

UNIVERSIDADE VILA VELHA – ES
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DE ECOSISTEMAS

**MODELAGEM GEOCLIMÁTICA DA DISTRIBUIÇÃO DE ESPÉCIES DE
LECYTHIDACEAE NUM PANORAMA DE MUDANÇAS CLIMÁTICAS**

LUANA GASPAR DO NASCIMENTO LOPES

VILA VELHA
JULHO / 2017

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Tese apresentada à Universidade Vila Velha,
como pré-requisito do Programa de Pós-
graduação em Ecologia de Ecossistemas, para
a obtenção do título de Doutora em Ecologia.

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Catálogo na publicação elaborada pela Biblioteca Central / UVV-ES

L864m Lopes, Luana Gaspar do Nascimento.
 Modelagem geoclimática da distribuição de espécies de
 Lecythidaceae num panorama de mudanças climáticas / Luana
 Gaspar do Nascimento Lopes – 2017.
 103 f.: il.

 Orientador: Ary Gomes da Silva.
 Coorientadora: Aryane Luna Peixoto.
 Tese (doutorado em Ecologia de Ecossistemas) -
 Universidade Vila Velha, 2017
 Inclui bibliografias.

 1. Ecologia. 2. Botânica – Vegetal. 3. Mudanças climáticas.
 I. Silva, Ary Gomes da. II. Peixoto, Aryane Luna. III. Universidade
 Vila Velha. III. Título.

CDD 577

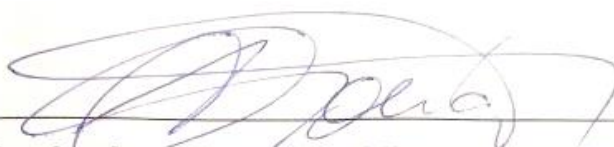
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Aprovada em 27 de julho de 2017,

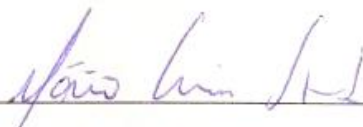
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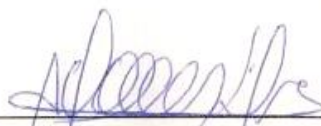
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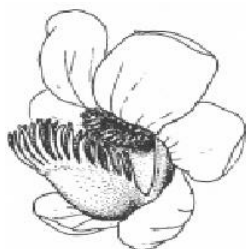


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Orientador



***“Não são espécies mais fortes que sobrevivem,
nem as mais inteligentes,
e sim as mais suscetíveis a mudanças.”***

Charles Darwin

Aos meus pais Gilberto e Janiere pelo apoio incondicional.

A Alexandre Lopes, por todo seu amor e suporte, ao nosso filho Cauã. Tudo só é possível por e com vocês!

AGRADECIMENTOS

Aos meus pais, Gilberto e Janiere, pelo carinho, amizade, compressão, ensinamentos, companheirismo e por me proporcionarem o bem mais valioso que qualquer ser humano pode ter, a educação.

Agradeço de forma incondicional ao meu marido. Ele foi o alicerce que me fez relevar as dificuldades, que me deu sustentação nas horas difíceis, que me ouviu muitas vezes falar de coisas que ele não fazia a mínima ideia do que se tratava e, ainda assim, no final, dizer que daria tudo certo. Agradeço pelo amor, pelo companheirismo, pela paciência e pelo o incentivo.

Agradeço ao Profº Ary Gomes da Silva pela dedicação, paciência, preocupação, ensinamento e, principalmente, pelas sugestões valiosas durante essa grande jornada. Mais uma vez, agradeço imensamente ao meu orientador.

A Michel Ribeiro, por disponibilizar os registros de ocorrência da família Lecythidaceae no Estado do Espírito Santo.

Aos professores da Pós-Graduação em Ecologia da UVV, por auxiliarem no processo de minha formação profissional.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), pela bolsa de doutorado.

A todos os amigos pelo apoio e incentivo que, direta ou indiretamente, influenciaram esse trabalho.

A todos, muito obrigada!

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LISTA DE ABREVIATURAS

AUC – *Area Under Curve*

CCSM 4 – *Community Climate System Model 4*

CNCFlora – Centro Nacional de Conservação da Flora

CO₂ – Gás carbônico

GBIF – *Global Biodiversity Information Facility*

GBIF – Sistema Global de Informação Sobre a Biodiversidade

IPCC – *Intergovernmental Panel on Climate Change*

IUCN – *União Internacional para a Conservação da Natureza e dos Recursos Naturais*

LGM – *Last Maximum Glacial*

LIG – *Last Interglacial*

LPM – *Minimum Training Presence*

Maxent – *Maximum Entropy Model*

MDE – Modelo de Distribuição de Espécie

MNE – Modelo de Nicho Ecológico

PCA – Análise de Componentes Principais

RCPs – *Representative Concentration Pathways*

ROC – *Receiver Operating Characteristic*

SIG – Sistema de Informações Geográficas

TSS – *True Skill Statistic*

RESUMO

LOPES, Luana Gaspar do Nascimento, D.Sc, Universidade Vila Velha - ES, julho de 2017. **Modelagem Geoclimática da distribuição de espécies de Lecythidaceae num panorama de mudanças climáticas.** Orientador: Ary Gomes da Silva. Co-orientadora: Aryane Luna Peixoto.

Modelos de distribuição de espécies, também conhecidos como modelos bioclimáticos ou modelos de nicho ecológicos, têm sido aplicados em inúmeras questões ecológicas, inclusive para avaliar os efeitos das mudanças climáticas sobre as espécies. Nesse sentido, em resposta às flutuações climáticas, a distribuição de algumas espécies poderá sofrer mudanças ou, ainda, as espécies poderão se deslocar para novas áreas adequadas. Contudo, isso dependerá de sua capacidade em dispersar e de características ambientais. As espécies da família Lecythidaceae são consideradas importantes no monitoramento das alterações da composição florestal causadas por distúrbios antropogênicos e alterações climáticas. Como tal, avaliamos o efeito da mudança climática na distribuição de cinco espécies na família Lecythidaceae (*Couratari macrosperma*, *Cariniana ianeirensis*, *Lecythis lurida*, *Lecythis pisonis* e *Couratari asterotricha*) em diferentes escalas de tempo no Brasil. Hipotetizamos que os padrões geográficos da distribuição de espécies arbóreas nesta família podem ser influenciados pelo padrão climático de temperatura e pela distribuição de precipitação. Para testar essas hipóteses, baseamo-nos na modelagem de nicho ecológico, que é uma das abordagens mais utilizadas e relevantes para prever mudanças na distribuição de espécies. A modelagem de nicho ecológico usa associações entre variáveis ambientais e registros de ocorrência da espécie para estimar modelos que representam as condições ambientais favoráveis à espécie. Neste trabalho foram estudadas espécies de Lecythidaceae com características ecológicas distintas, incluindo uma espécie endêmica da Floresta Atlântica (*Couratari asterotricha*). Foram gerados modelos para os cenários passados (Último interglacial 132.000, Último Máximo Glacial 21.000 e médio Holoceno 6.000 anos atrás) utilizando o Programa Maxents 3.3.3k. Além disso, geramos modelos para os cenários presente e futuro (2050 e 2070) utilizando o cenário otimista e pessimista. De acordo com nossos resultados, as projeções de diferentes cenários climáticos no passado indicam que houve mudanças consideráveis nas condições ambientais e nas áreas de adequação das espécies estudadas (capítulo I). Em cenários futuros (2050 e 2070), quase todas as espécies tiveram uma redução nas áreas adequadas nos cenários otimistas e pessimistas (capítulo II). O terceiro capítulo modelou a distribuição potencial de uma espécie endêmica (*Couratari asterotricha*), para produzir mapas preditivos que podem permitir novos levantamentos direcionados em áreas de ocorrência da espécie prevista pelo modelo. Nesse sentido, os resultados apresentados reforçam fortemente a importância dos modelos de nicho ecológico como ferramenta de predição e suas perspectivas de aplicabilidade para prever áreas adequadas para o estabelecimento de espécies sob diferentes projeções climáticas.

Palavras-chave: Lecythidaceae. Mudanças climáticas. Modelagem de Nicho Ecológico.

ABSTRACT

LOPES, Luana Gaspar do Nascimento, D.Sc, University of Vila Velha - ES, julho de 2017. **Geoclimatic modeling of the distribution of species of Lecythidaceae in a panorama of climatic changes.** Advisor: Ary Gomes da Silva. Coorientador: Aryane Luna Peixoto.

Models of species distribution, also known as bioclimatic models or ecological niche models, have been applied to many ecological questions, including assessments of the effects of climate change on species distributions. In response to climatic fluctuations, the distribution of some species may change or species may move to new areas. However, this will depend on their ability to disperse and on environmental characteristics. Species of the family Lecythidaceae are considered important in monitoring forest composition changes caused by anthropogenic disturbances and climate change. As such, we evaluated the effect of climate change on the distribution of five species in the Lecythidaceae family (*Couratari macrosperma*, *Cariniana ianeirensis*, *Lecythis lurida*, *Lecythis pisonis*, and *Couratari asterotricha*) at different time scales in Brazil. We hypothesized that the geographical patterns of tree species distribution in this family may be influenced by climate pattern of temperature and rainfall distribution. To test this hypothesis, we relied on ecological niche modeling, which is one of the most frequently used and relevant approaches to predict changes in species distribution. Ecological niche modeling uses associations between environmental variables and species occurrence records to estimate models that represent favorable environmental conditions for the species. Here, we studied species of Lecythidaceae with different ecological characteristics, including one species that is endemic to the Atlantic Forest (*Couratari asterotricha*). Models for past scenarios (last interglacial 132,000, last glacial maximum 21,000, and mid-Holocene 6,000 years ago) were generated using Program Maxent 3.3.3k. Furthermore, we generated models for the present and future (2050 and 2070) using optimistic and pessimistic scenarios. According to our results, projections of different climatic scenarios in the past indicate that there have been considerable changes in environmental conditions and areas of suitability of the species studied (chapter I). In future scenarios (2050 and 2070), almost all species had a reduction in suitable areas in both the optimistic and pessimistic scenarios (chapter II). The third chapter modeled the potential distribution of an endemic species (*Couratari asterotricha*), to produce predictive maps that may allow new targeted surveys in areas of strongly predicted species occurrence. The presented results strongly reinforce the importance of ecological niche models as a predictive tool, and their applicability to predict suitable areas for the establishment of species under different climatic projections.

Keywords: Climate Change. Ecological Niche Modeling. Lecythidaceae

1. INTRODUÇÃO

Atualmente vivenciamos alterações no clima global, em decorrência do aumento da temperatura terrestre causado pela intensificação do efeito estufa. Desde a década de 1950, evidências científicas apontam para a possibilidade inequívoca de mudança no clima. Dentre as implicações prováveis das mudanças climáticas, está a alteração na distribuição geográfica de espécies da flora e fauna. O que nos parece claro é que a rapidez prevista para as modificações do clima, inclusive no que diz respeito à variabilidade e aos eventos extremos, pode ser o grande obstáculo, pois as respostas das espécies às mudanças climáticas podem incluir extinções, adaptações ou mudanças nas amplitudes de distribuição geográfica (DINIZ-FILHO e BINI, 2008).

Dessa forma, é primordial entender como as espécies, a dinâmica e a composição dos ecossistemas locais podem ser afetados pelas mudanças climáticas e como responderão a essas perturbações. Assim, é fundamental identificar quais são as características que tornariam as espécies mais vulneráveis a essas mudanças. Nesse sentido, a importância e carência de informações sobre a distribuição geográfica das espécies da família Lecythidaceae nos motivaram a avaliar a influência das alterações climáticas sobre essas espécies, em uma escala temporal, abrangendo desde o Quaternário (a partir do Último Interglacial) até o futuro. Destaca-se que há poucos trabalhos sobre a distribuição dessa família no Brasil e poucas pesquisas visando o conhecimento de sua distribuição futura e passada já foi realizada.

A família está representada no Brasil com 10 gêneros e aproximadamente 119 espécies, sendo que a maior parte se encontra na Amazônia (SMITH et al., 2014); e a Floresta Atlântica se configura como centro secundário de diversidade da família (MORI, 1995) com 19 espécies, sendo que 60% é endêmica deste domínio, apresentando maior riqueza e diversidade na floresta de tabuleiro, seguida da floresta de encosta e restinga (RIBEIRO et al. 2014). A presença de espécies de Lecythidaceae tem sido usada por botânicos e ecólogos como indicador de florestas preservadas.

Este trabalho propõe o uso de espécies de Lecythidaceae como indicadoras de mudanças ambientais em áreas de floresta tropical, embasadas na tradição de que as espécies são adaptadas aos ambientes em que vivem e que alterações em tais ambientes podem promover mudanças observáveis nas características dessas espécies.

Nesse sentido, modelar a distribuição dessas espécies é de fundamental importância, pois se torna possível inferir o ambiente em que viveram (paleoambiente) e das mudanças que este possa ter sofrido, por comparação com o que se passa atualmente. Inventariando as preferências individuais de cada espécie é possível definir janelas ecológicas dos atributos comuns no habitat. Já que há determinadas espécies que, por si só, definem um determinado tipo de ambiente, não podendo existir em outro qualquer. A utilização dessas espécies como indicadoras ambientais, são ferramentas preciosas para tentar compreender as condições físicas e biológicas que caracterizaram o ambiente e na identificação de acontecimentos responsáveis por mudanças (graduais e bruscas) eventualmente operadas ao longo do tempo.

O conhecimento do potencial de ocorrência de uma espécie com importância ambiental, como a família Lecythidaceae, facilita a definição de medidas direcionadas à conservação das espécies, bem como permite estudos de monitoramento, principalmente quando se considera cenários decorrentes dos efeitos de mudanças climáticas. Além disso, o uso de técnicas de modelagem de distribuição geográfica de espécies tem um grande potencial em situações nas quais é preciso tomar decisões, mas ainda não existe disponível um conjunto de informações sistematizado. Assim, é tarefa fundamental identificar as características das espécies, que as tornam resistentes ou susceptíveis a mudança climática, para que possamos verificar como os parâmetros ambientais podem influenciar os padrões de biodiversidade; tendo em vista que para preservar a biodiversidade é necessário conhecer a distribuição e a abundância das espécies (DOBSON et al. 1997; ARAÚJO & WILLIAMS 2000).

Nesse sentido, a modelagem preditiva, baseada na teoria de nicho se constitui uma ferramenta útil ao fazer associações entre dados de ocorrência de espécies e variáveis climáticas através de processos computacionais que resultam em modelos das condições e tolerâncias climáticas necessárias à sobrevivência das espécies.

Com base no histórico apresentado, algumas hipóteses são levantadas: (1) os padrões geográficos de distribuição de espécies arbóreas de Lecythidaceae são determinados por padrões climáticos; (2) Mudanças no padrão climático de distribuição de temperatura e pluviosidade podem modificar os padrões geográficos de distribuição das espécies ao longo do tempo; (3) Mudanças climáticas extremas podem provocar extinção de espécies devido à supressão de habitats possíveis para sua distribuição.

Para responder essas questões, foi realizado a modelagem de nicho para conhecer a área de ocorrência potencial atual, passada e a futura. Com os resultados

obtidos neste estudo foi produzido um artigo científico, apresentado aqui na forma de Capítulo 1: ***An outlook of geoclimatic modeling based on the current patterns of distribution of tropical species of Lecythidaceae.***

O Capítulo 1 está focado em como as áreas ambientalmente adequadas para as espécies estavam distribuídas no passado, considerando os impactos das oscilações climáticas durante o Quaternário, e em como o clima pode ter contribuído para moldar a distribuição atual da espécie. A hipótese utilizada é que as mudanças climáticas podem ter influenciado o padrão de distribuição dessas espécies ao longo do tempo. Este artigo foi formatado nas normas da revista *Ecological Modelling*.

No segundo capítulo, foi realizado a modelagem de distribuição de espécies para conhecer a área de ocorrência potencial atual e no futuro. O capítulo 2 se intitula: ***Modeling of climatic aptitude of arboreal species in the face of climate change scenarios in Brazil.*** Ele aborda o impacto futuro das mudanças climáticas sobre três espécies de Lecythidaceae. As condições atuais foram projetadas para dois níveis de emissão de gás carbônico, um mais otimista (com menores taxas de emissão) e outro mais pessimista (com maiores taxas). Este artigo foi formatado nas normas do *Journal of Ecology*.

O terceiro, e último capítulo, trata da modelagem de distribuição potencial de uma espécie tida como endêmica no Estado do Espírito Santo, com o título: ***Ecological niche modeling of the Couratari asterotricha Prance (Lecythidaceae): prediction new areas of occurrence.*** A formatação utilizada neste capítulo segue as normas da revista *AoB Plants*

Com efeito, esta pesquisa evidencia sua importância na medida em que contribuirá com melhor conhecimento sobre o provável efeito das mudanças climáticas na distribuição geográfica das espécies da família de Lecythidaceae, bem como possibilitará ou criará condições para identificar quais dessas espécies são mais vulneráveis as mudanças climáticas, através do mapeamento de sua distribuição potencial que permitirá prever a persistência de ocorrência dessa espécie em diferentes cenários temporais, já que há uma necessidade premente em se estudar e desenhar esses efeitos sobre a vegetação.

É necessário considerar, por sua vez, que as questões das mudanças climáticas por meio da modelagem climática se mostra instrumento estratégico para estimar a área climaticamente favorável para a ocorrência da espécie alvo, identificar outras áreas favoráveis para a ocorrência da espécie alvo ou de espécies filogeneticamente próximas, auxiliar no planejamento de coletas, estudos de

reintrodução de espécies, impactos da introdução de espécies exóticas, analisar e avaliar como esses eventos climáticos podem provocar graves consequências econômicas, sociais e ambientais.

Noutro aspecto, conquanto não dissociado do primeiro, esses estudos tendem a trazer implicações imprescindíveis aos projetos conservacionistas pela influência direta sobre a persistência de espécies e pela produção de informações a respeito da sua distribuição geográfica. Nesse sentido, contemporaneamente, mais do nunca, revela-se fundamental os estudos que visem antecipar a natureza e magnitude de possíveis alterações das mudanças climáticas sobre a biodiversidade. Em função disso, os modelos de nicho ecológico são instrumentos que surgiram com a proposta de preencher as lacunas de conhecimento sobre os limites geográficos de espécies de interesse e ainda podem ajudar na formulação de novas hipóteses sobre os mecanismos que determinam a distribuição dessas espécies (GUISAN e ZIMMERMANN, 2000).

2. FUNDAMENTAÇÃO TEÓRICA

A modelagem de distribuição de espécie é normalmente baseada no conceito de nicho ecológico de uma espécie, traduzindo-se “[n]um conjunto de condições ecológicas com as quais as populações conseguem se manter” (HUTCHINSON, 1981). No entanto, a tarefa de modelagem desenvolvida pelas ferramentas atualmente disponíveis é baseada principalmente em um conceito mais específico; *in casu*, o de nicho fundamental, que “consiste no conjunto de condições sob as quais a espécies pode existir na ausência de fatores bióticos limitantes, como competição, predação e parasitismo” (ACIESP, 1997).

Nesse sentido, o nicho ecológico corresponde ao conjunto de condições e recursos nos quais os indivíduos de uma espécie são capazes de sobreviver, crescer e reproduzir; e serve como base para estimar os locais de ocorrência das espécies (DE MARCO JR e SIQUEIRA, 2009). Para Brown e Lomolino (1998), a amplitude de distribuição geográfica das espécies pode ser interpretada como a tradução espacial de seus nichos ecológicos ou, dito doutra forma, significa que as espécies ocorrem onde as condições ambientais são adequadas e não ocorrem onde os recursos e/ou condições ambientais requeridos estão ausentes.

As principais interpretações do nicho ecológico, assim como a estruturação e a colocação conceitual, são devidas a Grinnell (1917), Elton (1927) e Hutchinson (1957). Grinnell trabalhou com variáveis correspondentes a fatores ambientais expressos geograficamente em escalas espaciais pequenas (PETERSON et al., 2011), entretanto, na sua concepção, o nicho não era exatamente um atributo da espécie, mas sim do espaço (GIANNINI et al., 2012). Posteriormente, as ideias de Elton (1927) trouxeram novas perspectivas ao conceito de nicho, que passou a ser empregado para descrever o modo de vida dos organismos ao invés de seus locais de vida (BEGON et al., 2007).

Assim, Elton (1927) caracterizou o nicho das espécies como sendo o seu papel funcional na cadeia alimentar. Ele deu ênfase nos impactos, tanto do ambiente sobre as espécies quanto das espécies sobre os seus ambientes (GIANNINI et al., 2012) e trabalhou com variáveis ambientais em escala local (PETERSON et al., 2011), considerando principalmente as interações entre as espécies, particularmente as relações alimentares (WHITTAKER et al., 1973).

Ressalta-se, entretanto, que a contribuição mais substancial é devida a Hutchinson, no ano de 1957. Ele fez uma grande contribuição na Ecologia ao

caracterizar o nicho de uma espécie como um hipervolume “*n dimensional*”, definido como o nicho fundamental, onde todos os pontos desse hipervolume correspondem a representações de estados do ambiente, de variáveis físicas, químicas e biológicas, que possibilitam a sobrevivência de uma espécie sem limites pré-determinados (HUTCHINSON, 1957); de acordo com esse conceito, as condições ambientais é que limitam a abundância e distribuição de uma espécie. Destarte, toda espécie é limitada por um número de fatores ambientais, em um período de tempo determinado e dentro de sua distribuição geográfica.

Seguindo a definição de Hutchinson (1957), o ambiente de uma espécie pode ser representado pela construção de um espaço multidimensional onde cada eixo ou dimensão representa uma variável ambiental diferente. Esse conceito considera que todos os fatores bióticos (também chamados de variáveis recurso ou bionômicas) e abióticos (também chamadas de variáveis condição ou cenopoéticas) agem em conjunto para delimitar o nicho da espécie (SOBERÓN, 2007). Hutchinson também realizou a distinção entre nicho fundamental, que é um espaço multidimensional em que a espécie consegue reproduzir e sobreviver indefinidamente; e entre nicho realizado, que é uma parte do nicho fundamental em que a espécie consegue permanecer mesmo em competição com outras (POLECHOVÁ e STORCH, 2008). A diferença entre o nicho ocupado e o nicho fundamental ocorre, pois, a distribuição das espécies não é apenas determinada pelas condições ambientais, mas também por diferentes fatores resultantes da complexa expressão de sua ecologia, capacidade dispersiva e história evolutiva (PERSONS e DAWSON, 2003; PULLIAM, 2000).

Jorge Soberón em uma série de trabalhos resumiu esses conceitos teóricos em um diagrama, que descreve alguns dos resultados da interação dos fatores que determinam a distribuição de uma espécie: diagrama Biótico-Abiótico-Mobilidade, mais conhecido como diagrama BAM (Figura 1) (SOBERÓN e PETERSON, 2005; SOBERÓN, 2007; SOBERÓN e NAKAMURA, 2009). Neste caso, o nicho de uma espécie seria delimitado por três espaços independentes, mas que interagem: biótico (B), abiótico (A) e movimento (M).

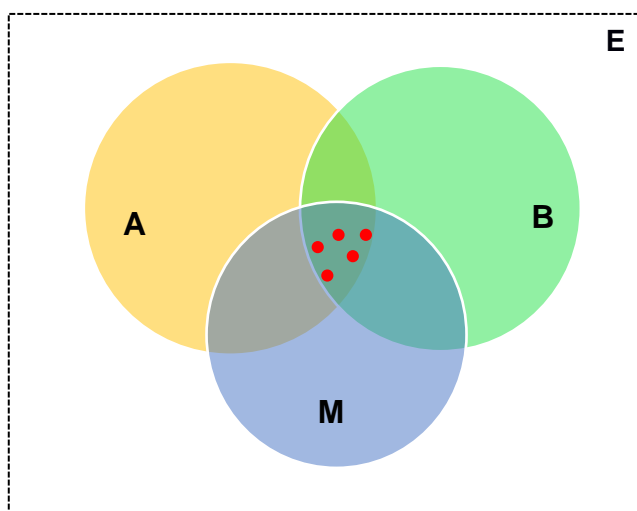


Figura 1. Diagrama BAM, mostrando as intersecções entre variáveis cenopoéticas (A) bionômicas (B) e de movimento (M) que condicionam a ocorrência de uma espécie em um determinado local. A letra E representa o espaço geográfico em que a espécie está inserida. Adaptado de Sóberon (2007).

Os autores usam o diagrama como uma representação abstrata do espaço geográfico. O diagrama indica que a espécie poderá estar presente em um determinado ponto onde três condições são satisfeitas: região (A) as condições abióticas devem ser favoráveis para a espécie, ao qual Peterson e Soberón (2012) chamam de nicho fundamental existente. A região (B) é a área, onde as condições bióticas estão disponíveis para a espécie e a terceira região (M) é onde a espécie poderá estar presente somente se for acessível, considerando a capacidade de dispersão da espécie a partir de áreas de distribuição onde a espécie está estabelecida. A área de intersecção entre a região (B) e a região (A) é a expressão geográfica do nicho realizado, região que pode ser potencialmente invadida porque os dois tipos de condições (A e B) são favoráveis, mas a espécie ainda não foi capaz de alcançá-la dadas as barreiras à dispersão; e, finalmente, a intersecção desta área com a região (M) é obtido a distribuição geográfica da espécie (Soberón e Peterson 2005).

Outro conceito que surge com a teoria de Hutchinson é de Espaço Geográfico e Espaço Ambiental (Figuras 2 e 3). Esta dualidade entre o espaço ambiental e geográfico (biotope *sensu* Hutchinson) é conhecida como “dualidade de Hutchinson” (COLWELL e RANGEL, 2009). O espaço geográfico (bidimensional) refere-se à localização espacial da espécie, enquanto o espaço ambiental (multidimensional) refere-se ao nicho dimensional de Hutchinson.

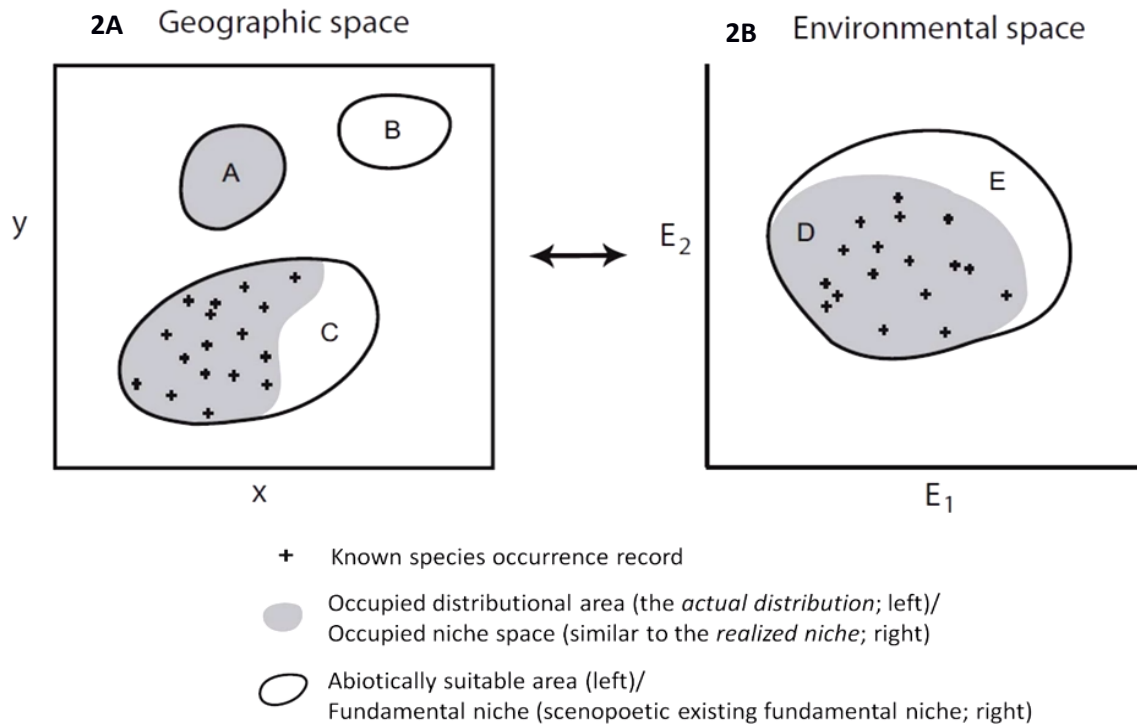


Figura 2: Espaço geográfico e ambiental para uma espécie hipotética.

Fonte: Person 2007; Peterson et al., 2011.

A figura 2A representa o espaço geográfico (dimensional) e a distribuição real da espécie (áreas ocupadas) pode ser observada no sombreado cinza, contudo é possível verificar que a área A está ocupada, mas a espécie não foi detectada. Dentro do espaço geográfico, as linhas contínuas representam áreas com condições abióticas adequadas para a ocorrência da espécie (distribuição potencial). Cabe ressaltar, entretanto, que algumas regiões da distribuição potencial podem não ser habitada pelas espécies devido a interações bióticas ou limitações de dispersão.

Na ilustração do espaço ambiental (multidimensional) a parte do nicho ocupado pela espécie (nicho realizado) é representado por uma área cinzenta. Desse modo, é possível perceber que os registros de ocorrência observados podem não identificar a extensão do nicho ocupado (por exemplo, a área sombreada ao redor da letra D não inclui locais conhecidos). A linha contínua no espaço ambiental retrata o nicho fundamental, que representa toda a gama de condições abióticas dentro das quais a espécie é viável.

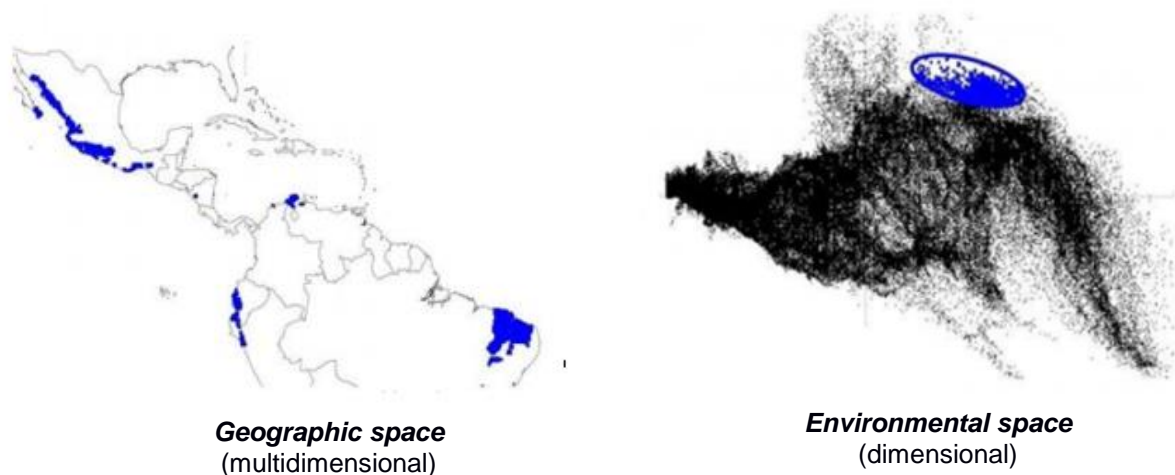


Figura 3. Limites entre duas dimensões: dimensão geográfica e a dimensão ecológica (Dualidade de Hutchinson). O círculo azul no espaço ambiental representa as condições ambientais do nicho fundamental de uma espécie e os respectivos pontos azuis no mapa são áreas geográficas que apresentam essas condições ambientais, ou seja, as áreas de distribuição potencial da espécie.

Fonte: Soberón e Nakamura, 2009.

Soberón (2007), faz uma separação interessante entre modelagem de distribuição potencial e nicho. O autor separa esse conceito da mesma forma que Hutchinson (1957; 1981) o fez em seu trabalho clássico: o sub-espaço de condições e o sub-espaço de recursos. Esse conceito considera que todos os fatores bióticos (também chamados de variáveis recurso ou bionômicas) e abióticos (também chamadas de variáveis condição ou cenopoéticas) agem em conjunto para delimitar o nicho da espécie (SOBERÓN, 2007).

De acordo como o exposto por De Marco Jr. e Siqueira (2009), os dados ambientais disponíveis devem apenas representar o sub-espaço de condições e não o nicho completo da espécie. Além disso, é bastante provável que os pontos de ocorrência tomados representem áreas em que as condições são favoráveis, mas podem existir outras áreas com condições semelhantes, mas que a presença da espécie é impedida por interações interespecíficas. Hutchinson identificou esse conceito como nicho pós-interativo ou realizado e é ele a base correta para a modelagem com os dados disponíveis.

Soberón (2007) reforça esse argumento distinguindo entre nicho Grinnelliano (que apenas leva em consideração as condições do ambiente) e nicho Eltoniano (que leva em conta as interações entre espécies). Ou seja, o nicho Grinnelliano pode ser definido fundamentalmente por variáveis abióticas, chamadas de cenopoéticas, que apresentam autocorrelação espacial e estão relacionadas com a fisiologia da espécie.

O nicho Eltoniano é focado nas variáveis chamadas bionômica, o que significa dizer que as interações bióticas e dinâmicas de consumo dos recursos, interações entre as espécies e as interações dos seus recursos locais e as outras espécies. O que é preciso ressaltar é que os conceitos de Nicho Grinnelliano e Nicho Eltoniano são relevantes para o entendimento da distribuição das espécies no espaço. Contudo, o nicho Eltoniano é mais fácil de medir em escala grande, que tem maior resolução. Já o nicho Grinnelliano se encaixa melhor às escalas pequenas, com resolução mais baixa, nas quais as áreas de distribuições são tipicamente definidas (SOBERÓN, 2007; SOBERÓN e NAKAMURA, 2009; PETERSON, 2011).

O trabalho de Prinzing et al., (2002), sugere que os fatores bionômicos não afetam o padrão de distribuição de espécies em macroescala, e sim em microescala. As interações bióticas causariam “ruídos” na distribuição geográfica das espécies quando consideradas grandes escalas espaciais, restringindo sua ocorrência em um ou outro local, ao invés de restringir efetivamente sua amplitude geográfica. Esse efeito ficou conhecido como ruído Eltoniano (SOBERÓN e NAKAMURA, 2009).

Na maior parte das aplicações de modelagem potencial de distribuição de espécie se considera que o nicho ecológico é o modelo básico que sustenta a possibilidade de produzir predições sobre a ocorrência de espécies (PETERSON 2001; THUILLER et al., 2005; ELITH et al. 2006). De acordo com De Marco e Siqueira (2009), essa argumentação é consistente, à medida que o nicho ecológico é definido como o conjunto de condições e recursos nos quais os indivíduos de uma espécie são capazes de sobreviver, crescer e reproduzir. De tal modo que o conhecimento dessas condições e recursos deve servir para predizer os locais de ocorrência da espécie.

Nessa perspectiva, considera que as condições ambientais são fatores importantes na determinação da distribuição das espécies principalmente em escalas espaciais pequenas de menor resolução (SOBERÓN e PETERSON 2005; SOBERÓN 2007). Uma vez que estes fatores definem o nicho das espécies no espaço ecológico de maneira similar ao conceito moderno de nicho fundamental (HUTCHINSON, 1957; SOBERÓN e NAKAMURA, 2009).

Em vista disso é possível definir que o nicho fundamental representa as combinações de variáveis ambientais diversas que permitem a sobrevivência dos indivíduos e a manutenção das populações. Enquanto o nicho realizado é um subconjunto do nicho fundamental e representa a área ocupada pela espécie, que pode ser menor que seu nicho fundamental devido à influência humana, interações bióticas (competição interespecífica, predação, etc.), ou barreiras geografias que

dificultam a dispersão e colonização, ou seja, uma série de fatores que podem evitar que a espécie habite locais onde as condições atendem ao seu potencial ecológico (HUTCHINSON, 1957; PULLIAM, 2000; ANDERSON e MARTINEZ-MEYER, 2004). Não por acaso, Guisan e Thuiller (2005) nos mostram que o que observamos na natureza são nichos ecológicos realizados, ou seja, pares de nicho ecológico fundamental disponíveis onde a espécie não foi excluída por interações bióticas e limitações de recursos.

Em suas colocações, Brown e Lomolino (2006) chamam a atenção para algumas considerações que devem ser observadas ao se pretender explicar os padrões de distribuição e abundância, tais como: o fato de ser “muito simplista assumir que as condições ambientais são igualmente favoráveis para uma espécie em todas as localidades onde ocorre”; certas localidades podem ser tão favoráveis que as taxas de natalidade excede a de mortalidade, produzindo excesso de indivíduos que migram para outras áreas, servindo como “habitat fonte”; já outras localidades podem ser tão desfavoráveis que a taxa de mortalidade excede a de natalidade, mas podem ser habitadas para manter a população local. Deste modo, conclui-se que pode haver locais com condições favoráveis e que são inabitados e locais onde apesar das condições desfavoráveis, são habitados.

Nesse sentido, uma espécie tem sua área de distribuição limitada tanto na escala geográfica (que corresponde a distribuição total da espécie) quanto na ecológica (distribuição local da espécie), ou seja, existem áreas em que a espécie pode ou não existir (CERQUEIRA, 1995). E com relação à abundância, esta tende a ser maior para uma espécie onde todos os parâmetros do nicho estão em uma amplitude favorável, e rara ou ausente onde um ou mais fatores ambientais atuam fortemente como limitante (BROWN e LOMOLINO, 2006).

A teoria de nicho ecológico suporta fortemente uma das principais ferramentas utilizadas atualmente, a Modelagem de Nicho Ecológico (GUISAN e ZIMMERMANN, 2000; SOBERÓN, 2007), a qual é baseada principalmente no nicho Grinnelliano. Antes de considerarmos as demais questões envolvendo essa ferramenta, é preciso entender as diferentes terminologias utilizadas para os modelos de nicho ecológico (MNEs), que também têm sido chamados de modelos de envelope bioclimático ou modelo de distribuição de espécies (MDEs) (ELITH e LEATHWICK, 2007).

Nesse sentido, ainda que ambos os termos são encontrados em muitos trabalhos como sinônimos, alguns autores propõem diferenciações entre Modelagem de Distribuição de Espécie e Modelagem de Nicho Ecológico (PETERSON e

SOBERÓN, 2012; PETERSON et al., 2011). Para Peterson e Soberón (2012), a modelagem preditiva tem sido chamada por alguns autores de Modelagem de Nicho Ecológico (MNE) e, por outros, de Modelagem de Distribuição de Espécies (MDE). Soberón (2010) sugere que a distribuição geográfica não está somente relacionada com o nicho ecológico, mas também inclui outros fatores, os quais nem sempre podem incluídos na modelagem. Nesse sentido, segundo o autor, os modelos de nicho têm sido validados universalmente através da comparação entre ocorrência no espaço geográfico, embora eles sejam, estritamente falando, modelos de nicho ecológico e não de distribuição geográfica (SOBERON e PETERSON, 2005).

Já para Jiménez-Valverde et al., (2008), o termo modelagem de nicho deveria ser evitado, pois além de ser complexo, implica em considerar os efeitos tanto dos fatores bióticos quanto dos bióticos que atuam sobre o organismo. E, ainda, os autores defendem que os modelos são capazes de projetar simulações da distribuição das espécies no espaço geográfico, entretanto não oferecem uma descrição do nicho das espécies, já que, embora haja disponibilidade de dados relacionados com condições ambientais, os dados sobre interações ainda são escassos ou de difícil interpretação. Isso significa dizer que a maioria dos exemplos na literatura tem utilizados apenas as variáveis abióticas em suas análises e assim a modelagem deveria ser considerada com modelagem de distribuição e não de nicho (ARAÚJO e GUIBAN, 2006; JIMÉNEZ-VALVERDE et al., 2008; PHILLIPS, 2008; ELITH e LEATHWICK, 2009; GIANNINI et al., 2012).

O modelo de nicho ecológico é embasado tecnicamente por três pilares fundamentais: a informação sobre as espécies (tolerância fisiológica a partir de dados de ocorrência), as variáveis ambientais (variáveis preditoras) e os próprios métodos analíticos (funções ou modelos que relacionam as informações sobre as espécies aos preditores ambientais). Dentro dessa perspectiva, o princípio geral da Modelagem de Nicho Ecológico é obter um mapa de adequabilidade ambiental, a partir de um modelo que descreve o nicho das espécies (PEARCE e FERRIER, 2000; GUIBAN et al., 2002; THUILLER, 2003).

Seguindo essa lógica, a ferramenta de modelagem nicho utiliza variáveis abióticas do lugar onde se registrou a ocorrência das espécies para construir um modelo do nicho utilizado por elas em todos os pontos de ocorrência conhecidos da espécie. A partir desse modelo, ela projeta as condições ambientais propícias para a ocorrência das espécies para locais em que a ocorrência não é conhecida e gera um mapa de distribuição potencial ao longo da área considerada.

A partir das variáveis analisadas no treino do modelo, a análise também pode extrapolar a ocorrência das espécies em outros períodos de tempo ou em outras regiões geográficas. Com base nisso, as projeções para o futuro ou reconstruções para o passado, por exemplo, são resultados do estabelecimento entre a distribuição conhecida da espécie e as variáveis abióticas da região onde a espécie se encontra, identificando, assim outras regiões que as espécies poderão habitar ou as mudanças na distribuição das áreas ambientalmente adequadas tanto no futuro quanto no passado (HEIKKINEN et al., 2006).

Portanto, o mapa de adequabilidade define quais locais são mais ou menos adequados à sobrevivência da espécie focal, dados seus requerimentos ecológicos (vale dizer, o modelo), o que é chamado de distribuição geográfica modelada ou mapa preditivo (ELITH e LEATHWICK, 2009; FRANKLIN, 2009). As áreas que satisfazem as condições do nicho realizado das espécies representam a sua distribuição potencial, enquanto as zonas geográficas em que elas realmente habitam constituem sua distribuição realizada (PHILLIPS et al., 2006). Mesmo quando um modelo é baseado nas exigências de nicho de uma espécie, as áreas que predizem a presença são geralmente maiores que a distribuição realizada, já que poucas espécies ocupam todas as áreas que satisfaçam seus requerimentos de nicho. Isto se deve a muitos fatores, como barreiras geográficas para dispersão, interações bióticas e modificações humanas no ambiente (GUISAN e THUILLER, 2005).

Como foi exposto, os modelos de nicho ecológicos têm se mostrado úteis especialmente no planejamento de ações de conservação, chamando a atenção para espécies ou ecossistemas ameaçados. É importante ressaltar, entretanto, que os modelos projetados precisam ser analisados com cautela, considerando, principalmente, as características biológicas e ecológicas de cada espécie avaliada, assim como outras variáveis como a fragmentação ambiental e outros impactos antrópicos sobre as espécies.

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CAPÍTULO I
REVISTA ECOLOGICAL MODELLING

An outlook of geoclimatic modeling based on the current patterns of distribution of tropical species of Lecythidaceae¹

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ABSTRACT

The expansion and/or retraction of biomes in the glacial and interglacial periods of the Quaternary had arisen new opportunities for speciation. This set of climatic fluctuations had a direct influence on the composition and structuring of the biodiversity of the Neotropical region, potentially reflecting the population dynamics of the species. Thus, studies on particular species produce key information on how climate, geological, and geographic changes have altered the demographic history of populations. In this context, ecological niche modeling is an important tool to predict changes in species distributions due to climate change using past climate scenarios. In this work, we used the algorithm of maximum entropy implemented in Maxent 3.3.3k to model the niche of four species of Lecythidaceae (*Cariniana ianeirensis*, *Couratari macrosperma*, *Lecythis lurida*, and *Lecythis pisonis*). These species, as important components of tropical ecosystems, constitute a good model for origin and evolution studies. The family Lecythidaceae is considered one of the 10 plant families of major interest for

¹ Abbreviations: LGM- Last Glacial Maximum; LIG- last interglacial

conservation and research because it has many species with restricted distribution and/or there are insufficient data about the conservation status of most of its species. To simulate the area of potential species distribution in past climatic scenarios, the present models were designed for scenarios during the mid-Holocene (6,000 years before present), the Last Glacial Maximum (21,000 years before present), and the last interglacial (132.000 years before present) periods.

Keyword: Maxent; Lecythidaceae; Climate changes; Ecological niche modeling; Geographic Information System; Quaternary.

1. Introduction

Lecythidaceae range from small to very large trees that grow mainly in hygrophilous forests below 1.000 m elevation, with few species occurring in savannas, várzeas, and forests over 1.000 m above sea level (Mori and Prance, 1981). The family has pantropical distribution and includes 25 genera and 300 species (Souza and Lorenzi, 2012) classified into four subfamilies: Planchonioideae, Foetidioideae, Napoleonaeoideae, and Lecythidoideae. The first three subfamilies are from the Old World and the fourth subfamily is limited to the New World, with the exception of *Asteranthos brasiliensis* Desf., a Napoleonaeoideae from the upper Negro River floodplain in Brazil (Mori and Prance, 1981). The subfamily Lecythidoideae have exclusively a Neotropical distribution and possibly form a monophyletic taxon (Mori et al., 2007; Prance and Mori, 2004). In Brazil, the members of this subfamily compose a high percentage of the Amazon forest, both in species richness and abundance (Mori et al., 2001). Although with fewer species, the Atlantic Coastal Forest constitutes another important distribution ecosystem of this subfamily (Mori, 1995).

The knowledge of the potential for occurrence of environmentally important species, such as the family Lecythidaceae, facilitates the definition of measures aimed at the conservation of species and allows the conduct of monitoring studies. In this context, understanding the spatial dimension from the analysis of geographic distribution is also a prerequisite for evolutionary studies (Morrone, 2004).

Quaternary climatic fluctuations encompass climatic cycles of different amplitudes and durations (alternations between colder and drier periods and between hotter and wetter periods) and have been considered a determinant historical factor in successive fragmentation processes during the extension of tropical forest cover (Bonnefille, 2007). In the Southern Hemisphere this period seems to have involved an alternation of dry and humid conditions, with forested biomes and savannas constantly changing in distribution (Haffer, 1997). This set of climatic fluctuations had a direct influence on the composition and structuring of the biodiversity of the Neotropical region, potentially reflecting the population dynamics of the species throughout evolutionary time.

In general, the climate had become progressively colder and drier after the last interglacial period (LIG; ~125,000 years ago) and until the Last Glacial Maximum (LGM; ~21,000 years ago), and then it became more hot and humid in the mid-Holocene (~6,000 years ago) (Nogués-Bravo et al., 2008). It is important to emphasize

that all the evidence strongly supports that past climate changes were extremely important events that had contributed to the change in vegetative pattern at both spatial and temporal scale. During this long period of great climatic oscillations, several species of organisms have undergone changes in their geographic distributions expressed in different ways for each region of the planet (Hewitt, 2004). As a consequence, many species/populations had their genetic structures modified or they reached extinction (Awise and Walker, 1998; Vanzolini, 1992; Vuilleumier, 1969).

Ecological niche modeling and predictions of past scenarios help to better understand the influence of climate in natural environments. The ecological niche models are statistical algorithms that use climatic and environmental variables to reconstruct the niche of a species and to predict areas in which the environment is favorable to the existence of this niche (Peterson and Soberón, 2012; Peterson et al., 2011; Soberón and Peterson, 2005). Considering that niche requirements of species may vary slowly (Peterson et al., 1999), it is possible to use the reconstructed niche from the recent species occurrences and project it into the past. This approach has already been used to study several important issues in paleobiology such as glacial refugia, megafauna extinctions, and impacts of past climate changes on species diversity and distribution (Lima-Ribeiro et al., 2012; Nogués-Bravo et al., 2008; Svenning et al., 2011; Varela et al., 2010; Werneck et al. 2012).

In this regard, predictive modeling of species distribution based on Hutchinson's ecological niche theory (1957) is a useful tool for making associations between species occurrence data and climatic variables through computational processes and producing models of the climatic conditions and climate tolerances necessary for species survival (Anderson et al., 2003).

In this context, the objective of this study is to analyze the ecological niche modeling of four tree species in the family Lecythydaceae for current and past climatic conditions (LIG, LGM, and mid-Holocene). The four species of Lecythydaceae *Couratari macrosperma* A.C. Smith, *Cariniana ianeirensis* R. Knuth, *Lecythis lurida* (Miers) Mori, and *Lecythis pisonis* Cambess constitute a good model for studies on the origin and evolution since they represent important components of tropical ecosystems.

2. Materials and methods

For these models, the occurrence records of *C. ianeirensis*, *C. macrosperma*, *L. lurida* and *L. pisonis* were obtained using data sources available from Species Link (<http://www.splink.cria.org.br/>) and Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>). A total number of 352 occurrence records of *L. lurida*, 90 of *Couratari macrosperma*, 37 of *Cariniana ianeirensis*, and 510 of *L. pisonis* were obtained.

To characterize the climate requirements of the species, we used a set of 19 bioclimatic layers representing temperature and precipitation combinations in the last 50 years with a resolution of 2.5 arc min (Hijmans et al., 2005); these layers were obtained from the WorldClim website (www.worldclim.org/verson1). The environmental layers considered were as follows: (1) Annual Mean Temperature; (2) Mean Diurnal Range; (3) Isothermality; (5) Max Temperature of Warmest Month; (6) Min Temperature of Coldest Month; (12) Annual Precipitation; (13) Precipitation of Wettest Month; (14) Precipitation of Driest Month; (18) Precipitation of Warmest Quarter; and (19) Precipitation of Coldest Quarter. To reduce the multicollinearity among the 19 bioclimatic variables, the variables with Pearson correlation $r \geq 0.75$ were eliminated. This reduction of the predictor variables resulted in the inclusion of 10 variables for the models.

For niche modeling, we opted for the maximum entropy algorithm implemented in the Maxent 3.3.3k program (Phillips and Dudík, 2008). This algorithm has outperformed other modeling methods that have been also based on species presence registers in performance tests (Elith et al., 2006; Phillips et al., 2006). To run the model, convergence threshold was set to 1.0E-5 with 500 iterations and 10,000 background points and auto features and random seed options on.

The dataset was submitted to 10 replicates of the model, with a cross-validation (bootstrap type) with reset, in which the data were divided into two independent sets, 70% of the data were used for calibration and 30% to validate the model (Pearson, 2007). The final model used was based on the average of the 10 repetitions performed by the program. The model was evaluated by using the parameters of area under the curve (AUC), omission rate, and probability p (binominal probability) (Pearson, 2007).

Maxent estimates the most uniform distribution (maximum entropy) within the study area by taking into account the environmental information obtained from species presence registers and their distribution environment (Phillips et al., 2006). In addition,

Maxent has been shown to be more efficient in predictive modeling of species distribution (Elith et al., 2006; Hernandez et al., 2006; Mateo et al., 2010). Its use is facilitated because it does not rely on absence data (Elith et al., 2010), information that is difficult to obtain and unreliable for the tropical region (Graham et al., 2004).

A classification proposed by Yang et al. (2013) recognizes five classes of potential habitats: inadequate habitat (0.0–0.2), poorly suitable habitat (0.2–0.4), suitable habitat (0.4–0.6), highly suitable habitat (0.6–0.7), and extremely suitable habitat (0.7–1.0). For each model, the area of the optimum distribution was calculated and classified as approximate or very high (0.6–1.0).

To simulate the area of potential distribution of species in past climatic scenarios, the present models were designed for scenarios during the average mid-Holocene 6,000 years before present, during the LGM 21,000 years before present, and during the LIG 132,000 years before present. The final maps were made with the help of ArcGIS 10 software (Esri Inc., Redlands, CA, USA).

3. Results

The AUC values of the obtained models were higher than 0.9, which according to the classification for AUC values proposed by Metz (1986), indicate that the models are highly accurate. The results of the binomial test indicated that the models generated were significantly different from those expected at random ($p < 0.001$) and showed high AUC values (>0.90) and low omission errors (Table 1).

SPECIES	CURRENT			MID-HOLOCENE		
	AUC model	<i>P</i>	Default rate	AUC model	<i>P</i>	Default rate
<i>C. macrosperma</i>	0.942	0.000	0.111	0.945	0.000	0.088
<i>C. ianeirensis</i>	0.909	0.001	0.092	0.923	0.001	0.089
<i>L. lurida</i>	0.952	0.000	0.072	0.958	0.000	0.084
<i>L. pisonis</i>	0.948	0.000	0.076	0.948	0.000	0.960
SPECIES	LGM			LIG		
	AUC model	<i>P</i>	Default rate	AUC model	<i>P</i>	Default rate
<i>C. macrosperma</i>	0.951	0.000	0.109	0.939	0.000	0.104

<i>C. ianeirensis</i>	0.906	0.000	0.084	0.905	0.000	0.101
<i>L. lurida</i>	0.953	0.000	0.087	0.955	0.000	0.077
<i>L. pisonis</i>	0.951	0.000	0.085	0.946	0.000	0.097

Table 1- Results of the modeling procedure for four species of the Lecythydaceae family in different climatic scenarios (mid-Holocene, Last Glacial Maximum and Last Interglacial).

Projections indicated that there had been considerable changes in environmental conditions for these species over time. Particularly, the size of the current potential distribution of *Couratari macrosperma* and *L. lurida* was higher than that in the mid-Holocene, whereas the area of *Cariniana ianeirensis* and *L. pisonis* presented a loss of 52.9% and 14.7%, respectively. Between the LIG and LGM periods, the results of the niche modeling showed a loss of area for all species except for *C. macrosperma* whose area increased by 71.8% (Table 2).

SPECIES	CURRENT	MID-HOLOCENE	LGM	LIG
<i>C. macrosperma</i>	162,31	132,39	102,71	59,79
<i>C. ianeirensis</i>	862,29	1831,80	825,45	2019,74
<i>L. lurida</i>	147,76	138,19	138,19	143,02
<i>L. pisonis</i>	141,28	165,59	67,45	204,00

Table 2. Optimum distribution area (0.6 -1.0) in different climatic scenarios (each pixel has 2.5 arc-min). This evaluation was used to estimate the loss/ gain changes of areas (in Km²) suitable for four species of Lecythydaceae.

The projections indicated that during the LGM (21,000 years) and LIG period (132,000 years), there were considerable changes in the environmental conditions of these species (Table 2). The geographic distribution of the studied species was strongly influenced by the global variation in temperature and humidity. However, the species responses followed a different pattern.

The projections based on the current climate showed that the areas of optimal stability of *Couratari macrosperma* resumed expanding in the mid-Holocene (Fig. 1a). The current distribution model predicted areas of optimal suitability in the state of Acre and between the coast of São Paulo and Sergipe. The model showed that during the LGM (21,000 years before present) the area of environmental suitability of this species increased, whereas the area of the other three studied species decreased or was altered during the climatic oscillations. In the LGM, the area of optimum suitability of *C. macrosperma* was restricted to the Amazonian phytogeographic domain, mainly in

the southeastern Roraima, northern Pará, and southern Amapá. During the LIG period, the model for *C. macrosperma* (Fig. 1d) predicted an area of optimal suitability between the coast of Bahia and Pernambuco (phytogeographical domain of the Atlantic Forest) and an isolated point of high suitability in northwestern Roraima. There was evidence of a contact zone in the past between the Amazon and Atlantic Forest. In the mid-Holocene, the area of environmental suitability increased in Roraima, Acre, and along the coast between Rio de Janeiro and Bahia (Table 2).

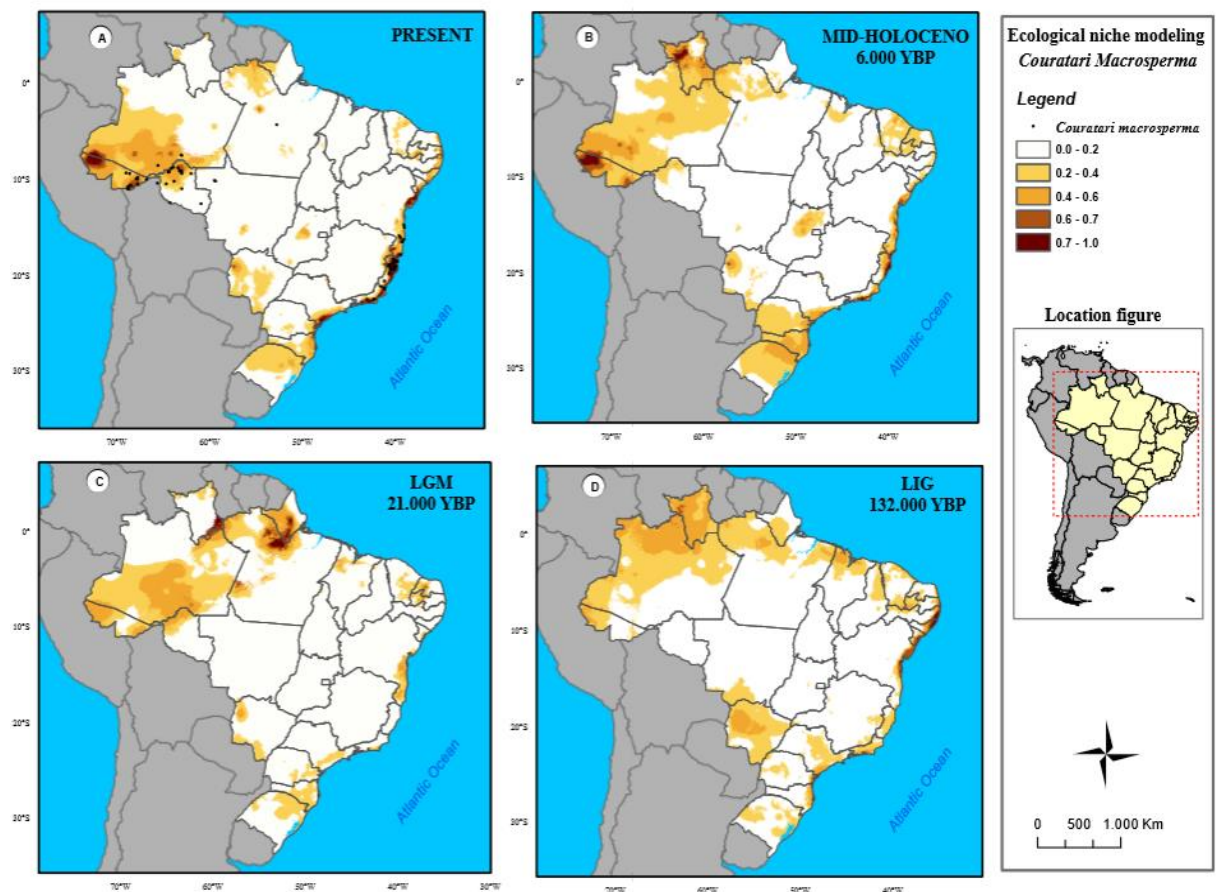


Fig.1. Areas with high environmental suitability (0.6-1.0) in the Brazilian territory for *Couratari macrosperma* A.C. Smith in past climatic scenarios.

According to the LIG scenario, *Cariniana ianeirensis* presented an area of broad suitability (Fig. 2d), extrapolating the phytogeographical domains of the Amazon and the Atlantic Forest (Fig. 2d). The climate change in the scenario of the LGM to conditions that were drier than they are today probably caused the retraction of this species mainly to the Amazonian phytogeographical domain and the coastal strip north of Espírito Santo, with a disjunction in southern Brazil (Fig. 2c). According to the model generated for *C. ianeirensis*, the environmentally adequate area of this species expanded during the mid-Holocene in relation to the LGM (by 121, 9%). In the present-day scenario, the area of suitability retracted from the Amazonian phytogeographical domain and

concentrated in the South Region, west of Mato Grosso do Sul, and along the coast from the state of Alagoas to São Paulo (Fig. 2a).

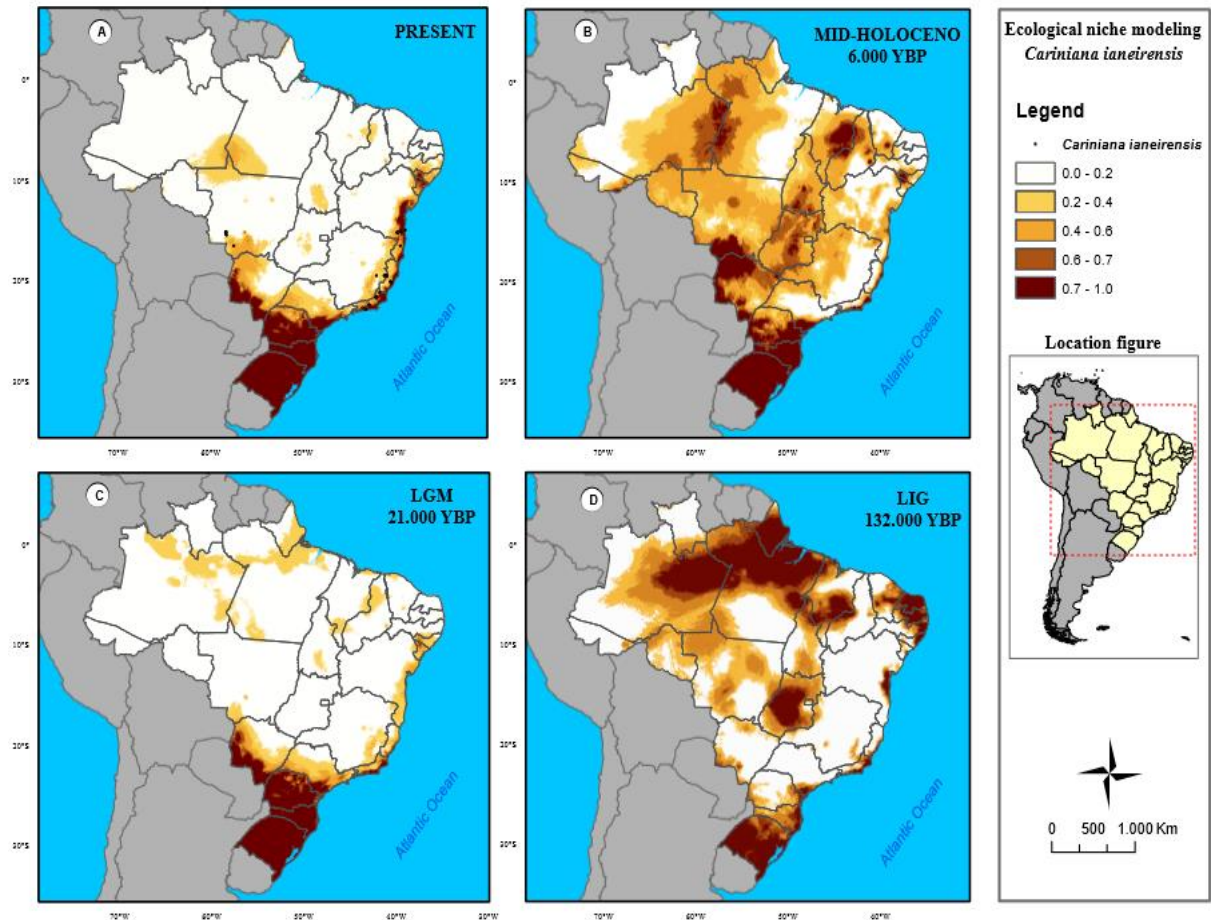


Fig.2. Areas with high environmental suitability in the Brazilian territory for *Cariniana ianeirensis* R. Knuth in past climatic scenarios.

The reconstructed distribution of *L. lurida* was similar with the model proposed for *L. pisonis*, with some particularities. During the LIG period, *L. lurida* concentrated mainly in an area northeast of Pará and north of Tocantins (Fig. 3d). In general, there was a slight decrease (3.4%) in environmentally suitable areas during the LGM period compared to the LIG (Table 2). Namely, during the LGM there was a small reduction in propitious conditions for optimal adaptation, resulting in a displacement of the area of species occurrence mainly to the coastal region between Pernambuco and Rio de Janeiro, north of Pará, east of Amapá, and in an isolated location in Maranhão (Fig. 3c). The *L. lurida* model predicts a retraction of the area of distribution during the LGM, followed by a period of stability in population size in the mid-Holocene and a subsequent increase in the current period (Table 2). In the mid-Holocene, the area of optimum suitability for the species expanded to northern Piauí, Ceará, and Paraíba, covering similar areas that were present during the LGM. The model of the present-

day scenario of this species concentrated the suitable area mainly in the coastal strip, with a vestige in northern Pará and Maranhão and an isolated point in Mato Grosso do Sul (Fig. 3a).

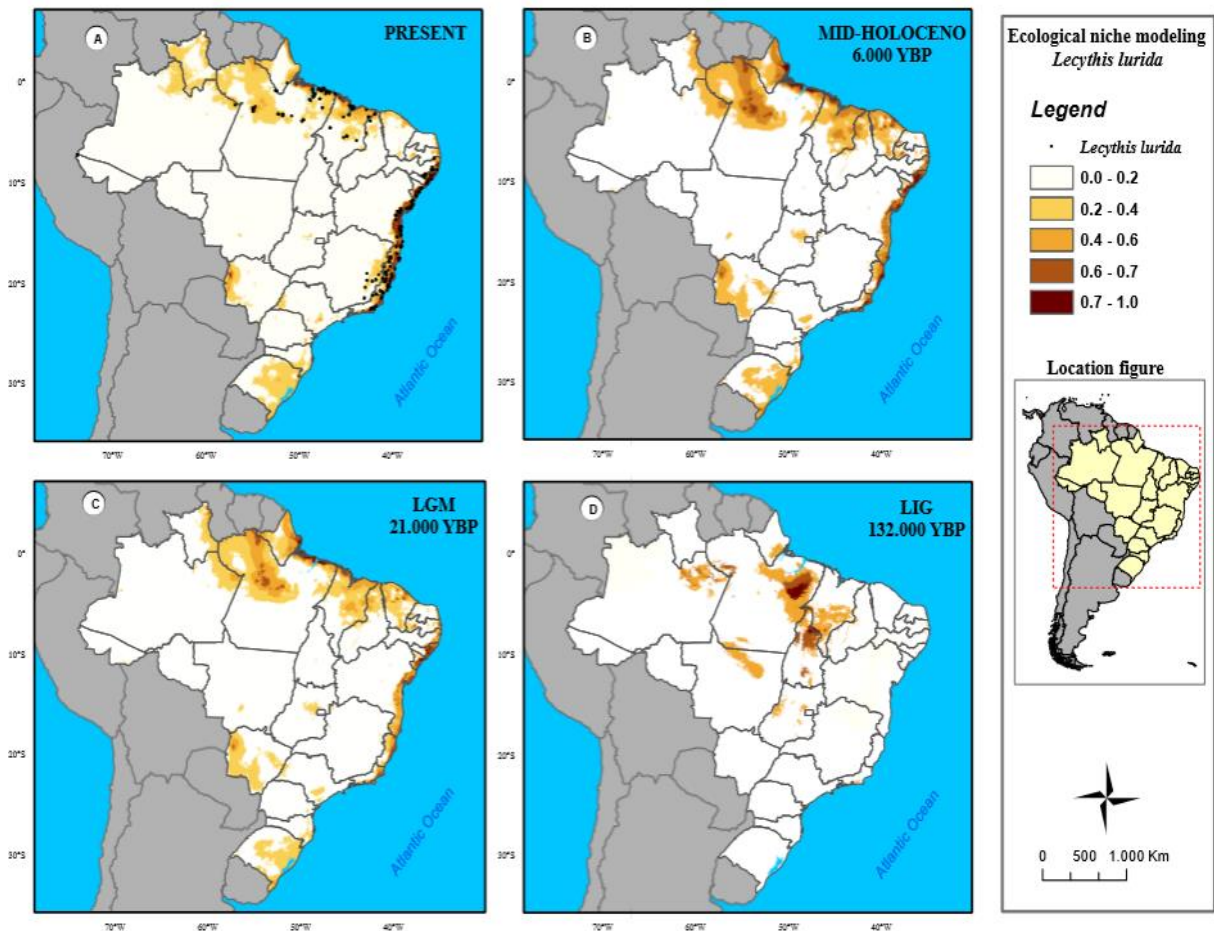


Fig.3. Areas with high environmental suitability in the Brazilian territory for *Lecythis lurida* (Miers) Mori in past climatic scenarios.

In the LIG scenario, the models suggested that the ideal adequate area of distribution of *L. pisonis* was concentrated in the northeastern Amazonia, Pará, Tocantins, western Maranhão, northern Mato Grosso, eastern Goiás, southern Minas Gerais, and northern São Paulo (Fig. 4d). The models for this species predicted a marked change in its area of occurrence during the LGM, limiting it from the coast of Paraíba to southern Bahia and isolated points in Maranhão, Pará, Roraima, and Mato Grosso (Fig. 4c). The model of the present-day scenario concentrated the species mainly in the coastal strip and along the Amazon River (Fig. 4a), which was very similar to the distribution pattern during the mid-Holocene. During the LGM, the model predicted that the area of occurrence of *L. lurida* underwent retraction (by 67%) in relation to the area in LIG, and it was followed by an increase during the mid-Holocene and a retraction in the current period (Table 2).

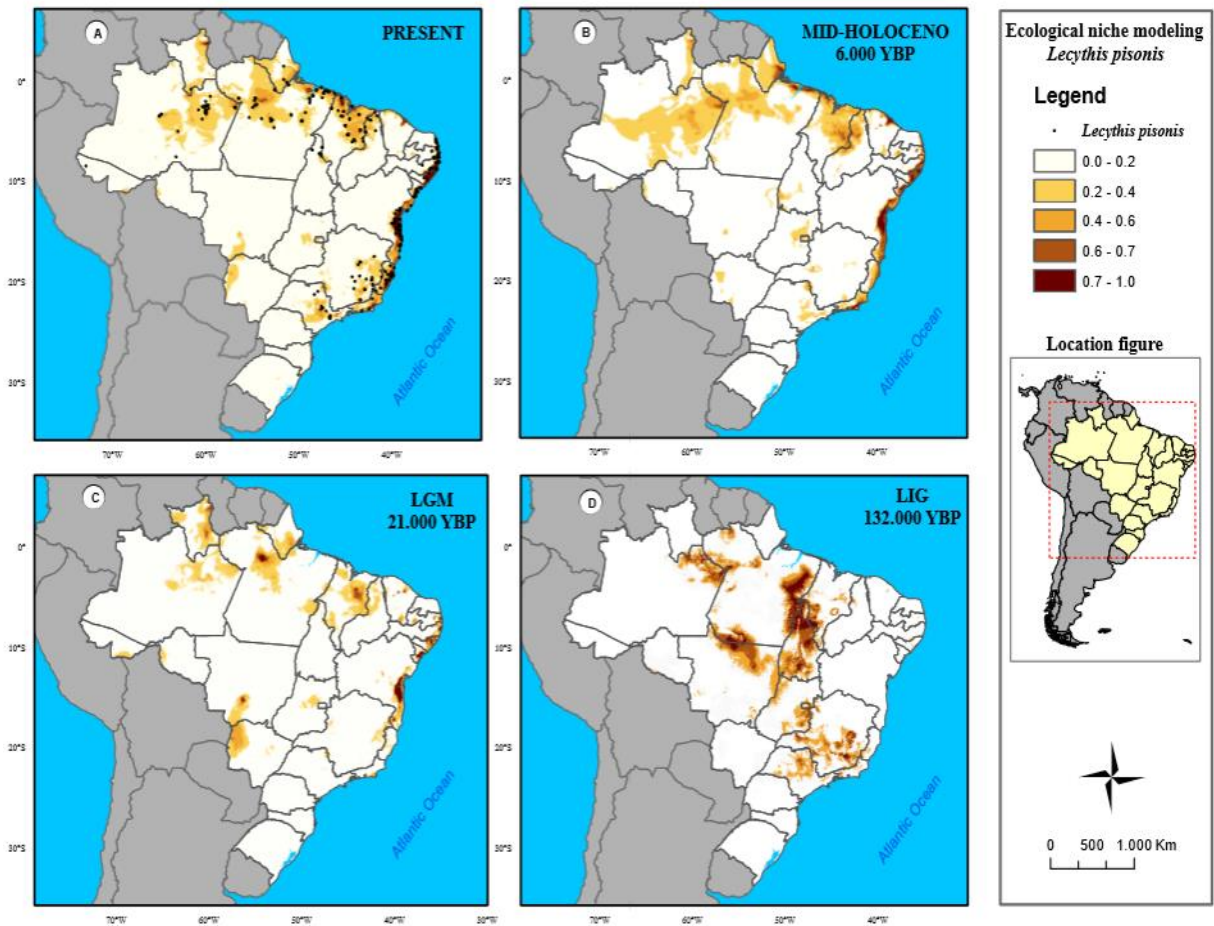


Fig.4. Areas with high environmental suitability in the Brazilian territory for *Lecythis pisonis* Cambess in past climatic scenarios.

In the mid-Holocene, the prediction maps point to an increase in the area of high suitability for the four studied species, with the exception of *L. lurida*, which occupied the same area since the LGM period. The comparison between predicted and past distributions indicates changes in the general distribution of species. In the modeling of climatic changes from the current period to the LGM, it is possible to perceive both increase and decrease in optimal areas. The selected species presented different distribution patterns related to specific environmental conditions within their tolerance range. Thus, we suggest that species sensitivity may depend on their ecological properties related to regional patterns of exposure to climate change.

4. Discussion

Couratari macrosperma has records of well-spaced occurrence, with disjunct distribution in flood-free forests from the south-central and southwestern regions of the

Brazilian Amazon to the Atlantic Rainforest (Mori et al., 2010). The species is distributed in Bahia, Espírito Santo, Rio de Janeiro, Pará, Western Amazonia, northern Bolivia, and Peru (Smith et al., 2016). Potential distribution models show an expansion of the optimal suitability of areas during the LIG period up to the current period (Table 2).

The model generated for *Cariniana ianeirensis* evidenced a retraction in the area of suitability of the species, mainly in the Amazonian phytogeographic domain of the present period in relation to the average mid-Holocene (Fig. 2b). There was also a considerable reduction in the area of suitability during the LGM; in contrast, its area of distribution increased considerably in the mid-Holocene and LIG (Table 2). The species is distributed from Rio de Janeiro to Bahia, in Mato Grosso, and in Bolivia, with more than 90% of the analyzed collections being outside the protected areas (Smith et al., 2016). The species is listed as threatened in the IUCN red list (IUCN 2014). It was the only species that presented an area of optimal suitability concentrated in the south.

The distribution of *L. lurida* indicates that this species has registere in the state of Rio de Janeiro to Alagoas (eastern Brazil) and Eastern Amazon, although part of the habitat occurs in fragmented areas that are in decline (Smith et al., 2016). The species is endemic to Brazil and listed as lower risk according to IUCN (IUCN 2014). Potential distribution models include areas in the Atlantic phytogeographical domain (coastal strip) and a disjunct area in the eastern Amazon Forest (Fig. 3). The models predicted a retraction of the species distribution during the LGM period, stability in the potential area during the average mid-Holocene, and a subsequent increase in distribution in the present (Table 2).

Lecythis pisonis is native to eastern Brazil and the Brazilian Amazon and mainly distributed in Eastern Amazon, along the Amazon River, and in Colombia and Peru. In eastern Brazil, it is common in fragments of primary forests and agricultural lands of Espírito Santo and Bahia (Smith et al., 2016). The models predicted a reduction of the species distribution during the LGM period; increased considerably in mid-Holocene, and a reduction in distribution in the present (Table 2).

Palynological data from the LGM period suggest colder and drier conditions during this period compared to the present which resulted in an expansion of savanna vegetation and a reduction in the rainforest (Behling, 2002). However, these events were not strong enough to wipe out the species, but they caused only a retraction and/or alteration of the areas of suitability of the studied species. The distribution of

species adapted to wet climates retracted during the driest glacial periods, expanding later over the same areas during the humid Pleistocene periods (Lima et al., 2014; Palma-Silva et al., 2009; Turchetto-Zolet et al., 2012). The combined effects of reduced annual rainfall and lower temperatures led to habitat shrinkage and fragmentation of the studied species, except for *Couratari macrosperma*, whose area of suitability expanded in the glacial period (Table 2). Interglacial periods, with similar characteristics to the current climate, would have provided, in an inverse way, ideal conditions for the expansion of forest biomes and the retraction of open formations (Vonhof and Kaandorp, 2010) as shown in Figs. 2-4.

In the mid-Holocene, a significant expansion of the optimal area (0.6–1.0) of the species is well supported by our results. During this period, *Cariniana laneirensis*, *L. pisonis*, and *Couratari macrosperma* exhibited a larger area of continuous potential distribution compared to those in the LGM, whereas the distribution area of *L. lurida* remained stable (Table 2). According to Mayle et al. (2004), tropical forests may have expanded more than once in the late Holocene due to increased rainfall.

Based on the hypothesis that current disjunct areas are the remnants of a more continuous distribution in the past, it is important to verify whether adequate conditions for species occurrence existed in the intermediate areas that would allow the dispersion and occupation of the present disjunct areas. Therefore, the occurrence of plant taxa with a disjunct distribution between the Amazon and the Atlantic Forest reinforces the possibility of previous connections due to expansion events in South America (Batalha-Filho et al., 2013; Carvalho, 2013; Oliveira et al., 1999). This hypothesis based on the distribution of *Lecythis pisonis* has been also discussed by Mori and Prance (1981).

In the present study, we detected fragments of potential areas of distribution that connect these disjunct areas during the LIG (Figs 1d and 2d) and the mid-Holocene (Figs. 3b and 4b). The results suggest the distributive dynamics of the species, signaling past links of the Neotropical forests, as well as providing indications about the climatic conditions of their different parts that may have affected their past spatial displacements.

The study by Batalha Filho et al. (2012) similarly points to two periods during which there could have been a connection between these biota, an older one (from the middle to the end of the Miocene) and a more recent one (Pliocene to Pleistocene). Today, there are three sites that were the regions of contact between these forests. One of them, located between the southeastern Amazon and southern Atlantic Forest,

is an important connecting area. The other occupies two areas in northeastern Brazil—one adjacent to the north coast spreads along the coastal zone of the States of Maranhão, Piauí, Ceará, and Rio Grande do Norte and the other extends through the states of Tocantins and Bahia in inner northeastern Brazil (Batalha Filho et al., 2012; Costa, 2003). Thus, the projected models support the hypothesis of connection along the route adjacent to the coast.

The projected models also illustrated a possible differentiation of the Atlantic Forest into two distinct biogeographic units, one in the northern region and the other in the southern part of the forest, with the Doce River acting as a divider. Other biogeographic studies demonstrated a historical division of species into the southern area and northern area of the Atlantic Forest domain (Costa, 2003; Perret et al., 2006). Paleoclimatic studies by Cheng et al. (2013) reported that the changes in precipitation and temperature regime differed between the southern and northern sections of the Atlantic Forest since the LGM (21,000 years ago). Most studies agree that there is a historical separation between the northern and southern parts of the domain, and the boundaries between the two are coincident with the valley of the Doce River in northern Espírito Santo State (DaSilva and Pinto da Rocha, 2011; Fiaschi and Pirani, 2009; Goldani et al., 2006; Müller, 1973; Silva et al., 2004).

The knowledge about geographic distribution of a given taxon is the first step toward understanding the processes that are responsible for diversification of different groups (Fiaschi and Pirani, 2009). Although each species has its own distribution pattern, pattern repetition may reflect past and paleoclimatic connections as they are related to current limiting environmental factors. Therefore, the distribution of certain species is directly associated with both ecological and historical issues (Marchioretto et al., 2009).

To study the geographic distribution of a species means to understand the complex expression of its ecology and evolution, which are influenced by several factors that operate at different intensities and scales, such as the evolutionary history of the species and its dispersion capacity (Brown and Lomolino, 2006). Each population has a limited range of tolerances to climate variables, i.e., it has a climate envelope (Corlett and Westcott, 2013). This climate envelope may change with changes in climate, altering the distribution of populations over time, which will allow the populations to remain within the envelope, eventually resulting in changes in the global distribution of species (Corlett and Westcott, 2013). Although ecological niche models generally assume that species respond to their abiotic tolerances, it is widely

recognized that other factors related to biotic interactions and biogeographical or evolutionary processes also influence the pattern of species distribution (Wiens and Donoghue, 2004; Wisz et al., 2013).

5. Conclusions

The results presented herein strongly reinforced the importance of ecological niche models as a prediction tool and their applicability in modeling, particularly of an ecologically important group of species such as Lecythidaceae. In this regard, modeling studies provided a better understanding of the effects of climatic variables on the current species distribution and allowed assessments under different climatic scenarios in the past. Given the scenario of environmental changes, knowledge about the distribution of these species aims to increase the information about the diversity of this important family, thus becoming an indispensable tool for the conservation and management of natural resources.

Funding: This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Conflicts of interest: None.

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Modeling of climatic aptitude of arboreal species in the face of climate change scenarios in Brazil

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ABSTRACT

This study aimed to evaluate the influence of climate change on the distribution of three species of the Lecythidaceae family, and to predict possible changes in future climatic scenarios for Brazil by using ecological niche modeling. The MaxEnt algorithm (maximum entropy) was used in two different scenarios, one pessimistic (A2) and the other optimistic (B2), for the years 2050 and 2070. It also evaluated the reduction of habitat percentage of the species based on climate change scenarios through the

Geographic Information System (GIS). All models were significant ($p < 0.001$), presented high AUC values (> 0.90) and low omission errors. The results showed that a reduction in the suitable habitats in scenarios (A2 and B2) and periods (2050 and 2070) analyzed, exception *C. macrosperma* (B2-2050) and *L. lurida* (A2 2070). The largest area loss (close to 76.3%) is verified for *C. macrosperma* between the current scenario and the A2-2050 scenario.

Keyword: MaxEnt; Lecythydaceae; Climate changes; Ecological niche modeling.

1. INTRODUCTION

Climate change has contributed to significant changes in the geographical distribution of species over the previous decades (Walther et al., 2002; Root et al., 2003; Parmesan, 2006). In addition to altered distribution patterns, some species have decreased in abundance, leading to fears that climate change may result in widespread decline and loss of species (Thomas et al., 2004; Deustsch et al., 2008). Predicting the potential impacts of climate change on areas of high species richness faces a particular challenge due to the lack of accurate data for a large number of species, especially tropical forest biomes that are at high risk of loss of biodiversity as a result of climate change (Huntingford et al., 2008). Therefore, it is crucial to understand how species, dynamics, and composition of local ecosystems can be affected by, and how climate change will respond to, these disturbances.

The geographical distribution of each species reflects a complex expression of its ecology and evolutionary history, in which several factors such as biotic and abiotic conditions, access to the regions, and the capacity of adaptation to new conditions operate (Soberón & Peterson, 2005). Thus, the current distribution limits of species are not only conditioned by their ecological and physiological characteristics, but also depend on the geographic space where their evolution and speciation occurred (Segurado, 2000). Therefore, the distribution areas of a species are the convergence of various aspects of biology and ecology, including body size, population density, dispersion potential, resource availability, ecological interactions, physiological constraints, and adaptive mechanisms that shape the species throughout its evolutionary history (Brown et al., 1996).

Within this perspective, understanding the importance of each of these factors and the degree of interaction between them in spatial structuring of species

distributions is of primary interest in ensuring the effective conservation of biodiversity. In the case of plants, global climate change can affect geographic distribution, life cycle, biological interactions, and many other factors (Thuiller et al., 2008). As a result, studies aiming to anticipate the nature and magnitude of climate change-related changes in biodiversity are critical.

In this scenario, Ecological Niche Modeling will be used as the basis of this study. Ecological niche models (MNEs) have also been called bioclimatic envelope models, or species distribution model (MDES) (Elith & Leathwick, 2007). Specifically, this tool relates species distribution data (occurrence or known locations) to information on the environment and/or characteristics of these sites (Elith & Leathwick, 2009; Franklin, 2010; Hartley et al., 2010). An environmental model is intended to relate a particular characteristic or phenomenon (dependent variable or response variable) with environmental factors (independent variables or covariables), whose variation in space are the justification for extrapolation across the study area.

Recently, the use of Ecological Niche Models has increased in the scientific literature and has proven to be a very effective tool in several areas of science (Peterson et al., 2011; Vaz et al., 2015). The use of ecological niche modeling has been an important tool for predicting suitable areas for the establishment of species under current and future climatic projections (Beaumont et al., 2008; Franklin, 2010; Nori et al., 2011; Collevatti et al., 2013). In general, this type of model has been influenced by Hutchinson's concept of niche (Lavergne et al., 2010). Several examples of species distribution modeling have been applied in predicting the effects of climate change, including Peterson et al., 2001; Oberhauser & Peterson, 2003; Siqueira & Peterson, 2003; Araujo et al., 2006; Colombo, 2007; Carnaval et al., 2009; Kramer et al., 2010; Loiselle et al., 2010; Pearman et al., 2010; Saupe et al., 2011; Watt et al., 2011; Klamt et al., 2011; Maiorano et al., 2011; Zimbres et al., 2012.

The Lecythidaceae family are environmental indicators, making them excellent model organisms for studies of biogeography. Studies of this family make for interesting ecological niche modeling, constituting important representatives for studies on the evolution and conservation of biodiversity. The use of these species as environmental indicators are valuable to try to understand the physical and biological conditions that characterize the environment, and for the identification of events responsible for changes (gradual and abrupt) that may occur over time.

In this context, the objective of this study is to evaluate the potential impact of climate on the geographic distribution of three species of Lecythidaceae (*Couratari macrosperma* A.C. Smith, *Cariniana ianeirensis* R. Knuth and *Lecythis lurida* Miers), considering the current climate and future climate change scenarios, and how to contribute to the understanding of the influences of climate changes in relation to the limits of the ecological niche for survival in these species. This understanding is important because of the ecological role these species represent in the composition, structure, and function of forest ecosystems.

2. MATERIALS AND METHODS

Three tree species of Lecythidaceae (*Cariniana ianeirensis*, *L. lurida* and *Couratari macrosperma*) were analyzed. The occurrence data of each species was searched using data sources, available from Species link and the Global Biodiversity Information Facility (GBIF). The occurrence records of 352 *L. lurida*, 90 *C. macrosperma*, and 37 *C. ianeirensis* obtained from different sources (Gbif, Species link) were used.

To characterize the needs of species in terms of climate, we used a set of 19 bioclimatic layers that represent combinations of temperature and precipitation in the

last 50 years with a resolution of 2.5 arc-min (Hijmans et al., 2005), to be combined with points of occurrence of the species, and then produced the models. These layers were obtained from the Worldclim website (www.worldclim.org/version1) for the present period, for 2050 and for 2070. The environmental layers considered were as follows: (1) annual mean temperature; (2) mean diurnal range; (3) isothermality; (5) max temperature of the warmest month; (6) min temperature of the coldest month; (12) annual precipitation; (13) precipitation of the wettest Month; (14) precipitation of the driest month; (18) precipitation of the warmest quarter; (19) precipitation of the coldest quarter. In addition, we use an elevation variable. To reduce the multi-collinearity of environmental variables, a multivariate statistical method of principal component analysis (PCA) was applied, selecting the variables with Pearson correlation $r \geq 0.80$. This reduction of the predictor variables resulted in the inclusion of eleven variables for the models.

To predict future conditions, the same eleven layers projected for the 2050 and 2070 periods were used. Future projections were obtained from the global climate models CCSM4 (Community Climate System Model), and are based on the projections developed by the Intergovernmental Panel on Climate Change. Projections are based on data from the fifth report, based on two future scenarios of CO₂ emission, RCPs (Representative Concentration Pathways) RCP 4.5 (optimistic scenario) and RCP 8.5 (pessimistic scenario) (IPCC, 2013).

The RCP 4.5 scenario corresponds to CO₂ emission levels of 650 ppm (parts per million), and a temperature increase of 1.8°C (± 0.7) for the year 2080. This is the more desirable scenario, in which the level of CO₂ in the atmosphere stabilizes just after 2100. However, the RCP 8.5 scenario, which corresponds to CO₂ emission levels of 1370 ppm and an increase in temperature of 3.7°C (± 0.9), is admittedly the most likely to occur (Schardong et al., 2014).

We used the MaxEnt algorithm, which consists of a prediction or inferential method based on presence data (Philips et al., 2006), to estimate the probability of the species being present given a certain environment (Elith et al., 2011). The MaxEnt algorithm is one of the most widely used methods (Vaz et al., 2015); it is a machine learning and statistical method (Franklin, 2009), which associates records of single presence species with bioclimatic variables, according to the principle of maximum entropy (Elith et al., 2011). The MaxEnt approach is especially useful because it can be applied to analyze presence data only (Wisz et al., 2008), a form of data that is frequently collected in tropical regions (Feeley & Siman, 2011). We used the MaxEnt software package available online (<http://www.cs.princeton.edu/~schapire/maxent/>), and its standard with 500 interactions.

The data set was submitted to 10 replicates of the model, with a cross-validation (bootstrap type) with replacement, in which the original data of each species were randomly divided into calibration (70%) and evaluation subsets (30%) (Fielding and Bell 1997). The area under the Operating Characteristic Curve (ROC curve) was applied to estimate the quality models (Fielding & Bell, 1997). The ROC analysis is based on the measure of sensitivity, which corresponds to the true positive rate (absence of omission error), compared to the specificity (overshoot error). In this way, the ROC analysis evaluates the ability of the model to correctly predict the occurrence of the species. For a level of interpretation, the closer the area under curve (AUC) value is to 1.0, the less the results are due to the random prediction model (Phillips et al., 2006).

For visualization and further analysis, we imported the results of the MaxEnt models predicting the presence of the species (interval 0-1) into a classification proposed by Yang et al. (2013), with five classes of potential habitats being regrouped: Inadequate habitat (0.0-0.2); poorly suitable habitat (0.2-0.4); Suitable habitat (0.4-

0.6); Highly suitable habitat (0.6-0.7); Extremely suitable habitat (0.7-1.0). For each model, the area of optimum distribution was calculated, and classified as approximate or very high (0.6-1.0). Based on this information, we evaluated the percentage reduction of the appropriate surface area of the species in the future climate change scenario. All of these procedures were performed with ArcGIS 10 software (Esri Inc., Redlands, CA, USA).

3. RESULTS

The models obtained for all species presented AUC values higher than 0.9 and can be considered to be exact. According to Metz (1986), AUC values above 0.9 indicate that the quality of the model is excellent and values between 0.8-0.9 indicate a model of good quality. The modeling results can be seen in the maps below. All models were significant ($p < 0.001$), had high AUC values (> 0.90), and low omission.

Table 1 - Results of the modeling procedure for three species of the Lecythidaceae, with a pessimistic (A2) and an optimistic (B2) profile in scenario of future climate changes for the years 2050 and 2070.

SPECIES	PESSIMISTIC								
	CURRENT			A2(2050)			A2(2070)		
	AUC model	<i>P</i>	Default rate	AUC model	<i>P</i>	Default rate	AUC model	<i>P</i>	Default rate
<i>C. macrosperma</i>	0.942	0.000	0.101	0.955	0.000	0.076	0.944	0.000	0.095
<i>C. ianeirensis</i>	0.909	0.001	0.116	0.949	0.001	0.057	0.943	0.000	0.078
<i>L. lurida</i>	0.952	0.000	0.095	0.962	0.000	0.075	0.962	0.000	0.067
SPECIES	OPTIMISTIC								
	CURRENT			B2(2050)			B2(2070)		
	AUC model	<i>P</i>	Default rate	AUC model	<i>P</i>	Default rate	AUC model	<i>P</i>	Default rate

<i>C. macrosperma</i>	0.942	0.000	0.101	0.953	0.000	0.085	0.956	0.000	0.085
<i>C. ianeirensis</i>	0.909	0.001	0.116	0.954	0.001	0.064	0.943	0.001	0.005
<i>L. lurida</i>	0.952	0.000	0.095	0.960	0.000	0.076	0.961	0.000	0.067

According to our results, almost all species found a reduction in the appropriate occurrence areas in scenarios (A2 and B2) and periods (2050 and 2070) analyzed, exception *C. macrosperma* (B2-2050) and *L. lurida* (A2 2070) (Table 2). The when comparing the current scenario to the A2-2050 scenario, the largest area loss (close to 76.3%) was verified for *C. macrosperma*. The second species that presented the greatest loss of area was *C. ianeirensis* when the current scenario was compared to scenario B2-2050 (67.2%) and to A2-2050 (63.9%). The model also projected an expansion of the appropriate areas for *L. lurida* (plus 465%), when comparing A2-2050 and A2-2070 scenarios (Table 2). In addition to the alteration of the amount of area predicted as adequate, the association between these data demonstrates the reorganization between areas considered as adequate and inadequate. The results of the proportions test showed a significant loss of areas considered environmentally adequate for the three species.

Table 2. Optimum distribution area (0.6 -1.0) in different climatic scenarios (each pixel has 2.5 arc-min). This evaluation was used to estimate the loss/ gain changes of areas (in Km²) suitable for three species of Lecythidaceae, with a pessimistic (A2) and an optimistic (B2) profile in scenario of future climate changes for the years 2050 and 2070.

SPECIES	CURRENT	A2 2050	A2 2070	B2 2050	B2 2070
<i>C. macrosperma</i>	162,31	38,46	37,58	169,91	70,97
<i>C. ianeirensis</i>	862,29	311,47	319,81	283,16	403,11
<i>L. lurida</i>	147,76	99,49	563,02	117,81	109,20

The variables that contributed most to the suitability of the areas with optimal distribution for the current climate and the modeling of climate change for the different CO₂ emission scenarios (RCP 4.5 and RCP 8.5) were: daily thermal amplitude (2); maximum temperature of the hottest month (5); precipitation of the wettest month (13); and precipitation of the driest month (14).

C. macrosperma presents well-spaced occurrence records, prevailing in the western Amazon and eastern Brazil (Figure 1a). Regarding the modeling itself, from the probabilistic data presented, it can be said that the generated model had a satisfactory performance, since the AUC was close to one, that is, different from the random one and the binomial probability was 0.000 in all scenarios, indicating the low probability of this model being generated at random (Table 1).

Future distribution models showed a reduction in the distribution area in almost all scenarios of greenhouse gas emissions, with the exception of scenario B2 2050 (increased by 4.7% compared to the current scenario). The values for area reduction of *C. macrosperma* were high in scenarios A2 (2050) and B2 (2070): 76.3% and 58.2%, respectively (Table 2). Future models projected significant reductions in the areas predicted by the potential distribution model in the Western Amazon. There is also an area of high concentration of the species in scenario B2-2050 in the state of Rio Grande do Sul (Figure 1c).

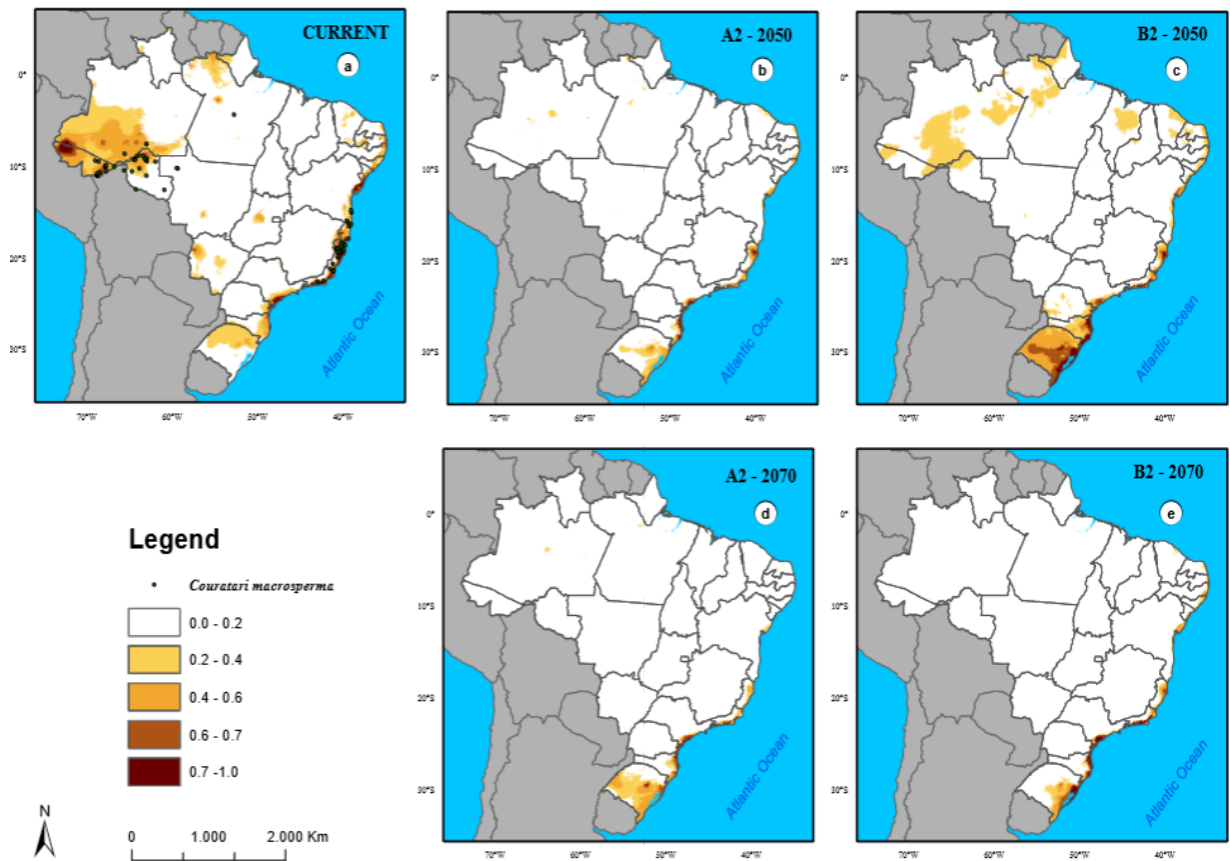


Fig. 1. Suitable habitat areas of *C. macrosperma* A.C. Smith, considering a pessimistic (A2) and optimistic (B2) scenario of future climate changes for the years 2050 and 2070.

Cariniana ianeirensis also performed well, with high AUC, and low binomial probability (Table 1). This species has records of occurrence from Rio de Janeiro to Bahia, and in the state of Mato Grosso (Figure 2a). The values of area reduction of *C. ianeirensis* were high in scenarios A2 and B2 (2050): 63.9% and 67.2%, respectively. This is particularly concerning as the species is already on the IUCN red list. A significant shrinkage of the areas predicted by the models with the future scenarios (A2 and B2) was observed, mainly in the phytogeographic region of the Atlantic Forest, with a concentration of areas of high suitability, mainly in the State of Rio Grande do Sul (Fig. 2).

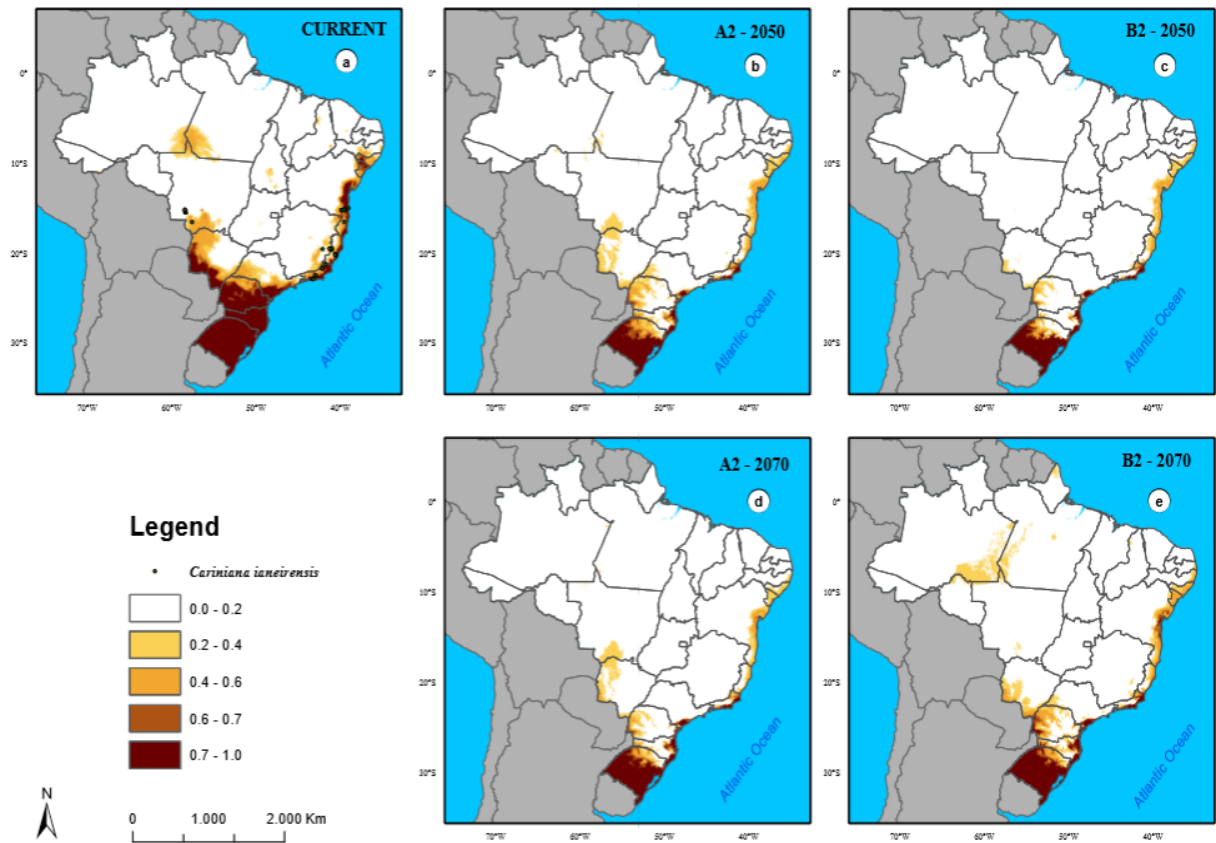


Fig. 2. Appropriate habitat areas of *C. inaneirensis* R. Knuth, considering a pessimistic (A2) and optimistic (B2) scenario of future climate changes for the years 2050 and 2070.

Finally, we have the predictive modeling for *Lecythis lurida*. This species is distributed in the States of Pará, Maranhão, Piauí, Pernambuco, Bahia, Sergipe, Minas Gerais, Espírito Santo and Rio de Janeiro (Figura 3a). The generated models had a high AUC rate and the binomial probability was 0.000 in all scenarios, indicating the low probability of this model being generated at random (Table 1).

The comparison of current distribution models with those in future scenarios of climate change shows a reduction in the probability of occurrence of the species (Table 1), except for the scenario A2 2070 (considerable increase of the species by 465.9%) (Figure 3d). The model for future distribution, under scenarios of climatic changes, presented substantial changes in the distribution areas of the species and presented a reorganization of the appropriate sites in the Amazonian geographic domain (Figure

3); this may be related to the magnitude of climate change, which when more drastic, make previously inadequate areas appropriate.

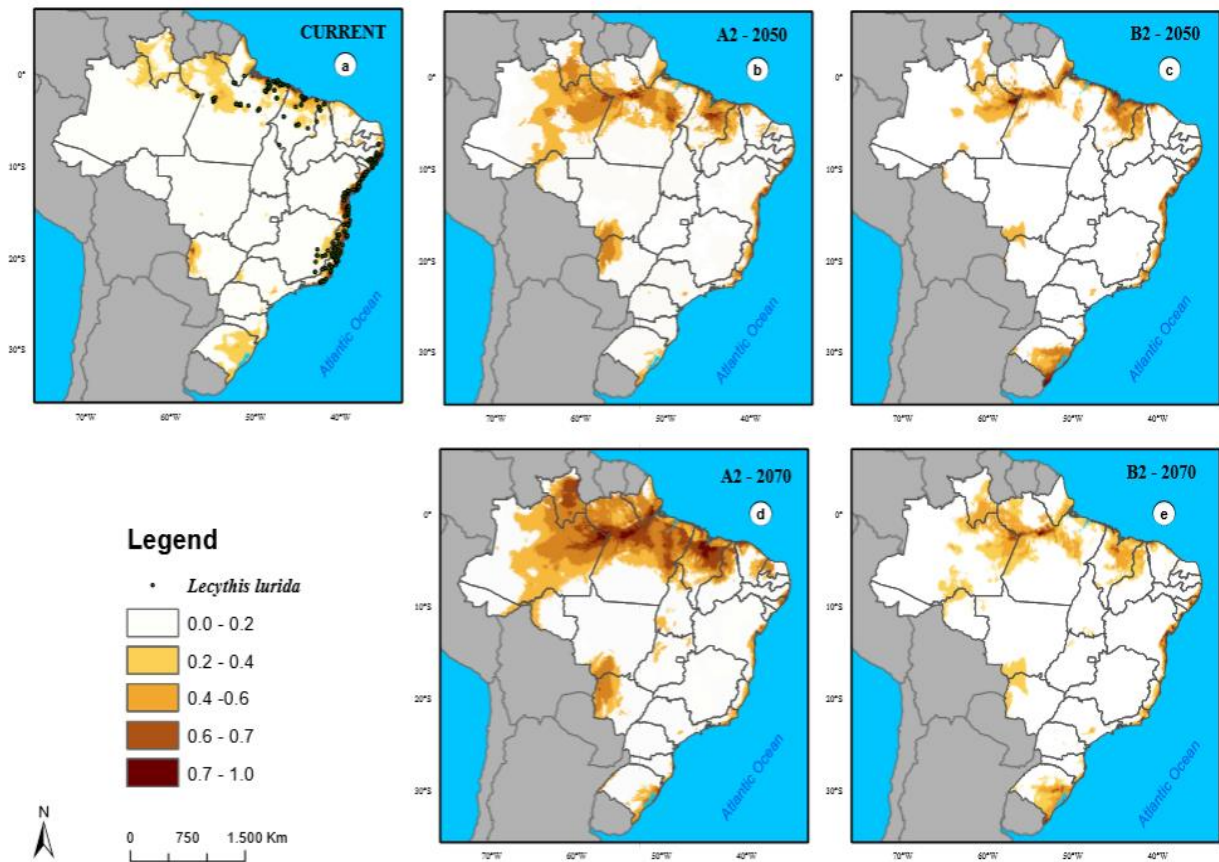


Fig. 3. Appropriate habitat areas of *L. lurida* (Miers), considering a pessimistic (A2) and optimistic (B2) scenario of future climate changes for the years 2050 and 2070.

The developed climatic scenarios were crossed with the thematic maps of the original occurrence of the evaluated species, resulting in a worrisome forest scenario, in which part of the species would not occupy extensive areas if future projections of temperature increase are to be realized. Many models indicated the displacement and retraction of areas considered environmentally suitable for the species. However, it is important to understand that the geographic distribution, usually obtained through ecological niche models, does not reflect the effects of dispersion and biotic interactions (Soberón, 2010), because we are mostly dealing with the potential distribution and not with the actual distribution of the species.

4. DISCUSSION

The expected speed of climate change, including variability and extreme events, can be a major obstacle, as species responses to climate change may include extinctions, adaptations, or changes in the range of geographic distribution (Diniz-Filho & Bini, 2008). In this way, it is crucial to understand how species, dynamics and composition of local ecosystems can be affected by climate change, and their response to such changes. With respect to the environmental, one of the main impacts of climate change is the change in environmental suitability in the species' current or potential future habitats, since climatic and physical factors can influence, at different intensities and scales, the ecologically- and evolutionarily-determined distribution of species (Pearson & Dawson, 2003).

Thus, niche conservatism or the tendency of species to retain characteristics of their fundamental niche is one of the factors responsible for the impact of climate change on world biota (Wiens & Graham, 2005). Faced with the impossibility of rapid migrations to all plant formations, it is foreseeable that an overlap will occur between the distribution ranges of species that today occupy different habitats. With the appearance of one and disappearance of others, new combinations will be created, which would allow both the emergence of new ecological interactions and the disruption of interactions previously established among species; however, this will depend on their ability to disperse and the characteristics of the environment. Some studies have shown that many species respond to climate change with niche conservatism, as opposed to rapid evolutionary changes that can enable greater climate tolerance (Parmesan & Yohe, 2003); species with strong niche conservatism will be more susceptible to extinctions, while others tend to adapt to new changes.

In our models, we detected major changes in the areas of species suitability in the phytogeographic domain of the Amazon and in the Atlantic Forest; one of the possible causes of these changes in location and habitat sizes is the fact that the climate change scenarios tested show changes in precipitation and temperature. It is known that amongst the several factors that restrict the survival of a species, temperature is one of the most important (Costa et al., 2012; Ribeiro & Navas, 2012).

According to the latest IPCC report (2013), it is very likely that there will be an increase in temperatures throughout South America, with higher warming projected in southern Amazonia and reduced precipitation in the eastern Amazon, northeast and east of Brazil. In addition, an increase in precipitation extremes should occur during the dry season (Christensen et al., 2013). These predictions have led to a negative outlook for neotropical biodiversity, and some studies (e.g. Siqueira & Peterson, 2003; Miles et al., 2004; Colombo, 2007; Colombo & Joly, 2010; Zimbres et al., 2012), already point to possible extinctions of species.

Buckeridge (2007) also states that, in the context of biodiversity, the loss of species involves the additional loss of associations at higher levels of complexity, such as ecosystems and communities. Therefore, an increase in greenhouse gas emissions may imply significant climate change in the coming decades; hence, consequent potential loss of biodiversity and disruption of ecological services should be seriously evaluated (Gatti, 2013). As per Buckeridge (2007), if the disruptive changes are too rapid, some species may not be able to migrate and adapt in time to a suitable environment and thus would be in danger of disappearing. Therefore, in the terrestrial environment, tree species would be the most drastically affected because many of these species have a long-life cycle, are already very well adapted to relatively restricted microclimatic conditions, and thus would have a limited chance of finding a new habitat. According to Aleixo et al. (2010), following recent changes in natural

landscapes, climate change predicted for the future is the second-most important factor threatening the biodiversity of Brazilian biomes.

As demonstrated by several authors (Ackerly et al., 2003; Cianciaruso et al., 2011; Carlson et al., 2016), the response of a plant to an environmental stimulus can vary within and between species. This occurrence of variation is also supported by the fact that species occupy distinct preferential niches. Tropical plant species may be sensitive to variations in climate, which biological systems are slow to respond to, potentially leading to a decrease in species diversity (Magrin et al., 2007). For the future scenarios, a notable reduction was observed in the areas of suitability for the three species (Table 2). This shrinkage in distribution patterns can be explained by the increase in temperature and decrease in precipitation in South America, which were pointed out by Magrin et al. (2007) and Christensen et al. (2013).

In this sense, the vulnerability of species to climate change can directly be linked to exposure, climatic variation in areas occupied by species, the degree of tolerance and the ability of the species to adapt to these climatic variations. In response to climatic fluctuations, the distributions of some species may contract or expand or the species may move to more favorable climatic habitats (Parmesan & Yohe, 2003). Understanding the ability of species to expand into suitable new habitats and change their distributional boundaries when exposed to climate change is important to delineate the probabilities of species-specific extinction (Thomas et al., 2004; Loarie et al., 2008).

According to Geng et al. (2012), widely distributed species can use a wide variety of resources and tolerate different environmental conditions or physiological stresses, and thus, such species can develop in a larger area. Likewise, Murray et al. (2002) emphasized that species with differently sized distribution areas may respond differently to environmental variations. Since functional attributes usually vary on a

wide spatial and temporal scale, these reflect characteristics adaptive to the environment in which the species have been inserted.

5. CONCLUSION

The models of the current and future potential distributions of Lecythidaceae species had good performance, with results being far from those of random prediction. The presented maps showed variation in the extent of areas considered environmentally adequate for future projections (A2 and B2) along with changes in the areas themselves, thus revealing sites previously not predicted by current potential distribution models. In this context, elucidation of the patterns of the geographic distribution of species is relevant for a spatial and ecological understanding of biodiversity and interrelationships within ecosystems.

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CAPÍTULO III

REVISTA AoB PLANTS

Ecological niche modeling of the *Couratari asterotricha* Prance (Lecythidaceae): prediction new areas of occurrence

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ABSTRACT

Habitat loss and fragmentation are typically considered the main causes of extinction. In a few decades, several species might be extinct, especially endemic ones with restricted geographical distributions, occurring only in specific environments, wherein they are well adapted. Thus, providing ecological information and a better understanding of the factors and processes that shape species distribution are

important for conservation planning. In this context, given the importance and the lack of information on the geographic distribution of *Couratari asterotricha* (family Lecythidaceae), we carried out prediction of the potential distribution regions of the species. We used the principle of maximum entropy (Maxent 3.3.3k.), with a database composed of 12 natural occurrence points, obtained through the work of Ribeiro *et al.* 2014 and from seven bioclimatic layers, for modelling. The suitable areas predicted by the model were consistent with the actual distribution of the species, shaped primarily by annual precipitation, isothermal temperature, mean temperature of the driest quarter, and the average temperature of the coldest quarter. The models predicted environmental suitability mainly in the north of the State of Espírito Santo. The major probability of occurrence of this species includes the coastal line, where occurrence records are already available, as well as in Bahia, Rio de Janeiro. There was an isolated point in Pantanal where there is no existing record of the occurrence of the species. Ecological niche modeling is a way of understanding and interpreting the biological and ecological phenomena that occur in ecosystems, and the most common strategy to determine the current or potential distribution of a species and the main factors that may influence it. Suitability models can be used to fill existing gaps in the geographic distribution limits of the species, apart from being an auxiliary tool in conservation decision-making.

KEYWORDS: Conservation; Ecological Niche Modeling; Endemism; Maxent; Rare species.

INTRODUCTION

A detailed knowledge of the natural history and biology of a species, as well as the information about its geographical distribution and its potential for occurrence, are of great importance for conservation (Papes and Gaubert 2007). Environmental suitability modeling is a powerful tool to overcome the lack of knowledge about the geographical distribution limits of species (Bustamante and Seoane 2004; Giovanelli *et al.* 2008), and for their conservation (Carroll *et al.* 2001). Thus, it becomes a particularly important approach in situations where there is little available data for the species or there is a need for immediate decision-making with the best information available.

Niche modeling is a technique that estimates associations between environmental (climatic) aspects and the regions of occurrence to characterize the tolerance for environmental variation and to plot indices of environmental suitability in locations where there is no known occurrence (Franklin 2009; Peterson *et al.* 2011). However, the unavailability of reliable species occurrence data remains one of the great challenges in modeling, as the datasets are often incomplete, inaccurate, or spatially biased about the true species distribution (Araújo and Guisan 2006). In Brazil, information on the distribution of species is still very scarce, even in biodiversity hotspots such as the Atlantic Forest (Myer *et al.* 2000).

Studies with endangered or rare species are even more difficult to perform because there is little information available on the biology, ecology, and physiology of these organisms. There are typically very few records of their occurrence in the literature and their distribution is frequently restricted. These issues can be mitigated using computational techniques and statistical methods to generate models that indicate the geographic areas with a high degree of environmental suitability for the occurrence of the species being evaluated.

In the literature, there are very few studies on the geographical distribution of Brazilian flora using niche modeling techniques, mainly focus on rare species. Moreover, most ecological niche modeling studies have focused on species with wide geographic distribution. Some papers have been recently published on the potential geographic distribution of rare and/or restricted species, which contributed to a better evaluation of the importance of these species in the planning and adoption of conservation strategies (Engler *et al.* 2004; Guisan *et al.* 2006; Peterson and Papes 2006; Young 2007; Papes and Gaubert 2007; Slatyer *et al.* 2007).

Several recent studies have indicated a high richness of flora in Espírito Santo, but the region is still poorly explored (Thomaz and Monteiro 2007; Giaretta *et al.* 2013; Dutra *et al.* 2015; Luber *et al.* 2016). Several species new to science have been described in the state in the last few decades, confirming this great diversity in flora and pointing out the need for new research to fill in the gaps in the existing knowledge (Leme and Silva 2001; Vianna and Fontella 2002; Amorim 2003; Chautems *et al.* 2005; Coelho 2006; Filardi 2011; Machado and Filho 2012; Ribeiro *et al.* 2015).

Couratari astrotricha is endemic to the Atlantic Forest, with records of occurrence only in the state of Espírito Santo (Prance 1981; Mori 1990; Mori *et al.* 1990; Smith *et al.* 2012). The species is characterized by hermaphrodite trees up to 31 m in height, which flower during the period from March to May; the pollination is probably by bees, and fruiting occurs in the interstice from June to September (CNCFlora 2017). The species is on the red list of the IUCN (International Union for Conservation of Nature), as endangered (IUCN 2014).

Species with restricted distribution are the most susceptible to anthropogenic disturbances or natural stochastic events, and therefore, they should be treated as vulnerable (Giulietti *et al.* 2009); the presence of a small number of individuals in these species makes them susceptible to extinction (Primack and Rodrigues 2001).

Therefore, the present study used ecological niche modeling to estimate the current area of occurrence of *C. asterotricha* and to predict new areas of occurrence. Thus, we hope to guide new collection efforts to possible areas of occurrence, as foreseen by the projected model, as well as indicate the potentially important areas for conservation.

METHODS

To characterize species requirements with respect to the current climate, we used a set of 19 bioclimatic layers, representing combinations of temperature and precipitation for the past 50 years, with a resolution of 2.5 arc-min (Hijmans *et al.* 2005). The environmental variables were subjected to a correlation test, and those that presented a Pearson correlation coefficient (either positive or negative) higher than 0.8 were discarded.

These layers were obtained from the Wordclim website (www.worldclim.org). The environmental layers considered the following variables: (3) isothermality, (4) temperature seasonality, (6) minimum temperature of the coldest period, (7) annual temperature range, (9) mean temperature of the driest quarter, (11) mean temperature of the coldest quarter, (12) annual precipitation, and (14) precipitation during the driest period. All the climatic variables used had a resolution of 2.5 min.

The potential distribution model was generated using the software Maxent 3.3.3e (Phillips *et al.* 2006), using the following options: create response curve, logistic result format, result in asc type file, make prediction figures, make Jackknife to measure the importance of variables, and the automatic dependency functions of variables. The parameters used in the model had a threshold convergence of 1.0E-5, with 500 interactions and 10,000 backgrounds points, random seed, and maintained using the program regularization multiplier (RM) parameter. The dataset was subjected

to 10 replicate runs of the model, with a cross-over (bootstrap) with replacement, wherein the data were divided into two independent sets, containing 70% and 30% of the data, used to calibrate and validate the model (Pearson 2007).

The Maxent assumes a uniform distribution and performs a series of interactions, where the weight associated with the environmental variables and the functions are adjusted to maximize the information potential of the sampled locations (Phillips *et al.* 2006), since we used only the data for presence. High values of the function indicate favorable conditions for the studied species (Phillips 2005). These values were then used to estimate the distribution, as generated by the program, for the entire geographical space.

This particular algorithm was because it has been demonstrated to perform well, when there is only species data with a few points of occurrence, as indicated by several studies on Maxent (Hernandez *et al.* 2006; Papes and Gaubert 2007; Pearson *et al.* 2007; Bueno 2012), including endemic organisms of the Atlantic Forest (Giovenelli *et al.* 2010).

To validate the model, areas with high chances of species occurrence need to be identified. For this, the map of environmental suitability gradient was transformed into a binary map, where it was possible to distinguish areas of high and low environmental suitability, according to a specific threshold. The minimum training presence (LPM) threshold was used, which has been suggested as the most suitable for modeling rare species with conservation objectives (Pearson *et al.* 2007). In this sense, the use of this threshold is justified and recommended for modeling with few points of occurrence (Pearson *et al.* 2007). Of course, it is also important that all occurrence points that are a part of the sample are correctly identified, and are not subject to errors of species identification or georeferencing.

The model was evaluated based on the variation of the omission error rate in the test data set as a function of a suitability threshold in the Receiver Operating Characteristic (ROC) curve. The contributions of the different variables in the normalized gain of the model were also analyzed, when omitted and when modeled alone. Further details of the evaluation of distribution models based on maximum entropy can be found in publications by Phillips *et al.* (2004, 2006), Phillips and Dudík (2008), and Elith *et al.* (2011).

The LPM classifies the pixels with probability values equal to or greater than those found in the real presence locations of the species (used in the generation of the model) as - presence of the species in the binary model. Pixels with probability values of occurrence below this conversion threshold are classified as - absence of the species (Pearson *et al.* 2007). A problem that could result from this methodology of choosing the Minimum Threshold is that a reduction in omission rates would mean predicting the occurrence of the species everywhere (Freeman and Moisen 2008). However, the model overreach rates were low for the species (Table 1).

After the creation of the binary maps, referring to the current distribution models, a confusion matrix was made: a matrix of hits and errors associated with the prediction of the models. Through the confusion matrix, the values for sensitivity, specificity, accuracy, and TSS (True Skill Statistic) were obtained (Table 1) (Allouche *et al.* 2006; Giannini *et al.* 2012).

RESULTS

For elaboration of the potential distribution model, we used the confirmed information of 12 records of occurrence of *C. asterotricha*, as reported by Ribeiro *et al.* (2014). The model design suggested appropriate areas that were superior to those described in the original distribution of the species (Figure 1). The projected model

identified an apt area of estimated 89,676 km² for the species, largely within the morphoclimatic domain of the Atlantic Forest, but with a small spot of suitable area appearing isolated in Pantanal (Figure 1).

The variables that contributed most to explaining the area suitability for *C. asterotricha* were: annual precipitation, isothermality, mean temperature of the coldest quarter, and mean temperature of the driest quarter. Analyzing the relationship of the variables to the 12 points of occurrence of *C. asterotricha*, it was observed that it tends to inhabit lowland regions, with an average altitude of 200 m and an average temperature of 23 °C. The rainfall regime, referring to the places where the occurrence of *C. asterotricha* was recorded, presented an average annual precipitation of 1,300 mm. In this region, the pre-dominant climate is tropical with dry winter (Aw) (Alvares *et al.* 2013).

The model was considered statistically significant ($p < 0.01$) and had a good performance in the identification of suitable habitats, presenting a high AUC value (0.994 ± 0.002) and 0% omission error. In general, it is recognized that AUC values equal to or greater than 0.5 are robust and reliable, and among the highest values, the forecast would have a low commission and default rate (Anderson *et al.* 2003; Wisz *et al.* 2008; Thorn *et al.* 2009; Giovanelli 2010; Loiselle *et al.* 2010; Giannini *et al.* 2012). Considering that the maximum value that this test can assume is less than 1 (0.994 in this case), and that the AUC varies with the natural amplitude of the species niche (Phillips *et al.* 2004), the evaluated indicators suggest that the model performs satisfactorily in the estimation of the suitability distribution of the potential habitat of *C. asterotricha*.

This study constituted the first systematic prospection of *C. asterotricha* at a national level. The application of different criteria in the evaluation of the obtained model shows that the predictions were significantly superior to those expected from a

random process of attribution of suitability to the map cells of the study area (Figure 1).

Generally, for models that use only occurrence records, sensitivity is a measure of performance that is assessed along with the omission rate (Peterson *et al.* 2002; Peterson *et al.* 2011). The higher the sensitivity and the lower the default rate, the better the performance of the model (Brotons *et al.* 2007). The confusion matrix of the current distribution model also presented a high success rate (99%) for the total number of points of presence and pseudo-absence, corroborating the predictive quality of the model. The performance of the model reached high sensitivity in the predicted model. The maximum value of sensitivity (one) and the minimum omission rate (zero) were observed for the model (Table 1).

DISCUSSION

The Atlantic Forest is known to have high rates of endemism and species richness, representing one of the richest biodiversity repositories worldwide, despite the intense deforestation suffered (Ribeiro *et al.* 2009). Among the tropical biomes, the Atlantic Forest is one of the most threatened ones, with only 11.6% of its original forest cover remaining (Ribeiro *et al.* 2009). Much of this forest is in a mosaic of small, disconnected fragments (Joly *et al.* 2014), which, in most cases, do not exceed 50 ha (Ribeiro *et al.* 2011). Due to such strong anthropogenic impact, and given its high rates of endemism and diversity, the Atlantic Forest is included in the list of the 25 priority areas for world conservation, known as diversity hotspots (Myers *et al.* 2000; Mittermeier *et al.* 2004).

Couratari asterotricha is an endemic species, which is geographically restricted, with records of known occurrence only in the State of Espírito Santo. It is concentrated mainly in the northern part of the state in the reserve areas (Ribeiro *et al.* 2014). This

species is distributed in the forest edges and non-flooded lands (both high and plain), presenting both inside the dense primary forest, as in secondary formations (Mori 1990; Mori *et al.* 1990; Lorenzi 2002).

The board forest extends from Pernambuco to Rio de Janeiro, with a central area located south of Bahia and north of Espírito Santo. It occurs in the narrow coastal strip formed by the tertiary deposits from barrier formation (Rizzini 1997). The existence of endemic plant taxa in the forest of trays led several authors to suggest the region between the south of Bahia and the north of Espírito Santo as one of the centers of endemism in the tropical coastal forests of Brazil (Mori *et al.* 1981; Rizzini 1997; Thomas *et al.* 1998). The geographical characteristics, combined with the great altitudinal variety, promote high species diversity and endemism (Morellato and Haddad 2000; Pereira 2009; Ribeiro *et al.* 2009; Haddad *et al.* 2013).

In this sense, *C. asterotricha* trends to rarity, combined with the threats of its distribution area, becomes a species for an interesting study that could contribute to the knowledge of biodiversity and conservation. As endemic species tend to be naturally rare and geographically restricted, the knowledge about their biology and distribution, as well as their niche remains limited (Serra *et al.* 2012). It is worth noting that the study of the biological phenomenon of rarity has been gaining importance in recent times, especially because rarity is considered a precursor to extinction (Martins 2012) and a predictor of vulnerability. Therefore, rare species need to be further studied (Stebbins 1980; Goerck 1997; Davies *et al.* 2000; Hubbell 2001). The study of rare species in Brazil, especially in forests, is still emerging (Martins 2012).

The models of potential species distribution are widely used in cases where the geographical limits of the occurrence of a species are unknown (Giovanelli *et al.* 2008). However, this knowledge can also help gain insights into the interesting aspects of the biology of the organism, provide useful information for its conservation, and contribute

to the implementation of strategies to protect endangered species (Godown and Peterson 2000; Guisan and Thuiller 2005).

Species with restricted distribution use a small variety of resources and have a small range of tolerance towards different environmental conditions or physiological stresses, as they adapt to relatively homogeneous environments, thus, developing in a smaller area; while species with wide distribution use a extensive variety of resources. Murray *et al.* (2002) emphasized that species with different sizes of distribution area might respond differently to the environmental variations.

In this context, the variation in plant morphological characteristics in response to environmental conditions (Gratani 1996, 2014; Westoby 1998; Weier *et al.* 1999; Ackerly *et al.* 2000, Garnier *et al.* 2001) has been used to describe the relationship between distribution area and environmental tolerance (Wright *et al.* 2004), as well as to understand the underlying ecological processes (Diaz and Cabido 2001; McGill *et al.* 2006). These attributes usually reflect an adaptation of the species to the environment (Wright *et al.* 2004, Picotte *et al.* 2009; Geng *et al.* 2012), being directly responsible for the collection of resources necessary for plant development, such as light, water, and nutrients (Ackerly 2003).

Although ecological niche models assume that species respond to their abiotic environment, it is widely recognized that other factors, driven by biotic interactions and biogeographical or evolutionary processes, also influence species distribution patterns (Wiens and Donghue 2004; Wisz *et al.* 2013). The fact that environmental variables exert a dominant control over species distribution is well known (Wright 1983; Woodward and Willian 1987; Kreft and Jetz 2007).

Upon analyzing the seven variables used in the construction of suitability models of *C. asterotricha*, it was possible to establish spatial relationships that helped understand the range of conditions tolerated by the species in regions suitable for its

establishment. For example, suitable temperature ranges for the occurrence of *C. asterotricha* could be traced, as ranging from 20 °C to 26 °C. The average altitude that the species was recorded at was approximately 200 m, indicating that this species does not tend to disperse to higher altitudes, in contrast with the lowland environments. Restricted species present preferential niche, with specific edaphoclimatic characteristics.

Knowing these parameters, even before the execution of the models, makes it possible to delimit the appropriate areas for field expeditions, thus, reducing the cost and time spent in establishing criteria for species-oriented demand.

Climatic variables such as annual precipitation, isothermal temperature, cooler quarter temperature, and even dry season average temperature, appear as the most significant factors, acting on the distribution of the species under study. In the model projections, the annual rainfall was the most important, indicating that the species is very sensitive to this factor. These variables are associated with some basic energetic and physiological needs of the species, suggesting that energy or water balance variables are essential for plants (Wright 1983; Currie 1991; Austin *et al.* 1996).

The modeling area for Brazil presented a more restricted distribution in the morphoclimatic domain of the Atlantic Forest, with only a small spot of suitable region appearing alone in the Pantanal. There are no records yet for this species in the state of Rio de Janeiro and Bahia. However, the performance of inventories focused on these localities might generate new records of occurrence. If *C. asterotricha* also occurs in these regions, this would configure an optimistic scenario for its conservation. Therefore, it is important to discover new populations of the species to improve the distribution data. These complexes deserve attention, not only for the conservation of this species, but also from a biodiversity viewpoint in general.

The fact that the present potential distribution model identifies a region outside the limits of the Atlantic Forest morphoclimatic domain as suitable, despite it being an endemic species of this domain (probably an over-prediction error), does not disqualify the generated model. Overestimations need not necessarily be prediction errors, as, according to the predictors used, the models indicate the potential distribution, in the absence of limits of dispersion, biotic interactions, and evolutionary and biogeographic processes (Wiens and Donoghue 2004; Wisz *et al.* 2013).

Modeling aims at understanding and interpretation of the biological and ecological phenomena that occur in ecosystems. It is the most common strategy to determine the current or potential distribution of a species and the main factors that might influence it (Jetz *et al.* 2012).

The generated model did not indicate a probability of finding *C. asterotricha*. However, it suggested areas that could be inferred as appropriate habitats for its occurrence. Given that the current and potential distribution of species is fundamental for the conservation of biodiversity, the generated niche models are important tools that subsidize studies and applications aimed at the species threatened with extinction. However, the predictions of a model can only be trusted if they differ from a random chance-based prediction, and it is important to point out that all models have a prediction error, precisely because models are a simplification of reality (Franklin 2009).

A cut threshold was established to evaluate the performance of the model, with the objective of indicating suitable regions for the establishment of *C. asterotricha*, with the awareness that the areas predicted as suitable were dependent on the criterion used. When there are very few known points of occurrence of the species of interest, excessive restriction of the cut threshold can render the model unusable (Nenzén and Araújo 2011).

Deciding the threshold value was intrinsically related to the objective of this study, i.e., to identify areas potentially suitable for *C. asterotricha*, thus, increasing the possibility of searching the species. Therefore, the use of LPT applies in cases where a more comprehensive forecast is intended, as its ecological interpretation is simple (Pearson *et al.* 2007). In this context, we identified the regions that are at least as plausible as the current points of occurrence.

Studies that seek to find new populations of species with restricted distribution are quite useful when there is a lack of knowledge about the real geographic distribution, associated with the scarcity of information on the population size of the species. Species with these characteristics should be the main targets for conservation actions, since small populations are more susceptible to extinction for a variety of reasons, including loss of genetic variability, demographic stochasticity, and environmental fluctuations (Gaston 1998).

CONCLUSION

The occurrence data allowed the development of the potential habitat model for Brazilian morphoclimatic domains. The model predicted environmental suitability and a probability of species occurrence in the coastal board in the north of Espírito Santo, where records already exist, as well as in Bahia, Rio de Janeiro, and an isolated point in Mato Grosso, regions that do not yet have records of occurrence of the species. It is important to point out that the developed model represents the fundamental niche of *C. asterotricha* and not the realized niche, which results from the interception of the suitability determined by the abiotic factors.

In view of the rarity, the degree of threat, and the continuous degradation of the habitat of *C. asterotricha*, there is an urgent need to continue research on the biology and ecology of the species and its monitoring. In this sense, niche modeling can be

used as an auxiliary tool in decision-making regarding the conservation of the species, as well as assisting in the identification of regions that have similar environmental conditions to the species occurrence sites, and might direct future inventories. In this sense, encouraging and supporting the availability of data from various biological collections is of vital importance for the conservation of the species, besides contributing to increase the scientific knowledge.

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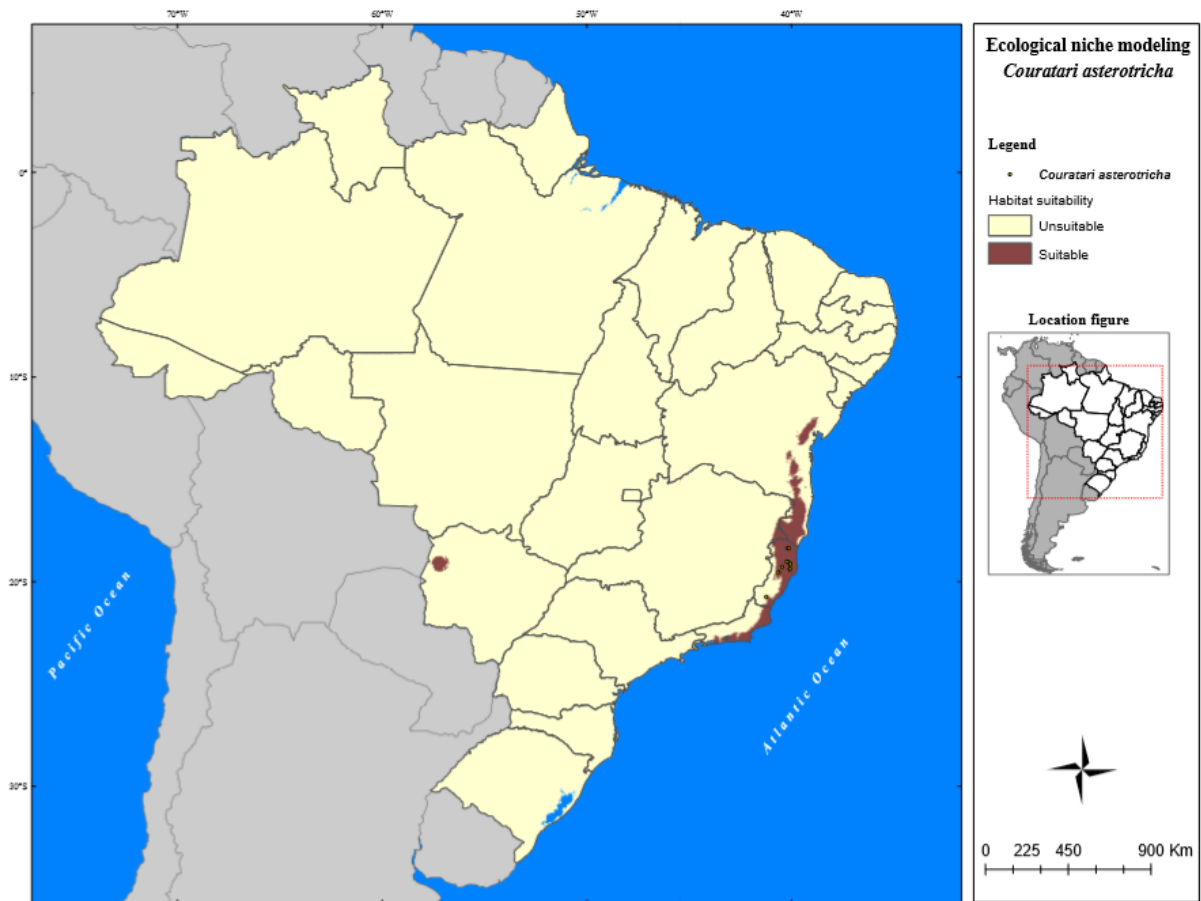


Figure 1. Representation of the suitability of the habitat of *Couratari asterotricha* in Brazil. In brown areas predicted as the presence of the species, in yellow areas predicted as an absence.

Table 1: Metrics for the evaluation of the model *C. asterotricha*

Measures	Values
<i>Overflow error</i>	0,167361
<i>Error omission</i>	0,000000
<i>Sensitivity</i>	1,000000
<i>Specificity</i>	0,832639
<i>Acuracy</i>	0,999174
<i>TSS</i>	0,832639
<i>Hit rate</i>	1211 (99%)
<i>Error rate</i>	1 (1%)

CONSIDERAÇÕES GERAIS

Nossos resultados confirmaram as hipóteses levantadas, apontando que os padrões geográficos de distribuição de espécies arbóreas de Lecythidaceae podem ser influenciados pelo clima, na condição atual, bem como ser prevista através de modelagens em condições pretéritas e futuras. Também foi considerando que as mudanças no padrão climático de distribuição de temperatura e pluviosidade podem modificar os padrões geográficos de distribuição das espécies ao longo do tempo, conforme evidenciados nos modelos gerados para as espécies em estudo.

Esse trabalho teve com intuito contribuir para reunir dados dos levantamentos das espécies da família Lecythidaceae, preenchendo uma lacuna de conhecimento ao sistematizar essas informações acerca da ocorrência das espécies dessa família e de suas áreas potenciais em diferentes períodos temporais. Assim, estudos futuros poderão ser realizados para testar outras espécies, para garantir o máximo de levantamentos, a fim de testar as hipóteses dos efeitos das mudanças climáticas sobre outras espécies.

No primeiro capítulo, modelamos o nicho ecológico, predizendo a distribuição potencial e reconstruindo a distribuição geográfica pretérita em diferentes cenários climáticos (médio Holoceno, LGM e LIG). Avaliamos os efeitos das mudanças climáticas através das alterações das áreas de adequabilidade ótimas (contração ou expansão). As projeções dos modelos indicam que a área de adequabilidade das espécies no presente foi maior do que no médio Holoceno, com exceção de *C. ianeirensis* e *L. pisonis*, que apresentaram perda de área de adequabilidade; já entre o LIG e o LGM as espécies apresentaram retração, exceção *C. macrosperma* que apresentou um aumento de área de adequabilidade.

Os modelos projetados, ainda, evidenciaram uma possível conexão pretérita de espécies com distribuição disjunta entre a Floresta Amazônica e Atlântica, além de evidenciar uma possível diferenciação da Floresta Atlântica em duas unidades biogeográficas distintas, sendo uma ocorrendo na região norte e outra na porção sul, tendo o Rio Doce como divisor. Outra questão que merece ser mencionada e aprofundada em estudos futuros refere-se aos processos de especiação e riqueza de espécies em florestas tropicais (Floresta Amazônica e Atlântica), tendo em vista que os processos que geram essa diversidade ainda são muito discutidos (teoria dos refúgios, rios como barreiras, hipótese dos muses, teoria geotectônica e hipótese dos gradientes ou de diversificação parapátrica).

No segundo capítulo, ao considerar tanto os cenários presente quanto os futuros, os modelos indicaram efeitos consideráveis das alterações climáticas na distribuição potencial das espécies em estudo. Os resultados, em função dos cenários climáticos, independentemente do grau em que ocorreram as mudanças, evidenciam que a maioria das espécies estudadas terão redução do percentual do habitat das áreas de distribuição ótima e reorganização dos locais adequados e inadequados, devido às mudanças que ocorrerão no regime de precipitação e temperatura, em função da sensibilidade destas espécies a estas variações. Nesse sentido, é importante incrementar as observações nas áreas onde a aptidão climática pode se alterar no futuro, já que os resultados dos modelos apontam elevado grau de susceptibilidade dessas espécies as alterações climáticas.

O terceiro capítulo, aborda uma espécie endêmica da Floresta Atlântica *C. asterotricha*, que possui carência de trabalhos básicos sobre sua biologia, estudo da história natural e ciclos de vida que podem ser amenizadas com inventários em áreas pouco estudadas e/ou desconhecidas. Para tal, estas pesquisas devem estar acompanhadas de elementos que facilitem estes estudos, como mapas de

adequabilidade ambiental que direcionam esforços para áreas apropriadas. Guardadas as devidas proporções, os resultados apresentados neste estudo podem contribuir para a mudança deste panorama. Ademais, percebe-se na literatura que há poucos trabalhos sobre distribuição geográfica da flora brasileira utilizando técnicas de modelagem de nicho, principalmente de espécies raras, já que a maior parte dos estudos de modelagem de nicho ecológico tem se concentrado em espécies de ampla distribuição geográfica.

Nesse sentido, os resultados apresentados nos três capítulos reforçam fortemente a importância dos modelos de nicho ecológico como ferramentas de predição e as suas perspectivas de aplicabilidade para modelagem em diferentes períodos temporais (presente, passado e futuro). Faz-se necessário, diante das atuais alterações climáticas e perda de biodiversidade, ter um conhecimento mais aprofundado da distribuição das espécies, tendo em vista que estas passam por um processo dinâmico de evolução de nicho sob o qual as espécies podem migrar ou se adaptar mediante mudanças nas condições ambientais.

Nesse contexto, cresce o aumento da atividade de pesquisa relacionada com os efeitos das mudanças climáticas, sobre a biodiversidade, indicando que se trata de uma preocupação global. Não obstante, ainda assim existem lacunas geográficas que precisam ser supridas, tendo em vista que grande parte dos estudos são principalmente provenientes da América do Norte e Europa, sendo ainda poucos trabalhos desenvolvidos por autores brasileiros. Outra fonte de dificuldade é que dados de coletas biológicas tendem a ser escassos e/ou limitados em abrangência, principalmente em regiões tropicais, onde a grande diversidade biológica dos ecossistemas torna esse tipo de inventário uma tarefa onerosa e inviável em curto prazo.

Por fim, podemos entender que o conhecimento sobre a modelagem de nicho ecológico é um eficaz instrumento para o entendimento da distribuição geográfica das espécies vegetais, permitindo auxiliar a estratégia conservacionista para a mitigação dos efeitos das mudanças climáticas. Estudos dessa magnitude, especificidade e complexidade podem melhorar significativamente as previsões dos impactos das mudanças climáticas sobre as espécies, além de fornecerem dados baseados em evidências, com informações que irão subsidiar tomadas de decisões pelos gestores de como ecossistemas estão respondendo às mudanças climáticas. Dentro dessa perspectiva, ainda que haja limitações, estas, por si só, não são impeditivas de uma análise coerente e crítica sobre seus resultados, na medida em que os modelos de distribuição potencial de espécies revelam-se de extrema utilidade no contexto ora apresentado.