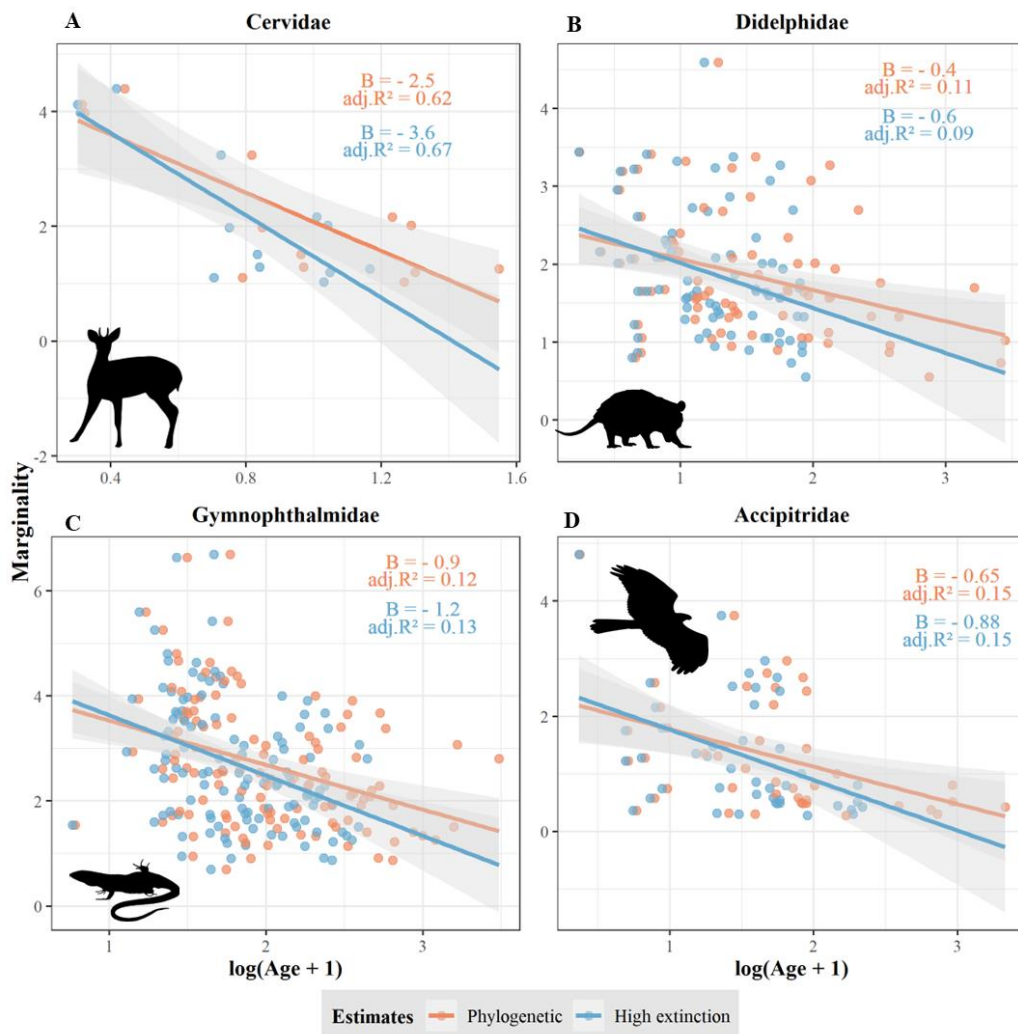


Figure 4. Relationship between species age and weighted marginality. The x-axis represents the species age log transformed and the y-axis represents the weighted marginality. The Phylogenetic model (line), or the species age calculated from the branch lengths of time-calibrated phylogenies, parameters ($B = \text{Beta}$; $\text{adj.R}^2 = \text{adjusted R}^2$; $\text{pseudo.R}^2 = \text{pseudo R}^2$), and observations (dots) are depicted in orange. The High extinction model, or the corrected species age considering a 0.9 extinction fraction, parameters ($B = \text{Beta}$; $\text{adj.R}^2 = \text{adjusted R}^2$; $\text{pseudo.R}^2 = \text{pseudo R}^2$), are depicted in blue. The adjusted R^2 correspond to linear models with low or none phylogenetic signal in the residuals. The pseudo R^2 correspond to PGLS when the linear model presented a high phylogenetic signal in its residuals. (A) Cervidae; (B) Didelphidae; (C) Gymnophthalmidae; (D) Accipitridae.

Age vs. Specialization

For Squamates, one family (4%), Phyllodactylidae ($p = 0.001$; Figure 5A), presented a negative age-specialization relationship. For Amphibians, one family (~5%), Leptodactylidae ($p < 0.001$; Figure 5D) presented a negative age-specialization relationship. The two models passed the FDR test and were supported by the background and high extinction model (Table SM2).

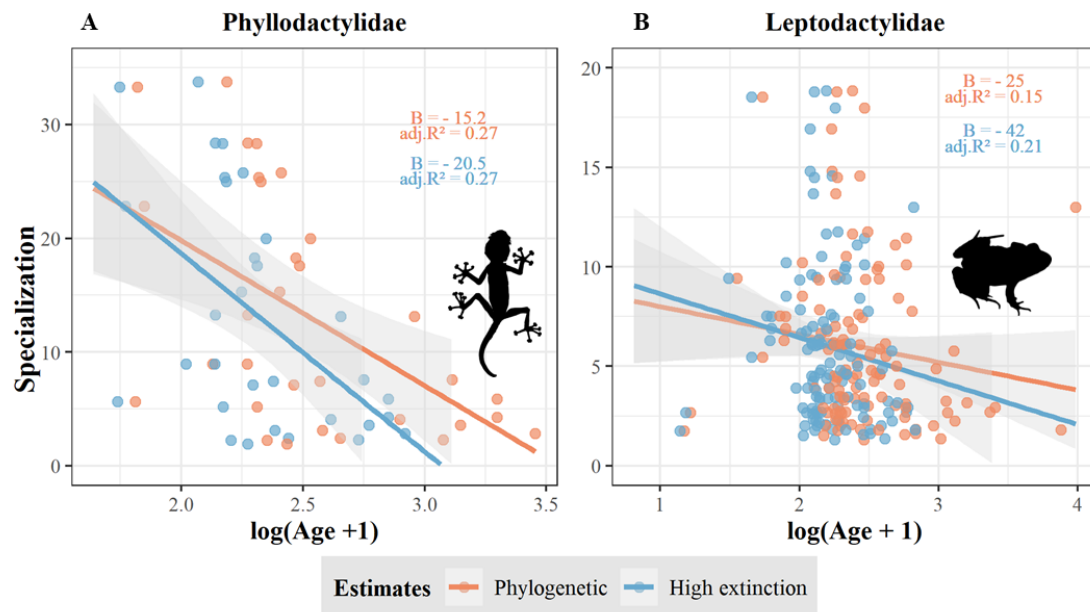


Figure 5. Relationship between species age and weighted specialization. The x-axis represents the species age log transformed and the y-axis represents the weighted specialization. The Phylogenetic model (line), or the species age calculated from the branch lengths of time-calibrated phylogenies, parameters ($B = \text{Beta}$; $\text{adj.R}^2 = \text{adjusted R}^2$; $\text{pseudo. R}^2 = \text{pseudo R}^2$), and observations (dots) are depicted in orange. The High extinction model, or the corrected species age considering a 0.9 extinction fraction, parameters ($B = \text{Beta}$; $\text{adj.R}^2 = \text{adjusted R}^2$; $\text{pseudo. R}^2 = \text{pseudo R}^2$), are depicted in blue. The adjusted R^2 correspond to linear models with low or none phylogenetic signal in the residuals. The pseudo R^2 correspond to PGLS when the linear model presented a high phylogenetic signal in its residuals. (A) Phyllodactylidae, and (B) Leptodactylidae.

Discussion

Our study showed little evidence of the relationship between species age and niche position. Specifically, we found 44 significant relationships (adding families and genera) from 1778 fitted models (2.5%) for Neotropical biomes assessment. A similar trend was present in the weighted marginality, with 4 significant relationships out of 274 fitted models (1.46%). Nevertheless, and evaluating only significant models for Neotropical biomes, 32 out of 44 (73%) and all weighted marginality models were negative relationships, i.e., marginality decreases with species age. These negative relationships confirm our expectation, at least in this small subset of neotropical tetrapods, that older species have centric niche positions than younger ones. Complementarily, there is little evidence of the relationship between species ages and specialization. This matches our overall expectation of specialization not being influenced by species ages due to niche partitioning during adaptive diversification. We found 32 significant relationships from 1778 fitted models (1.8%) for Neotropical biomes assessment. Similarly, we found five significant relationships out of 274 fitted models (1.8%) for weighted specialization. Evaluating only significant models, for Neotropical biomes, 18 out of 32 (56%), and for weighted specialization, 4 out of 5 (80%) presented a negative relationship, suggesting that specialization decreases with species age; i.e., older species are more generalist. Endotherms (Mammals and Aves) showed overall lower values of marginality and specialization than Ectotherms (Squamates and Amphibians). Endotherms are less marginal on average probably due to their endurance to less benign Neotropical biomes such as Montane grasslands and shrublands or Temperate grasslands savannas and shrublands (Rolland & Salamin 2016, Rolland *et al.* 2018). Ectotherms may be more specialized due to their lower dispersal abilities when compared with endotherms, and thus, having to partition niche space by diverging ecologically to promote species coexistence (Araujo *et al.* 2005, Smith & Green 2005, Araújo *et al.* 2006). The phylogenetic models almost did not differ from the background extinction models because the estimated extinction rate in phylogenies was mostly zero (Rabosky 2010). Similarly, the high extinction models usually supported the phylogenetic models in size effect and direction. Thus, in general terms, the corrective function caught the same signal as the phylogenetic ages.

Given the lack of generality in our results, especially in ages vs. marginality, we can infer two possible alternatives. The first is to conclude that the pattern doesn't exist and assume that the relationships we found, particularly those that passed the false discovery rate, across the neotropical tetrapods are exceptions. The second alternative is to take these robust relationships as a signal of a plausible pattern whose processes we must better explore. That is, we should revisit the underlying assumptions of our theoretical background, identify alternative hypotheses, and examine the operationalization of our variables (Travassos-Britto *et al.* 2021, Fristoe *et al.* 2023). For example, let's consider the most important concept of our work: niche space, here defined as the global environmental conditions of a region. Due to this definition, we used the niche space in a Grinnellian fashion, i.e., only encompassing abiotic factors (Grinnell 1917, Peterson 2003). However, we assumed that niche partitioning, which assigns niche position and homogenizes specialization, is driven by competitive interactions, future works should consider biotic interactions, i.e., Eltonian fashion, to define the niche space (Elton 1927, Leibold 1995). Thus, making this distinction and understanding its implications clarifies several aspects of the niche filling trajectory (Soberón 2007). In the same sense, we framed niche space into biomes within Neotropics, arguing that they are proper geographic realms where species share an evolutionary history (Mucina 2019). Nevertheless, we realized during the CENFA that many species inhabit at least two biomes, which complicated our assertion of unified niche space, causing ambiguity in the marginality and specialization measurements. One approach to contour this problem could be framing the niche space to biogeographical regions, defined as geographically distinct assemblages of species and, thus, plausible units of shared evolutionary history and biotic interactions (Vilhena & Antonelli 2015, Edler *et al.* 2017).

In the introduction we highlighted the shortfalls associated with measuring species ages from the branch lengths of time-calibrated phylogenies. Regarding the extinction shortfall, the phylogenetic models didn't differ from the background extinction models because the phylogenies suggest that the extinction rate for most groups is zero, which is highly unlikely due to the actual extinction trends driven by anthropogenic pressures (Barnosky *et al.* 2011, Cowie *et al.* 2022). Likewise, regarding the speciation mode shortfall, phylogenetic age and the corrective function estimations assume a bifurcating speciation mode; however, adaptive radiations generate groups of ecologically distinct and sympatric species, and sympatric speciation is mostly associated with a budding

speciation mode (Anacker & Strauss 2014, Skeels & Cardillo 2019; but see Rundell & Price 2009), which would produce a high miscalculation rate of species age through phylogenies (Cid et al. 2023, second chapter). Besides these shortfalls, species age probably fails to represent genuinely the evolutionary history of species. It seems related to the problem of using phylogenetic proximity as equivalent for ecological similarity because species age and phylogenetic relatedness are assumed to be proxies for complex processes. Probably the best way to contour these issues and move further the understanding of research areas related to these variables is to use the phylogenies as backbones as stated by Swenson (2019). In our context, this approach would map the niche position of species onto the phylogeny to infer the concrete evolutionary history of this trait (Ricklefs 2006, Sedio *et al.* 2013) For example, Quintero *et al.* (2022) characterized the niche breadth, defined by temperature and precipitation, of Avian species and evaluated the evolution of this trait within the clade using a phylogenetic model that accounts for heterogeneous evolutionary rates. Complementarily, adding the reconstruction of niche space, through species distributions and paleoenvironmental data, would help us to assess the clades' niche preemption trajectory concretely (see Tanentzap *et al.* (2015)).

Due to common theoretical background and variables, our study is related to the Age-dependent extinction (ADE) literature. ADE is a pattern that assumes species longevity as predictor of extinction probability, and presents different directions (i.e., positive, negative, and neutral) both in the empirical and theoretical realm (Hagen *et al.* 2018, Januario 2021). Among the hypotheses that predict a negative ADE, where older species are less extinction prone, the most representative is the “Age-and-Area hypothesis” (Willis 1922). It posits that older species have had more time to disperse and colonize, and, therefore, they possess larger spatial distributions which decrease their vulnerability to environmental changes or local extinctions. To our knowledge, this ADE hypothesis has only been tested once in extant species, with inconclusive evidence (Tanentzap *et al.* 2020). However, in the context of our study, this hypothesis could be reformulated, given that the specialization metric (a proxy of niche breadth which is correlated to species spatial distribution (Slatyer *et al.* 2013)) had less relationship to species age than marginality, to “Age-and-Niche position” hypothesis, where older species have had more time to position themselves in the center of the niche space. Additionally, central niche positions had been related to species local abundance and

occupancy, determinants of species survivance (Vela Díaz *et al.* 2020). Thus, in this framework, older species would be less extinction prone because they occupy less marginal niche positions. By contrast, the “Time-and-specialization hypothesis” predicts a positive ADE, where older species possess higher extinction probabilities (Pearson 1995, Clavel *et al.* 2011). It posits that specialization is higher in older species due to the time their niches had to track the environments; this niche narrowing would increase their vulnerability before any biotic or abiotic change (Poisot *et al.* 2011). Our study didn’t demonstrate a clear relationship between Neotropical tetrapods age and specialization. Even the small subset with a significant relationship, presented a negative direction, suggesting that older species are more generalist which goes against the “Time-and-specialization hypothesis”. Nevertheless, Raia *et al.* (2016) showed that specialization should also be assessed by the degree of spatial overlap among species within clades because it would explicitly evaluate niche partitioning. To foster a better understanding of the relationship between species age and specialization, future studies should consider, besides climatic specialization, the spatial overlap dynamics of species within clades.

At first glance, the lack of generality in our results would seem like an endpoint on whether there is a historical imprint in extant species regarding the niche filling trajectory. Nevertheless, we think of this study as an exploratory analysis from which is possible to learn about the interplay between macroevolution and macroecology (McGill *et al.* 2019, Travassos-Britto *et al.* 2021). Of course, it is needed to evaluate the underlying assumptions of our theoretical expectations, particularly regarding the niche space characterization, and to reformulate our methodological approach, e.g., the implementation of phylogenetic information for reconstructing explicitly the niche filling and partitioning trajectory. Despite the uncertainties associated with the calculation of our variables and the small subset of significant groups, the trend of older species occupying centric niche positions is a clear imprint of how different groups, from distinct taxonomic ranks and ecological functions, had preempted and partitioned the niche spaces represented by the Neotropical biomes. We didn’t manage to bring evidence about a plausible macroevolutionary-macroecological law, maybe it doesn’t exist, but we did manage, through our failed search for generality, to rise plausible venues for future studies in the theoretical and empirical realms.

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SUPPLEMENTARY MATERIAL

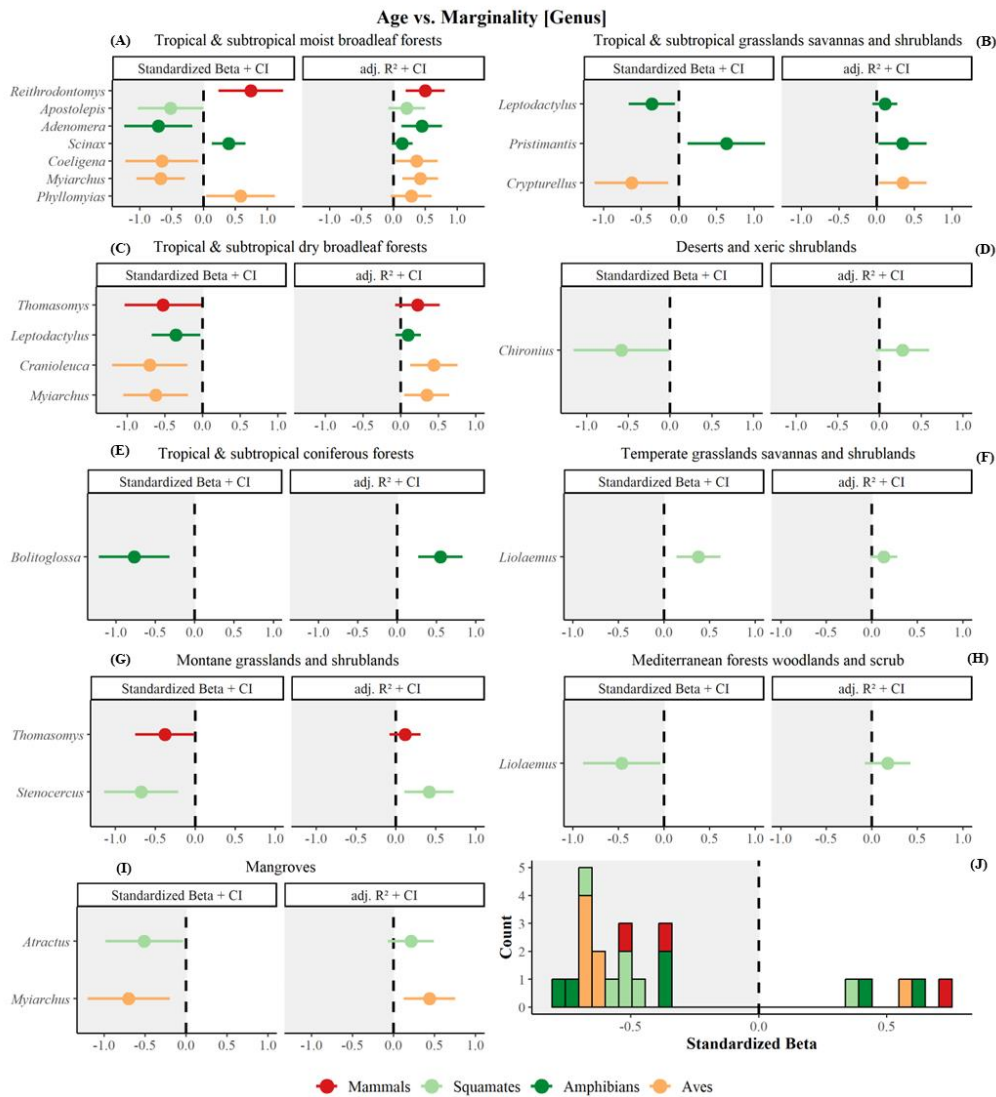


Figure SM1. Relationship between species age and marginality for each Neotropical biome at genus level. The significant groups are dots colored according to the class they belong: Mammals (red), Squamates (light green), Amphibians (green), and Aves (orange). The x-axis represents the parameter values and the y-axis shows the family names. Left panels in each biome stand for the standardized Beta and the correspondent confidence interval (CI) of each significant model. Right panels in each biome stand for the adjusted R^2 and the correspondent CI of each significant model. The dashed black line intersects the zero on the x-axis to separate the gray panel (negative values) from the white panel (positive values). A) Tropical & subtropical moist broadleaf forests; B) Tropical & subtropical grasslands savannas and shrublands; C) Tropical & subtropical dry broadleaf forests; D) Deserts and xeric shrublands; E) Tropical & subtropical coniferous forests; F) Temperate grasslands savannas and shrublands; G) Montane grasslands and shrublands; H) Mediterranean forests woodlands and scrub; I) Mangroves; and J) Standardized Beta histogram; x-axis represents the Beta values and y-axis the count.

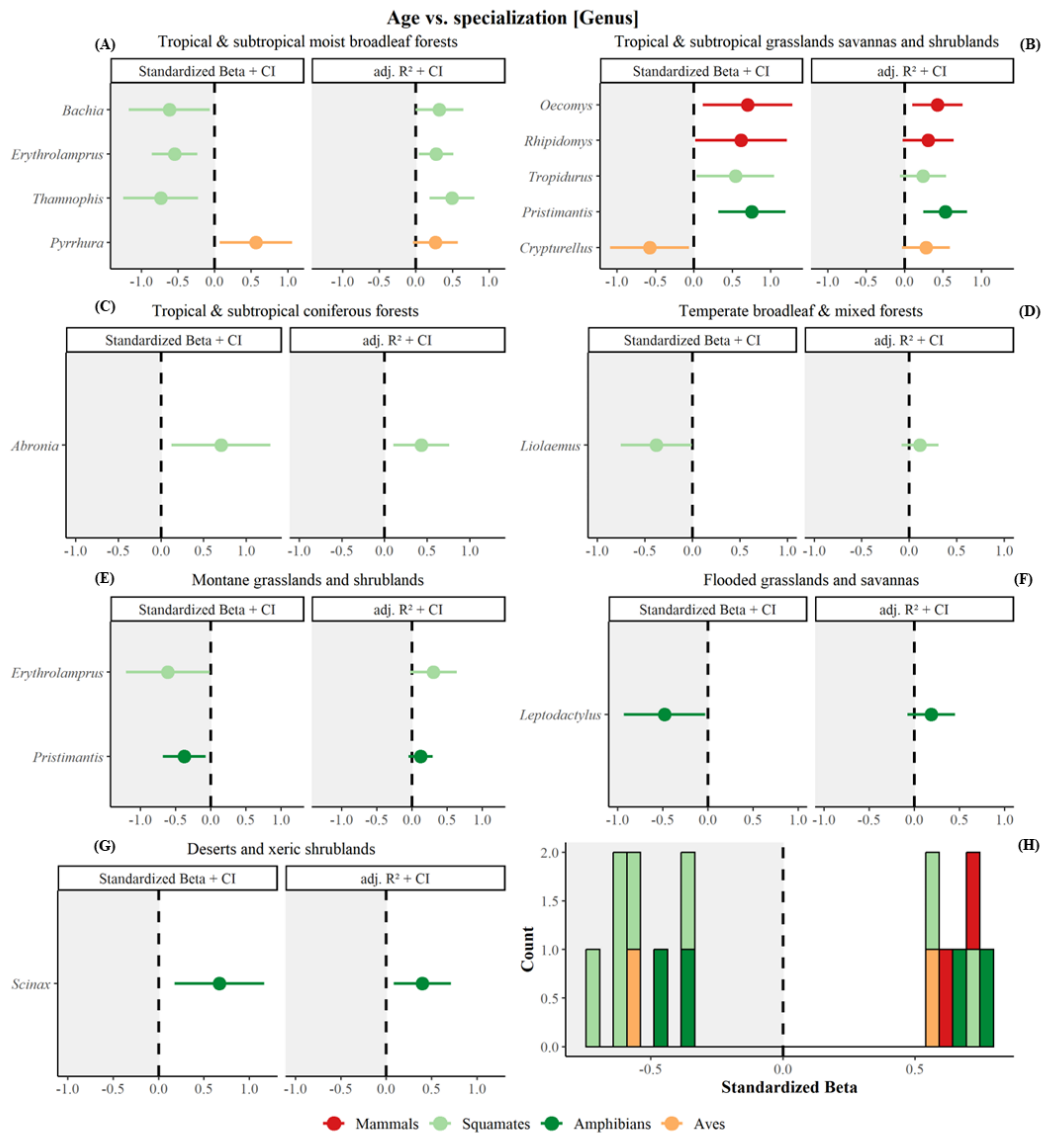


Figure SM2. Relationship between species age and specialization for each Neotropical biome at genus level. The significant groups are dots colored according to the class they belong: Mammals (red), Squamates (light green), Amphibians (green), and Aves (orange). The x-axis represents the parameter values and the y-axis shows the family names. Left panels in each biome stand for the standardized Beta and the correspondent confidence interval (CI) of each significant model. Right panels in each biome stand for the adjusted R² and the correspondent CI of each significant model. The dashed black line intersects the zero on the x-axis to separate the gray side (negative values) from the white side (positive values). A) Tropical & subtropical moist broadleaf forests; B) Tropical & subtropical grasslands savannas and shrublands; C) Tropical & subtropical coniferous forests; D) Temperate broadleaf & mixed forests; E) Montane grasslands and shrublands; F) Flooded grasslands and savannas; G) Deserts and xeric shrublands; and H) Standardized Beta histogram; x-axis represents the Beta values and y-axis the count.

Table SM1. Age vs. Marginality (weighted) regressions table for the significant groups with Tetrapod Class (Class), Taxon inside the Class (Taxon), term (term), estimate (estimate), standar error (std.error), statistic (statistic), p-value (p-value), adjunted R squared (adj.r.squared), Pagel lambda (pagel), Bloom K (bloom), False Discovery rate p-value (p-value (FDR)), Number of species (N.species), model (model).

Age vs. Marginality (weighted)												
Class	Taxon	term	estimate	std.error	statistic	p-value	adj.r.squared	pagel	bloom	p-value (FDR)	N. species	model
Mammals	CERVIDAE	Intercept	4.610	0.564	8.172	0.000	0.617	0.000	0.365	0.020	13	lm
		Beta	-2.530	0.561	-4.511	0.001						
		Intercept	4.610	0.564	8.172	0.000	0.617	0.000	0.365	0.020	13	background
		Beta	-2.530	0.561	-4.511	0.001						
		Intercept	5.059	0.596	8.488	0.000	0.666	0.000	0.338	0.009	13	high
	Beta	-3.582	0.717	-4.993	0.000							
	DIDELPHIDAE	Intercept	2.467	0.209	11.820	0.000	0.110	0.000	0.112	0.025	75	lm
		Beta	-0.400	0.126	-3.179	0.002						
		Intercept	2.467	0.209	11.820	0.000	0.110	0.000	0.112	0.025	75	background
		Beta	-0.400	0.126	-3.179	0.002						
Squamates	GYMNOPHTHALMIDAE	Intercept	4.383	0.421	10.422	0.000	0.122	0.144	0.193	0.001	118	lm
		Beta	-0.848	0.204	-4.162	0.000						
		Intercept	4.383	0.421	10.422	0.000	0.122	0.144	0.193	0.001	118	background
		Beta	-0.848	0.204	-4.162	0.000						
		Intercept	4.781	0.500	9.560	0.000	0.129	0.129	0.191	0.001	118	high
		Beta	-1.147	0.268	-4.280	0.000						
		Intercept	2.428	0.394	6.157	0.000						0.156
Beta	-0.650	0.218	-2.986	0.005								
Aves	ACCIPITRIDAE	Intercept	2.428	0.394	6.157	0.000	0.156	0.000	0.080	0.074	44	background
		Beta	-0.650	0.218	-2.986	0.005						
		Intercept	2.646	0.468	5.649	0.000	0.152	0.000	0.082	0.085	44	high
		Beta	-0.875	0.297	-2.949	0.005						

For the model categories: lm (linear model); background (background extinction model); high (high extinction model).

Table SM2. Age vs. Specialization (weighted) regressions table for the significant groups with Tetrapod Class (Class), Taxon inside the Class (Taxon), term (term), estimate (estimate), standar error (std.error), statistic (statistic), p-value (p-value), adjunted R squared (adj.r.squared), Pagel lambda (pagel), Bloom K (bloom), False Discovery rate p-value (p-value (FDR)), Number of species (N.species), model (model).

Age vs. Specialization (weighted)												
Class	Taxon	term	estimate	std.error	statistic	p-value	adj.r.squared	pagel	bloom	p-value (FDR)	N. species	model
Squamates	PHYLLODACTYLIDAE	Intercept	53.434	10.709	4.990	0.000	0.267	0.000	0.207	0.024	34	lm
		Beta	-15.234	4.219	-3.611	0.001						
		Intercept	53.434	10.709	4.990	0.000	0.267	0.000	0.207	0.024	34	background
		Beta	-15.234	4.219	-3.611	0.001						
		Intercept	62.483	13.170	4.745	0.000	0.268	0.000	0.209	0.023	34	high
		Beta	-20.495	5.669	-3.615	0.001						
Amphibians	LEPTODACTYLIDAE	Intercept	73.401	13.126	5.592	0.000	0.146	0.098	0.085	0.000	129	lm
		Beta	-25.554	5.337	-4.788	0.000						
		Intercept	73.401	13.126	5.592	0.000	0.146	0.139	0.062	0.000	129	background
		Beta	-25.554	5.337	-4.788	0.000						
		Intercept	103.733	15.709	6.603	0.000	0.211	0.089	0.053	0.000	129	high
		Beta	-42.037	7.091	-5.928	0.000						

For the model categories: lm (linear model); background (background extinction model); high (high extinction model).

Conclusões

Obtivemos as seguintes conclusões:

Capítulo I – *The Clade Replacement Theory: A framework to study Age-dependent extinction*

- Mostramos a falta de consenso teórico e empírico ao respeito da relação entre a idade das espécies e a probabilidade de extinção (ADE).
- Propomos a teoria de substituição de clados (CRT) como uma estrutura plausível para gerar predições concernentes ao sentido de ADE.
- Formalizamos CRT a partir de duas proposições: i) Efeito de incumbência por parte de um clado antigo sobre o espaço de nicho, inibindo a colonização e dominância de um clado novo; ii) Mudança ecológica que afeta negativamente ao clado antigo, oferecendo uma oportunidade ecológica para o clado novo.
- Deduzimos que o sentido do ADE é definido pela mudança ecológica. Se não acontecer, o ADE é negativo, i.e., espécies mais antigas possuem menor probabilidade de extinção. Se acontecer, o ADE é positivo, i.e., espécies mais recentes possuem menor probabilidade de extinção.

Capítulo II – *Approximating species age from phylogenies under different speciation modes and extinction*

- Ao avaliar as taxas de erro associadas com a estimação da idade por meio de filogenias descobrimos que o erro é maior para especiação por brotamento e anagenético independentemente do cenário de extinção.
- Mostramos que quando o clado diversifica predominantemente sob especiação bifurcativa a idade filogenética possui uma taxa baixa de erro, porém, esta cresce exponencialmente quando a taxa de extinção aumenta.
- Nosso estimador probabilístico possui boa eficiência na correção do erro da idade filogenética, especialmente em cenários de extinção alta. Porém, deve ser utilizado quando a diversificação do clado seja predominantemente bifurcativa.
- Aconselhamos precaução com as inferências feitas a partir das idades estimadas por meio do comprimento dos ramos das filogenias.

Capítulo III – *Species age and niche position: An exploratory analysis*

- Os tetrápodes neotropicais endotérmicos foram menos marginais e especialistas do que os ectotérmicos, provavelmente devido a capacidade maior de dispersão e tolerância dos primeiros.
- Não há generalidade na relação entre idade e posição de nicho para os tetrápodes neotropicais, mas os grupos que forma significativos, mostraram uma relação negativa; i.e., as espécies mais antigas ocuparam posições de nicho mais centrais.
- Não há generalidade na relação entre idade e especialização para os tetrápodes neotropicais, mas os grupos que forma significativos, mostraram uma relação negativa; i.e., as espécies mais antigas foram menos especialistas climáticos.

Novas sendas

Durante a elaboração dos capítulos nos deparamos com novas perguntas:

Capítulo I – *The Clade Replacement Theory: A framework to study Age-dependent extinction*

- A primeira proposição da teoria de substituição de clados (CRT) é efeito de incumbência por parte de um clado sobre o espaço de nicho, inibindo a colonização e diversificação de clados novos. Dita argumentação possui várias suposições não declaradas, como a equivalência funcional entre os membros dos diferentes clados, assim como as dinâmicas de ocupação do nicho, tanto em posição como no particionamento deste. Acreditamos que a exploração teórica e empírica desses processos dentro do contexto de CRT possuem potencial para pesquisas de qualidade e interesse geral para a macroevolução.
- A segunda proposição da CRT é mudança ecológica, a qual produz de fato a substituição do clado antigo pelo clado recente. Seria interessante avaliar, nas evidências de substituição passiva descritas na introdução, a existência de dita mudança ecológica. Especificamente sua definição e proporções, pois não está clara sua escala temporal, é dizer, como um transtorno ecológico teria implicações na diversificação de dois ou mais clados.
- Finalmente, o objetivo que não cumprimos (pelo tempo e as dinâmicas próprias de uma tese) de simular no Gen3sis ou em outra plataforma as nossas premissas do CRT e sua influência no ADE.

Capítulo II – *Approximating species age from phylogenies under different speciation modes and extinction*

- Além de procurar um método geral que melhore a estimação da idade filogenética, acreditamos que um caminho mais interessante, em termos eco-evolutivos, seria pesquisar a possibilidade de inferir o modo de especiação das espécies por meio de análises espaciais, associados com a especiação geográfica, e modelagens filogenéticas de reconstrução de nichos ancestrais.

Capítulo III – *Species age and niche position: An exploratory analysis*

- Acreditamos que uma definição mais abrangente do espaço de nicho seja necessária. É dizer, considerar diferentes abordagens para não limitar o espaço de nicho à tradição Grinelliana, variáveis climáticas, e incorporar em estudos futuros variáveis de interação biótica.
- Reconstrução do espaço de nicho ancestral a partir de dados paleoclimáticos, fósseis, e modelos filogenéticos que permitam reconstruir as distribuições do passado dos clados. Utilizar a filogenia e os dados das espécies atuais para reconstruir verdadeiramente a história evolutiva do clado.