UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Mário Sérgio Muniz Tagliari

# As diferentes dimensões das mudanças climáticas no espaço-tempo: de uma análise biogeográfica ao efeito regional dentro de um sistema socioecológico

Florianópolis
2021

Mário Sérgio Muniz Tagliari

# As diferentes dimensões das mudanças climáticas no espaço-tempo: de uma análise biogeográfica ao efeito regional dentro de um sistema socioecológico

Tese submetida ao Programa de Pós-Graduação em Ecologia, da Universidade Federal de Santa Catarina, para a obtenção do título de Doutor em Ecologia.

Orientador: Prof. Nivaldo Peroni, Dr.
Coorientador: Ghislain Vieilledent, Dr.

Florianópolis
2021

Ficha de identificação da obra elaborada pelo autor,
através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Tagliari, Mário Sérgio Muniz
As diferentes dimensões das mudanças climáticas no espaço tempo: de uma análise biogeográfica ao efeito regional dentro de um sistema socioecológico / Mário Sérgio Muniz Tagliari ; orientador, Nivaldo Peroni, coorientador, Ghislain Vieilledent, 2021.
236 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós Graduação em Ecologia, Florianópolis, 2021.

Inclui referências.

1. Ecologia. 2. Mudanças climáticas. 3. Modelos Ecológicos de Nicho. 4. Araucaria angustifolia. 5. Adansonia spp.. I. Peroni, Nivaldo. II. Vieilledent, Ghislain. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. IV. Título.

Mário Sérgio Muniz Tagliari

# As diferentes dimensões das mudanças climáticas no espaço-tempo: de uma análise biogeográfica ao efeito regional dentro de um sistema socioecológico

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Prof. Moeses Rodrigo Danner, Dr.
Departamento de Agronomia, Universidade Tecnológica Federal do Paraná

Profa. Michele de Sá Dechoum, Dra.
Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina (ECZ, CCB, UFSC)

Prof. Tiago Montagna, Dr.
Departamento de Fitotecnia, Centro de Ciências Agrárias, Universidade Federal de Santa Catarina (FIT, CCA, UFSC)

Prof. Pedro Higuch, Dr.
Departamento de Engenharia Florestal, Centro de Ciências Agroveterinárias, Universidade do Estado de Santa Catarina

Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de Doutor em Ecologia.

ICP-Edu
Documento assinado digitalmente
Nei Kavaguichi Leite
Data: 17/11/2021 16:42:54-0300
CPF: 629.700.972-49
Verifique as assinaturas em https://v.ufsc.br

Prof. Dr. Nei Kavaguichi Leite
Coordenador do Programa de Pós-Graduação em Ecologia

ICP-Edu
Documento assinado digitalmente
Nivaldo Peroni
Data: 17/11/2021 12:07:02-0300
CPF: 132.475.048-00
Verifique as assinaturas em https://v.ufsc.br

Prof. Nivaldo Peroni, Dr.
Orientador

Florianópolis, 2021

Dedico esta tese à minha família. Aos MAPAs. Eterna fonte de aprendizado e reflexão. Obrigado para hoje e sempre por todo apoio incondicional, seja ele emocional, espiritual, pa(fra)ternal. Cresci num universo caótico, mas com bondade determinística.

# AGRADECIMENTOS

Inúmeras sensações transpassam pelo meu sistema nervoso. Há, provavelmente, uma boa dose de hormônios atuando, e que me fazem sentir um “nó” em minha garganta. É engraçado, pois apesar de viver uma realidade onde os fenômenos e processos tendem a ser explicados ou estão em vias de serem explicados, ainda carrego expressões românticas para descrever essa cascata emotiva apenas por lembrar de todos que me acompanharam até aqui.

Deixo meu eterno agradecimento ao acaso, por eu apenas ser uma entidade orgânica que vive, e já viveu, mais de três décadas de maneira “inconsequente”. Mas o acaso, em muitas vezes, foi vencido pelo determinismo de algumas pessoas. São três em especial. Meu pai – Mário; mãe – Maris; e meu amado irmão – Marcus. O que eu fui, sou e serei é um reflexo de seus ensinamentos. Vocês são eu e eu sou vocês. O modo como vejo o mundo é com simplicidade. É na simplicidade que o mais complexo se torna belo. Vocês me ensinaram isto. Este agradecimento se estende à toda família Muniz Tagliari. Obrigado por todos os suportes possíveis. Télinha, Dona Lia e Dona Lory, vocês são parte fundamental nisto. Álvaro Tagliari é o engenheiro neste suporte. Agradeço em especial a dois tutores mágicos que encontrei no caminho: Nivaldo Peroni e Ghislain Vieilledent. Acho pouco provável encontrar duas pessoas que insistem tanto em mim. Palavras são poucas para ilustrar a gratidão que tenho pelos ensinamentos, modos de ver o mundo e carinho recebido por vocês. Nivaldo, obrigado por me fazer sentir capaz. Ghislain, obrigado por insistir tanto comigo. Ao longo desta formação agradeço aos companheir@s que topei e levarei. Querido Julhy Bogoni, Grazi, Kauan, Victor, Jonatas, Gisele, Selvino e Aline: desnecessário imaginar uma realidade alternativa frente a esta bela surpresa de coexistirmos. João, você sempre voltará da França. Lembrando deste país que traz um cheiro de baguette à tese agradeço a minha família musical francesa: Manu e Sayu. Também vivi por pouco mais de um ano em uma casa de cientistas – e me descobri; obrigado ao Pablito, Papá Diegô e Maurício pelo amparo na empreitada. Desculpem-me pelos incômodos e tijolos no telhado. Sem esquecer dos companheir@s Marcelo, Rafa, Maristela, Leo, Clarissa, Lorena, Macarena, Edu (professor), Edu (filho), Angelet, Márcio, Artur, Dani Boto e Raffaello. Sem dúvidas, à equipe do Seu Tavares: Fofo, Carlito e Felipe! E aos grandes amigos do “Ciência no Bar”: Carol Levis, Bernardo Flores, Bárbara Segal e Pablo Amorim. Pensando no efeito borboleta agradeço à Patrícia Ceccato por me incentivar a fazer curso de francês – este foi o pontapé inicial para uma empreitada mundo afora; a Paulo Hoffmann – que simplesmente acreditou em mim em um momento de angústia e desilusão com a profissão Biólogo; e à Paola Bongiovani – que involuntariamente me levou a trabalhar com o Ghislain. Deixo meu agradecimento à Profª Estela e à Elza – duas pessoas espetaculares que muito me ensinaram. Agradeço à família maravilhosa do Gedeoni e Lucimar em Urubici. Sempre dedicarei as implicações deste projeto ao Patrick. Agradeço muito à família Hoppen nesta empreitada final: Milton, Vera, Carolina e a Angela Hoppen. Em especial à Angela Hoppen pelo amor, companheirismo, apoio, carinho, suporte, leveza, aprendizado e paz de espírito.

Agradeço ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina e pelo Cirad – Montpellier – França por me acolherem e me integrarem neste universo acadêmico. Por fim, agradeço aos companheiros eternos: Santoro, Dolores, Murilage, Julhy, Belinho, Jhonny, Lotchão, Renanzão, Pitchoni, Saiman, Cris, Mauricião, Dal'ignea, Cebola, Jussara, Martin, Dudu e Radamés. Enfim, obrigado. Cada um faz parte disso tudo.

Eu cheguei de muito longe. E a viagem foi tão longa. E na minha caminhada, obstáculos na estrada, mas enfim aqui estou (...) Mas não vou ficar calado, com as coisas que eu vi, no conforto acomodado, como tantos por aí.

(Erasmo Carlos - 1971)

# RESUMO

São inúmeras as facetas sobre como, onde e por que as espécies respondem aos efeitos das mudanças climáticas no curto, médio e longo prazo. Compreender a escala de efeitos, e as suas implicações na biodiversidade, constitui aspecto imprescindível do entendimento sobre as mudanças climáticas. Um dos efeitos mais característicos e descritos na literatura é que as espécies se redistribuirão para elevadas altitudes, ou migrarão para latitudes maiores como reflexo do aumento das temperaturas. Nesta tese, busquei avaliar os efeitos das mudanças climáticas usando espécies vegetais tropicais emblemáticas, pertencentes a dois gêneros distintos. A implicação desta escolha se deve ao efeito-cascata que potencialmente ocorrerá ao preservá-las, pois estas se comportam como espécies-chave ecológicas e culturais e, assim, influenciam positivamente a sociobiodiversidade. No Capítulo 1 avaliei quais fatores abióticos, além da temperatura média, podem influenciar nos padrões de redistribuição das espécies frente às mudanças climáticas, usando as sete espécies de baobás existentes em Madagascar (*Adansonia* spp.). A implicação alcançada sobre o efeito distinto de variáveis abióticas nas espécies estudadas pôde ser estendida para toda a extensão da faixa latitudinal tropical. Mostramos que as espécies de baobás mais vulneráveis tendem a se redistribuir não em direção aos polos, como esperado por causa do aumento da temperatura média, mas que elas potencialmente migrarão em direção ao equador, tendo a sazonalidade da temperatura como fator mais importante. No Capítulo 2 foram estudados os efeitos potenciais das mudanças climáticas na Floresta de Araucárias, ecossistema característico da Mata Atlântica, que ocorre principalmente na paisagem cultural típica do sul, e em esparsas manchas no sudeste brasileiro. Avaliamos os efeitos das mudanças climáticas na redistribuição da *Araucaria angustifolia* (araucária) levando em conta a eficiência das Unidades de Conservação para a proteção da espécie, o efeito do uso-do-solo, e a potencial conectividade – tanto no presente quanto no futuro – dos remanescentes previstos da espécie. Mostramos que são necessárias mais Unidades de Conservação para proteger os remanescentes da araucária, e que tanto as Unidades de Conservação quanto os remanescentes projetados de ocorrência da espécie não estarão conectados no futuro. Demonstramos que a espécie terá seu nicho bioclimático reduzido a maiores altitudes, atualmente não inseridos em Unidades de Conservação e, principalmente, restritos ao planalto serrano catarinense a partir de 2050. Nos dois primeiros Capítulos usei os Modelos Ecológicos de Nicho correlativos – que usam variáveis abióticas combinadas com dados reais de ocorrência da espécie – para descrever os padrões de redistribuição e vulnerabilidade das espécies, no tempo e no espaço. Porém, nos dois últimos Capítulos avaliei

o efeito das mudanças climáticas sob outra perspectiva: o que gera resiliência frente às mudanças climáticas? Explorou-se também as limitações comuns dos Modelos Ecológicos de Nicho. Para responder a esta pergunta; primeiramente eu entrevistei agricultores extratores de pinhão em 4 estados (PR, SC, RS, SP) e avaliei o conhecimento ecológico tradicional (TEK) acerca da araucária e seu principal recurso – o pinhão. Por meio de questionários semiestruturados, busquei informações que descrevessem o conhecimento sobre as variedades de pinhão, como períodos de desenvolvimento ao longo do ano; aspectos fenológicos das variedades de araucária frente às mudanças climáticas; assim como caracterizei o perfil socioeconômico dos entrevistados e as sua percepções sobre os efeitos das mudanças climáticas na distribuição das araucárias. No terceiro Capítulo buscamos avaliar como o TEK pode contribuir para a resiliência da Floresta de Araucárias. Por meio de um modelo teórico de *feedbacks* geramos dois modelos antagônicos: (i) como medidas restritivas interagem com o TEK e a preservação da Floresta de Araucárias; (ii) e como o TEK e o manejo colaborativo interagem com a conservação da floresta. Ficou demonstrado que o modelo que avaliava o TEK juntamente com o manejo colaborativo gera um *feedback* positivo em relação a preservação do ecossistema. Tal feedback indica que o sistema pode aceitar estados alternativos, que não se limitem apenas à preservação das matas. Isso permitiu inferir que este modelo alternativo (ao qual chamamos de *bottom-up*) pode favorecer a expansão da Floresta de Araucárias, e contribuir para uma maior resiliência a distúrbios, dentre eles o desmatamento e as mudanças climáticas. Por fim, no quarto Capítulo explorei as consequências caso as mudanças climáticas afetem por completo a Floresta de Araucárias, sob o contexto de ser um sistema socioecológico. Novamente explorei as informações coletadas nas entrevistas semiestruturadas. Porém, calculamos os serviços ecossistêmicos que o TEK fornece, e como a perda deles pode ser um sinal de alerta para a disrupção completa do sistema. Para avaliar a potencial disrupção do sistema socioecológico, eu resgatei na literatura os principais estudos que usaram Modelos Ecológicos de Nicho correlativos para a araucária, e geramos uma fórmula linear que avalia a potencial disrupção do sistema socioecológico em 2050 e 2070 (i.e., baseado na projeção de perda potencial dos remascentes de distribuição da araucária). Mostramos que a garantia da resiliência frente às mudanças climáticas da Floresta de Araucárias reside no TEK, e que os grupos humanos que usam e manejam a araucária, principalmente pequenos agricultores extratores de pinhão, são imprescindíveis para a implementação bem-sucedida de medidas colaborativas e de conservação. Meus resultados, por fim, exploram distintas interpretações e implicações das mudanças climáticas em diferentes escalas espaço-temporais. Contudo, eles trazem fortes subsídios que as tomadas de decisão possam ser aplicadas das mais diversas

formas, desde políticas internacionais até avaliações locais dentro de um sistema socioecológico. Além disso, evidencia a vulnerabilidade das espécie-chaves escolhidas, e que sem as devidas medidas de preservação, ao menos sobre estas espécies-chaves, podemos evidenciar drásticos efeitos-cascata de perdas na sociobiodiversidade de ambos ecossistemas.

**Palavras-chave:** Mudanças climáticas; Modelos Ecológicos de Nicho; *Araucaria angustifolia*; *Adansonia* spp.; Redistribuição de espécies; Floresta de Araucárias; Madagascar; Sistemas socioecológicos

# ABSTRACT

There are several facets about how, where, and why species respond to the effects of climatic change in the short, medium, and long term. Understanding the scale of effects and implications on biodiversity are also essential aspects of climate change. One of the most characteristic effects described in the literature is that species will redistribute to higher altitudes or seek higher latitudes with increasing temperatures. In the present Thesis, I propose to assess the effects of climate change using emblematic tropical plant species belonging to two distinct genera. The implication of this choice is due to the cascade effect that will potentially occur by preserving them, considering that both are ecological and cultural keystone species, thus positively influencing sociobiodiversity. In Chapter I, it was studied which abiotic factors in addition to the annual mean temperature could influence the patterns of species redistribution in the face of climate change, using the seven species of baobab trees existing in Madagascar (*Adansonia* spp.). The implication reached about the distinct effect of abiotic variables in the studied species could be extended to the entire extension of the tropical latitudinal range. We have shown that the most vulnerable baobab species tend to redistribute not towards the poles, as previously expected by the increase in mean temperature, but they will potentially migrate equatorward owing to temperature seasonality as the most important factor. In Chapter II, we studied the potential effects of climate change in the Araucaria Forest, a characteristic ecosystem of the Atlantic Forest, which occurs mainly in the typical cultural landscape of the south – and sparse patches in southeastern Brazil. We have evaluated the effects of climate change on the redistribution of *Araucaria angustifolia* (Araucaria), considering the effectiveness of Protected Areas in preserving the target species, the effect of land use, and the potential connectivity - both in the present and in the future - of the species' predicted remnants. We showed that more Protected Areas are necessary to protect Araucaria remnants, as these areas and the projected remnants of Araucaria will not be connected in the future. The species will have its bioclimatic niche reduced to higher altitudes, outside current Protected Areas, restricted to the Santa Catarina highlands from 2050. In the first two Chapters, I used the correlative Ecological Niche Models, which use abiotic variables combined with real data on the occurrence of the species, to describe the redistribution patterns and vulnerability of this species in time and space. However, in the last two Chapters, I assessed the effect of climate change from another perspective: which aspects promote resilience against climate change? This perspective allowed me to explore common limitations of Ecological Niche Models. I also explored the common limitations of Ecological Niche Models. To answer the question, I first interviewed pinhão extractors in 4 states (PR, SC, RS, SP) and evaluated the Traditional Ecological Knowledge (TEK) about the Araucaria and its main resource, the pinhão. Through semi-structured questionnaires, I searched for information that describes knowledge about pinhão varieties, such as its development periods throughout the year; phenological aspects of Araucaria varieties in a scenario of climate change; as well as characterized the socioeconomic profile of the interviewees and their perceptions about the effects of climate change on the distribution of Araucarias. In the third chapter, we assessed how TEK could contribute to the resilience of the Araucaria Forest. Through a theoretical feedback model, we generate two antagonistic models: (i) how restrictive measures interact with the TEK and the preservation of the Araucaria Forest; and (ii) how TEK and collaborative management interact with forest conservation. We demonstrated that the evaluated TEK model through collaborative management generates positive feedback regarding the preservation of the ecosystem. Such feedback indicates that the system can accept alternative states that are not limited to forest preservation. This allowed us to infer that this alternative model (called *bottom-up* system) can favor the expansion of the Araucaria Forest and contribute to greater resilience to disturbances, including deforestation and climate change. Finally, in the fourth chapter, I explored the consequences of climate change completely affects the Araucaria Forest, under the context of being a socio-ecological system. Over again, I studied the information previously collected in the semi-structured interviews. However, we have calculated the ecosystem services that the TEK provides and how their loss can be a warning sign of complete system disruption. To assess the potential disruption of the socio-ecological system I retrieved the main studies that used correlative Ecological Niche Models for Araucaria and generated a linear formula to assesses the potential disruption of the socio-ecological system in 2050 and 2070 (i.e. based on the projection of a potential loss of the remnants of Araucaria distribution). We have shown that the guarantee of the Araucaria Forest resilience to climate change lies in the TEK and that these human groups who use and manage Araucaria are essential for the successful implementation of collaborative and conservation measures. Finally, my results explore different interpretations and implications of climate change at different spatiotemporal scales. They evidenced strong subsidies to be applied in diverse ways to decision-making, from international policies to local assessments within a socio-ecological system. Furthermore, it reinforces the vulnerability of the chosen key species and that without the proper preservation measures, at least for them, we can suffer from drastic cascade effects on sociobiodiversity.

**Keywords:** Climate change; Ecological Niche Models; Species redistribution; Araucaria Forest; Madagascar; Socioecological systems.

# LISTA DE FIGURAS

## INTRODUÇÃO

## CAPÍTULO I

**CAPÍTULO II**

**CAPÍTULO III**

**CAPÍTULO IV**

# LISTA DE TABELAS

## CAPÍTULO I

**CAPÍTULO II**

**CAPÍTULO III**

**CAPÍTULO IV**

# LISTA DE ABREVIATURAS E SIGLAS

CET Conhecimento Ecológico Tradicional
$CH_4$ Metano
$CO_2$ Dióxido de carbono
IPCC *Intergovernmental Panel on Climate Change*
MEN Modelos Ecológicos de Nicho
$NO_2$ Óxido de nitrogênio
PR Paraná
RCP *Representative Concentration Pathways*
RESEX Reserva Extrativista
RS Rio Grande do Sul
SC Santa Catarina
SP São Paulo
TEK *Traditional Ecological Knowledge*
UC Unidade de Conservação
UFSC Universidade Federal de Santa Catarina
UPI Unidades de Proteção Integral
UUS Unidades de Uso Sustentável

# SUMÁRIO

# 1 INTRODUÇÃO

## 1.1 MUDANÇAS CLIMÁTICAS: DO GLOBAL AO LOCAL, EFEITOS SOBRE A BIOGEOGRAFIA CLIMÁTICA

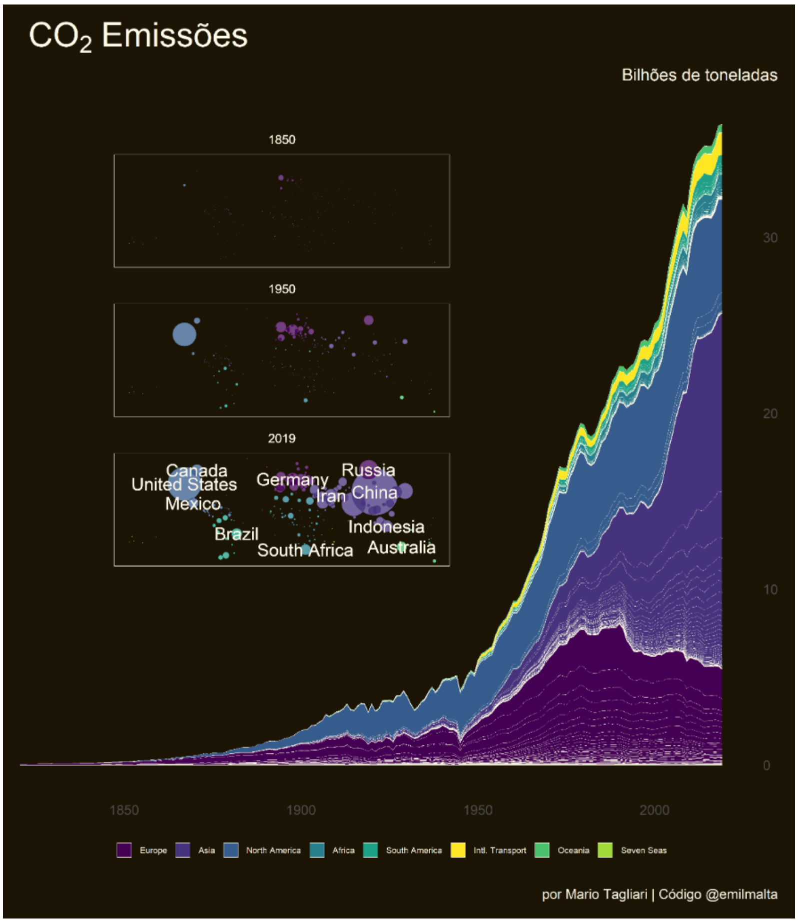
A revolução industrial, iniciada no século XVIII, é indiscutível como um marco para a humanidade. Em termos tecnológicos e produtivos, é inegável a importância deste fato histórico para a transformação social. Combinada com visões prematuras sobre a relação da produção e os recursos extraídos do meio – os quais seriam inesgotáveis – a pegada ecológica antrópica modificou drasticamente a relação "pessoas X meio" desde o século XVIII. O que se observou com este marco foi a aceleração das alterações antrópicas sobre o meio ambiente, especialmente no que tange ao uso descontrolado de recursos naturais e emissão de elementos potencialmente poluentes e tóxicos ao meio.

Dentre estes elementos, o dióxido de carbono ($CO_2$), o metano ($CH_4$) e o óxido nitroso ($NO_2$) demandam particular atenção ao efeito que exercem sobre os ciclos biogeoquímicos, com impactos diretos à manutenção climática. Naturalmente, estes gases estão presentes na atmosfera, devido a processos metabólicos, bioquímicos e biogeoquímicos, que se autorregulam, proporcionando a homeostase dos sistemas. Entretanto, conforme é possível perceber em dados históricos (IPCC, 2021), a partir da revolução industrial a concentração destes gases na atmosfera vem aumentando significativa e aceleradamente, de forma que o balanço químico se torna comprometido, interferindo na ciclagem destes elementos e incorporação natural nos ciclos biogeoquímicos.

Estes gases são oriundos de atividades industriais e queima de combustíveis fósseis (derivativos de petróleo e turfa), principalmente, mas também se correlacionam com o acelerado desmatamento, exposição de superfície de solo, queima de vegetação, expansão da agricultura monocultora e da pecuária de corte, por exemplo. Na Figura 1, pode-se perceber como há uma aceleração expressiva e exponencial na concentração de $CO_2$ na atmosfera, bem como os principais países emissores desde 1850 (dados obtidos em: <https://ourworldindata.org/co2-and-other-greenhouse-gas-emissions>).

Como consequência direta da emissão dos gases supracitados, observam-se mudanças nos padrões climáticos em escala global. A emissão de $CO_2$, $CH_4$ e $NO_2$ estão intimamente associados ao efeito estufa, quando impedem as trocas de calor entre a superfície e a atmosfera. Desta forma, observa-se o aumento da temperatura média da terra, com elevação em relação às médias históricas, em uma constante ao longo do tempo. Segundo o Painel Intergovernamental sobre Mudanças Climáticas (IPCC), são feitas previsões para o aumento médio da temperatura da superfície terrestre e oceânica, indicando cenários possíveis de acordo com o nível de emissão de carbono na atmosfera (IPCC; PACHAURI; MEYER, 2015). Os modelos indicam que, em um cenário positivo, na mais baixa previsão de emissões de carbono, a temperatura média da terra dele elevar-se em 0,3 ºC até 2050 (IPCC, 2015, 2021). Entretanto, sabe-se que este cenário é praticamente inalcançável, uma vez que a desaceleração nas emissões de gases estufa ainda não contempla o necessário para alcançar as menores elevações de temperatura (RIAHI *et al.*, 2011). A comunidade científica lida, atualmente, com a previsão de um cenário mais pessimista, onde pode-se esperar uma elevação média de 4,8 ºC até o final deste século, ou seja, até 2100 (IPCC, 2021). Tal cenário pessimista é conhecido como *business as usual*, ou seja, considera que o padrão de emissões típico do século XX continuará – e aumentará proporcionalmente – até 2100 (RIAHI *et al.*, 2011).

Figura 1- O aumento de emissões de dióxido de carbono no planeta em bilhões de toneladas, entre 1850 até 2019. Os principais emissores são: Asia, Europa e América do Norte. Países da América do Sul e do continente africano – e que abrigam gigantescas algumas das principais florestas tropicais – emitem uma quantidade de dióxido de carbono próxima ao que emitem o transporte internacional de mercadorias, a Oceania e o tráfego marítimo nos sete mares. No quadro comparativo entre 1850-2019, os círculos representam proporcionalmente a emissão de dióxido de carbono.



Fonte: Elaborado pelo autor (2021).

A projeção de elevação de temperaturas tem outras consequências bastante severas ao clima. Por exemplo, a mudança no padrão e regime de chuvas. Com temperaturas mais altas, em períodos prolongados, já se observam impactos no regime e distribuição das chuvas, cuja irregularidade vem causando efeitos locais e regionais mais intensos nas secas ou estiagens, ou, ao contrário, alagamentos, devido a tempestades ou precipitações excessivas em um curto espaço de tempo (ANDERSON-TEIXEIRA *et al.*, 2013). Este efeito no regime hidrológico leva à preocupação sobre a disponibilidade de recursos hídricos, que podem afetar não apenas a distribuição humana, mas também alterar o padrão de distribuição da biodiversidade, contraindo áreas de habitat de determinadas espécies de ambientes úmidos, como na Mata Atlântica, na Floresta Amazônica, ou demais florestas tropicais úmidas.

Outro fator que desperta preocupação de estudiosos do clima refere-se aos eventos extremos. Conhecidas como ondas de calor, do inglês *heat waves*, este fenômeno relaciona-se com a elevação igual ou superior a 5ºC da média histórica para o período, por ao menos 6 dias consecutivos. Este calor intenso tem sido correlacionado com a mortalidade massiva de fauna e flora, além de propiciar efeitos de queimadas mais intensas em períodos de seca nas áreas sob sua influência (BRODIE; POST; LAURANCE, 2012). Desta forma, percebe-se que as elevações de temperatura, seja na temperatura média e/ou em extremos climáticos, associam-se outros efeitos em menor escala. Combinados, estes parâmetros vêm alterando os padrões climáticos locais, regionais e globais, com influência direta na distribuição, resiliência e adaptação dos organismos sujeitos a estes fenômenos.

De forma contundente, pode-se afirmar que as mudanças climáticas já alteraram a distribuição espacial da biodiversidade. Este efeito é observado especialmente nas regiões tropicais (CHEN *et al.*, 2009; FADRIQUE *et al.*, 2018; FEELEY; SILMAN; DUQUE, 2016), que mais severamente vêm sofrendo com as alterações nos padrões climatológicos interativos entre escalas de efeitos resultantes das mudanças climáticas. O aumento das temperaturas médias e os regimes de precipitação anômalos, somados a eventos climáticos extremos fazem que as espécies distribuídas no globo testem os limites climáticos (ANDERSON-TEIXEIRA *et al.*, 2013; GARCIA *et al.*, 2014; RODRÍGUEZ-CASTAÑEDA, 2013). Por esta razão, espera-se que além das modificações nos limites das zonas climáticas, também sejam observadas alterações na biogeografia como resposta às variações no clima.

A biogeografia é um ramo correlato à ecologia que se preocupa em observar, descrever e entender o porquê da distribuição da biodiversidade. Preocupa-se em caracterizar a distribuição das espécies em seus biomas, zonas climáticas e em gradientes, sejam eles altitudinais (das planícies costeiras até áreas de altitude), bem como latitudinais (acompanhando o gradiente físico-químico de distribuição da energia solar, chuvas, ventos, entre outros componentes abióticos) (VIOLLE *et al.*, 2014). Apesar de observar o presente, a biogeografia tem um componente fundamental na análise dos processos e fenômenos do passado, que se correlacionam com os atuais padrões de distribuição da biodiversidade (VELLEND, 2010). Estes processos podem ser entendidos em três esferas:

A) Evolução: quando os organismos conseguem se adaptar às condições abióticas e estabelecer relações bióticas na comunidade, e aqueles mais aptos, sendo capazes de gerar prole, acabam por influenciar na composição genética de sua população;

B) Extinção: quando, por processos locais, a espécie deixa de existir em determinado habitat. Entretanto, devido à redução populacional em outras áreas, e sem o fluxo gênico e menor capacidade de dispersão e colonização, a dinâmica populacional inviabiliza a manutenção da espécie, que se torna extinta globalmente;

C) Dispersão: mecanismos que as espécies utilizam para colonizar novos espaços de habitat, adequados à manutenção de suas populações. Vale ressaltar que mesmo sob condições ótimas, a espécie pode não se estabelecer em determinado habitat, por processos de competição biótica por recursos, que inviabilizam o estabelecimento e expansão de determinadas populações frente a outras, mais bem adaptadas e/ou competidoras (VELLEND, 2010).

Todos estes processos se aplicam aos estudos da biogeografia climática e da distribuição da biodiversidade em gradiente abiótico (DE KORT *et al.*, 2021), e o entendimento do nicho fundamental e realizado das espécies (SOBERÓN; ARROYO-PEÑA, 2017). Conforme o entendimento do nicho Hutchinsoniano, o nicho de uma espécie é composto de *n* dimensões, que incluem as características abióticas e bióticas. As espécies, dentro destas dimensões, possuem faixas de tolerância para cada um destes parâmetros, e o equilíbrio ótimo entre estes fatores pode ser entendido como o seu nicho fundamental (SOBERÓN; ARROYO-PEÑA, 2017). Entretanto, considerando também o estabelecimento de interações bióticas, como competição e predação, por exemplo, as espécies encontram verdadeiramente uma faixa mais restrita de condições ótimas para o seu estabelecimento e crescimento populacional, entendido como seu nicho realizado (SOBERÓN; ARROYO-PEÑA, 2017). De acordo com o nicho realizado, a espécie distribui-se em determinado espaço geográfico, o que caracteriza a sua biogeografia. A percepção de que fenômenos passados interferiram na biogeografia atual de uma espécie permite a compreensão dos processos adaptativos, evolutivos e dispersivos que resultaram em sua ocorrência; enquanto o entendimento dos processos atuais e futuros contribui para as predições à sua capacidade de adaptação e redistribuição para habitats que correspondam às suas dimensões de nicho, com características fundamentais similares ao seu ótimo do nicho realizado (GODSOE *et al.*, 2017; SOBERÓN; ARROYO-PEÑA, 2017).

Há um consenso de que espécies terão que se adaptar para encontrar áreas que correspondam aos seus nichos climáticos e, consequentemente, evitar potenciais extinções locais no futuro (JONES *et al.*, 2013). Dentre estas estratégias adaptativas, é esperado que as espécies intensifiquem seus processos de migração, expandindo seus limites de distribuição enquanto colonizam áreas de habitat mais favoráveis à manutenção de suas populações. Examinando especificamente as espécies florestais sob influência do aumento da temperatura média, existem predições de que aquelas espécies adaptadas em zonas temperadas ou tropicais, de áreas mais frias ou montanhosas, tenham seu nicho climático reduzido, o que seria uma forçante de migração para maiores altitudes (LENOIR *et al.*, 2010; PECL *et al.*, 2017; WILSON *et al.*, 2019). Espera-se também que estas espécies devam alterar seus isotermos em direção às maiores latitudes (COLWELL *et al.*, 2008; LENOIR; SVENNING, 2015).

A temperatura média, comumente, é a principal variável a ser mensurada quando estudamos os efeitos das mudanças climáticas nas respostas bióticas das espécies. Isto se deve a alguns fatores principais. O primeiro deles é a simplicidade de mensuração do parâmetro, tanto em campo quanto em escala experimental, requerendo baixo esforço de coleta de dados e o uso de equipamentos de simples manipulação e calibração. Em segundo, a temperatura é um fator determinante da fenologia e ontogenia das espécies, sendo determinante nos processos fisiológicos do desenvolvimento e reprodução. E por fim, como comentado até aqui, o estabelecimento das zonas climáticas e dos nichos climáticos é determinante para a distribuição da biodiversidade em gradientes elevacionais e latitudinais, compondo e estruturando as fitofisionomias em ambientes terrestres (SENTINELLA *et al.*, 2020; TEWKSBURY; HUEY; DEUTSCH, 2008). A correlação da temperatura com a altitude e latitude se aplica também com a concentração de $CO_2$ na atmosfera (HARRIS *et al.*, 2014). Consequentemente, o aumento global de $CO_2$ na atmosfera (Figura 1) leva incontáveis espécies a alterar suas distribuições potenciais no espaço na busca pelos seus respectivos isotermos (COLWELL *et al.*, 2008; LENOIR *et al.*, 2008; LENOIR; SVENNING, 2015). Predizer como as espécies se comportarão em cenários futuros de condições abióticas, entendendo a ecologia de seus nichos fundamental e realizado, é uma promissora ferramenta para monitoramento e conservação da biodiversidade.

## 1.2 MODELAGEM DE NICHO APLICADA A MODELOS VEGETAIS: DA CARACTERIZAÇÃO DE FITOFISIONOMIAS À ESTRATÉGIAS DE CONSERVAÇÃO

Ao longo dos anos, e considerando as dimensões de nicho conforme predito por Hutchinson, outros estudos, como o de Soberón e Arroyo-Peña (2017), dedicam-se a prever as dimensões que compõe o nicho fundamental de uma espécie, e que podem influenciar na sua distribuição, seja por suprimi-las em seus habitats originais ou determinar a sua expansão para outras zonas. Estes estudos também se preocupam em determinar as mudanças dos espaços n-dimensionais e nicho de espécies-chave, que são determinantes para a estruturação de comunidades e funcionamento ecossistêmico (MEURANT *et al.*, 2018). Estas espécies, ainda que não sejam dominantes em abundância relativa, quando suprimidas de uma comunidade podem causar impactos sobre as demais espécies em desproporção ao total de indivíduos da comunidade. Isto por conta de suas interações bióticas e dos recursos que provêm para outras espécies que coexistem no mesmo habitat (PERES, 2000).

Ao considerarmos as espécies vegetais, podemos observar que além de fornecerem os mais diversos recursos para as comunidades ecológicas, elas também são responsáveis pela estruturação de habitats. Conforme descrito por Mills, Soulé e Doak (1993), a supressão de espécies-chave tem implicações diretas aos grupos com os quais estas espécies se relacionam. Para definir a importância de espécies vegetais na estruturação e organização de uma determinada comunidade, Peres (2000) cunhou o termo "Recursos de Plantas-Chave" (*Keystone plant resources*). Uma espécie-chave vegetal produz recursos sazonalmente críticos para uma comunidade. No caso das espécies-chave vegetais, estas fornecem recursos que, quando ausentes, podem trazer prejuízos de estruturação para a comunidade. Tais recursos podem ser as flores, o néctar, os frutos, as sementes ou mesmo raízes. Quando da ausência de tais recursos alimentares e de abrigo, há um especial impacto sobre outros grupos-dependentes, tais como os polinizadores, consumidores de sementes e mesmo outras plantas de hábito epifítico (MILLS; SOULÉ; DOAK, 1993). Em ecossistemas terrestres ao redor do globo, é indissociável a interação estabelecida entre plantas-chave como fornecedoras de recursos durante períodos de escassez para outras espécies da biota (PERES, 2000). Plantas-chave ecológicas também podem ser classificadas também como "espécies-chave culturais" (*Cultural keystone species*), ou seja, espécies que exercem influência histórica e de identificação em culturas humanas, além de serem fontes de recursos para povos indígenas e populações tradicionais (GARIBALDI; TURNER, 2004). Nem toda espécie-chave ecológica pode ser uma espécie-chave cultural, e vice-versa. Entretanto, o papel ‘chave-cultural’, na maioria das vezes, é indissociável da importância e relevância ecológica da espécie na estruturação de uma comunidade e na delimitação da fitofisionomia (MELLO; PERONI, 2015). Por exemplo, temos os baobás (*Adansonia* spp.) no continente africano (WICKENS, 2008), assim como as espécies vegetais dos neotrópicos, dentre elas a castanheira-do-Brasil (*Bertholletia excelsa*) na Amazônia; ou a erva-mate (*Ilex paraguariensis*) e a araucária (*Araucaria angustifolia*), sendo que estas duas últimas foram imprescindíveis na formação de uma paisagem cultural no sul do Brasil (BAUM, 1995; BOGONI; GRAIPEL; PERONI, 2018; DOS SANTOS *et al.*, 2009; FERREIRA *et al.*, 2021; TAGLIARI *et al.*, 2021)

Considerando o seu papel ecológico fundamental para a constituição e delimitação de fitofisionomias, as espécies arbóreas vêm sendo estudadas na perspectiva das mudanças climáticas; e como as alterações nos parâmetros abióticos podem influenciar em sua distribuição e abundância dentro dos sistemas florestais (CASTRO *et al.*, 2019; VIEILLEDENT *et al.*, 2013a; WILSON *et al.*, 2019). Existem diferentes estratégias para traçar medidas de mitigação e conservação frente às mudanças climáticas e seus impactos na estrutura de comunidades. Em relação aos efeitos potenciais das mudanças climáticas sobre a biodiversidade, o primeiro passo é a identificação do alvo de estudo, pois, como já comentado, as avaliações das espécies-chave podem indicar possíveis mudanças sistêmicas (JOHNSON; OBER; ADAMS, 2017)., bem como revelar alterações secundárias nas relações bióticas estabelecidas. Ainda que todas as espécies possam – senão devem – ser avaliadas quando aos possíveis impactos que as mudanças globais no clima possam exercer sobre suas dinâmicas de comunidades, este esforço amostral não se mostra viável, dada a extensão da biodiversidade. Sendo assim, selecionar uma espécie focal, sobre a qual maiores esforços em estudos e conservação sejam direcionados, pode ser uma estratégia mais eficiente de manejo e conservação, implicando em resultados benéficos ao longo prazo para a manutenção do funcionamento sistêmico (JOHNSON; OBER; ADAMS, 2017).

Uma vez definido este alvo, o pesquisador deve encontrar estratégias para acessar e mensurar a vulnerabilidade das espécies e/ou população focais, para então extrapolar tais efeitos da dinâmica populacional sobre a estrutura da comunidade ou estabilidade ecossistêmica (JOHNSON; OBER; ADAMS, 2017). Após esta etapa, cabe ao pesquisador propor opções de gestão e manejo, seja em forma de identificação de áreas importantes para a conservação; identificando aquelas regiões que são determinantes para a dinâmica populacional das espécies-chave; elaborando planos de manejo, propondo novas legislações para proteção da biodiversidade, ou criando quadros de biodiversidade locais (ARAÚJO *et al.*, 2019;

JOHNSON; OBER; ADAMS, 2017).

Uma das estratégias de conservação, adotadas em consonância com os resultados de levantamento de espécies prioritárias, é o estabelecimento e monitoramento de Unidades de Conservação em uma determinada região. As unidades de conservação são áreas destinadas à conservação e manejo da biodiversidade, e são regulamentadas pelo Sistema Nacional de Unidades de Conservação da Natureza (SINUC), promulgada pela Lei 9.985 de18 de julho de 2000 (BRASIL, 2000). No Brasil, por exemplo, elas são divididas entre Unidades de Proteção Integral (UPI) e Unidades de Uso Sustentável (UUS), havendo diferentes subcategorias para cada um dos dois grupos. Nestas unidades, delimitam-se as espécies, comunidades, ecossistemas, fitofisionimais, interações bioculturais relevantes, áreas com potencial extrativista sustentável entre outros, como fatores prioritários de conservação. Após essa análise, as Unidades de Conservação são criadas e classificadas em categorias respectivas ao propósito que se espera alcançar.

Um dos principais objetivos de uma Unidade de Conservação é a preservação de espécies, sejam elas chave para um ecossistema ou não. Contudo, quando uma unidade busca preservar uma determinada espécie na sua área criada, ela apresenta limitações. A delimitação de áreas prioritárias à conservação observa somente os registros de ocorrência real destas espécies, e seus limites bióticos de ocorrência, baseado no nicho realizado previamente conhecido. Entretanto, com um mundo em transformação, a tomada de decisão sobre como gerir áreas de conservação torna-se deficitária, uma vez que os limites de distribuição e as áreas de habitat favoráveis, no futuro, tendem a modificar-se, especialmente com as mudanças climáticas (CATEN *et al.*, 2017; FERRO *et al.*, 2014; MARCHIORO; SANTOS; SIMINSKI, 2020; RIBEIRO, RIBEIRO *et al.*, 2018; SOARES-FILHO *et al.*, 2010), afetando tanto o nicho realizado quanto o fundamental. Neste processo de migração, redistribuição ou mesmo de restrição de habitat para as espécies, considerar os cenários futuros de sua distribuição é fundamental para a tomada de decisão sobre os limites e as áreas prioritárias para o estabelecimento de tais unidades. Cabe, então, a aplicação de novas ferramentas para a melhor identificação de áreas prioritárias para conservação que abranjam os novos possíveis limites de distribuição de uma determinada espécie, de forma a possibilitar sua dinâmica populacional e, consequentemente, o funcionamento sistêmico (CATEN *et al.*, 2017; LEMES; MELO; LOYOLA, 2014; SOARES-FILHO *et al.*, 2010).

Entre as ferramentas mais comumente utilizadas por ecólogos para descrever a distribuição potencial de uma espécie estão os Modelos de Distribuição de Espécies (MDE), também denominados de Modelos Ecológicos de Nicho (MEN) (ARAÚJO *et al.*, 2019; ELITH *et al.*, 2006; ELITH; FRANKLIN, 2013; ELITH; KEARNEY; PHILLIPS, 2010; GUISAN; ZIMMERMANN, 2000; NAIMI; ARAÚJO, 2016). Através de ferramentas de modelagem computacional amparadas pelo uso dos algoritmos estatísticos, o uso e aplicação de MEN buscam respostas para perguntas como: quais as áreas de distribuição futura de determinada espécie? Qual a distribuição de habitats futuros que sejam ideais para a dispersão e ocorrência desta espécie? Quais possíveis contrações/expansões de habitat podem ser esperadas? Qual porcentagem de distribuição potencial de uma determinada espécie ocorre dentro da rede de Unidades de Conservação?

Em sua essência, os MEN se embasam nas concepções teóricas da teoria de nicho de Hutchinson. As modelagens consideram um cenário atual de distribuição, com identificação da ocorrência de indivíduos e/ou populações. Por sua vez, são levantados dados de parâmetros abióticos (i.e., pluviosidade, temperaturas médias, máximas e mínimas, regime de ventos, entre outros) com a ocorrência de determinada espécie. Ao cruzarem-se as dimensões dos parâmetros abióticos ideais para determinada espécie, ou seja, seu nicho fundamental, pode-se determinar as áreas que, futuramente, conterão as características ideais de habitat para o estabelecimento de suas populações (ARAÚJO *et al.,* 2019; ELITH *et al.*, 2006; FODEN *et al.,* 2019).

Modelos de nicho, deste modo, utilizam dados de ocorrência e abundância de uma determinada espécie no tempo e espaço, e correlacionam estes dados com informação ambiental e/ou espacial (ELITH; LEATHWICK, 2009). Os modelos gerados permitem compreender e prever a distribuição potencial das espécies, taxas de extinção locais, avaliar a eficácia de unidades de conservação existentes, além de apontar locais prioritários para a conservação (PORFIRIO *et al.*, 2014). A disponibilidade de gigantescas bases de dados com acesso livre (como a ocorrência de espécies e dados climáticos/ambientais), combinada com a criação de programas de modelagem práticos e didáticos (como “ecospat”, “Biomod2”, “sdm”; DI COLA *et al.*, 2017; GEORGES; THUILLER, 2013; NAIMI; ARAÚJO, 2016$^{a}$, respectively), possibilitaram que inúmeros pesquisadores conseguissem gerar suas próprias avaliações, estimulando um crescimento exponencial dos estudos envolvendo os modelos de nicho (LOBO; JIMÉNEZ-VALVERDE; HORTAL, 2010; FOURCADE; BESNARD; SECONDI, 2018).

Modelos de nicho podem possuir diferentes níveis de complexidade, devido às inúmeras etapas para sua construção. Por exemplo, o mínimo para gerar um modelo de nicho envolve: (i) seleção de variáveis resposta e como os dados de ocorrência da espécie são confiáveis; (ii) variáveis preditoras e como elas realmente influenciam na ecologia de uma espécie ou se são apenas redundantes, p. ex. altitude e temperatura; (iii) construção do modelo e a escolha dos testes estatísticos condizentes com os dados; (iv) a avaliação do modelo, ou seja, se as métricas para avaliar o modelo são condizentes com o que é proposto pelo pesquisador, ou se os dados foram separados previamente para teste e treino, culminando na acurácia e realismo desta avaliação; (v) interpretação dos resultados do modelo e como eles descrevem realmente a ecologia da espécie (ARAÚJO, *et al.*, 2019; FODEN *et al.*, 2019).

Vale ressaltar, entretanto, que os MEN não são determinísticos, uma vez que fornecem ao pesquisador uma base para a identificação de áreas onde as condições abióticas seriam próximas do ideal para a ocorrência e estabelecimento de populações de espécies-alvo para a conservação. Tantas são as etapas para gerar um modelo de nicho, que apesar de parecer simples, erros e más-interpretações são muito comuns, mostrando a necessidade de uma avaliação robusta (veja ARAÚJO *et al.*, 2019). Modelos de nicho são ferramentas imprescindíveis para a conservação biológica, uma vez que apontam prós e contras de unidades de conservação, indicam áreas prioritárias para conservação, apontam zonas potenciais de convergência entre diferentes espécies, além de destacar a vulnerabilidade que espécies se encontram ou se encontrarão no futuro (DUFLOT *et al.*, 2018).

Desta feita, a última etapa deste ciclo - correlação entre variáveis, geração de modelos e proposição de áreas prioritárias - seria a implementação de tais resultados, onde tomadores de decisão avaliam as medidas propostas baseando-se nos resultados obtidos nos modelos, transformando-os em efetivas políticas público-ambientais (FODEN *et al.*, 2019). Nesta tese, primeiramente busquei: (i) identificar espécies-chave ecológicas e culturais que vêm sofrendo os efeitos das mudanças climáticas; (ii) mensurar a vulnerabilidade destas espécies por meio dos MEN; (iii) propor medidas de preservação e conservação de acordo com os resultados apresentados; e (iv) avaliar a dimensão que os efeitos das mudanças climáticas podem alcançar nas espécies-alvo e implicações potenciais na biodiversidade tropical em diferentes escalas espaço-temporais. Não me limitei apenas a elaborar estudos usando os MEN e propor medidas de manejo e mitigação aos impactos das mudanças climáticas sobre as espécies-chave avaliadas. O segundo momento desta tese foi que uma vez acessada a vulnerabilidade das espécies-alvo às mudanças climáticas, decidi identificar, avaliar e descrever quais aspectos conferem resiliência dentro de um sistema socioecológico frente às mudanças climáticas, uma vez que modelos de nicho são incapazes de incorporar esse tipo de análise (ARAÚJO, *et al.*, 2019; DORMANN *et al.*, 2012).

## 1.3 INTERAÇÕES ENTRE ESCALAS E SEUS EFEITOS EM ESPÉCIES-CHAVE

Com base na literatura anteriormente citada, torna-se evidente a importância de se correlacionar os parâmetros abióticos com aspectos da biologia das espécies, para a determinação de possíveis impactos às suas dinâmicas populacionais em resposta a estressores (DUFLOT *et al.,* 2018; FODEN *et al.*, 2019; GODSOE *et al.,* 2017; GUISAN; ZIMMERMANN, 2000). Também foi revisitado o papel que as mudanças climáticas, em diferentes escalas, podem exercer sobre os organismos. Entretanto, outro aspecto de investigação e análise torna-se necessário no contexto da ecologia aplicada: a análise de interação entre escalas de estressores, para uma avaliação mais realística dos efeitos que tais fatores, em associação, podem exercer sobre a biota e, consequentemente, sobre a biogeografia de determinada espécie. Ademais, é preciso considerar o papel que o manejo e o uso humano de espécies de importância cultural podem ter para a sua conservação, no contexto das mudanças abióticas que interfiram na dinâmica das populações nativas.

Em estudos ecológicos, alguns conceitos são controversos, e entre eles, o uso e aplicabilidade do conceito de “estressor”. Recentemente, foi compreendido e proposto por Piggott, Townsend e Matthaei (2015) que estressores são variáveis oriundas de atividades humanas. As variações em parâmetros abióticos como resultado de processos mediados por ações humanas podem ter efeitos diversos, sejam eles positivos ou negativos, mas que alteram, em relação a um nível de referência, o fitness individual, a dinâmica populacional, a estrutura e o funcionamento de comunidades e ecossistemas e a resiliência de um determinado sistema frente a distúrbios (DE BRUIJN *et al.*, 2017; FOLKE *et al.*, 2010). Sendo assim, não apenas os fatores, mas a interação entre eles e a escala em que atuam são determinantes dos efeitos que possam exercer, em todas as escalas da organização biológica.

Neste contexto, são discutidos também os efeitos de sinergismo, antagonismo e nulidade, derivados então de aproximações toxicológicas e incorporadas, ao longo do século XX, aos estudos relacionados à abordagem da toxicologia ambiental e, em seguida, à ecotoxicologia. Ainda segundo Piggot, Townshead e Matthaei (2015), estes conceitos não são plenamente aplicáveis a estudos de ecologia, uma vez que o referencial, ou seja, sobre qual organismo se verifica o efeito, é o fator que direciona a determinação positiva, negativa ou nula do estressor aplicado e/ou investigado. Em Ecologia, os sistemas são complexos, e o contexto, ambiente, momento histórico e ambientação dos organismos é igualmente relevante para este tipo de inferência. Considerarei as definições destes autores, que propõe uma classificação baseada nos seguintes preceitos:

A) Direção e magnitude da resposta - interpretação positiva, negativa ou nula do estressor;

B) Efeito acumulativo – quando é possível determinar a combinação dos efeitos dos estressores em relação à condição padrão;

C) Efeito de interação - efeito de desvio em relação ao modelo combinatório, quando há uma adição (positiva ou negativa) em relação ao modelo padrão da associação.

A aplicação destes conceitos encontra-se diretamente relacionada com a interpretação de modelos ecológicos para a distribuição de espécies. Valendo-nos das premissas de ecologia de nicho, e considerando os limites de tolerância a cada um dos parâmetros que compõe o seu espaço multidimensional, observar as respostas dos organismos à associação de estressores é fundamental à compreensão da aplicabilidade dos modelos (LAENDER, 2018). A partir da interpretação dos *ranges* de tolerância simultânea a estressores diferentes, pode-se, por exemplo, avaliar efeitos associativos e inerentes à dinâmica ambiental, que ultrapassem as condições médias dos parâmetros abióticos registrados em diferentes escalas, ou compreender a estocasticidade destes fenômenos (LAENDER, 2018).

Relacionando tais conceitos à teoria de nicho de Hutchinson, entende-se que a associação entre os limites de tolerância entre os diferentes fatores abióticos que compõe o espaço multidimensional do nicho caracteriza o nicho realizado da espécie. Além das condições médias toleradas pelas espécies, deve-se considerar os limites extremos de eventos estocásticos, que podem declinar, em curto espaço de tempo, o tamanho da população ou comprometer o seu *fitness*, de tal forma que não seja possível reestabelecer sua dinâmica populacional. Entre eles, o efeito da sazonalidade da temperatura ou mesmo de eventos climáticos extremos (i.e., tempestades, maior incidência de fogo, secas prolongadas, geadas), que podem ser determinantes, por exemplo, para as avaliações da dinâmica populacional ao longo do tempo em uma escala local (CRIMMINS *et al.*, 2011; GARCIA *et al.*, 2014).

Neste embasamento, é possível perceber como as condições abióticas de diferentes escalas atuam entre si. Os efeitos das mudanças climáticas, com a elevação média das temperaturas ou as ondas de calor associam-se a processos locais, como perda de cobertura vegetal, que intensificam o efeito da elevação térmica e amplitude diária de temperaturas. Ou seja, é possível perceber como padrões globais intensificam-se em escalas locais, considerando o efeito acumulativo de processos abióticos, e a interatividade no compartimento biótico juntamente com a atividade antrópica em escala local (por exemplo, ver os trabalhos desenvolvidos por Hoffmann *et al.* (2018) e Maxwell *et al.* (2018)).

Considerar todos estes fatores é fundamental para uma melhor seleção, delimitação e observação do sucesso das áreas destinadas à conservação, dos processos de reintrodução de espécies ou do manejo florestal, que podem ser alcançados com resultados mais próximos da realidade sistêmica. Quando se trata de espécies-chave para a conservação, a interatividade de parâmetros abióticos que possam interferir na dinâmica populacional ganha ainda mais relevância. Estas espécies, além do seu valor ecológico inerente, normalmente também estão sob a pressão antrópica para exploração de recursos, e em se tratando daquelas arbóreas, especialmente a exploração madeireira. Desta feita, as modelagens e previsões de distribuição de habitat podem dar aos pesquisadores uma dimensão sobre as possíveis áreas onde, futuramente, a espécie possa existir, delimitando tanto as áreas para a conservação como, quando pertinente, contribuindo a planos de manejo que permitam a exploração sustentável em longo prazo.

## 1.4 MANEJO SUSTENTÁVEL E SERVIÇOS ECOSSISTÊMICOS

Com as mudanças de paradigmas sociais e culturais, a cada dia se valorizam mais os serviços ecossistêmicos, entendendo-se que o funcionamento e conservação dos sistemas naturais trazem benefícios ao bem-estar humano e ao planeta (METZGER *et al.*, 2019; REID *et al.*, 2005). O conceito de serviços ecossistêmicos foi elaborado com a contribuição de diversas disciplinas e pela própria evolução da ecologia, com a melhor delimitação de conceitos aos estudos da biosfera, dos organismos e das interações entre processos abióticos e bióticos. Ainda assim, por ser um ramo bem desenvolvido dentro da ecologia, os estudos florestais em muito contribuíram para as atuais definições e delimitações do que são os serviços ecossistêmicos (PATTERSON; COELHO, 2009).

Vale ressaltar, como analisado no trabalho de Schröter *et al.* (2017), que os conceitos de serviços ecossistêmicos e sustentabilidade, como os entendemos hoje, estão muito próximos e correlacionados. De forma geral, os serviços fornecem subsídios para o bem-estar humano, tanto para a atual quanto para as futuras gerações[1]. Apesar de sustentabilidade ser um conceito mais abstrato e idealístico, com relação ao status atual e futuro da conservação das funções sistêmicas e ecológicas, ambos os conceitos partilham a compreensão que a redução da biodiversidade afeta sobremaneira a seguridade humana em médio e longo prazo. Isto porque a biodiversidade é responsável por prover serviços fundamentais, tais como recursos alimentares, atuar no balanço climático e sequestro do carbono, participação na regulação do ciclo hidrológico e ciclos biogeoquímicos dos elementos, entre outros, que garantem a

---

[1] De acordo com os autores, "[...] *ecosystem services describe the ecological structures and functions appropriated as a means to increase human well-being* [...]" / "[...] serviços ecossistêmicos descrevem as estruturas e funções ecológicas apropriadas com a finalidade de aumentar o bem-estar humano" (SCHRÖTER *et al.,* 2017, p. 35, tradução nossa).

homeostase sistêmica capaz de suprir as necessidades humanas e o bem-estar ambiental para a nossa sobrevivência.

Um fator importante para a avaliação da relevância dos serviços ecossistêmicos é como as mudanças climáticas afetam a provisão, regulação e suporte dos mais diversos tipos de serviços (MALHI *et al.*, 2020; SCHRÖTER *et al.*, 2017). Como discutido ao longo deste embasamento teórico, as mudanças climáticas, seja em escala global ou local, têm o efeito deletério e significativo sobre a biodiversidade (BELLARD *et al.*, 2012; WATSON *et al.*, 2019). Desta forma, considerar os impactos que as mudanças no clima exercem sobre a biodiversidade, a estrutura e dinâmica de comunidades e funcionamento de ecossistemas pode dar o direcionamento sobre a dimensão das perdas, tanto em escala espacial quanto temporal. Este tipo de consideração também é relevante para planejamentos estratégicos de manejo e ações de conservação (WATSON *et al.*, 2019; YU *et al.*, 2020). Especialmente, quando se trata de ecossistemas potencialmente ameaçados pelas mudanças mais extremas do clima, ou mesmo espécies-chave para a estruturação de comunidades biológicas e sistemas sociais dependentes destes recursos.

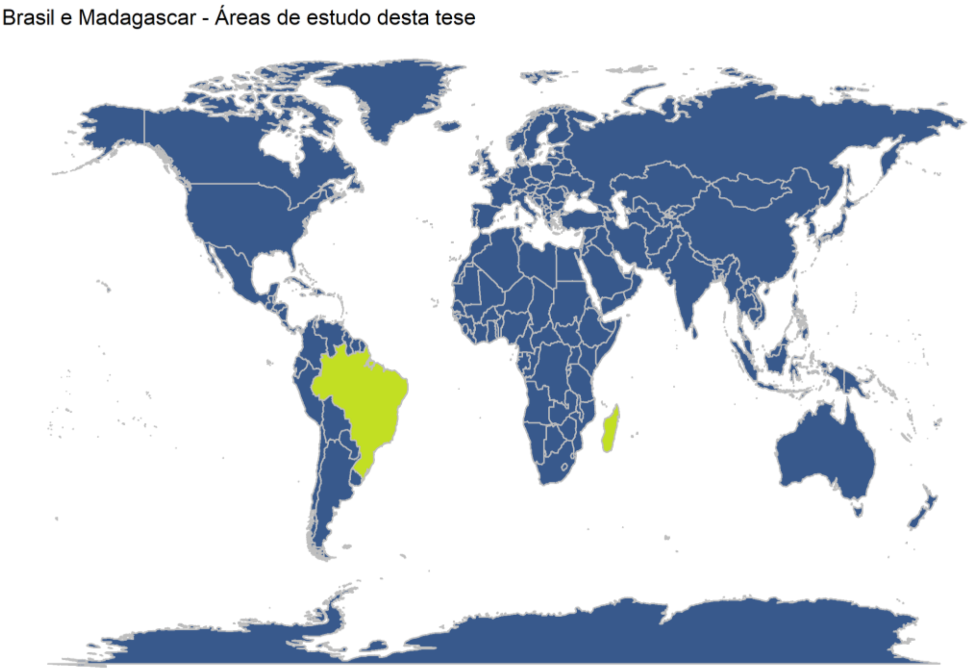
As mudanças climáticas também podem servir como elemento para avaliar a resiliência de sistemas socioecológicos, ou seja, sistemas em que grupos humanos locais interagem, manejam e promovem benefícios para o ecossistema e vice-versa, como feedbacks, interdependência e resiliência (FOLKE *et al.*, 2010). A resiliência de sistemas socioecológicos está relacionada com a capacidade de adaptação e de continuar estável frente à uma potencial alteração ou fator de impacto (BERKES; COLDING; FOLKE, 2000). As florestas distribuídas no planeta abrigam incontáveis sistemas socioecológicos, incluindo aqueles estruturados por povos indígenas, comunidades tradicionais, ou até mesmo agricultores familiares (DE SOUZA, *et al.*, 2006; FATORIĆ; CHELLERI, 2012).

Estes sistemas socioecológicos são formados por pessoas que ocupam, transformam e modificam paisagens, pelo manejo e domesticação de espécies vegetais de interesse para as comunidades (LEVIS *et al.*, 2018; TAGLIARI, *et al.*, 2021). Dentre aquelas de interesse para manejo, localizam-se as de utilidade para fornecimento de madeira (i.e., construção, lenha, confecção de embarcações de pesca; CRUZ *et al.*, 2020; OROFINO *et al.*, 2018), usadas como recurso alimentar direto (sejam folhas, raízes ou frutos; FERREIRA *et al.*, 2021; QUINTEIRO; ALEXANDRE; MAGALHÃES, 2019) e também o valor medicinal e espiritual, através dos ritos de cura e devoção às divindades (WICKENS, 2008). Todas estas formas de conhecimento sobre o uso de espécies vegetais, que incluem as espécies-chave para a estruturação dos sistemas ecológicos, constituem saberes tradicionais, que muito contribuem para a construção da história de um povo e o entendimento da evolução do ambiente onde a comunidade se estabelece.

Deste modo, alinhar políticas públicas com pessoas que detêm conhecimentos tradicionais permite elaborar estratégias e planos de manejo sustentável, de forma a promover a conservação e manutenção dos recursos naturais. Duas são as principais estratégias que podem ser apontadas como mecanismos de conservação ambiental, envolvendo o estabelecimento de Unidades de Conservação (UCs). Como já comentado, no Brasil, estas são classificadas entre as destinadas para Proteção Integral (PI) ou Uso Sustentável (US) (BRASIL, 2000). Nesta última, nas categorias de Floresta Nacional, Reserva Extrativista e Reserva de Desenvolvimento Sustentável, atividades de manejo, extrativismo e restauração são visadas e desejáveis, de forma a promover o desenvolvimento da área concomitantemente à conservação dos recursos naturais (PACHECO; NEVES; FERNANDES, 2018). Estas estratégias de manejo devem ser desenvolvidas pelos povos nativos que já ocupam historicamente a região, e que devem ter voz e participação na elaboração nos planos de manejo e na proposição das estratégias de restauração (BERKES *et al.*, 2000). Desta forma, percebe-se que a implementação de UCs têm também o papel fundamental de promover o manejo colaborativo e integrativo, que seja responsável socialmente com os povos originários e tradicionais, e efetivo no alcance da proposição de conservação da biodiversidade e manutenção dos serviços ecossistêmicos. Entretanto, essas reservas específicas que valorizam e promovem o manejo colaborativo e integrativo não representam 1% do total de UCs de Uso Sustentável na Mata Atlântica brasileira (PACHECO; NEVES; FERNANDES, 2018).

As áreas tropicais e subtropicais são prioritárias para conservação, seja pelo elevado endemismo (MYERS, 1988), pressões antrópicas, como uso do solo, urbanização e desmatamento (REZENDE *et al.,* 2018), além dos impactos das mudanças climáticas (FEELEY; SILMAN; DUQUE, 2016). Ao se delimitar áreas prioritárias para conservação nas faixas tropical e subtropical, não se permitem generalizações, ou seja, traçar estratégias semelhantes para toda uma faixa latitudinal tropical. É necessário avaliar especificamente os aspectos bióticos, abióticos, socioculturais e econômicos de cada região (TAGLIARI *et al.*, 2021), permitindo a elaboração de efetivas medidas de manejo, conservação ou monitoramento de espécies. A seguir, apresentam-se aspectos relevantes sobre duas formações florestais tropicais sujeitas à influência de estressores climáticos: a Floresta Ombrófila Mista (Floresta de Araucárias) no Brasil e a Floresta Tropical Úmida de Madagascar, cujas espécies-chave vegetais – a *Araucaria angustifolia* (Bertol.) Kuntze e os baobás (*Adansonia* spp.), respectivamente – foram utilizadas para explorar, mensurar, discutir e analisar as distintas facetas das mudanças climáticas na dinâmica espaço-temporal (Figura 2).

Figura 2 - Áreas de estudo desta tese. Em Madagascar, nós avaliamos como variáveis climáticas específicas influenciam diferentemente no padrão de redistribuição das sete espécies vegetais de baobás. Já no Brasil, apesar da dimensão gigantesca deste país, nós utilizamos uma área de estudo dentro do domínio/bioma da Mata Atlântica: a Floresta de Araucárias, distribuída principalmente no sul do país e com manchas específicas de ocorrência na região sudeste.



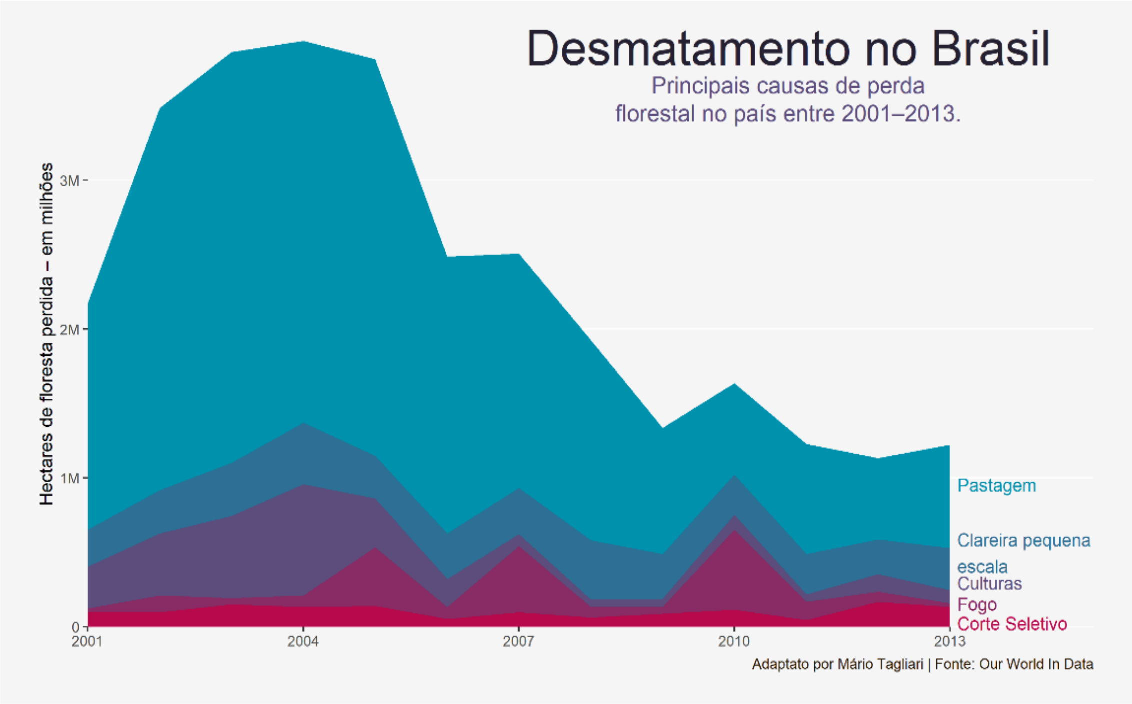
Fonte: Elaborado pelo autor (2021).

### 1.4.1 Floresta Ombrófila Mista: a importância da Floresta das Araucárias na Mata Atlântica

Historicamente no Brasil, dois biomas têm especial importância na construção social e estruturação de comunidades tradicionais, dependentes de seus recursos: a Mata Atlântica e a Amazônia. Ambos os ambientes florestais foram moldados, transformados e coevoluíram com grupos humanos e comunidades tradicionais. A floresta Amazônica, que se distribui entre os países ao norte da América do Sul, tem a maior porção de sua distribuição no Brasil. O processo de domesticação de plantas na Amazônia, além de transformar a paisagem, também garantiu segurança alimentar para suas comunidades humanas (LEVIS *et al.*, 2018). Já a Mata Atlântica estende-se pelo litoral brasileiro, compondo-se de diferentes fitofisionomias entre florestas e campos.

Apesar de conter elevada biodiversidade, além de alta concentração de espécies endêmicas (REZENDE *et al.*, 2018; ZACHOS; HABEL, 2011), a Mata Atlântica vem sendo, historicamente, um dos ecossistemas mais ocupados e degradados pela ação humana (RIBEIRO *et al.*, 2009). Originalmente, diferentes povos indígenas ocupavam os ambientes da Mata Atlântica, utilizando-se de seus recursos para a subsistência. Após a invasão colonizadora europeia do século XVI, este ambiente foi altamente explorado, especialmente quanto aos recursos florestais, para obtenção de madeira, especiarias e gêneros alimentares, além do uso do solo para a agricultura, pecuária e mineração. Ao longo dos séculos, o cenário não vem se mostrando muito diferente em termos de ocupação humana e superexploração dos recursos naturais, sendo mais significativos nos domínios da Mata Atlântica e Cerrado – que se tornaram hotspots da biodiversidade –, mas também ao longo dos demais domínios brasileiros, i.e. Amazônia, Caatinga, Pantanal e Campos de Altitude (Pampas) (SANQUETTA; MATTEI, 2006). Como é possível observar na Figura 3, as principais causas de perda de cobertura vegetal no Brasil até 2013, desde o começo do século XXI, são a abertura de áreas para a pastagem e criação de gado, seguindo-se da prática agrícola, manejo florestal através de fogo e corte seletivo. Esta figura, apesar de alarmante, ainda não está atualizada para os anos 2016-2021, cujo aumento vertiginoso do desmatamento e queimadas possivelmente teve respaldo político da era Bolsonaro (LEVIS *et al.*, 2020). Por exemplo, em 2020, a taxa de desmatamento na Amazônia brasileira foi a maior de toda a década (SILVA JUNIOR *et al.*, 2021).

Figura 3 - As principais causas de perda de biodiversidade no Brasil entre 2001 e 2013.



Fonte: Elaborado pelo autor (2021).

Ademais, o cenário também é crítico na Mata Atlântica, onde remanescentes originais da floresta úmida não passam de 25% em projeções otimistas (REZENDE *et al.*, 2018), sendo comumente aceito que apenas 11–16% dos remanescentes ainda existam. A perda de cobertura vegetal nesta fitofisionomia está intimamente ligada à ocupação humana. A Mata Atlântica vem congregando grande número de cidades e adensamentos populacionais ao longo da história, pois além da obtenção de recursos há que se considerar as facilidades de acesso e conectividade entre as cidades, que anteriormente se caracterizavam apenas como vilarejos e pequenas comunidades. Entretanto, esta conectividade humana representou uma fragmentação ao ambiente, com a perda de áreas florestais fundamentais para o trânsito e migração de espécies, avanço de bordas florestais (i.e., efeito de borda) e perda potencial da conectividade genética entre populações. Este fato preocupa particularmente os pesquisadores, que identificam na fragmentação de habitat um evento perigoso, potencialmente contributivo ao processo de extinção local e como consequência, levando a perda de biodiversidade e da caracterização de fitofisionomias (JOLY; METZGER; TABARELLI, 2014). A Mata Atlântica, consequentemente, é um *hotspot* da biodiversidade e reconhecida como uma das 36 áreas mundiais prioritárias para a conservação (RIBEIRO *et al.*, 2011). Este status foi alcançado devido à ampla variabilidade de habitats, fitofisionomias e biodiversidade, como já comentado, e a sua composição em mosaico, resultante de processos locais, regionais e globais que determinam características climáticas, de composição de solo e disponibilidade hídrica específicas (ESSER; NEVES; JARENKOW, 2019; REZENDE *et al.*, 2018; TABARELLI *et al.*, 2010). De acordo com Meyers (1988), um *hot spot* em uma área de floresta tropical compreende três características básicas para a denominação: i. elevado endemismo de espécies de fauna e flora; ii. elevado risco de extinção, devido a processos locais e baixo fluxo gênico; e iiii. altas taxas de contração de suas áreas originais, intensificando os efeitos de borda e a pressão sobre o fluxo gênico.

Um dos ecossistemas pertencentes à Mata Atlântica mais alterados e possivelmente sob ameaça, tanto de histórica pressão antrópica quanto dos efeitos das mudanças climáticas, é representado pela Floresta Ombrófila Mista ou Floresta de Araucárias. Distribuída essencialmente na região sul do Brasil e com pequenas manchas de ocorrência nas áreas de altitude no sudeste brasileiro (HUECK, 1953; REIS; LADIO; PERONI, 2014), a sua área atual de distribuição é representativamente muito menos ampla do que fora outrora, quando havia uma continuidade em sua distribuição ao longo do sul e sudeste brasileiro, em detrimento dos atuais remanescentes e manchas florestais. A espécie que dá nome à formação, a araucária (*Araucaria angustifolia*), tem importância histórica de uso por populações humanas. O uso de suas sementes – pinhão – com alto potencial calorífico, integrava a dieta de grupos indígenas do tronco linguístico Jê no passado (ROBINSON *et al.*, 2018). Em contrapartida, tais grupos indígenas favoreceram a expansão da Floresta de Araucárias para além de seus limites naturais (BITENCOURT; KRAUSPENHAR, 2006; LAUTERJUNG *et al.*, 2018; REIS; LADIO; PERONI, 2014). Essa interação entre grupos humanos e a araucária se mantém no presente, onde agricultores familiares e os poucos povos indígenas que coexistem na região da Floresta de Araucárias, cuja área de ocorrência possuía mais de 200.000 km² no passado – mas hoje restam entre 10 e 20% dos remanescentes originais (REZENDE *et al.*, 2018; RIBEIRO *et al.*, 2009).

Esses grupos humanos contribuem com a manutenção, uso, manejo, extrativismo (ADAN *et al.*, 2016; MONTAGNA *et al.*, 2019; QUINTEIRO; ALEXANDRE; MAGALHÃES, 2019; TAGLIARI; PERONI, 2018) e a transformação da paisagem deste ecossistema em uma paisagem cultural (REIS *et al.*, 2018). Do ponto de vista de escala, o sistema socioecológico existente na Floresta de Araucárias é ideal para avaliar como as mudanças climáticas promovem vulnerabilidade tanto para sua espécie-chave, a *A. angustifolia*, quanto para os grupos humanos ali inseridos. Considerando as possíveis alterações na distribuição da espécie devido aos fatores climáticos, em associação aos estressores antrópicos, é necessário que estudos preditivos sejam feitos, focando em áreas para manejo e conservação da araucária, planejando estratégias para a conectividade populacional e manutenção de habitat. Ademais, é possível sugerir medidas de conservação específicas para a espécie, levando em conta o sistema socioecológico como um todo, e não apenas a sua espécie (e.g. BERGAMIN *et al.*, 2019; CASTRO *et al.*, 2019; MARCHIORO; SANTOS; SIMINSKI, 2020; WILSON *et al.*, 2019).

### 1.4.2 A Floresta Tropical Úmida em Madagascar

Na costa sudeste africana, Madagascar é um país insular de grande extensão e que vem recebendo atenção global para a conservação (SCALES, 2011; VIEILLEDENT *et al.*, 2017; WAEBER *et al.*, 2015). A biodiversidade de Madagascar torna as suas áreas florestais hotspots para a conservação (MORELLI *et al.*, 2020), considerando também as elevadas taxas de endemismo e os mosaicos de paisagem que constituem suas fitofisionomias. As florestas são divididas em quatro tipos, de acordo com as regiões climáticas: florestas úmidas ao leste, florestas secas ao oeste, florestas espinhosas ao sul e florestas de manguezais ao noroeste (VIEILLEDENT *et al.*, 2018). Como discutido por Waeber *et al.* (2015), os esforços para a conservação destes sistemas, entretanto, são desiguais, e marcadamente podem comprometer as estratégias de conservação de espécies-chave em cada uma destas ecorregiões em longo prazo.

Assim como em quaisquer regiões do globo, as florestas de Madagascar estão sob a influência dos efeitos das mudanças climáticas, que podem comprometer o funcionamento sistêmico e levar à supressão, ou mesmo extinção local de espécies relevantes na estruturação de fitofisionomias. No caso específico, as espécies de baobás (*Adansonia* spp.) são as que despertam maior preocupação quanto aos efeitos que o estresse advindo das mudanças nos parâmetros abióticos, relacionados com as mudanças climáticas, podem causar sobre as populações. Dentre as sete espécies registradas no país, seis são endêmicas (*A. grandidieri, A. suarezensis, A. madagascariensis, A. perrieri, A. rubrostipa, A. za*) (WAN *et al.*, 2021) e, portanto, altamente vulneráveis a eventos estocásticos e pressões antrópicas, contributivos ao declínio e extinção de suas populações.

A possível ameaça às populações de baobás transcende a preocupação ecológica, embora a supressão destas espécies seja fator decisivo na estruturação das comunidades biológicas e caracterização da paisagem no país. As espécies de baobás têm importância e relevância socioecológica para as populações tradicionais do país. As suas folhas constituem recurso alimentar perene, altamente citado entre as principais espécies de plantas de consumo frequente das populações africanas (ZONNEVELD *et al.*, 2021). Já a espécie *A. digitata* (L., 1759), que tem ampla distribuição tanto em Madagascar quanto no continente africano, é utilizada como matéria prima para diversos usos e produtos, de acordo com a parte da planta (WICKENS, 2008). Além das folhas, cascas e frutos também são usados com fins alimentares, além das aplicações medicinais. As sementes também têm interesse para a aplicação como alimento, extração de óleos para medicina, obtenção de energia e uso em produtos de higiene e beleza (MARIOD; SAEED MIRGHANI; HUSSEIN, 2017; WICKENS, 2008). Como recurso usado por povos tradicionais, já há uma elevada demanda pelos recursos advindos do baobá, interesse que se expande como produto de exportação e exploração para indústrias farmacêuticas e de cosméticos.

Esse aumento na demanda por recursos florestais pode agravar ainda mais a problemática ambiental no país. Conforme os dados históricos sobre a cobertura vegetal na ilha, parcela significativa de áreas florestais já foram perdidas em decorrência de atividades como extração madeireira para construção e recurso energético, plantio agrícola e abertura de áreas de pastagem para gado, atividades que, indiretamente, relacionam-se ao baixo desenvolvimento humano e elevada pobreza dos núcleos urbanos (SCALES, 2011). Segundo Vieilledent *et al.* (2018), as perdas de cobertura vegetal representaram 44% entre a década de 1950 e 2010, sendo a perda mais significativa nas áreas de florestas úmidas, com redução de 50% da área original. Seguem-se as perdas, em ordem decrescente de magnitude, para as florestas secas, espinhosas e mangues, com 29%, 19% e 2%, respectivamente. Além de uma ameaça potencial para os ecossistemas, com iminente perda da biodiversidade e aumento expressivo das taxas de extinção, estas perdas de cobertura vegetal representam também uma ameaça à conservação das espécies endêmicas de baobás (VIEILLEDENT *et al.*, 2018, 2013b).

Ainda neste contexto, é válido ressaltar o papel que as mudanças climáticas podem exercer sobre a ecologia destas espécies, uma vez que as alterações abióticas alteração a adequabilidade de habitat. Conforme o trabalho de modelagem desenvolvido por (WAN *et al.*, 2020), ocorrerão alterações significativas na distribuição e disponibilidade de habitat para todas as espécies endêmicas de baobás, relacionadas aos cenários preditivos de aumento das temperaturas globais (WAN *et al.*, 2020). Ainda que algumas áreas possam ser expandidas e exploradas pelas espécies, há uma maior tendência identificada de que estes habitats sejam contraídos. Espera-se igualmente que a competição interespecífica possa ser determinante na resiliência e estabelecimento das populações em outras áreas, ou mesmo responsável pelo seu sucesso em migrar e estabelecer-se em novos ambientes.

Diante destes fatores, a investigação associativa entre os cenários preditivos para a adequabilidade de habitat das espécies de baobá ocorrentes em Madagascar, frente à sua importância socioecológica, torna-se um importante estudo de caso para manutenção das interações socioecológicas no país. A partir da identificação de estressores e áreas de maior vulnerabilidade, podem ser traçados planos e estratégias mais eficazes para o manejo participativo e medidas de conservação mais adequadas para a prover condições necessárias à resiliência das populações.

## 1.5 OBJETIVOS

### 1.5.1 Objetivo Geral

Avaliar o papel das mudanças climáticas sobre a distribuição de duas espécies-chave na estruturação de sistemas florestais, descrever o grau de vulnerabilidade das mesmas e identificar aspectos que gerem em sistemas socioecológicos, como o manejo colaborativo, para traçar estratégias de conservação da sociobiodiversidade.

### 1.5.2 Objetivos Específicos

- Capítulo 1 - Título - “Nem todas as espécies vão migrar em direção aos polos conforme o clima esquenta: o caso das sete espécies de baobás em Madagascar”

a) Usar uma abordagem conjunta para identificar o nicho climático e a distribuição potencial das 7 espécies de baobá em Madagascar;
b) Descrever o padrão de redistribuição das espécies frente aos parâmetros abióticos das mudanças climáticas;
c) Descrever o papel de cada variável climática na distribuição de cada espécie, e indicar a relevância dos descritores para a construção de modelos ecológicos de nicho;
d) Avaliar como os padrões de redistribuição das espécies frente às mudanças climáticas podem se estender a faixa tropical mundial de acordo com as anomalias climáticas calculadas.

- Capítulo 2: Título - “Populações relictuais de *Araucaria angustifolia* estarão isoladas, pobremente protegidas e não conectadas sob efeito das mudanças climáticas e uso do solo no Brasil”.

a) Avaliar a distribuição potencial da araucária dentro da sua área de ocorrência original;
b) Descrever a porcentagem de remanescentes no presente e no futuro, considerando o uso do solo (land-use) e as mudanças climáticas;
c) Desenvolver modelos para o cálculo da conectividade dos remanescentes projetados na paisagem;
d) Avaliar o grau de vulnerabilidade e o padrão de redistribuição da araucária na paisagem.

- Capítulo 3: Título - “Manejo colaborativo como estratégia para aumentar a resiliência da Mata de Araucárias”.

a) Compreender como estratégias de conservação restritivas (*top-down*) e colaborativas (*bottom-up*) afetam a resiliência do sistema de estudo;
b) Avaliar os feedbacks e a dinâmica dos dois modelos de conservação: *top-down* e *bottom-up*;

c) Descrever os riscos e benefícios de implementação para ambas as estratégias de conservação;
d) Propor uma perspectiva crítica e alternativa ao manejo e para o aumento da resiliência no sistema socioecológico da Floresta de Araucárias.

- Capítulo 4: Título - "A disrupção de um sistema socioecológico: como o Conhecimento Ecológico Tradicional pode ser a chave para preservar a Floresta de Araucárias no Brasil sob efeito das mudanças climáticas?".

a) Avaliar como as mudanças climáticas poderão afetar aspectos socioeconômicos, ecológicos, etnoecológicos e provisão de serviços ecossistêmicos na Floresta de Araucárias;
b) Como comunidades tradicionais podem aumentar a resiliência da Floresta de Araucárias;
c) Descrever a perda potencial de serviços ecossistêmicos pela percepção de pequenos agricultores frente às mudanças climáticas.

# 2 CAPÍTULO I - NOT ALL SPECIES WILL MIGRATE POLEWARD AS THE CLIMATE WARMS: THE CASE OF THE SEVEN BAOBAB SPECIES IN MADAGASCAR.

(Nem todas as espécies vão migrar em direção aos polos conforme o clima esquenta: o caso das sete espécies de baobás em Madagascar)

Artigo publicado no periódico *Global Change Biology* – GCB (ISSN: 1365-2486) https://doi.org/10.1111/gcb.15859 – Capa da Edição (Volume 27, Dezembro de 2021)
Área de Avaliação: Biodiversidade
Classificação A1 (Quadriênio 2017-2020).

Parque Nacional Mar d'Ambre, Madagascar. Exemplar imponente de *Adansonia madagascariensis.*

Fonte: Foto de Mário M. Tagliari, 2015.

# Not all species will migrate poleward as the climate warms: the case of the seven baobab species in Madagascar

**Running head**: Baobabs redistribution as climate warms

Mario MUNIZ TAGLIARI*, Pascal DANTHU, Jean-Michel LEONG POCK TSY, Cyrille CORNU, Jonathan LENOIR, Vítor CARVALHO-ROCHA, Ghislain VIEILLEDENT*

Correspondence to: mario.tagliari@posgrad.ufsc.br | ghislain.vieilledent@cirad.fr

- M. Muniz Tagliari (https://orcid.org/0000-0002-8746-3598), CIRAD, UMR AMAP, F-34398 Montpellier, France. Human Ecology and Ethnobotany Lab, ECOHE, Ecology and Zoology Department, Universidade Federal de Santa Catarina, Florianópolis, Brazil.
- P. Danthu (https://orcid.org/0000-0002-9607-8253), CIRAD, UPR HortSys, F-34398 Montpellier, France. HortSys, Univ Montpellier, CIRAD, Montpellier, France.
- J.-M. Leong Pock Tsy, FOFIFA, DRFGRN, 101 Antananarivo, Madagascar.
- C. Cornu, CIRAD, UMR TETIS, TETIS, Univ Montpellier, AgroParisTech, CIRAD, CNRS, IRSTEA, Montpellier, France.
- J. Lenoir (https://orcid.org/0000-0003-0638-9582), Unité de Recherche “Ecologie et Dynamique des Systèmes Anthropisés” (EDYSAN, UMR 7058 CNRS), Université de Picardie Jules Verne, F-80000 Amiens, France.
- V. Carvalho-Rocha (https://orcid.org/0000-0002-4747-1219), Amphibians and Reptiles Ecology Lab, LEAR, Ecology and Zoology Department, Universidade Federal de Santa Catarina.
- G. Vieilledent (https://orcid.org/0000-0002-1685-4997), CIRAD, UMR AMAP, F-34398 Montpellier, France. AMAP, Univ Montpellier, CIRAD, CNRS, INRA, IRD, Montpellier, France

## ABSTRACT

It is commonly accepted that species should move toward higher elevations and latitudes to track shifting isotherms as climate warms. However, temperature might not be the only limiting factor determining species distribution. Species might move to opposite directions to track changes in other climatic variables. Here, we used an extensive occurrence dataset and an ensemble modelling approach to model the climatic niche and to predict the distribution of the seven baobab species (genus *Adansonia*) present in Madagascar. Using climatic projections from three global circulation models, we predicted species' future distribution and extinction risk for 2055 and 2085 under two representative concentration pathways (RCPs) and two dispersal scenarios. We disentangled the role of each climatic variable in explaining species range shift looking at relative variable importance and future climatic anomalies. Four baobab species (*A. rubrostipa*, *A. madagascariensis*, *A. perrieri*¸ and *A. suarezensis*) could experience a severe range contraction in the future (> 70% for year 2085 under RCP 8.5, assuming a zero-dispersal hypothesis). For three out of the four threatened species, range contraction was mainly explained by an increase in temperature seasonality, especially in the North of Madagascar, where they are currently distributed. In tropical regions, where species are commonly adapted to low seasonality, we found that temperature seasonality will generally increase. It is thus very likely that many species in the tropics will be forced to move equatorward to avoid an increase in temperature seasonality. Yet, several ecological (e.g. equatorial limit, or unsuitable deforested habitat) or geographical barriers (absence of lands) could prevent species to move equatorward, thus increasing the extinction risk of many tropical species, like endemic baobab species in Madagascar.

**Key-words:** Baobabs; climatic anomaly; climate change; elevation; extinction risk; latitude; Madagascar; temperature seasonality; species distribution models, species range shift.

## 2.1 INTRODUCTION

Climate change has already modified the spatial distribution of tropical biodiversity (Chen et al., 2009; Fadrique et al., 2018; Feeley, Silman, & Duque, 2016). Increasing temperatures, anomalous precipitation regimes (Anderson-Teixeira et al., 2013) and more frequent and severe extreme events (e.g. heatwaves, droughts and wildfires; Garcia, Cabeza, Rahbek, & Araújo, 2014) all pose significant challenges to biodiversity by pushing species towards the limits of their climatic tolerances (Rodríguez-Castañeda, 2013). Temperature has been the main variable considered when studying biotic responses to climate change for several reasons. First, it is an easy to measure variable. The first reliable thermometers have been used to measure air temperature since the beginning of the 18th century (Fahrenheit, 1724). Second, temperature generally decreases with elevation and latitude and has been historically used to define habitat types on Earth (FAO, 2010; von Humboldt, 1817; Holdridge, 1947). Third, temperature is a known determinant of species biology and distribution (Sentinella, Warton, Sherwin, Offord, & Moles, 2020; Tewksbury, Huey, & Deutsch, 2008). Fourth, temperature is strongly correlated to $CO_2$ concentration in the atmosphere and is expected to significantly increase at the global scale in the future, in association with increasing $CO_2$ emissions due to human activities (IPCC, 2014). As a consequence, it is commonly accepted that species will move towards higher elevations (i.e. upslope) and latitudes (i.e. poleward) to track shifting isotherms as the climate warms (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008; Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008; Lenoir & Svenning, 2015).

However, it has also been observed that species may go "*against the flow*" under the effect of climate change: towards lower elevations (i.e. downslope) and lower latitudes (i.e. equatorward) to find suitable climate conditions (Lenoir et al., 2010). These unexpected directional range shifts may involve several potential determinants, e.g. indirect biotic response due to the combined effect of both climate warming and land-use change; changes in interspecific interactions such as competition release; sensitivity to other environmental gradients not conforming with upslope and poleward range shifts; physiological or evolutionary adaptations; and random shifts due to stochastic ecological processes (Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011; Lenoir et al., 2010; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). Yet, studies reporting species range shifts in response to anthropogenic climate change usually focus on two geographical dimensions solely – latitude and elevation (Lenoir & Svenning, 2015) – and one single climatic dimension, namely mean annual temperature. Hence, these studies disregard other relevant climatic predictors such as changes in precipitation regime, water balance, or temperature seasonality, which may force species to shift downward in elevation (Crimmins et al., 2011; Lenoir et al., 2010). Given that, it is extremely important to account for additional climatic variables different from the mean annual temperature and consider other potential ecological processes that could explain species range shifts in multiple directions.

The most commonly employed tools to predict current and future distribution of species under climate change from a set of observations and climatic predictors are correlative species distribution models (SDMs) (Elith & Graham, 2009; Foden et al., 2019; Guisan et al., 2013; Porfirio et al., 2014). The main outputs of these SDMs are maps of species potential distributions in the present and future. Nowadays, many easy-to-use softwares (the JAVA Maxent; Phillips, Anderson, & Schapire, 2006) or libraries (e.g. "*sdm*" and "*biomod2*"; Naimi & Araújo, 2016; Thuiller, Lafourcade, Engler, & Araújo, 2009) have been made available to easily derive such redistribution maps. Comparing present with future species distribution maps, one can assess species vulnerability to climate change by looking at species range shift, contraction, or expansion (Vieilledent, Cornu, Cuní Sanchez, Leong Pock-Tsy, & Danthu, 2013). Surprisingly, conservation studies that employ correlative SDMs to assess species vulnerability to climate change mostly do not disentangle the respective effect of predictor variables in explaining species range shift (Fourcade, Besnard, & Secondi, 2018). Thus, they fail at explaining the possible underlying mechanisms behind such changes. For example, in an article studying the vulnerability of three baobab species to climate change in Madagascar, Vieilledent et al. (2013) showed that *Adansonia suarezensis H. Perrier,* and *A. perrieri Capuron*, will likely become extinct by 2085. However, the study does not analyze the respective role of each variable in explaining species range shift and does not suggest potential mechanisms that could explain the species extinction. In addition, a recent study assessing the vulnerability of Madagascar endemic baobabs to future climate change also failed to explore the underlying mechanisms behind expected species range shifts (Wan et al., 2020).

To help fill this gap, we investigate here the specific role of a set of climatic variables in explaining shifts in species distribution associated with climate change. We chose the seven emblematic baobab species that can be found in Madagascar (*Adansonia* L. genus; Malvaceae family) for this purpose. Six of the seven species are endemic to Madagascar (*Adansonia grandidieri* Baill*., A. madagascariensis* Baill., *A. perrieri*, *A. rubrostipa* Jum. and Perr*., A. suarezensis*, and *A. za* Baill), while the remaining species also occurs in the African continent: *A. digitata* L. (Wickens 2008). Each of the seven baobab species are located in different regions of Madagascar, being adapted to different climates and could potentially have different responses to climate change. We gathered an extensive and unprecedented occurrence dataset obtained from more than 15 years of field prospection and photo-interpretation of high-resolution satellite images. We used an ensemble modelling approach to model the climatic niche and to predict the distribution of these seven species. Using SDMs and climatic projections, we assessed whether each species could experience range shift, contraction or expansion, and in which direction. Looking at the relative climatic variable importance and future climatic anomalies, we disentangled the role of each climatic variable in explaining species range shift. Based on species' extinction risk, we made suggestions to update the current baobab species conservation status. Finally, we attempted to generalize our results to other species in the tropics that should experience similar climatic anomalies in the future.

## 2.2 MATERIAL AND METHODS

### 2.2.1 Presence and pseudo-absence data

We used photo-interpretation of very high-resolution QuickBird (61 cm resolution: most of the cases, especially for baobab identification from the crown or by their projected shadow) and Spot5 (2.5 m resolution: only in few specific cases, such as dense and homogeneous forests) satellite images available on Google Earth (http://www.google.com/earth/index.html; see Yu & Gong, 2012) to locate *A. grandidieri* and *A. suarezensis* individual trees in Madagascar. To validate occurrence data from photo-interpretation, ground-truth verifications were conducted identifying baobabs trees by the basis of their crown size, shape and color during flowering period (see Vieilledent et al. 2013). Ground-truth verification was conducted during the flowering period to facilitate species identification and validation of species occurrence data (see Vieilledent et al., 2013 for further details). For the other five Malagasy baobab species (*A. digitata*, *A. madagascariensis*, *A. perrieri*, *A. rubrostipa*, and *A. za*) we used an extensive presence only data-set available thanks to prospective fieldwork (2000 to 2015) from the Cirad Madagascar team. During fieldwork, baobab trees were identified at the species level and georeferenced with a GPS to generate a unique occurrence data-set for all Malagasy baobab species.

Our raw data-set contains 137,285 occurrence records encompassing all seven Malagasy baobab species. First, we removed all points with coordinates outside Madagascar (only for *A. digitata* because occurrence records were also collected in Comoro islands). Then, for each of the seven species separately, we created a grid with 1-km² cell resolution covering the Madagascar territory and identified all cells that had at least one occurrence record for the focal baobab species. Finally, we removed all cells and respective presence observation data with incomplete bioclimatic information. For instance, the initial set of 1,686 occurrence records available for *A. suarezensis* was reduced to a total of 170-pixel units of 1-km$^2$ each (Table S1 for all baobabs species). Our observation sample size was sufficient to perform SDMs because the recommended minimum sample size (see van Proosdij, Sosef, Wieringa, & Raes, 2016) for narrow-ranged species (as for *A. perrieri* – 21 1-km2 grid cells) is as low as 3 while it is recommended to have at least 13 occurrence points for widespread species (as for *A. grandidieri* or *A. za* – 3,772 and 460 1-km2 grid cells, respectively). We randomly sampled 10,000 pseudo-absences (i.e. virtual absence data which are drawn to be representative of the environmental variability in the study-area; Barbet-Massin, Jiguet, Albert, & Thuiller, 2012) across all Madagascar for each species to constitute a presence/pseudo-absence data-set. By using pseudo-absences we used both presence and pseudo-absence information to predict species' habitat suitability and distribution, optimizing spatial and environmental discrimination (Senay, Worner, & Ikeda, 2013). Consequently, we aimed to have a good representativity of the climate variability in Madagascar and to be able to compute a relative probability of presence across the country.

### 2.2.2 Bioclimatic data

We used current (~1950-2000) and future (2055 and 2085) climatic data at 30 arc-seconds resolution (about 1 km at the equator) over the entire spatial extent of Madagascar. This data is freely available on MadaClim (https://madaclim.cirad.fr/). The MadaClim website provides climatic data for Madagascar obtained from the WorldClim (http://worldclim.org/bioclim/) and CGIAR-CCAFS climate data portal (http://www.ccafs-climate.org/). We selected four bioclimatic variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) to model species distribution which were weakly correlated among each other and easy to interpret with regard to baobab species distribution. Three of them were previously selected via a principal component analysis among all the 19 WorldClim bioclimatic variables (following Vieilledent et al. (2013): (1) mean annual precipitation – *prec* (mm.y-$^1$); (2) mean annual temperature – *tmean* (°C); (3) temperature seasonality – *tseas* (sd x 1000 ºC). In addition, we included a synthetic variable reflecting (4) climatic water deficit – *cwd* (mm). The *cwd* variable was computed from monthly precipitation (*mcprec*) and potential evapotranspiration (*pet*) using the following formula (**Equation 1**):

$$cwd = -\sum_i \quad min\ (mcprec_i \quad - pet_i, 0) \qquad \textbf{(1)}$$

Potential evapotranspiration is defined as the evaporation amount that would occur if a sufficient water source was available. We used the Thornthwaite formula (Thornthwaite, 1948) to compute the monthly potential evapotranspiration. The four selected bioclimatic variables are widely used (i) to define biomes globally, known as Holdridge Life Zones System (Holdridge, 1947) and (ii) as proxies for other bioclimatic variables. For instance, the mean annual temperature (tmean) is a proxy for solar radiation and temperature stress (Haigh, 2007). Additionally, the mean annual temperature may indicate potential losses of plant productivity (Hatfield & Prueger, 2015). The temperature seasonality (tseas) can be interpreted as a proxy for the growing season (Hatfield & Prueger, 2015) while the annual precipitation (prec) is a proxy for potential water availability (Amissah, Mohren, Kyereh, Agyeman, & Poorter, 2018). Finally, the climatic water deficit (cwd) can be indicative of water stress and drought periods (Fayolle et al., 2014; Stephenson, 1990).

For future climate data (2055 and 2085) we selected three different global circulation models (GCMs) from the World Climate Research Programme (CMIP5) (i.e., NorESM1-M, GISS-E2-R, and HadGEM2-ES) under two representative concentration pathways (RCPs: carbon dioxide emission scenarios) (i.e., RCP 4.5 and 8.5). The RCP 8.5 scenario is characterized by high concentration and increasing $CO_2$ gas levels emissions (Riahi, Grübler, & Nakicenovic, 2007; van Vuuren et al. 2011) and can be considered the most likely emission scenario in the absence of effective mitigation policies regarding $CO_2$ emissions, whereas RCP 4.5 is known as the "*mitigation scenario*" because of projected reduction of $CO_2$ gas levels emissions (van Vuuren et al. 2011). A recent discussion has been brought in the literature affirming that RCP 8.5 is a problematic scenario for near-term (2030-2050) emissions and indicate that RCP 4.5 is more likely than RCP 8.5 (Hausfather & Peters, 2020). Despite this recent discussion, we projected our main results under RCP 8.5 because: **(i)** we projected for long-term climate change (i.e. 2085) where projections presented by RCP 8.5 in 2100 are more probable than RCP 4.5 (Schwalm, Glendo & Duffy, 2020a); **(ii)** historical cumulative $CO_2$ emissions from 2005 to 2020 are more in accordance with RCP 8.5 than RCP 4.5 (Schwalm, Glendo & Duffy, 2020b); **(iii)** RCP 4.5 underestimate biotic feedbacks (e.g. changes in soil dynamics, forest fires frequency and severity, permafrost thaw) which accelerates warming, further supporting RCP 8.5 (Schwalm, Glendo & Duffy, 2020b); **(iv)** in our study we used RCP

8.5 for the sake of risk assessment and not to compare RCPs effectiveness, despite RCP 4.5 projected temperature by 2100 is 1.7-3.2 °C, whereas for RCP 8.5 is 3.2-5.4 °C (Fuss et al. 2014). As a consequence, the outputs of RCP 4.5 in our study are presented in the supplementary material.

### 2.2.3 Species distribution modeling: statistical algorithms, model performance and importance of bioclimatic variables

We selected four statistical algorithms to model the bioclimatic niche and distribution of the seven studied baobab species: generalized linear models (GLMs); generalized additive models (GAMs); random forests (RF); and Maxent. Algorithms selection included standard regression models, such as the parametric GLM and the non-parametric GAM, classification tree (RF), and maximum entropy approach (Maxent). We aimed to quantify output uncertainty and generate a gradient from robustness (GLM and GAM) to complex algorithms, i.e. RF and Maxent (Elith & Graham, 2009). The uncertainty quantification of predictive modeling follows the premise of the ensemble modelling approach (Araújo & New, 2007), which enables a consensus identification among all forecasts and the exploration of the full breadth of intermodal variability (Kujala, Moilanen, Araújo, & Cabeza, 2013).

As we used two regression models (GLM and GAM) and two machine learning approaches (RF and Maxent) to fit SDMs, the inclusion of 10,000 pseudo-absence points (background points for Maxent algorithm) is advised for better SDM outputs to obtain more accurate results (Barbet-Massin et al., 2012). We randomly split our presence/pseudo-absence data-set using 70% for model calibration (training data-subset) and 30% for model validation (testing data-subset) to evaluate the predictive performances of our SDMs (Hijmans, 2012). We repeated the cross-validation procedure five times. Model performance in predicting species presence-absence was estimated using four different and complementary metrics: Area Under the Receiving Operating Characteristics Curve (AUC); True Skills Statistics (TSS); Sensitivity (Sen); and Specificity (Spe; Liu, White, & Newell, 2011). We thus calculated the mean value of AUC and TSS metrics across the five testing data-subsets obtained from the cross-validation procedure for each selected algorithm. By doing this we were able to describe the modelling performance in predicting species presence-absence. We also computed AUC and TSS metrics across the full data-set.

The AUC computes the model probability to rank a randomly chosen presence site instead of a randomly absent site (Liu et al., 2011; Pearce & Ferrier, 2000) and is commonly used as an accuracy index for SDMs using ensemble modelling approaches (Hao, Elith, Guillera-Arroita, & Lahoz-Monfort, 2019). It is a threshold-independent index, and it is also independent to prevalence (Allouche, Tsoar, & Kadmon, 2006), which is the proportion of samples representing species presence (McPherson, Jetz, & Rogers, 2004). If AUC values are >= 0.9, the model is commonly considered as highly accurate (Thuiller et al., 2009). The TSS metric is a threshold-dependent index (Liu et al., 2011) and is computed with a probability threshold maximizing its values. TSS values range from -1 to 1, and accurate models (correctly predicting both presences and absences) lead to values close to one (Thuiller et al., 2009). The TSS index is equal to Sensitivity + Specificity - 1. Sensitivity is the probability of correctly predicting a presence while specificity is the probability of correctly predicting an absence (Liu et al. 2011). As well as the AUC index, TSS is not sensitive to prevalence (Allouche et al., 2006; Lawson, Hodgson, Wilson, & Richards, 2014), so we used both accuracy indexes to evaluate SDM outputs for rare (such as *A. perrieri*) or abundant (such as *A. grandidieri*) baobab species.

To evaluate the performance of the ensemble model based on committee averaging we used three previously mentioned metrics: TSS, Sen, and Spe, following Araújo and New (2007). We previously defined an evaluation threshold using the accuracy index TSS (i.e. minimum score of 0.6 or 60%) in order to: **(i)** remove "bad algorithms/models"; **(ii)** build our ensemble model; **(iii)** test and evaluate the ensemble model forecasting capability (i.e. predicting species presence-absence); and **(iv)** make the binary transformation for the committee averaging computation (Thuiller et al. 2009).

For each statistical algorithm, we calculated the relative variable importance among the four studied bioclimatic variables selected for the SDMs. The computation principle follows the one used for RFs, where one bioclimatic variable is shuffled over the full data-set or the testing data-subset. To compute variable importance (*I*), the model prediction is calculated in this shuffled data-set, and a correlation (Pearson's correlation) is computed between baseline predictions (*pred_ref*) and the shuffled predictions (*pred_shuffled*; see **Equation 2**).

$$I = 1 - cor\ (pre_{ref}, pred_{shuffled}) \quad \textbf{(2)}$$

We thus generated a rank according to the variable importance over the four statistical algorithms for each species. The rank was defined by calculating the mean obtained from 6 model runs (5 runs from the testing data-subset and 1 run from the full data-set). The rank with higher mean values indicates which bioclimatic variable is more important to explain the species distribution. We used the Biomod2 R package (Thuiller et al. 2009) to generate the SDMs.

### 2.2.4 Current species distribution, climatic niche and elevational range

For each species and each modelling algorithm, predicted probabilities of occurrence during the current period were binary transformed (0 for species absence and 1 for species presence) using the probability threshold maximizing TSS. Then, the current species distribution area (SDAp in $km^2$) was defined as the set of 1-$km^2$ pixels where two out of the four modelling algorithms predicted the presence of the focal species. When only one algorithm out of the four predicted a presence for a given species, it was considered as uncertain. The species was considered absent when none of the four algorithms predicted a presence.

To characterize each species bioclimatic niche, we randomly sampled 1,000 points in the current species distribution area and computed the density (i.e. frequency), mean values, and 95% quantiles for each of the four studied bioclimatic variables, as well as for elevation. Elevation data in Madagascar was obtained from the SRTM (Shuttle Radar Topography Mission) 90 m Digital Elevation Data available from the CGIAR-CSI GeoPortal. Elevation data was aggregated at 1 km resolution and is also available for download on the MadaClim website.

### 2.2.5 Ensemble forecasting and future species distribution

To predict species distribution area in the future, we used an ensemble forecasting approach (Araujo & New 2007). For each of the two RCPs separately (RCP 4.5 and RCP 8.5), we combined climatic projections obtained from the three different GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES) and across the four modelling algorithms (GLM, GAM, Random Forest, and Maxent). We thus obtained, for each species under each RCP and for each year (2055 and 2085), 12 maps of the future probability of presence. Again, the probability of presence was converted into binary data (0 for species absence and 1 for species presence) using the same probability threshold which maximizes TSS during current conditions. Species distribution area in the future (SDAf) was defined as the set of 1-$km^2$ pixels where most projections (6 out of 12) predicted the presence of the focal species. When less than 6 models out of the 12 predicted a presence, the species presence in the future was considered uncertain. The species was considered absent in the future when none of the 12 projections predicted a presence.

When predicting future range maps under each RCP for 2055 and 2085, we also considered two contrasting dispersal hypotheses, with the reality likely to fall in between. The full-dispersal hypothesis considers the possibility for all baobab species to colonize new climatically favorable sites outside the current species distribution range. The zero-dispersal hypothesis considers the impossibility for baobab species to naturally colonize new climatically favorable sites outside the current species distribution range. This can be due to unsuitable conditions (other than climate, such as land-use) outside the current species distribution area, or to that baobab species may not be able to disperse seeds due to geographical barriers or in the absence of animal dispersers (see Vieilledent et al. 2013).

### 2.2.6 Species range shift and vulnerability to climate change

To evaluate the effect of climate change and the vulnerability of the seven Malagasy baobab species, we calculated the percentage of area change between the future (SDAf) and present (SDAp) distribution range (in km²). To compute SDAf, SDAp, and mean elevational shifts, we extracted all presence points indicated as 'presence' by the ensemble modelling and calculated the changes for each of the investigated future scenarios (mean, 95% quantiles interval, and percentage of area change in km²). Focusing on the year 2085, under RCP 8.5 for the full-dispersal and zero-dispersal scenarios, we suggested updates for baobabs conservation management strategies given their future distribution and vulnerability to climate change according to the International Union for Conservation of Nature Red List (IUCN, 2012a). Finally, we calculated potential latitudinal and elevational species range shifts by extracting 1,000 random points inside each species distribution range projected for the present and the future (2055 and 2085), under both RCPs 4.5 and 8.5 scenarios and for the full-dispersal hypothesis.

## 2.3 RESULTS

### 2.3.1 Range contraction and vulnerability of baobab species to climate change

For all seven baobab species we obtained high True Skill Statistics (TSS) values for both the model cross-validation (Table S2) and the ensemble model (Table S3). For the ensemble model, the TSS was >=0.83 for all the species except for *A. za*, for which the TSS was equal to 0.67 due to a relatively lower specificity (Table S3). High TSS values indicate that the models can then be confidently used to predict the vulnerability of species to climate change. Four baobab species are expected to be highly vulnerable to climate change under RCP 8.5, whereas for RCP 4.5 three species are expected to be highly vulnerable. *Adansonia perrieri* and *A. suarezensis* might experience a complete range loss modelled by 2085 (under RCPs 4.5 and 8.5), and could face extinction, under both the full and zero -dispersal hypothesis (Figures 1, S2; Tables 1, S4). Still, under RCP 8.5, *A. madagascariensis* and *A. rubrostipa* could experience a contraction in modelled suitable range by 2085, and thus might be threatened by extinction, under both the full (≥ -32% area) and zero-dispersal hypothesis (≥ -71% area). The three other baobab species modelled under RCP 8.5 (*A. za*, *A. grandidieri* and *A. digitata*), are expected to be resilient to climate change (Figure S1). These species might experience a small range contraction (down to -3%) under the zero-dispersal hypothesis and a strong range expansion (from +118% for *A. za* up to +300% for *A. grandidieri and A. digitata*) when modelled under the full-dispersal hypothesis (Table 1). Under RCP 4.5 and zero-dispersal hypothesis *A. madagascariensis* is predicted to lose 8% of its current distribution area, indicating that the species might not be threatened (Figure S2). The projections under RCP 4.5 and full-dispersal hypothesis also indicated a strong range expansion from +78% for *A. za* up to +268% for *A. grandidieri* and *A. digitata* (Figure S2; Table S4). Among these three species, only *A. digitata* is expected to contract its modelled suitable range by 2085 under zero-dispersal hypothesis: -20% (Figure S2). Both *A. grandidieri* and *A. za* might not be affected according to this predictive scenario

### 2.3.2 Baobab species range shift in latitude and elevation

Among the four vulnerable baobab species, *A. suarezensis* and *A. perrieri* are expected to contract their range equatorward in 2085 under RCP 4.5 and for the full-dispersal hypothesis (both species are expected to go extinct under RCP 8.5 whatever the dispersal hypothesis). *Adansonia madagascariensis* is also expected to move equatorward while *A. rubrostipa* is expected to move poleward under RCP 8.5 and full-dispersal hypothesis (Figures 1, 2). For the three resilient species (*A. za*, *A. grandidieri* and *A. digitata*), their distributional ranges should expand equatorward (*A. za*), poleward (*A. digitata)*, or in both directions for *A. grandidieri* under RCP 8.5 and the full-dispersal hypothesis (Figure S1). Regarding shifts in elevation, all baobab species are expected to shift upward in the future (from +100 m for *A. za* to +351 m for *A. rubrostipa*; Figures 2 and S3) when considering the full-dispersal hypothesis and scenario RCP 8.5 (except for *A. perrieri* and *A. suarezensis* where we considered RCP 4.5). When considering RCP 8.5 and the zero-dispersal hypothesis all threatened baobab species are expected to shrink their distribution upward (Figure 2; Table 1). Under RCP 4.5 for 2085, baobabs are expected to remain at current elevational gradient or to move upwards until 2085 (Figure S4). The potential redistribution of these species in 2085 and RCP 4.5 indicates that the *A. digitata* and *A. rubrostipa* might move poleward, whereas the other species are expected to remain in similar latitudes in the future (Figure S4).

### 2.3.3 Climatic gradients and future climatic anomalies in Madagascar

We identified four main climatic gradients in Madagascar (Figure 3) which are important to subsequently interpret species distribution on the island. A first gradient shows a decrease of the mean annual temperature with elevation. A second one shows an increase in temperature seasonality associated with higher latitude (lower seasonality at the North, toward the Equator, higher seasonality at the South, toward the South pole). A third gradient shows a decrease in annual precipitation from East to West associated with dominant Eastern winds and orographic precipitation (higher precipitation in the East). Finally, a fourth gradient shows an increase of the climatic water deficit from East to West due to the combining effects of precipitation and temperature. Computation of future climatic anomalies in 2085 under RCP 8.5 shows a general increase in the mean annual temperature over the whole Madagascar (from +2.5 to +4.0 °C), with a stronger increase in the inner-land than on the coast. Temperature seasonality should also generally increase over the whole Madagascar, especially at the North of the island where the temperature seasonality anomaly should reach up to +3 °C. Precipitation should generally decrease over the island (from 0 to -300 mm/yr) with a stronger decrease in the North-East. Associated with the general increase in temperature and decrease in precipitation, the climatic water deficit should generally increase (from 0 to +1500 mm/yr) over the island and decrease should be stronger in the Western part of Madagascar (> 500 mm/yr).

### 2.3.4 Importance of each bioclimatic variable in explaining species redistribution

For *A. madagascariensis*, *A. perrieri*, and *A. suarezensis*, three out of the four potentially threatened baobab species in 2085 under RCP 8.5, the most important variable for explaining species distribution and thus redistribution was temperature seasonality (Figure 4 and Table 2). These three species are currently distributed in the Northern part of Madagascar

(Figure 1) and might experience, by 2085 under RCP 8.5, a significant increase in temperature seasonality (from +0,113 to +0,148 °C) inside their current distribution range (Figures 1 and 4, Table S5). For the fourth threatened species (*A. rubrostipa*), the most important variable was climatic water deficit (Table 2). This species could experience, by 2085 under RCP 8.5, a strong increase in climatic water deficit inside its current distribution range (+870 mm/yr; Figures 1, 3 and 4). The second most important variable for the four threatened species were either annual mean temperature (*A. madagascariensis*), mean annual precipitation (*A. rubrostipa* and *A. suarezensis*), or climatic water deficit (*A. perrieri*).

For *A. grandidieri*, and *A. za,* two out of the three non-threatened baobab species under RCP 8.5 in 2085, the most important variable for explaining these species distribution and redistribution was mean annual precipitation (Figure 4 and Table 2). Mean annual precipitation should not significantly change (from -31 to -70 mm/yr) inside the current distribution range of *A. grandidieri* and *A. za* (Figures 3, 4, and Table S5), which are two species already adapted to dry climate (precipitation < 1000 mm/yr, Figure S5; Table S5). The second most important variable for these two species was annual mean temperature which is expected to significantly increase inside the two species' distribution range in the future (+3.5 °C, Figure 3; Table S5), although not affecting their distribution (Figure 1). For *A. digitata*, the third non-threatened species, the two most important variables were temperature seasonality (+0,87 °C) and the climatic water deficit (+680 mm/yr). These two variables are expected to increase inside the species distribution range in the future (Figures 3, 4 and Table S5), although not affecting its distribution.

## 2.4 DISCUSSION

### 2.4.1 Vulnerability of baobab species to climate change and conservation status

We showed that four out of the seven Malagasy baobab species are expected to experience a strong range contraction under the effect of climate change (> 70% for year 2085 under RCP 8.5 and the zero-dispersal hypothesis) and could be strongly threatened with extinction according to our predictive scenarios. These four species are: *A. madagascariensis*, *A. perrieri*, *A. suarezensis*, and *A. rubrostipa.* Among these four species, *A. perrieri* and *A. suarezensis* could face a complete loss of their habitat by 2085 due in particular to an increase in the temperature seasonality in the future. The three other Malagasy baobab species, *A. grandidieri*, *A. za*, and *A. digitata* did not indicate any significant range contraction when modelled under climate change scenarios, except for *A. digitata* which might reduce its modelled distribution by 20% in 2085 under RCP 4.5 (Figure S2). For *A. grandidieri* and *A. za*, this resilience can be easily explained. *A. za* is a generalist species that can be found in a large range of climatic conditions and has a large distribution over Madagascar (Figures S1, S5). For *A. grandideri*, while it has a much narrower climatic niche than *A. za* and can be considered as a specialist species, it is already adapted to hot and dry climates (Figures 4, S1 and S5). Conversely, we did not find a simple explanation for the resilience of *A. digitata* under RCP 8.5 in 2085. Temperature seasonality and climatic water deficit (which are expected to increase in the future, Figure 3) were the most important climatic variables in explaining the distribution of this species (Figure 4). We hypothesize that the potential combination of the four climatic variables (which are rather close in terms of importance, Table 2) determines the large suitable habitat for the species in the future and its predicted resilience to climate change (Figure S1).

These results are in line with those obtained by Vieilledent et al. (2013) who have previously demonstrated, with different statistical models and IPCC climate scenarios, that both *A. perrieri* and *A. suarezensis* should become extinct by 2085 due to climate change, and that *A. grandidieri* should not be vulnerable to climate change. In a recent study, Wan et al. (2020) found contradictory results to ours: a resilience of *A. perrieri* and *A. suarezensis*, and a vulnerability of *A. za* to climate change. However, these conclusions were taken by using a much smaller dataset (245 occurrence points distributed among the 6 endemic Malagasy baobab species) than ours (4830 in total, see Table S1). In addition, their statistical approach was very limited in comparison to ours. Wan et al. (2020) used only one algorithm (Maxent), while we used four algorithms for both the ensemble modelling and the forecasting approach. In particular, the vulnerability of *A. za* to climate change found by Wan et al. (2020) seems to be in contradiction with its known biology and distribution as a generalist species (Figures S1, S2, S5 and Table S5).

In light of these results, we recommend updating the IUCN conservation status for the four threatened baobab species (Table 1) based on the risk assessment under RCP 8.5. We base our recommendations on the IUCN Red List Categories and Criteria version 3.1 (IUCN, 2012b). We recommend updating *A. madagascariensis* from "Near Threatened" to "Endangered A3c" (population reduction >= 50% in the future). For *A. suarezensis,* we recommend updating the conservation status from "Endangered B1ab + B2ab" to "Critically Endangered B1ab + B2ab" (complete extent of occurrence loss by 2085). For *A. perrieri*, we recommend updating the conservation status from "Critically Endangered C2a(i)" to "Critically Endangered C2a(i) + A3c" (few mature individuals and potential extinction in the long-term). Finally, for *A.*

*rubrostipa*, we recommend updating the conservation status from "Least Concern" to "Endangered A3c" (> 85% habitat loss in 2085). Climate change is not the only threat to Malagasy baobab species. The seven baobab species are also severely threatened by habitat loss associated with the rampant deforestation in Madagascar (Vieilledent et al., 2018) which prevents species from regenerating.

### 2.4.2 Species range shifts in latitude and elevation under climate change

We have shown in our study that temperature seasonality was the most important variable at explaining species distribution for three out of the four threatened Malagasy baobab species. These three species (*A. madagascariensis*, *A. perrieri*, and *A. suarezensis)* are currently distributed in the Northern part of Madagascar, close to the Equator line, where the seasonality is lower. These three baobab species might experience, by 2085 under RCP 8.5, a strong increase in temperature seasonality. This strong increase in temperature seasonality is expected to be general to all the Northern region of Madagascar. To track the change in temperature seasonality, these three species might move equatorward, where the temperature seasonality is lower. Specifically for *A. madagascariensis*, mean annual temperature was the second most important variable explaining its distribution, and could also influence the species redistribution equatorward, thanks to suitable habitats in Northeastern Madagascar in 2085. Several studies on climate change have considered that the general trend for species, under the effect of climate change, will be to shift their distribution upward or poleward to escape from the increasing mean temperature globally (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir et al., 2008; Parmesan & Yohe, 2003; Pecl et al., 2017; Vanderwal et al., 2013). Using emblematic Malagasy baobab species as an example, we demonstrate that this might not always be the case. Depending on both the bioclimatic variables that preferentially determine their distribution (the temperature seasonality in our study) and the future climatic anomalies (increase in temperature seasonality in our study), some species are expected to move in the opposite direction under the effect of climate change, i.e. equatorward.

In a review article, Lenoir et al. (2010) have examined the potential mechanisms that could push species to go "against the flow" under climate change. They underlined the importance of additional ecological processes, in addition to climate change, to explain observed downslope range shifts in a warming climate. These mechanisms encompass biotic interactions (release of the competition associated with species range shift under climate change) and land-use change (new suitable habitats available downward). In our study, we show that it is not necessary to invoke other processes than climate change to explain shifts in species distribution in opposite directions. Studying the past range shift of 464 Australian bird species, VanDerWal et al. (2013), showed that complex interactions between temperature, precipitation, and species-specific tolerances could result in multi-directional distribution shifts, including equatorward. In our study, we illustrate one simple climatic mechanism, based on the change in temperature seasonality, by which species can shift their distribution equatorward.

We have also shown that it is not contradictory for a species to move both equatorward and upward under climate change, as is the case for *A. perrieri*, *A. suarezensis*, and *A. madagascariensis* (Figure 2). This counter-intuitive range shift has already been reported for sub-mountainous forest plant species in France which have shifted their distribution both southward (i.e. equatorward in France) and upward (Kuhn, Lenoir, Piedallu, & Gégout, 2016). The explanation lies in the presence of mountainous areas towards the south of the species' current distribution areas. In Madagascar, the explanation is different. We have shown that temperature seasonality is much more correlated to latitude than to elevation and that conversely, mean annual temperature is much more correlated to elevation than to latitude (Figure S6). Consequently, a species can shift its distribution both equatorward and upward to track changes in both temperature seasonality and mean annual temperature, respectively. Moreover, assuming that a species moves towards the equator to track changes in temperature seasonality, it might be that the lands towards the equator are located at higher elevation, thus leading to an upward shift of the species.

### 2.4.3 Vulnerability of tropical species to change in temperature seasonality

Our findings could have strong implications regarding species response to climate change in the tropics. In tropical regions, species are adapted to low temperature seasonality (Hua, 2016; Janzen, 1967; Pacifici et al., 2017; Sheldon, Leaché, & Cruz, 2015). Because sunlight duration (~12 hours a day) and solar incidence do not change significantly throughout the year, the temperature seasonality in tropical regions close to the Equator is narrower in comparison with subtropical or temperate regions (Figure 5a). For instance, temperature seasonality influences plant species biology and traits as it determines the length of the growing season and their phenology, such as the date of foliation, flowering and fruiting (Pacifici et al. 2017; Wright, 1996).

Here we have shown that an increase in temperature seasonality could force species to shift their distribution equatorward. Looking at the projected change in temperature seasonality in 2085 under RCP 8.5, a general increase in temperature seasonality across the tropics is expected (up to +1°C for the standard deviation of the monthly temperatures), with a particularly marked change in the Amazon region (Figure 5b). As for *A. perrieri* and *A. suarezensis* in Madagascar, the species redistribution equatorward to track changes in temperature seasonality might be impeded by several geographic and climatic barriers. This might also happen through several tropical lands located on islands in the Caribbean, Indian Ocean, or Southeast Asia for example. On these islands, the absence of land equatorward could act as a geographical barrier for species moving equatorward due to climate change. In addition, much of the tropical natural areas have been degraded, largely because of deforestation (Hansen et al., 2020). This could also prevent species from finding suitable habitats equatorward in tropical forests. Finally, species already distributed at the equator will not be able to move toward areas with lower seasonality, in analogy with species already at the top of the mountain which cannot shift their distribution upward to track temperature changes.

To conclude, our study shows that not all species should migrate poleward or upward as the climate warms, which reinforces the results of previous studies (Kuhn et al. 2016, VanDerWal et al. 2013). Depending on the relative importance of the bioclimatic variables at explaining species distribution and regional climatic anomalies, shifts in species distribution can be multi-directional, including equatorward. We also underline the importance of the increase in temperature seasonality in the tropics that could potentially drag to extinction a large number of species adapted to low seasonality, among which three out of the seven emblematic baobab species of Madagascar.

## 2.5 DECLARATIONS

**Data availability** – Data (including the CIRAD baobab occurrence database in Madagascar) and code used to obtain the results of the present study are available on GitHub (https://github.com/ghislainv/baobabs_mada). The GitHub repository has been permanently archived in the CIRAD Dataverse (https://doi.org/10.18167/DVN1/LIALRR).

**Acknowledgments** – Authors would like to thank all the people who have contributed to baobab occurrence data collection in Madagascar since the 2000s, in particular Wilfried Ramahafaly, Lucien Rasoanaivoson, Marcelo Saïdoune Maharitra, and Emilson Rakotoarisoa. MMT thanks to Juliano Bogoni and Maurício Cantor for their useful insights during the writing of the manuscript. MMT also thanks Emanuel Sinic and Sayuri Kyota for their tremendous support between 2019 and 2020.

**Funding** - This work was funded by the FRB - FFEM (Fondation pour la Recherche sur la Biodiversité - Fond Français pour l'Environnement Mondial) through the BioSceneMada project (project agreement AAP-SCEN-2013 I). MMT and VCR received their PhD grants from the "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior" - Brazil (CAPES) - Finance Code 001. MMT received additional fundings from MAPA's Private Fund - Number 8052-7. MMT also received a fellowship from CIRAD ("Action Incitative: Soutien aux doctorants du Sud") for a three month visiting period at UMR AMAP in Montpellier in 2019.

**Conflicts of interest** – The authors declare they have no conflicts of interest.

## 2.6 REFERENCES

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Amissah, L., Mohren, G. M. J., Kyereh, B., Agyeman, V. K., & Poorter, L. (2018). Rainfall seasonality and drought performance shape the distribution of tropical tree species in Ghana. Ecology and Evolution, 8(16), 8582–8597. https://doi.org/10.1002/ece3.4384

Anderson-Teixeira, K. J., Miller, A. D., Mohan, J. E., Hudiburg, T. W., Duval, B. D., & DeLucia, E. H. (2013). Altered dynamics of forest recovery under a changing climate. Global Change Biology, 19(7), 2001–2021. https://doi.org/10.1111/gcb.12194

Araújo, M. B., & New, M. (2007, January 1). Ensemble forecasting of species distributions. Trends in Ecology and Evolution. Elsevier. https://doi.org/10.1016/j.tree.2006.09.010

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution, (SUPPL.28), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. Science, 333(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Chen, I. C., Shiu, H. J., Benedick, S., Holloway, J. D., Chey, V. K., Barlow, H. S., … Thomas, C. D. (2009). Elevation increases in moth assemblages over 42 years on a tropical mountain. Proceedings of the National Academy of Sciences of the United States of America, 106(5), 1479–1483. https://doi.org/10.1073/pnas.0809320106

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science (New York, N.Y.), 322(5899), 258–261. https://doi.org/10.1126/science.1162547

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science, 331(6015), 324–327. https://doi.org/10.1126/science.1199040

Elith, J., & Graham, C. H. (2009). Do they? How do they? Why do they differ? on finding reasons for differing performances of species distribution models. Ecography, 32(1), 66–77. https://doi.org/10.1111/j.1600-0587.2008.05505.x

Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., … Feeley, K. J. (2018). Widespread but heterogeneous responses of Andean forests to climate change. Nature, 564(7735), 207–212. https://doi.org/10.1038/s41586-018-0715-9

Fahrenheit, D. G. (1724). VIII. Experimenta & observationes de congelatione aquæ in vacuo factæ a D. G. Fahrenheit, R. S. S *Philosophical Transactions of the Royal Society of London*, The Royal Society, *1724*(33), 78–84.

FAO, U.N. Food and Agriculture Organization. (2012). Global Ecological Zones for FAO forest reporting: 2010 Update. Available at: http://www.fao.org/geonetwork/srv/en/main.home.

Fayolle, A., Swaine, M. D., Bastin, J.-F., Bourland, N., Comiskey, J. A., Dauby, G., Plumptre, A. J. (2014). Patterns of tree species composition across tropical African forests. Journal of Biogeography, 41(12), 2320–2331. https://doi.org/10.1111/jbi.12382

Feeley, K. J., Silman, M. R., & Duque, A. (2016). Where are the tropical plants? A call for better inclusion of tropical plants in studies investigating and predicting the effects of climate change. Frontiers of Biogeography, 7(4). https://doi.org/10.21425/f5fbg27602

Fourcade, Y., Besnard, A. G., & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. Global Ecology and Biogeography, 27(2), 245–256. https://doi.org/10.1111/geb.12684

Fuss, S., Canadell, J. G., Peters, G. P., Tavoni, M., Andrew, R. M., Ciais, P., … Yamagata, Y. (2014, January 1). Betting on negative emissions. *Nature Climate Change*. Nature Publishing Group. https://doi.org/10.1038/nclimate2392

Garcia, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. Science (New York, N.Y.), 344(6183), 1247579. https://doi.org/10.1126/science.1247579

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., … Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. Ecology Letters, 16(12), 1424–1435. https://doi.org/10.1111/ele.12189

Haigh, J. D. (2007). The Sun and the Earth's Climate. Living Reviews in Solar Physics, 4(1), 2. https://doi.org/10.12942/lrsp-2007-2

Hansen, M. C., Wang, L., Song, X. P., Tyukavina, A., Turubanova, S., Potapov, P. V., & Stehman, S. V. (2020). The fate of tropical forest fragments. Science Advances, 6(11), 1–10. https://doi.org/10.1126/sciadv.aax8574

Hao, T., Elith, J., Guillera-Arroita, G., & Lahoz-Monfort, J. J. (2019). A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. Diversity and Distributions, 25(5), 839–852. https://doi.org/10.1111/ddi.12892

Hatfield, J. L., & Prueger, J. H. (2015). Temperature extremes: Effect on plant growth and development. Weather and Climate Extremes, 10, 4–10. https://doi.org/10.1016/J.WACE.2015.08.001

Hausfather, Z., & Peters, G. P. (2020). RCP 8.5 is a problematic scenario for near-term emissions. *Proceedings of the National Academy of Sciences of the United States of America*. National Academy of Sciences. https://doi.org/10.1073/pnas.2017124117

Hijmans, R. J. (2012). Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology, 93(3), 679–688. https://doi.org/10.1890/11-0826.1

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965–1978. https://doi.org/10.1002/joc.1276

Holdridge, L. R. (1947). Determination of world plant formations from simple climatic data. Science, 105(2727), 367–368. https://doi.org/10.1126/science.105.2727.367

Wright, S. (1996). Phenological Responses do Seasonality in Tropical Forest Plants. In S. S. Mulkey, R. L. Chazdon, & A. P. Smith (Eds.), Tropical Forest Plant Ecophysiology (1st ed., Vol. 1, pp. 440–460). Springer US. https://doi.org/10.1007/978-1-4613-1163-8

IPCC. (2014). Climate change 2014: Synthesis Report. In: Core Writing Team, Pachauri, R.K. & Meyer L.A. (eds.). Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, pp. 151

IUCN. (2012a). The IUCN Red List of Threatened Species. Version 2012.2. Available at: www.iucnredlist.org

IUCN. (2012b). The IUCN Red List Categories and Criteria: Version 3.1. 2012b. Second ed. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. Am. Nat. *101*, 233–249. https://doi.org/10.1086/282487

Kuhn, E., Lenoir, J., Piedallu, C., & Gégout, J. C. (2016). Early signs of range disjunction of submountainous plant species: An unexplored consequence of future and contemporary climate changes. Global Change Biology, 22(6), 2094–2105. https://doi.org/10.1111/gcb.13243

Kujala, H., Moilanen, A., Araújo, M. B., & Cabeza, M. (2013). Conservation Planning with Uncertain Climate Change Projections. PLoS ONE, 8(2). https://doi.org/10.1371/journal.pone.0053315

Lawson, C. R., Hodgson, J. A., Wilson, R. J., & Richards, S. A. (2014). Prevalence, thresholds and the performance of presence-absence models. Methods in Ecology and Evolution, 5(1), 54–64. https://doi.org/10.1111/2041-210X.12123

Lenoir, J., Gégout, J. C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., … Svenning, J. C. (2010). Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography, 33(2), 295–303. https://doi.org/10.1111/j.1600-0587.2010.06279.x

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. Science (New York, N.Y.), 320, 1768–1771. https://doi.org/10.1126/science.1156831

Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography, (April 2014), 15–28. https://doi.org/10.1111/ecog.00967

Liu, C., White, M., & Newell, G. (2011). Measuring and comparing the accuracy of species distribution models with presence-absence data. Ecography, 34(2), 232–243. https://doi.org/10.1111/j.1600-0587.2010.06354.x

McPherson, J. M., Jetz, W., & Rogers, D. J. (2004). The effects of species' range sizes on the accuracy of distribution models: Ecological phenomenon or statistical artefact? Journal of Applied Ecology, 41(5), 811–823. https://doi.org/10.1111/j.0021-8901.2004.00943.x

Naimi, B., & Araújo, M. B. (2016). sdm: a reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*, 368375. https://doi.org/10.1111/ecog.01881

Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*, *7*(3), 205–208. https://doi.org/10.1038/nclimate3223

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change. Nature, 421, 37–42.

Pearce, J., & Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling, 133(0000), 225–245.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, 355(6332), eaai9214. https://doi.org/10.1126/SCIENCE.AAI9214

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine Taxa Track Local Climate Velocities. Science, 341, 1239–1242.

Porfirio, L. L., Harris, R. M. B., Lefroy, E. C., Hugh, S., Gould, S. F., Lee, G., … Mackey, B. (2014). Improving the Use of Species Distribution Models in Conservation Planning and Management under Climate Change. PLoS ONE, 9(11), e113749. https://doi.org/10.1371/journal.pone.0113749

Riahi, K., Grübler, A., & Nakicenovic, N. (2007). Scenarios of long-term socio-economic and environmental development under climate stabilization. Technological Forecasting and Social Change, 74(7), 887–935. https://doi.org/10.1016/j.techfore.2006.05.026

Rodríguez-Castañeda, G. (2013). The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. Global Ecology and Biogeography, 22(1), 118–130. https://doi.org/10.1111/j.1466-8238.2012.00795.x

Sheldon, K. S., Leaché, A. D., & Cruz, F. B. (2015). The influence of temperature seasonality on elevational range size across latitude: a test using. *Global Ecology and Biogeography*, *24*, 632–641. https://doi.org/10.1111/geb.12284

Schwalm, C. R., Glendon, S., & Duffy, P. B., (2020a) RCP 8.5 tracks cumulative $CO_2$ emissions. *Proceedings of the National Academy of Sciences of the United States of America*. 117, 19656–19657. https://doi.org/10.1073/PNAS.2007117117

Schwalm, C. R., Glendon, S., & Duffy, P. B. (2020b). Reply to hausfather and peters: RCP 8.5 is neither problematic nor misleading. *Proceedings of the National Academy of Sciences of the United States of America*. National Academy of Sciences. https://doi.org/10.1073/pnas.2018008117

Senay, S. D., Worner, S. P., & Ikeda, T. (2013). Novel Three-Step Pseudo-Absence Selection Technique for Improved Species Distribution Modelling. *PLoS ONE*, *8*(8). https://doi.org/10.1371/journal.pone.0071218

Sentinella, A. T., Warton, D. I., Sherwin, W. B., Offord, C. A., & Moles, A. T. (2020). Tropical plants do not have narrower temperature tolerances, but are more at risk from warming because they are close to their upper thermal limits. Global Ecology and Biogeography, 29(8), 1387–1398. https://doi.org/10.1111/geb.13117

Stephenson, N. L. (1990). Climatic control of vegetation distribution - the role of the water balance. *The American Naturalist*, *135*, 649–670.

Tewksbury, J. J., Huey, R. B., & Deutsch, C. A. (2008). Ecology: Putting the heat on tropical animals. Science, 320(5881), 1296–1297. https://doi.org/10.1126/science.1159328
Thornthwaite, C. W. (1948). An approach toward a rational classification of climate. Geographical Review, 38(1), 55–94.

Thornthwaite, C. W. (1948). An approach toward a rational classification of climate. *Geographical Review*, 38(1), 55–94.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD - A platform for ensemble forecasting of species distributions. Ecography, (32), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J., & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. Ecography, 39(6), 542–552. https://doi.org/10.1111/ecog.01509

van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., … Rose,

S. K. (2011). The representative concentration pathways: An overview. Climatic Change, 109(1), 5–31. https://doi.org/10.1007/s10584-011-0148-z

VanDerWal, J., Murphy, H. T., Kutt, A. S., Perkins, G. C., Bateman, B. L., Perry, J. J., & Reside, A. E. (2013). Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nature Climate Change, 3(3), 239–243. https://doi.org/10.1038/nclimate1688

Vieilledent, G., Cornu, C., Cuní Sanchez, A., Leong Pock-Tsy, J.-M., & Danthu, P. (2013). Vulnerability of baobab species to climate change and effectiveness of the protected area network in Madagascar: Towards new conservation priorities. Biological Conservation, 166, 11–22. https://doi.org/10.1016/j.biocon.2013.06.007

Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J. R., Allnutt, T. F., & Achard, F. (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. Biological Conservation, 222(January), 189–197. https://doi.org/10.1016/j.biocon.2018.04.008

von Humboldt, A. (1817). Des lignes isothermes et la distribution de la chaleur sur le globe. Paris, V.H. Perronneau, 1817, p. 145

Yu, L., & Gong, P. (2012). Google Earth as a virtual globe tool for Earth science applications at the global scale: progress and perspectives. *International Journal of Remote Sensing*. Taylor and Francis Ltd. https://doi.org/10.1080/01431161.2011.636081

Wan, J.-N., Mbari, N. J., Wang, S.-W., Liu, B., Mwangi, B. N., Rasoarahona, J. R. E., … Wang, Q.-F. (2020). Modeling impacts of climate change on the potential distribution of six endemic baobab species in Madagascar. Plant Diversity. https://doi.org/10.1016/j.pld.2020.07.001

Wickens, G. E. (2008). The Baobabs: Pachycauls of Africa, Madagascar and Australia. Springer Netherlands. https://doi.org/10.1007/978-1-4020-6431-9

## 2.7 FIGURES

Figure 1. **Species range contraction under climate change for the four threatened baobab species under RCP 8.5.** The four species are *A. madagascariensis*, *A. perrieri*, *A. rubrostipa*, and *A. suarezensis* (one species per row). **(a, e, i, m)** Occurrence points over Madagascar elevation map (elevation in m); **(b, f, j, n)** Current predicted species distribution. Legend indicates the number of models (0-4) predicting the species presence; **(c, g, k, o)** Projected species distribution in 2085 under scenario RCP 8.5 and the full-dispersal hypothesis. Legend indicates the number of models (0-12) predicting the species presence; **(d, h, l, p)** Projected species distribution in 2085 under scenario RCP 8.5 and the zero-dispersal hypothesis. Legend indicates the number of models (0-12) predicting the species presence. For the distribution maps, the species is assumed to be present (green areas) when a majority of models predicts a presence (votes >= 2 in the present, and >= 6 in the future). The species is considered absent (grey areas) when no model (votes = 0), or a minority of models (votes < 2 in the present, and < 6 in the future), predicts a presence. Maps for *A. perrieri* and *A. suarezensis*, two species distributed at the extreme North of Madagascar, have been zoomed in (black squares).

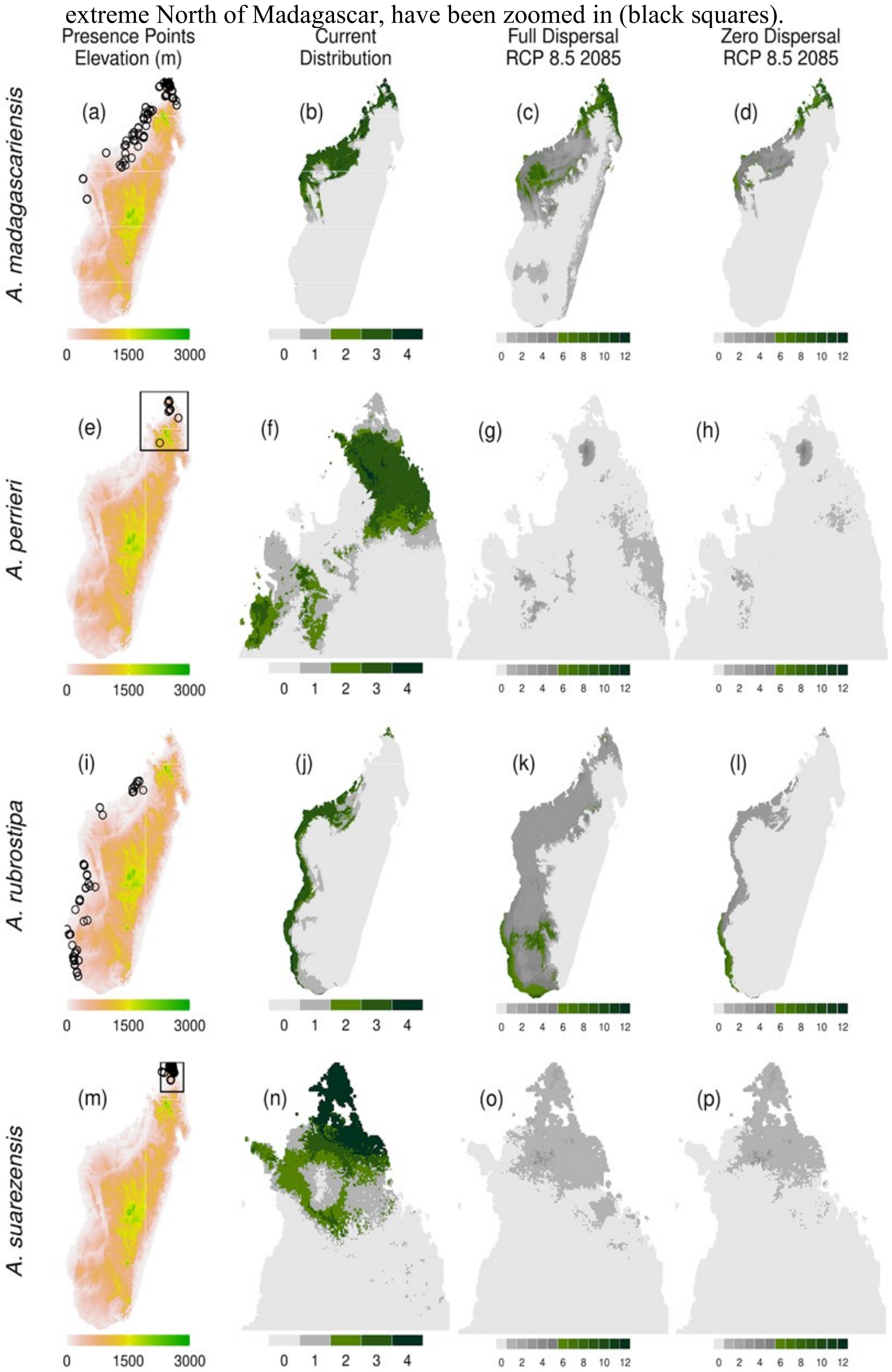


Figure 2. **Change in elevation and latitude for the most threatened baobab species.** We randomly sampled 1000 points inside the species predicted occurrence area in the present and in the future (due to the extremely reduced distribution area for *A. perrieri* and *A. suarezensis*, we only sampled 416 and 105 points, respectively for year 2085, and another 15 points for *A. suarezensis* in 2055). For *A. madagascariensis* and *A. rubrostipa* we considered the scenario RCP 8.5 and the full-dispersal hypothesis. Under RCP 8.5, both *A. perrieri* and *A. suarezensis* became extinct in 2055 and 2085. As a consequence, we used RCP 4.5 to show change in elevation and latitude for these two species. *A. madagascariensis* will migrate to higher elevation (a) under climate change scenarios for 2055 and 2085 and also change its latitudinal range to lower latitudes (i.e. equatorward) in 2085 (b). *A. rubrostipa* will move to higher elevations (e) and shift its latitudinal range to higher latitudes, i.e. poleward (f). Both *A. perrieri* and *A. suarezensis* will shift their range to more elevated areas (c,g) and lower latitudes, i.e. equatorward, especially *A. perrieri* (d), while *A. suarezensis* is expected to retain its niche at lower latitudes (h).

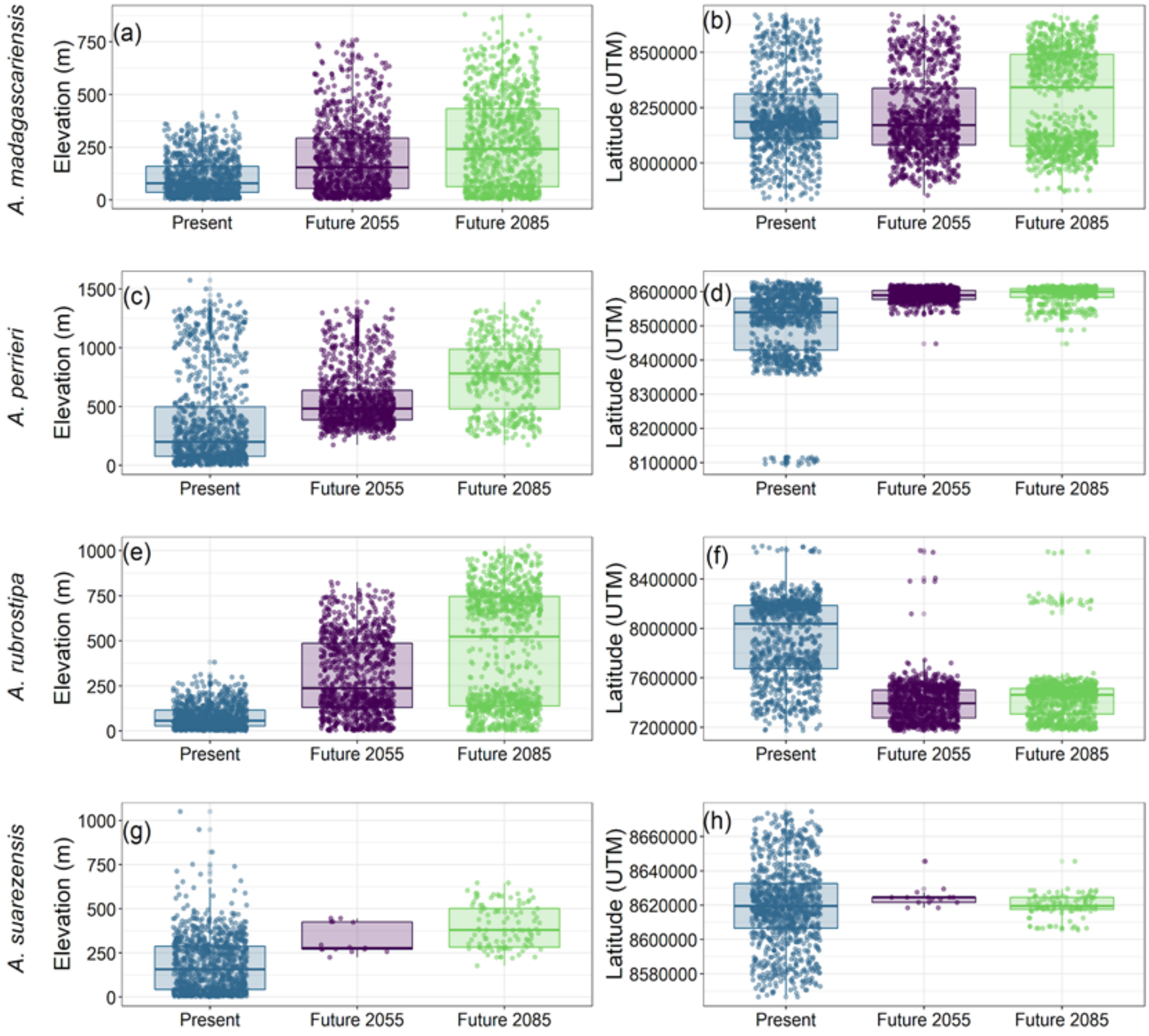


Figure 3. **Spatial variability of the climatic variables in Madagascar and map of the future climatic anomalies.** The four climatic variables used to perform the SDMs were considered: (a) annual mean temperature (Temperature in °C x 10); (b) temperature seasonality (T. seasonality, standard deviation of monthly temperatures x 1000); (c) annual mean precipitation (Precipitation in mm/y); (d) climatic water deficit (mm/y). Climatic anomalies (a’,b’,c’,d’) were computed as the difference between the mean of future climatic data in 2085 (2070-2100) and present (1970-2000) climatic data. Mean future climatic data in 2085 were computed from three GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES) under RCP 8.5. Four climatic gradients are well visible in Madagascar: (i) a North-South temperature seasonality gradient associated with latitude (low seasonality at the North, equatorward); (ii) a decrease in precipitation from East toward West Madagascar due to dominant Eastern winds and orographic precipitation (higher precipitation in the East); (iii) East-West water deficit gradient due to combining effect of both precipitation and temperature; and (iv) a decrease in mean temperature in more elevated areas. Temperature seasonality should increase for the whole Madagascar. This increase will be particularly important in the North of Madagascar (> +150) where seasonality is currently low. A general increase in temperature (> +3°C) is expected in 2085 over Madagascar with climate change, with a higher increase in the inner land than on the coast. All Madagascar should experience a decrease in precipitation. Decrease in precipitation is expected to be stronger in the East (between -150 and -300 mm.y-1). and a strong increase in the climatic water deficit.

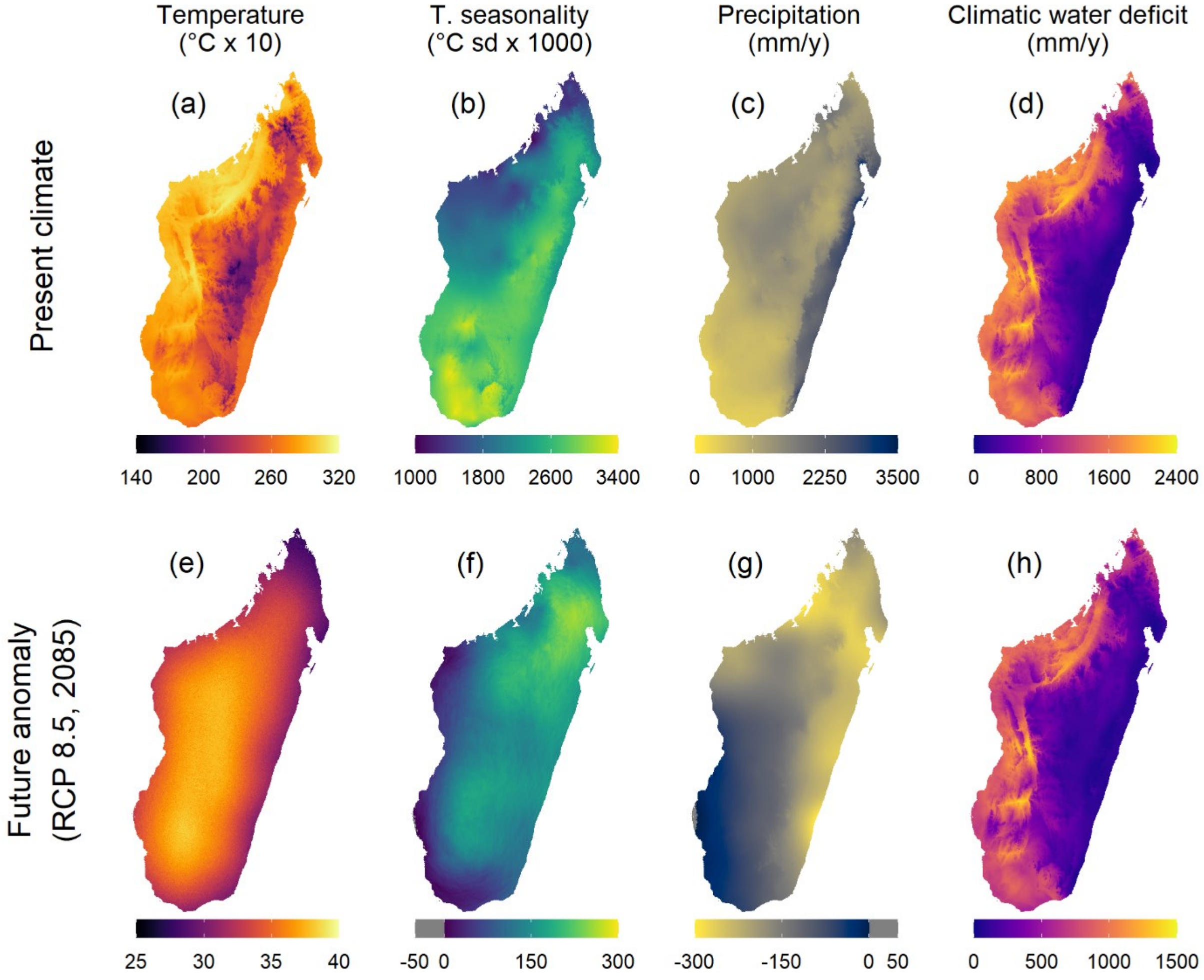


Figure 4. **Comparison of current (blue) and future (green) bioclimatic conditions experienced by each species within the current extent of their respective geographical ranges.** We selected only the two most important climatic variables determining species distribution. Left column (panels **a, c, e, g, i, k, m**) shows the first most important variables; Right column (panels **b**, **d**, **f**, **h**, **k**, **l**, **n**) shows the second most important variables. *Horizontal axis* represents one of the four bioclimatic variables: mean annual temperature (*temp* - °C x 10), temperature seasonality (°C, standard deviation [sd] x 1000), mean annual precipitation (mm/y), and climatic water deficit (mm). *Vertical axis* shows the distribution of values for that bioclimatic variable. Density plots show current (blue density plots) and future (2085, RCP 8.5, mean of 3 GCMs; green density plots). Dark-green shaded areas show current and future overlapping values. Bioclimatic envelope (current and future) of each variable was calculated within the current species distribution area (1000 random points extracted within occurrence areas indicated by the Ensemble approach). Vertical lines: dashed lines represent 95% bioclimatic envelope of future (green) and current (blue) variables within each species current distribution area; solid lines represent the computed mean value for current (blue) and future (green) bioclimatic data.

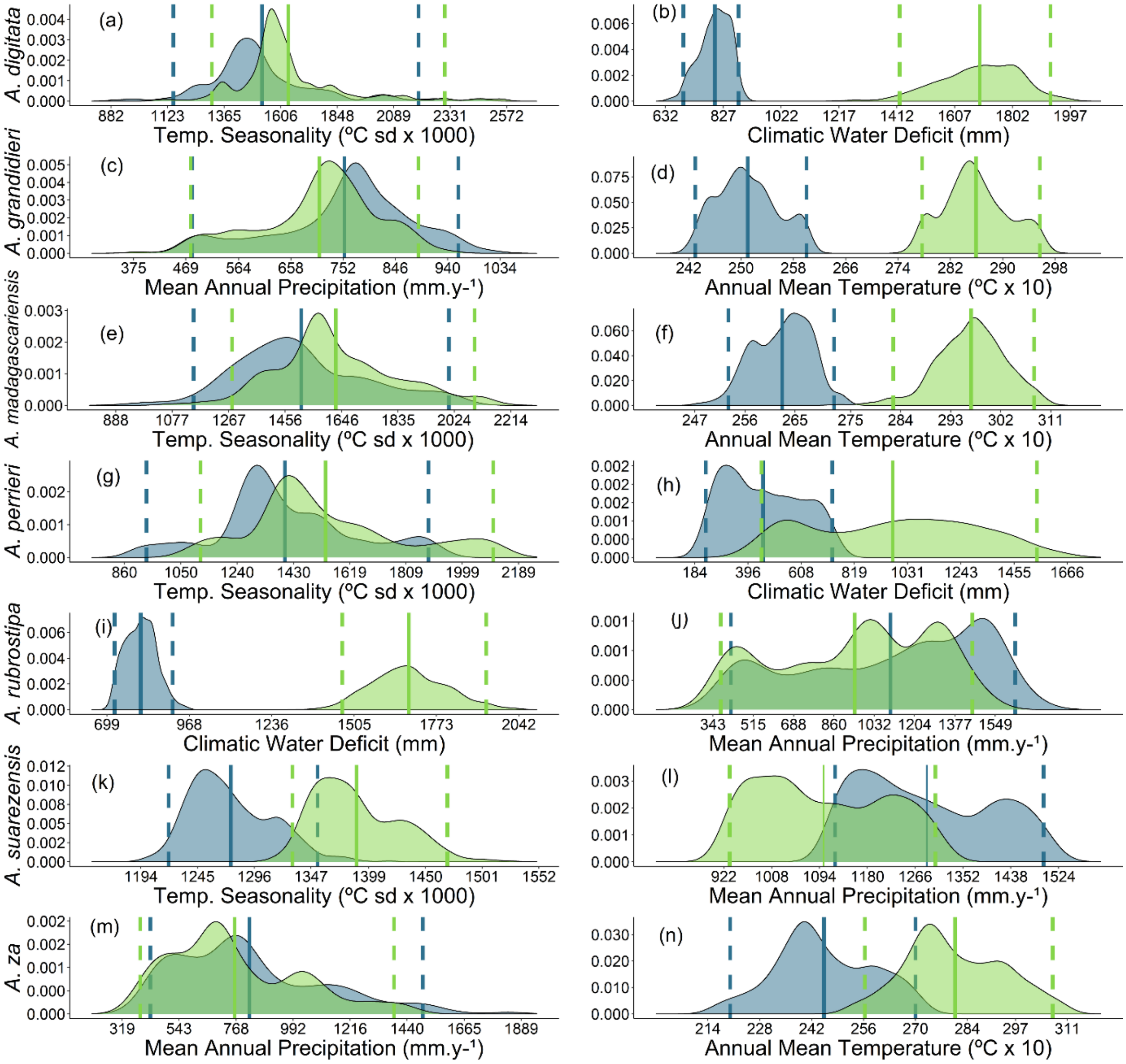
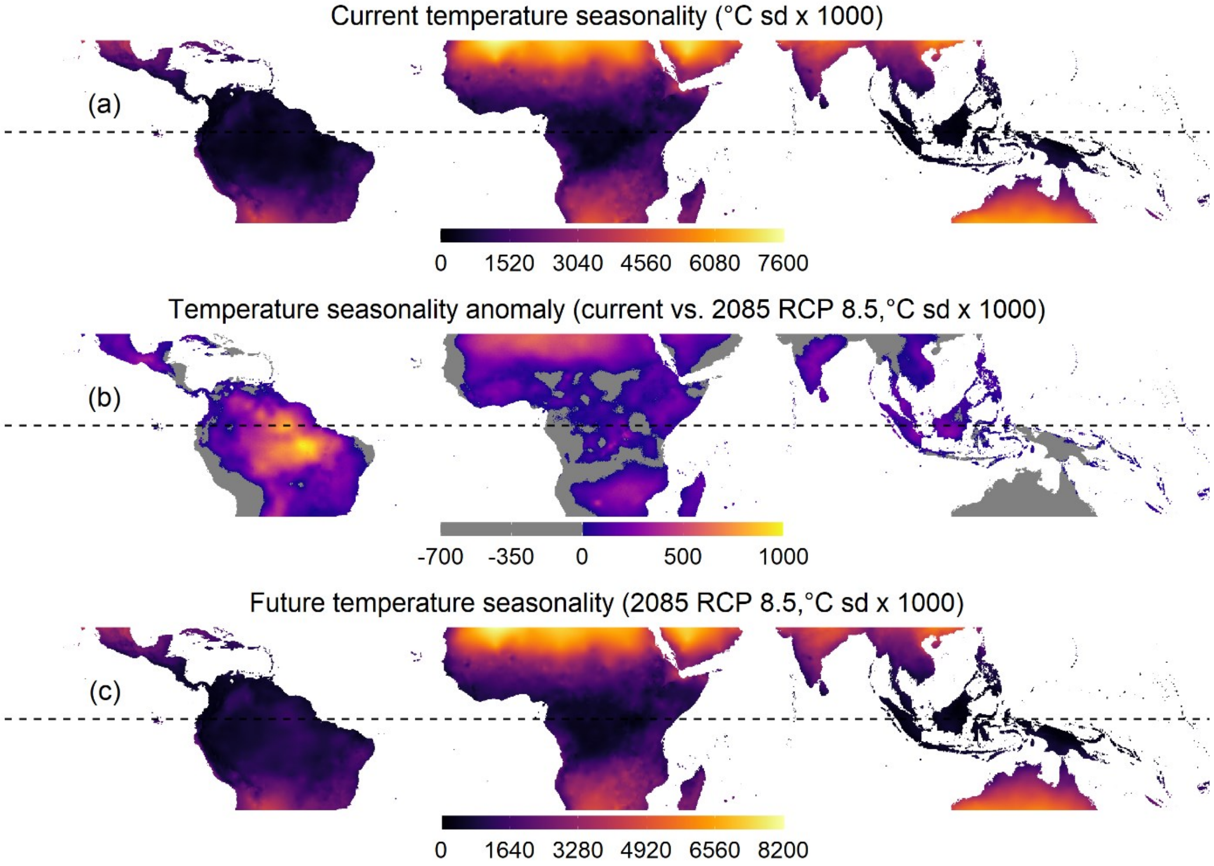


Figure 5. Map of temperature seasonality and future anomaly in the tropics. (a) Map of the temperature seasonality at 10’ resolution across the tropics. Black dashed line represents the equator. Intertropical regions in South America, Africa, Southeast Asia, and Oceania have similar low temperature seasonality values and temperature seasonality is decreasing from the poles to the equator. (b) Temperature seasonality anomaly obtained while comparing future temperature seasonality in 2085 under RCP 8.5 with current temperature seasonality. Future temperature seasonality in 2085 under RCP 8.5 is the mean of three GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES). Temperature seasonality will increase throughout most of the tropics, with a particular strong increase in South America. (c) Future temperature seasonality in 2085 under RCP 8.5. (mean of the three selected GCMs). Despite changes in temperature seasonality in the future, the gradient of temperature seasonality, with a lower temperature seasonality at the equator, will be conserved in the future.



Current temperature seasonality (°C sd x 1000)

Temperature seasonality anomaly (current vs. 2085 RCP 8.5,°C sd x 1000)

Future temperature seasonality (2085 RCP 8.5,°C sd x 1000)

## 2.8 TABLES

Table 1. Baobabs' vulnerability to climate change and elevational range shift in 2085 under scenario RCP 8.5. We calculated the species distribution area (km$^2$) in the present (SDAp) and future (SDAf) to describe the change in the species distribution area (Change SDAp SDAf %) according to two dispersal hypotheses (full and zero-dispersal). See IUCN Red List categories and criteria, version 3.1, second edition | IUCN Library System for criteria explanation.

| **Baobab species**<br>**IUCN status** | **SDAp (km$^2$)** | **Current mean elevation (m)** | **Dispersal hypothesis** | **SDAf (km$^2$)** | **Future mean elevation (m)** | **Change SDAp f (%)** | **IUCN Updated Status** |
|---|---|---|---|---|---|---|---|
| ***Adansonia digitata***<br>**Not assessed by IUCN** | 47 872 | 76 | Full | 194 447 | 195 | +306 | NT* |
| | | | Zero | 47 017 | 77 | -2 | |
| ***A. grandidieri***<br>**Endangered A2c*** | 27 651 | 135 | Full | 118 907 | 365 | +330 | EN A2c** |
| | | | Zero | 27 591 | 135 | 0 | |
| ***A. madagascariensis***<br>**Near threatened** | 92 311 | 105 | Full | 62 881 | 263 | -32 | EN A3c |
| | | | Zero | 26 878 | 102 | -71 | |
| ***A. perrieri***<br>**Critically endangered C2a(i)** | 14 872 | 377 | Full | 0 | Extinct | -100 | CR C2a(i) + A3C |
| | | | Zero | 0 | Extinct | -100 | |
| ***A. rubrostipa***<br>**Least concern** | 74 194 | 77 | Full | 44 833 | 428 | -40 | EN A3c |
| | | | Zero | 11 488 | 82 | -85 | |
| ***A. suarezensis***<br>**Endangered B1ab (i,ii,iii,iv,v) + B2ab (i,ii,iii,iv,v)** | 3347 | 194 | Full | 0 | Extinct | -100 | CR B1ab + B2ab |
| | | | Zero | 0 | Extinct | -100 | |
| ***A. za***<br>**Least concern** | 170 625 | 265 | Full | 372 134 | 365 | +118 | Least concern |
| | | | Zero | 166 254 | 271 | -3 | |

*IUCN criteria suggested for Madagascar; ** IUCN status defined by populational aspects for the referred species once our models did not predict vulnerability for this species.

Table 2. Relative importance of the four bioclimatic variables in determining species distribution. Here we present the variable mean rank of importance over the four statistical models for each species. Temperature seasonality was the most important variable in determining species distribution for four baobab species: *A. digitata*, *A. madagascariensis*, *A. perrieri*, and *A. suarezensis*. Precipitation was the most important for *A. grandidieri* and *A. za*, while climatic water deficit was the most important variable for *A. rubrostipa*. Abbreviations: Tmean for mean annual temperature; Tseas for temperature seasonality; Prec for mean annual precipitation; Cwd for climatic water deficit. The two most important variables for each species are in bold.

| Species | Mean Annual Temperature | Temperature Seasonality | Precipitation | Climatic Water Deficit | Most Important Variables (1st and 2nd) |
|---|---|---|---|---|---|
| ***A. digitata*** | 0.364 | 0.633 | 0.372 | 0.552 | Tseas/Cwd |
| ***A. grandidieri*** | 0.526 | 0.239 | 0.550 | 0.110 | Prec/Tmean |
| ***A. madagascariensis*** | 0.651 | 0.824 | 0.309 | 0.153 | Tseas/Tmean |
| ***A. perrieri*** | 0.369 | 0.954 | 0.336 | 0.518 | Tseas/Cwd |
| ***A. rubrostipa*** | 0.320 | 0.330 | 0.360 | 0.730 | Cwd/Prec |
| ***A. suarezensis*** | 0.211 | 0.987 | 0.620 | 0.150 | Tseas/Prec |
| ***A. za*** | 0.471 | 0.309 | 0.625 | 0.168 | Prec/Tmean |

## 2.9 SUPPORTING INFORMATION

### 2.9.1 Supplementary Figures

Figure S1. **Species range shift under climate change for the three resilient baobab species**. The three species are *A. digitata*, *A. grandidieri*, and *A. za* (one species per row). (a, e, i, m) Occurrence points over Madagascar elevation map (elevation in m); (b, f, j, n) Current predicted species distribution. Legend indicates the number of models (0-4) predicting the species presence (c,g,k,o) Projected species distribution in 2085 under scenario RCP 8.5 and the full-dispersal hypothesis. Legend indicates the number of models (0-12) predicting the species presence (d,h,l,p) Projected species distribution in 2085 under scenario RCP 8.5 and the zero-dispersal hypothesis. Legend indicates the number of models (0-12) predicting the species presence. For the distribution maps, the species is assumed to be present (green areas) when a majority of models predicts a presence (votes >= 2 in the present, and >= 6 in the future). The species is considered absent (grey areas) when no model (votes = 0), or a minority of models (votes < 2 in the present, and < 6 in the future), predicts a presence.

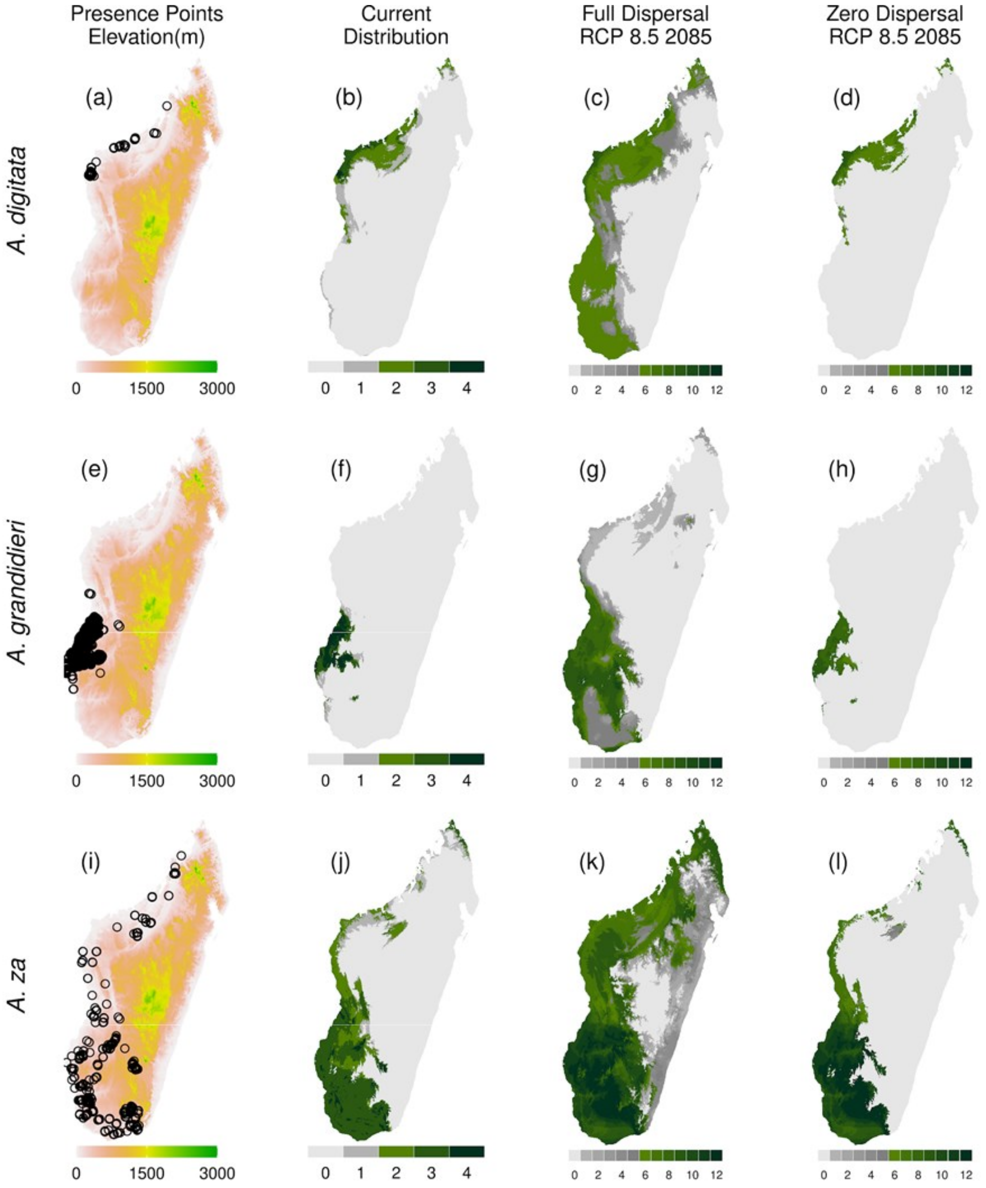


Figure S2. **Species range contraction under climate change (RCP 4.5) for all baobab species.** The seven species are *A. digitata*, *A. grandidieri*, *A. madagascariensis* (*A. mada.*), *A. perrieri*, *A. rubrostipa*, *A. suarezensis*, and *A. za* (one species per row). **(a, e, i, m, q, u, y)** Occurrence points over Madagascar elevation map (elevation in m); **(b, f, j, n, r, v, z)** Current predicted species distribution. Legend indicates the number of models (0-4) predicting the species presence; **(c, g, k, o, s, w, a')** Projected species distribution in 2085 under scenario RCP 4.5 and the full-dispersal hypothesis. Legend indicates the number of models (0-12) predicting the species presence; **(d, h, l, p, t, x, b')** Projected species distribution in 2085 under scenario RCP 4.5 and the zero-dispersal hypothesis. Legend indicates the number of models (0-12) predicting the species presence. For the distribution maps, the species is assumed to be present (green areas) when a majority of models predicts a presence (votes >= 2 in the present, and >= 6 in the future). The species is considered absent (grey areas) when no model (votes = 0), or a minority of models (votes < 2 in the present, and < 6 in the future), predicts a presence. Maps for *A. perrieri* and *A. suarezensis*, two species distributed at the extreme North of Madagascar, have been zoomed in (black squares).

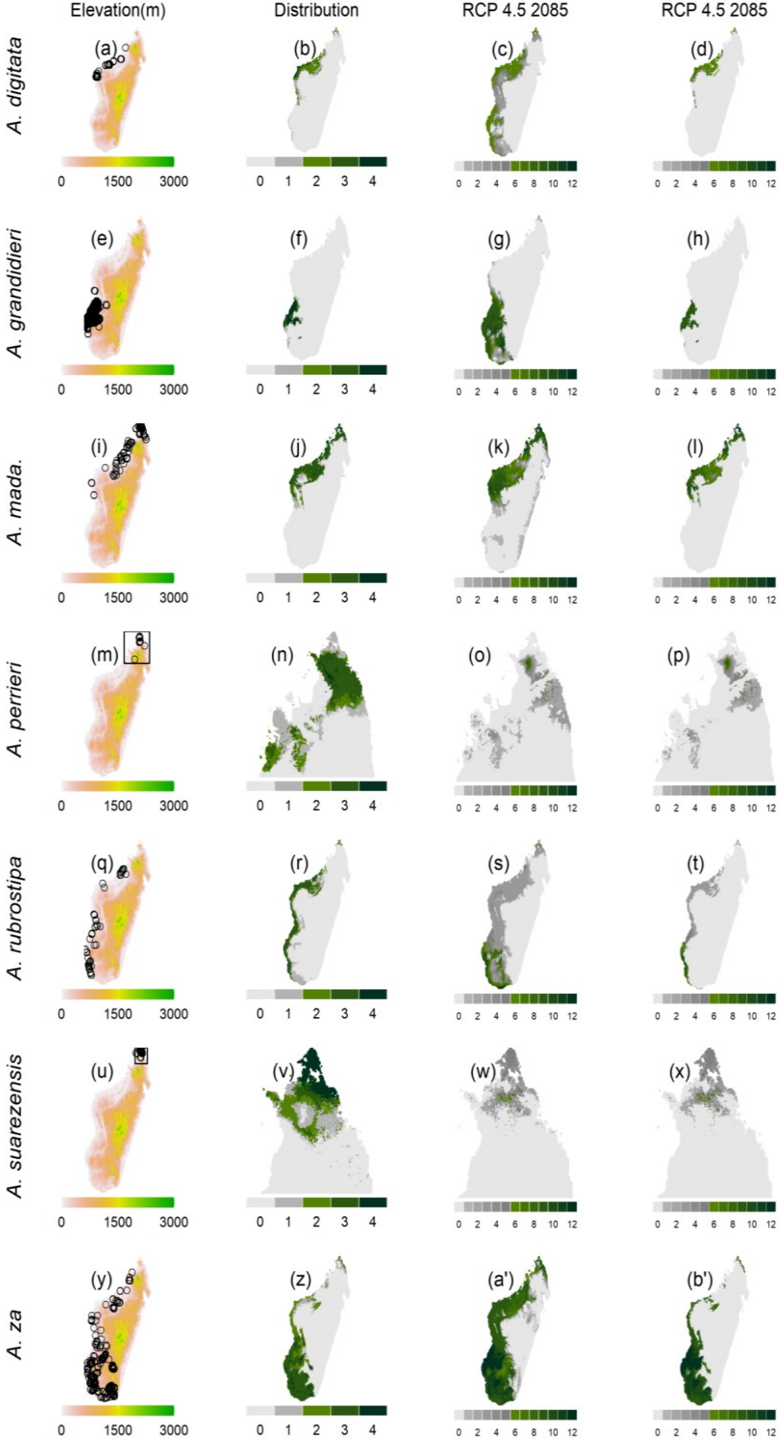


Figure S3. **Change in elevation and latitude for the climate-resilient baobab species.** We randomly sampled 1000 points inside the species predicted occurrence area in the present and in the future under RCP 8.5 scenario and full-dispersal hypothesis. **(a, b)** For *A. digitata*, the species should maintain stable its average elevational and latitudinal gradient from the current projection until 2085. **(c, d)** *Adansonia grandidieri* might move to higher elevations and shift its latitudinal range to lower latitudes. **(e, f)** *Adansonia za* could slightly shift its elevational gradient to more elevated areas in 2085 and higher latitudes, i.e. equatorward, from the present to 2085.

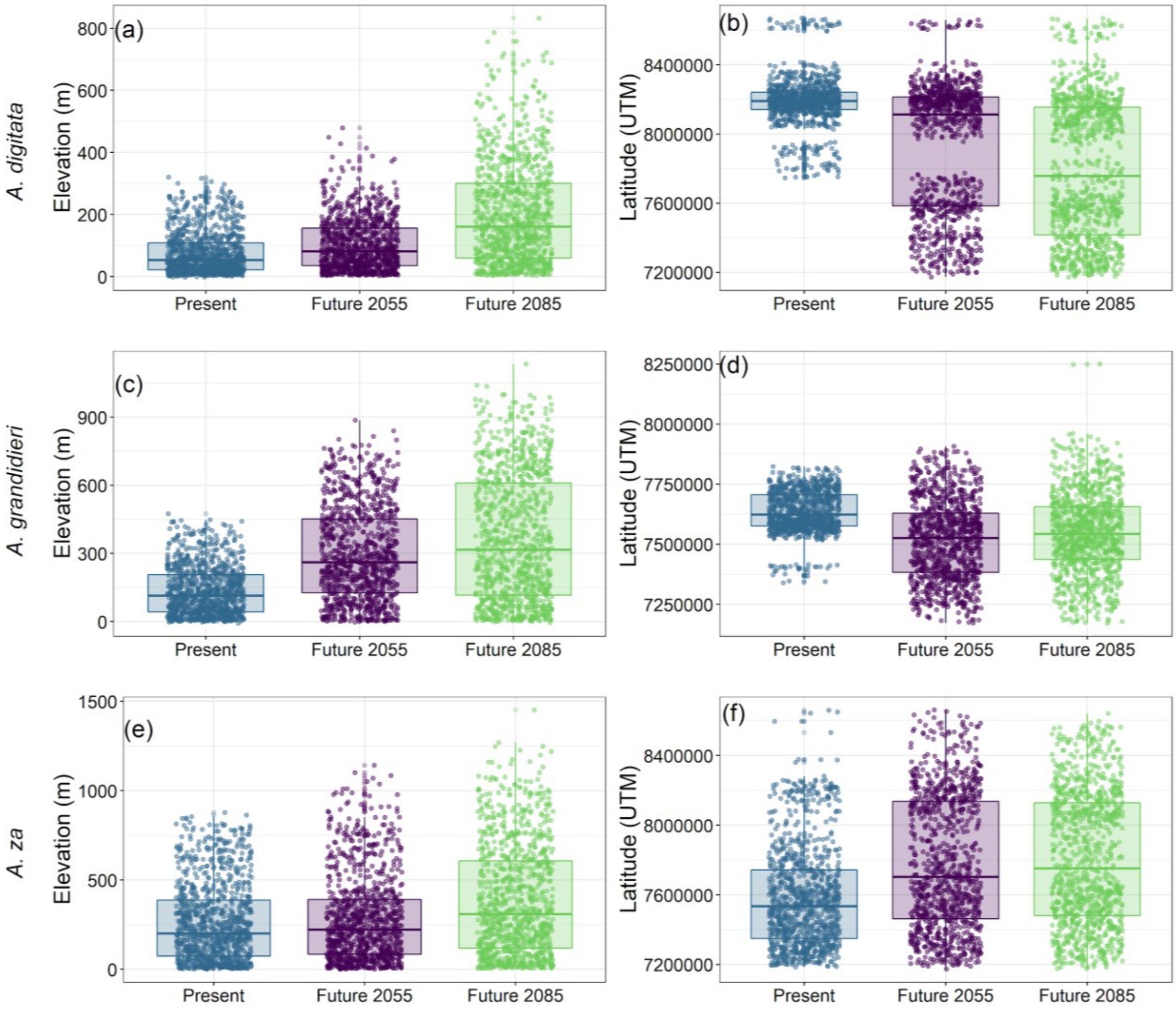


Figure S4. **Change in elevation and latitude for the all baobab species under RCP 4.5 in the present and under two future scenarios (2055 and 2085).** We randomly sampled 1000 points inside the species predicted occurrence area in the present and in the future (due to the extremely reduced distribution area for *A. perrieri* and *A. suarezensis*, we only sampled 416 and 105 points, respectively for year 2085, and another 15 points for *A. suarezensis* in 2055). **(a, c, e, g, i, k, m)** All species showed a tendency to maintain their current elevational range in the future or move upwards in 2055 or 2085 considering elevation. **(b, d, j)** Considering latitude distributional range, *A. digitata*, *A. grandidieri*, and *A. rubrostipa* are expected to move polewards in the future, while **(h, l, m)** *A. perrieri*, *A. suarezensis*, and *A. za* are expected to move equatorward, and **(f)** *A. madagascariensis* might keep stable its current latitudinal range in 2055 and 2085.

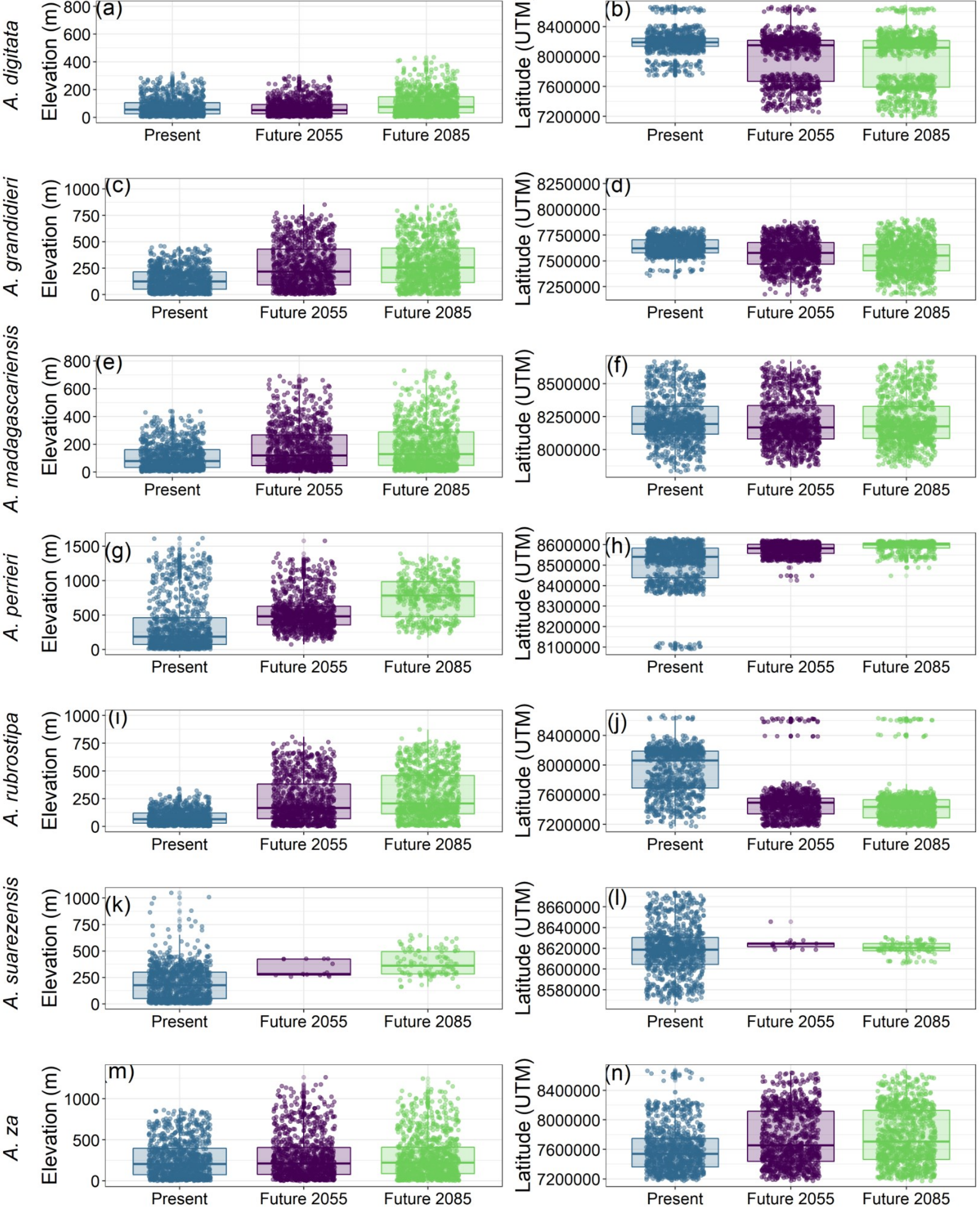


Figure S5. **Bioclimatic niche of the seven baobabs species found in Madagascar.** We computed species bioclimatic niche by randomly sampling 1000 points within each species distribution area for the four climatic variables selected in this study: annual mean temperature, temperature seasonality, mean annual precipitation, and climatic water deficit. Dashed lines (red) represent the climatic conditions through Madagascar. Baobab niche breadth indicates difference between species' climatic niche, with climatic specialist ones (*A. digitata* and *A. madagascariensis* – adapted to warmer temperatures –; *A. grandidieri* – adapted to higher seasonality in temperature and drier climate –; *A. perrieri* and *A. suarezensis* – adapted to lower seasonality in temperature), and generalist/ubiquitous species (*A. rubrostipa* and *A. za*), with a wider climatic niche which encompass almost every other baobab species bioclimatic niche.

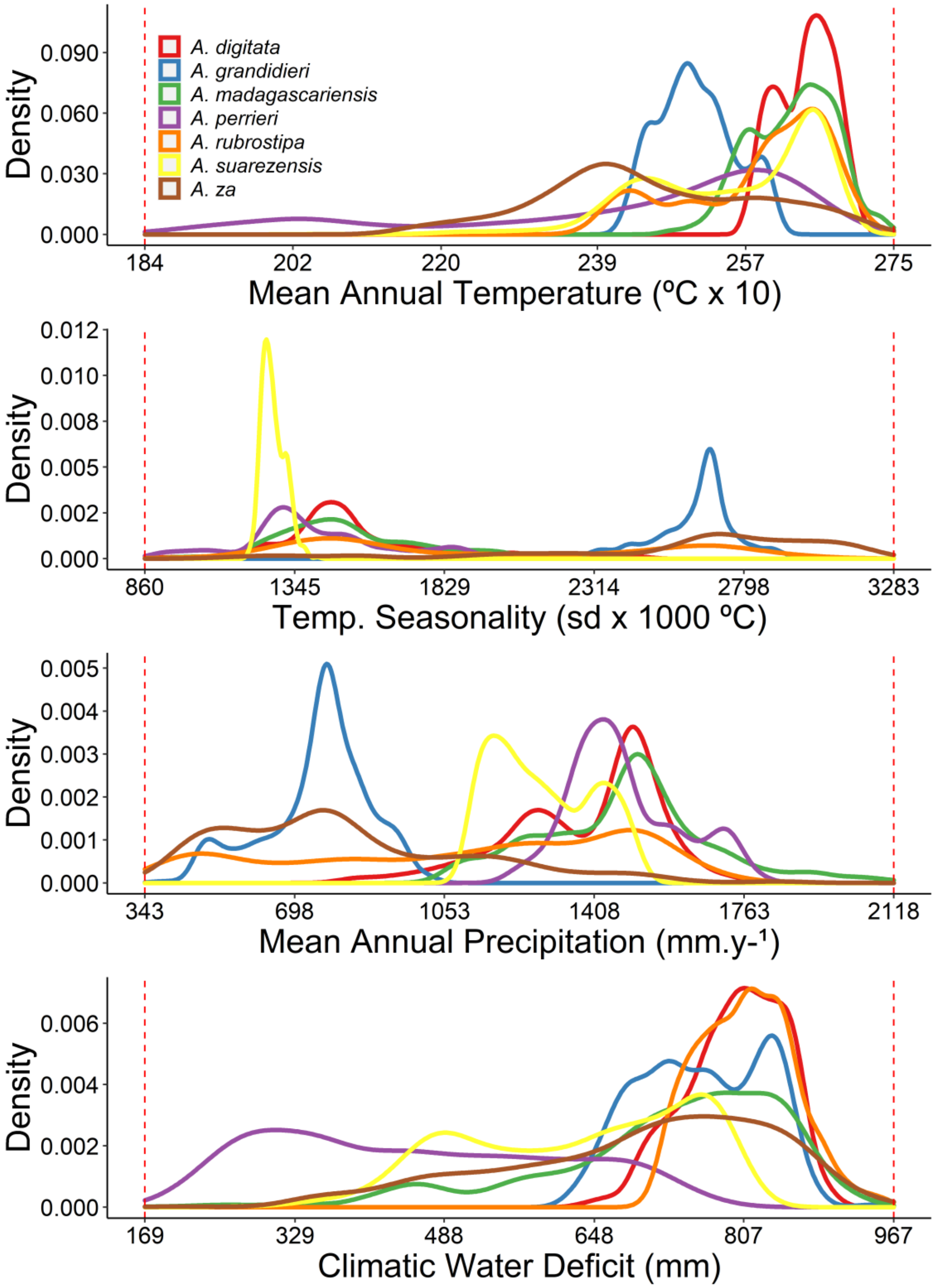
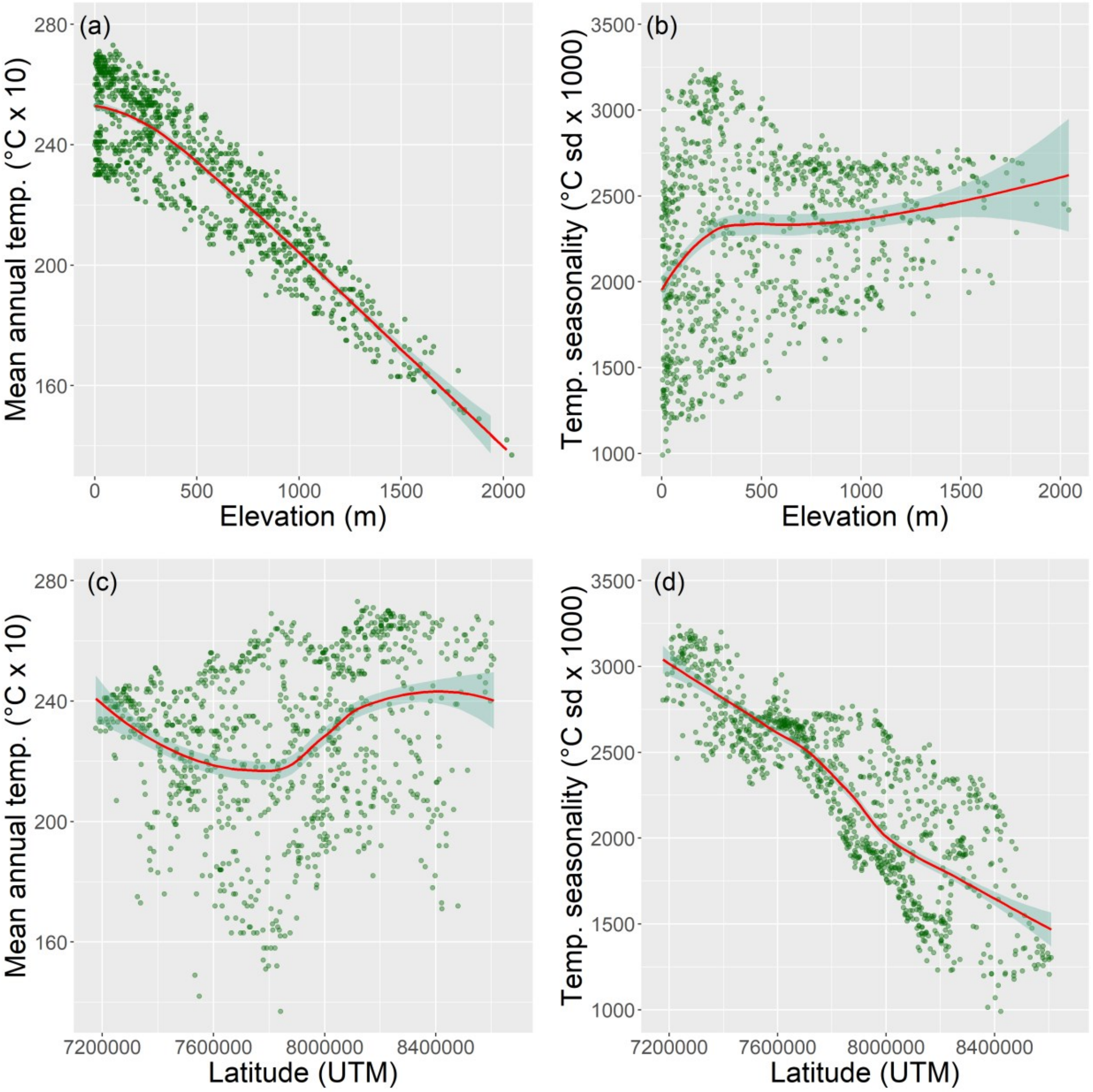


Figure S6. **Relationship between climatic, elevational, and latitudinal gradients in Madagascar.** We sampled 1000 random points through Madagascar extent. **(a)** Mean annual temperature is significantly lower as elevation increases. **(b)** Temperature seasonality remains stable as elevation increases, however, as elevation is > 1500 m, temperature seasonality might increase. **(c)** The mean annual temperature variation according to latitude in Madagascar. Mean annual temperature ranges between 22 °C to 25 °C across the entire country. **(d)** The temperature seasonality variation according to latitude in Madagascar. We see a decrease in seasonality from South (7200000 UTM) to North Madagascar (8400000 UTM). Shaded area surrounding the red line represents the smooth fitting values of the 1000 random points sampled.



## 2.9.2 Supplementary Tables

Table S1. Presence data-set used for the species distribution modeling (SDM). We computed the number of presence points with GPS coordinates for each species. Considering a 1-km² spatial grid covering Madagascar, we identified the cells including at least one presence point for each species independently. Doing so we obtained a presence data-set at 1-km² resolution for each species. We removed cells with incomplete associated bioclimatic data from the presence data-set.

| **Species** | **Number of initial presence points with GPS coordinates** | **Number of 1-km² cells with presence data** | **Number of 1-km² cells with presence data in Madagascar and complete bioclimatic data** |
|---|---|---|---|
| ***A. digitata*** | 1854 | 151 | 62 |
| ***A. grandidieri*** | 128 609 | 3772 | 3770 |
| ***A. madagascariensis*** | 1222 | 159 | 153 |
| ***A. perrieri*** | 150 | 21 | 21 |
| ***A. rubrostipa*** | 794 | 93 | 90 |
| ***A. suarezensis*** | 1686 | 174 | 170 |
| ***A. za*** | 2970 | 460 | 460 |

Table S2. Performance of the four statistical models in predicting species presence–absence. AUCc and TSSc indicate the mean of the Area Under the ROC Curve and the True Skills Statistics respectively after a 5-fold cross-validation procedure (data were split into 70% of the training data and 30% of test data). AUC full and TSS full indicate the Area Under the ROC Curve and the True Skills Statistics calculated for the full data-set (100% of the data).

| **Species** | **Model** | **AUC full** | **AUCc** | **TSS full** | **TSSc** |
|---|---|---|---|---|---|
| ***A. digitata*** | GLM | 0.972 | 0.955 | 0.900 | 0.903 |
| | GAM | 0.989 | 0.974 | 0.977 | 0.949 |
| | Random Forests | 1 | 0.969 | 0.999 | 0.927 |
| | Maxent | 0.970 | 0.967 | 0.859 | 0.875 |
| ***A. grandidieri*** | GLM | 0.991 | 0.991 | 0.951 | 0.951 |
| | GAM | 0.991 | 0.990 | 0.950 | 0.951 |
| | Random Forests | 1 | 0.994 | 0.988 | 0.965 |
| | Maxent | 0.989 | 0.989 | 0.936 | 0.936 |
| ***A. madagascariensis*** | GLM | 0.961 | 0.958 | 0.834 | 0.834 |
| | GAM | 0.966 | 0.963 | 0.834 | 0.837 |
| | Random Forests | 1 | 0.964 | 0.993 | 0.839 |
| | Maxent | 0.959 | 0.958 | 0.812 | 0.819 |
| ***A. perrieri*** | GLM | 0.993 | 0.954 | 0.967 | 0.913 |
| | GAM | 0.991 | 0.941 | 0.981 | 0.887 |
| | Random Forests | 1 | 0.960 | 1 | 0.917 |
| | Maxent | 0.987 | 0.987 | 0.924 | 0.946 |
| ***A. rubrostipa*** | GLM | 0.959 | 0.961 | 0.839 | 0.856 |
| | GAM | 0.962 | 0.963 | 0.831 | 0.858 |
| | Random Forests | 1 | 0.967 | 0.999 | 0.891 |
| | Maxent | 0.951 | 0.953 | 0.783 | 0.841 |
| ***A. suarezensis*** | GLM | 0.998 | 0.998 | 0.993 | 0.991 |
| | GAM | 0.999 | 0.998 | 0.995 | 0.993 |
| | Random Forests | 1 | 0.996 | 0.999 | 0.989 |
| | Maxent | 0.949 | 0.960 | 0.992 | 0.917 |
| ***A. za*** | GLM | 0.881 | 0.870 | 0.631 | 0.621 |
| | GAM | 0.893 | 0.880 | 0.676 | 0.655 |
| | Random Forests | 0.999 | 0.944 | 0.992 | 0.742 |
| | Maxent | 0.881 | 0.870 | 0.638 | 0.622 |

Table S3. Performance of the ensemble model based on committee averaging. Values of the threshold-dependents indices True Skill Statistics (TSS), Sensitivity, and Specificity are described below. Almost all TSS values were >= 0.83 except for *A. za*, where the TSS was 0.672 due to a relatively lower specificity. The performance metrics thus indicate good performance of the ensemble model by correctly predicting species presence/absence on committee averaging method.

| **Species** | **TSS** | **Sensitivity** | **Specificity** |
|---|---|---|---|
| ***A. digitata*** | 0.92 | 1.00 | 0.92 |
| ***A. grandidieri*** | 0.95 | 0.99 | 0.96 |
| ***A. madagascariensis*** | 0.83 | 0.99 | 0.84 |
| ***A. perrieri*** | 0.97 | 1.00 | 0.97 |
| ***A. rubrostipa*** | 0.85 | 0.97 | 0.87 |
| ***A. suarezensis*** | 0.99 | 1.00 | 0.99 |
| ***A. za*** | 0.67 | 0.94 | 0.72 |

Table S4. **Baobabs' vulnerability to climate change and elevational range shift in 2085 under scenario RCP 4.5**. We calculated the species distribution area (km²) in the present (SDAp) and future (SDAf) to describe the change in the species distribution area (Change SDAp SDAf %) according to two dispersal hypotheses (full and zero-dispersal).

| Baobab species IUCN status | SDAp (km²) | Current mean elevation (m) | Dispersal hypothesis | SDAf (km²) | Future mean elevation (m) | Change SDAp f (%) |
|---|---|---|---|---|---|---|
| *Adansonia digitata*<br>Not assessed by IUCN | 47 872 | 76 | Full | 91 692 | 100 | +92 |
| | | | Zero | 38 293 | 68 | -20 |
| *A. grandidieri*<br>Endangered A2c* | 27 651 | 135 | Full | 101 727 | 285 | +268 |
| | | | Zero | 27 651 | 135 | 0 |
| *A. madagascariensis*<br>Near threatened | 92 311 | 105 | Full | 123 913 | 184 | +34 |
| | | | Zero | 85 023 | 108 | -8 |
| *A. perrieri*<br>Critically endangered C2a(i) | 14 872 | 377 | Full | 427 | 762 | -97 |
| | | | Zero | 427 | 762 | -97 |
| *A. rubrostipa*<br>Least concern | 74 194 | 77 | Full | 53 367 | 283 | -28 |
| | | | Zero | 15 636 | 277 | -79 |
| *A. suarezensis*<br>Endangered B1ab (i,ii,iii,iv,v) + B2ab (i,ii,iii,iv,v) | 3347 | 194 | Full | 100 | 393 | -97 |
| | | | Zero | 100 | 393 | -97 |
| *A. za*<br>Least concern | 170 625 | 265 | Full | 304 482 | 294 | +78 |
| | | | Zero | 170 622 | 265 | 0 |

Table S5. Climate change within the current species distribution areas. We computed the climatic variables' mean and 95% quantiles within the current species distribution areas for the current and future climates. For the future climate, we considered the mean of the climatic projections of three GCMs (GISS-E2-R; HadGEM2-ES; NorESM1-M) for the year 2085 under RCP 8.5. Abbreviations: Temppf for mean annual temperature (in °C x 10); Tseaspf for temperature seasonality (in °C sd x 1000); Precpf for mean annual precipitation (in mm.y$^{-1}$); Cwdpf for climatic water deficit (in mm) in the present (p) and future (f).

| **Baobab species** | **Confidence interval** | **Tempp** | **Tempf** | **Tseasp** | **Tseasf** | **Precp** | **Precf** | **Cwdp** | **Cwdf** |
|---|---|---|---|---|---|---|---|---|---|
| ***A. digitata*** | *Mean* | 264 | 298 | 1525 | 1612 | 1390 | 1205 | 800 | 1680 |
| | *2.5%* | 258 | 291 | 1136 | 1267 | 953 | 937 | 691 | 1372 |
| | *97.5%* | 270 | 306 | 2246 | 2208 | 1665 | 1454 | 882 | 1926 |
| ***A. grandidieri*** | *Mean* | 251 | 286 | 2649 | 2729 | 746 | 715 | 764 | 1670 |
| | *2.5%* | 243 | 277 | 2338 | 2402 | 467 | 474 | 642 | 1447 |
| | *97.5%* | 260 | 296 | 2887 | 3045 | 956 | 895 | 877 | 1978 |
| ***A. madagascariensis*** | *Mean* | 263 | 296 | 1510 | 1623 | 1485 | 1298 | 724 | 1546 |
| | *2.5%* | 253 | 282 | 1133 | 1269 | 1110 | 986 | 399 | 980 |
| | *97.5%* | 272 | 308 | 2008 | 2101 | 1953 | 1733 | 890 | 1989 |
| ***A. perrieri*** | *Mean* | 243 | 272 | 1391 | 1539 | 1483 | 1257 | 465 | 962 |
| | *2.5%* | 192 | 223 | 948 | 1117 | 1262 | 1063 | 230 | 436 |
| | *97.5%* | 267 | 300 | 1890 | 2108 | 1764 | 1483 | 738 | 1563 |
| ***A. rubrostipa*** | *Mean* | 258 | 292 | 1972 | 2046 | 1088 | 969 | 808 | 1678 |
| | *2.5%* | 240 | 273 | 1224 | 1335 | 413 | 395 | 719 | 1455 |
| | *97.5%* | 270 | 306 | 2898 | 2921 | 1650 | 1451 | 913 | 1914 |
| ***A. suarezensis*** | *Mean* | 255 | 283 | 1275 | 1389 | 1288 | 1103 | 629 | 1242 |
| | *2.5%* | 233 | 259 | 1221 | 1333 | 1121 | 932 | 402 | 724 |
| | *97.5%* | 267 | 295 | 1357 | 1479 | 1498 | 1303 | 794 | 1653 |
| ***A. za*** | *Mean* | 245 | 280 | 2583 | 2668 | 830 | 760 | 689 | 1488 |
| | *2.5%* | 220 | 256 | 1282 | 1406 | 430 | 388 | 378 | 870 |
| | *97.5%* | 270 | 307 | 3183 | 3229 | 1524 | 1363 | 902 | 2010 |

# 3 CAPÍTULO II

## Relict populations of *Araucaria angustifolia* will be isolated, poorly protected, and unconnected under climate and land-use change in Brazil

(Populações relictuais da *Araucaria angustifolia* estarão isoladas, pouco protegidas e não conectadas sob mudanças climáticas e uso da terra no Brasil)

Artigo de qualificação
Publicado no periódico *Biodiversity and Conservation* – BIOC (ISSN: 0960-3115)
https://doi.org/10.1007/s10531-021-02270-z
Recebido em Fevereiro 2021 | Aceito em Julho-Agosto 2021

Área de Avaliação: Biodiversidade
Classificação A2 (Quadriênio 2017-2020).

A “conectividade” entre uma unidade de conservação e uma propriedade privada em uma área de transição dos Campos Gerais e Floresta Ombrófila Mista, Clevelândia - PR.

Fonte: Foto de Mário M. Tagliari, 2021.

# Relict populations of *Araucaria angustifolia* will be isolated, poorly protected, and unconnected under climate and land-use change in Brazil

Mario M. Tagliari*[a1], Ghislain Vieilledent[b2], Jonatas Alves[a3], Thiago C. L. Silveira[a4], Nivaldo Peroni[a5]

[a] Programa de Pós-graduação em Ecologia, Departamento de Zoologia e Ecologia, Laboratório de Ecologia Humana e Etnobotânica, 88010-970, Universidade Federal de Santa Catarina, Florianópolis, Brasil

[b] CIRAD, UMR AMAP, F-34398 Montpellier, France. AMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.

- 1 https://orcid.org/0000-0002-8746-3598
- 2 https://orcid.org/0000-0002-1685-4997
- 3 https://orcid.org/0000-0003-2123-7560
- 4 https://orcid.org/0000-0002-3163-479X
- 5 https://orcid.org/0000-0002-6770-5377

## ABSTRACT

One of Brazil's most threatened tropical biome is the Atlantic Forest. This biome has distinct forest formations, as the *Araucaria* Mixed Forest: a sub-tropical ecosystem distributed through southern and southeastern Brazil, where it is surrounded by Dense Ombrophilous Forest. The defining tree species of *Araucaria* Mixed Forest is *Araucaria angustifolia* (Bertol.) Kuntze (known as Araucaria): an endangered, relict, and historically managed conifer. Due to unsustainable exploitation during the twentieth century, the main strategy for Araucaria preservation was the creation of protected areas. However, protected area's coverage within Atlantic Forest remains scarce and might prevent connectivity between species' remnant patches. We thus evaluated the potential connectivity of projected Araucaria distribution in the present and future under climate and land-use changes, using a species distribution model with graph theory. Araucaria current connectivity – through the Mixed and Dense Forests – ranges entirely through the landscape, with 715 connecting arcs (212 within protected areas). However, only 7% of its current distribution is encompassed by protected areas. Under future climate change in 2085, connectivity is expected to decrease by 77% compared with current projections. In the future, Araucaria subpopulations will be concentrated at higher elevations in unprotected suitable areas. We suggest that specific regions in southern and southeastern Brazil might be targeted as priority conservation areas jointly to major existing protected areas. These areas will sustain Araucaria connectivity and protection. As a keystone species, by safeguarding Araucaria we protect the socioecological system in southern and southeast Brazil and potentially promote forest expansion.

**Key words**: Araucaria forests; Ecological Niche Modelling; Future climatic changes; Habitat fragmentation; Protected areas effectiveness; Species connectivity.

## 3.1 INTRODUCTION

Climate change threatens tropical biodiversity in distinct aspects (CHEN *et al.* 2011). Increased temperatures (ANDERSON-TEIXEIRA *et al.* 2013), changing precipitation regimes, and more frequent and severe climate extreme events, such as droughts or wildfires (GARCIA *et al.* 2014) are expected to affect entire biomes (RODRIGUES *et al.* 2006). One of the most threatened biomes in Brazil is the Atlantic Rainforest, which contains more than 1500 plant species vulnerable to extinction (SCARANO and CEOTTO 2015). Urbanization, deforestation, agricultural expansion, and climate change are some of the anthropic disturbances affecting the Atlantic Rainforest and its biodiversity (SCARANO; CEOTTO, 2015; REZENDE *et al.* 2018).

The Atlantic Rainforest biome has five forest ecosystems: (i) Dense Ombrophilous; (ii) Mixed Ombrophilous; (iii) Semi deciduous Seasonal; (iv) Deciduous Seasonal; and (v) Open Ombrophilous forests (Schneider *et al.* 2018). The Mixed Ombrophilous Forest, also known as *Araucaria* Mixed Forest, is characterized by species adapted to lower temperatures (CASTRO *et al.* 2019; WILSON *et al.* 2019). The original distribution of *Araucaria* Mixed Forest originally covered almost entirely southern Brazil besides specific areas in the country's southwestern region (VIBRANS *et al.* 2013), such as Mantiqueira Hills, at the High Rio Preto Microbasin (CASTRO *et al.* 2019; QUINTEIRO *et al.* 2019), along the borders of São Paulo, Minas Gerais, and Rio de Janeiro states. In these areas, remnant patches of *Araucaria* Mixed are surrounded by the Dense Ombrophilous Forest (hereafter Dense Forest). The prominent plant species of *Araucaria* Mixed Forest is the "Critically Endangered" — according to the International Union for Conservation of Nature — *Araucaria angustifolia* (Bert.) O. Kuntze (hereafter Araucaria).

Araucaria dominates the upper canopies and accounts for more than 40% of all trees within the Araucaria Mixed Forest (ROBINSON *et al.* 2018). It is a pioneer species and acts as a nurse-plant for other native tree seedlings (DUARTE *et al.* 2006; SÜHS *et al.* 2018). A rich plant diversity is found beneath its canopies, including plant species such as *Ilex paraguariensis*, *Mimosa scabrella*, or *Acca sellowiana*, strengthening ecological interactions (Castro *et al.* 2019). Not only plant diversity is found underneath Araucaria canopies. By comparing the biodiversity richness of Araucaria preserved patches with managed ones with exotic trees, such as *Pinus* and *Eucalyptus*, Fonseca *et al.* (2009) showed that preserved patches had richer biodiversity among 13 taxonomic groups, such as fungi, woody plants, spiders, galling insects, lichens, flatworms, opiliones, birds, and amphibians. Considering fungi, the Araucaria seedlings show a high dependency on arbuscular mycorrhizal fungi, indicating a relationship where Araucaria superficial roots develop on dead tree trunks and organic material while maintaining an active internal mycorrhizal community (MOREIRA *et al.* 2016). In preserved Araucaria remnants, soil invertebrate macrofauna is also richer than disturbed remnants, containing spider families, springtails, and earthworm species (de MORAIS PEREIRA *et al.* 2017). A rich insect community co-exists with Araucaria trees counting at least 100 species, such as coleopterans and hymenopterans developing under the bark, wood, and reproductive organs (MECKE *et al.* 2001). The attractiveness of Araucaria's highly nutritious nut-like seed, known as "*pinhão*" pulses Araucaria dispersal in the landscape, where parrots (*Amazona pretei*, *A. vinacea*), parakeet (*Pyrrhura frontalis*), and blue jay species (*Cyanocorax caeruleus* and *C. chrysops*) potentially carry the nut-like seeds from 10m to 500m in the landscape, contributing to both Araucaria and forest regeneration (SOUZA 2020). *Pinhão* seeds have been influencing and structuring mammal diversity, from mammal primary consumers (i.e. those feeding on seeds and fruits) to mean and apex-predators (BOGONI *et al.* 2020a). The nut-like peak production (from April to June) structures fauna diversity spatiotemporally (BOGONI *et al.* 2020b). Consequently, particularly due to the consumption of nutritious pinhão and the consequent structuring of local fauna, Araucaria is defined as an ecological keystone species (BOGONI *et al.* 2020b).

Moreover, human groups have interacted with Araucaria since Pre-Columbian times, promoting ecosystem expansion, given *pinhão* use and consumption (REIS *et al.* 2014; MELLO; PERONI 2015; LAUTERJUNG *et al.* 2018; ROBINSON *et al.* 2018). Currently, the management and consumption of pinhão promote economic and cultural benefits for smallholders in southern and southeastern Brazil (REIS *et al.* 2014, 2018; ADAN *et al.* 2016; TAGLIARI; PERONI 2018; QUINTEIRO *et al.* 2019). Local smallholder management systems maintain/preserve Araucaria Forest fragments due to *pinhão* use and consumption; a practice known as "conservation-by-use" (REIS *et al.* 2018). Given Araucaria's ecological, economic, and cultural aspects, the species is a relevant proxy as a whole because of its umbrella-conservation and ecological keystone aspects, influencing the entire ecosystem and its associated sociobiodiversity.

One of the main conservation strategies to curb anthropic threats is the establishment of protected areas (GRAY *et al.* 2016). Protected areas halt biodiversity loss, regulate ecological processes, and provide several ecosystem services (WATSON *et al.* 2014). However, the Atlantic Rainforest biome, which originally covered 17.4% of Brazilian territory (METZGER 2009), accounts for only 4% of Brazil's protected area network (OLIVEIRA *et al.* 2017). Ongoing problems faced by protected areas include population growth, logging, road expansion, fires, poor management, and lack of effectiveness in preserving biodiversity (OLIVEIRA *et al.* 2017). A primary goal of these areas is to buffer species from these historical drivers of species decline (MONZÓN *et al.* 2011) and long-term impacts, such as climate change (FERRO *et al.* 2014; SCARANO; CEOTTO 2015; CATEN *et al.* 2017). Climate change potentially requires species to shift their range to track suitable habitats (VIEILLEDENT *et al.* 2013; FODEN *et al.* 2019). This potential range shift may occur beyond the existing limits of the protected area network (PARMESAN 2006; VIEILLEDENT *et al.* 2013), influencing the protected area's effectiveness in conserving biodiversity. Chape *et al.* (2005) defined the extent of biodiversity distribution within protected areas as a metric to evaluate their effectiveness.

The effectiveness of the current protected area network to preserve Araucaria reveals that more areas are necessary to guarantee species preservation along the Atlantic Forest (CASTRO *et al.* 2019; MARCHIORO *et al.* 2020). Given climate change, Araucaria will shift its range and reduce its distribution in the future (WREGE *et al.* 2016; CASTRO *et al.* 2019; MARCHIORO *et al.* 2020), reducing the area in which the species is protected as well (CASTRO *et al.* 2019; MARCHIORO *et al.* 2020). Still, only the identification of potential priority conservation areas overlapped with the existing protected area network (CASTRO *et al.* 2019; WILSON *et al.* 2019) without evaluating the potential connectivity among species' remnant patches may mislead conservation efforts, especially due to land-use change (Joly *et al.* 2014). Previous studies only shed a light on potentially suitable areas for *Araucaria* remnant populations under climate change (CASTRO *et al.* 2019; WILSON *et al.* 2019). More recently, Marchioro *et al.* (2020) showed that climatically suitable areas under climate change for Araucaria would be also affected by land-use, which contributed to reducing potentially suitable areas for the species. We aimed to improve all these efforts for Araucaria conservation using the baseline of these previous studies targeting the Araucaria's vulnerability under both climate and land-use change and its potential connectivity among remnant patches. First, we followed their steps by projecting Araucaria current and future distribution under climate change scenarios. Second, we overlapped land-use in the Araucaria projected distribution to define clearly where Araucaria might occur despite habitat change. Third, we calculated the area of Araucaria occurrence already encompassed by the protected area network. Finally, we estimated the connectivity of the species remnant populations inside and outside protected areas to indicate (i) if the species is prone to be more isolated in the future; (ii) to show a light of hope in the Araucaria conservation scenario according to species' connectivity potential through the landscape; (iii) to describe which protected areas are playing a key role by conserving and protecting the species. The effectiveness of the current protected area network was thus assessed by calculating the potential Araucaria occurrence within protected areas (i.e., current and future; sensu CHAPE *et al.* (2005); and the Araucaria's potential connectivity in the present and under projected scenarios in 2085 considering land-use change and employing a Species Distribution Modelling approach).

No previous studies have evaluated the Araucaria's conservation potential within its natural occurrence area (i.e., the Mixed and surrounding Dense Forests) nor targeted the species connectivity capacity in the landscape under both climate and land-use change. To assess if Araucaria is effectively protected within its original distribution area, we evaluated the hypothesis on the topic of current and projected scenarios that potential connectivity among occurrence patches would be insufficient to connect Araucaria remnant populations. We expect that because of climate change these Araucaria relict populations will not be encompassed by the existing protected area network nor potentially connected throughout the landscape to major protected areas. Also, relict populations will be isolated in different subpopulations at higher elevations, preventing the connectivity among subpopulations, an unprecedented appraisal over Araucaria natural extent. We expect that by identifying refuge and climatically suitable areas for Araucaria species in the future, we could strengthen conservation efforts, such as the creation of ecological corridors, the identification of climatic refuge areas, and promote the creation and maintenance of new or existing protected areas to preserve these threatened ecosystems.

## 3.2 METHODS

### 3.2.1 Study area and species occurrences

Our study area covered the natural Araucaria occurrence area — the Mixed Ombrophilous Forest and Dense Ombrophilous Forest (Fig. 1). Occurrence points of Araucaria came from field surveys from Mars 2018 until January 2019, and from two databases: "*Global Biodiversity Information Facility Data Portal*" (GBIF, 2021); and "*Brazilian Biodiversity Portal*" (https://portaldabiodiversidade.icmbio.gov.br/portal/). Our raw dataset initially counted 953 occurrence points. We removed 8 duplicate points (same georeferenced position) in the raw dataset and another 121 occurrence points outside the study area (occurrence points within ecosystems that do not fit ecologically for Araucaria distribution, such as the Cerrado biome). We thus selected only occurrence points within 1 km² grid cells with complete climatic data used to perform the SDM. Our final dataset had 324 1 km² presence points. Our dataset encompasses properly the climatic variability and current *Araucaria* distribution because of extensive field-surveys throughout the Mixed and Dense Forests; besides our efforts to understand Araucaria phenology and ecology, which allowed us to correctly project Araucaria distribution; its level of threat, and its potential connectivity in the landscape.

### 3.2.2 Climatic dataset

Current and future climatic data came from the WorldClim Global Climate Database, Version 1.4 (http://worldclim.org/bioclim/), generated from interpolated climatic data from 1950 to 2000 (HIJMANS *et al.*, 2005). The 19 WorldClim bioclimatic variables consist of derived variables from (i) maximal, minimal, and average temperatures; and (ii) average precipitation; at 30 arc-seconds resolution (~1 km spatial resolution). The altitude variable was downloaded from the 'AmbData' website at 30 arc-seconds resolution — a specialized Brazilian website which supplies environmental and climatic variables for Species Distribution Modelling —(http://www.dpi.inpe.br/Ambdata/). To reduce multicollinearity among our variables and to follow the best practices in SDM construction (FOURCADE; BESNARD; SECONDI, 2018) we performed (i) Principal Component Analysis (PCA), (ii) correlation comparison among the 20 variables, and (iii) factor analysis. We also assessed Araucaria ecological aspects to select correctly the climatic variables to perform in the SDM, once biological knowledge is important for variables selection (PORFIRIO *et al.*, 2014). Based on these three criteria and ecological aspects of the target species, we selected 4 variables to use in our models: (i) annual mean temperature; (ii) mean diurnal range (iii) temperature seasonality, and (iv) annual precipitation (Fig. S1).

We selected three Global Circulation Models (GCMs) to simulate future climate for 2085 (average of 2071-2100) according to a hierarchical cluster grouping between nine GCMs correlated with the 19 WorldClim bioclimatic variables (VARELA; LIMA-RIBEIRO; TERRIBILE, 2015): NASA Goddard Institute for Space Studies E2-R Model — GISS-E2-R; and another hierarchical clustering selecting other two non-related GCM (Knutti *et al.* 2013): Hadley Global Environmental Model 2 — HadGEM-ES; and Norwegian Earth System Model 1 — NorESM-M, all available for download at the WorldClim website (https://www.worldclim.org/data/v1.4/cmip5.html). We considered two emissions scenarios (Representative Concentration Pathways) for climate projection in the future — RCPs 4.5 and 8.5. The RCP 4.5 or "mitigation scenario" is considered as a medium stabilization scenario according to its radiative forcing level for 2100 (van Vuuren *et al.* 2011), whereas the RCP 8.5, a “pessimistic scenario”, is characterized by continuous CO2 emission and temperature increase from 3.5°C to 5°C (BELLARD *et al.*, 2014; RIAHI *et al.*, 2011).

### 3.2.3 Land-use data

We used “*Mapbiomas Collection 5*” (1985-2019 data; Souza *et al.* 2020) land-use maps for the Atlantic Forest biome (https://mapbiomas.org/). These data are classified into five land-use categories (i.e. Forest; Non-Forest Natural Formation; Farming; Non-vegetated areas; and Watercourses). We selected three land-use categories from Mapbiomas collection and extracted specific sub-categories: (i) Farming (selection of the ‘Mosaic of Agriculture and Pasture’): a combination of both agriculture and pasture layer; (ii) Forest (selection of ‘Forest Plantation’) because *Pinus sp*. plantations for cellulose fiber production are economically important in southern Brazil; and (iii) Non-Vegetated Areas (selection of ‘Urban Infrastructure’). All spatial data were downloaded in their original resolution (30 m pixels) and were resampled to 30 arc-seconds resolution. We used these land-use sub-categories to further overlap with Araucaria projected distributions (i.e. current and future distribution). We defined a minimum percentage of land conversion (i.e. to visually compare our predictive maps and allow the calculation of area change under land-use) for each category before overlapping with Araucaria projected occurrence outputs. For ‘Forest Plantation’ and ‘Mosaic of Agriculture and Pasture’ we set a minimum of 30% of land conversion, while for ‘Urban Infrastructure’ we set a minimum of 50% of land change. For the calculation of “land-use” classes overlapped with projected occurrence maps, we used Quantum GIS with the “rasterize” function (QGIS Development-Team version 3.3, 2018).

### 3.2.4 Species Distribution Models

We selected five different algorithms for the SDM: (i) Artificial Neural Network (ANN); (ii) standard parametric GLM (Generalized Linear Model); (iii) non-parametric GAM (Generalized Additive Model); (iv) Maxent (Maximum entropy; (PHILLIPS; ANDERSON; SCHAPIRE, 2006); and (v) Random Forest (RF), based on classification trees (BREIMAN, 2001). We aimed to quantify output uncertainty and generate a gradient from robust (GLM and GAM) to complex algorithms, such as RF, Maxent, and ANN (ELITH; GRAHAM, 2009). We combined the outputs of the algorithms following the Ensemble Forecasting (EF) approach (ARAÚJO; NEW, 2007). Ensemble forecasting is a method to reduce uncertainty in SDMs, balancing the accuracy and robustness of SDM models via committee averaging (ARAÚJO; NEW, 2007; ZHANG *et al.*, 2015).

We computed current and future projections for Araucaria distribution according to the Araucaria presence dataset. We first randomly selected 10,000 pseudo-absences within the study area to generate a presence/pseudo-absence dataset. We thus randomly split our dataset for testing (30% for model validation) and training (70% for model calibration) to evaluate the predictive power of the SDM (HIJMANS, 2012). We repeated this cross-validation procedure ten times (ten model runs per each selected algorithm) using tested and training data to ensure that: (i) the ensemble model encompassed the entire occurrence dataset (Castro *et al.* 2019); (ii) because we used regression techniques in our modelling approach, i.e. GAM and GLM (BARBET-MASSIN *et al.*, 2012). We also made one run using the full dataset (i.e., no test and training data) for each selected algorithm, totalizing 55 model runs.

The ensemble modelling performance was evaluated over the full and split datasets using one threshold-independent accuracy index: AUC (Area Under the receiver operating Curve, which calculates the model's probability to rank a randomly chosen species presence site higher than a randomly chosen absence site (LIU; WHITE; NEWELL, 2011); and three threshold-dependent indexes: TSS (True Skills Statistics = Sensitivity + Specificity - 1). Sensitivity is the ratio of correctly predicted presences to the total number of presences, while Specificity is the ratio of correctly predicted absences to the total number of absences. The AUC varies from 0 to 1, and values > 0.9 indicate highly accurate capacity (THUILLER *et al.*, 2009; VIEILLEDENT *et al.*, 2013; WILSON *et al.*, 2019). TSS varies from -1 to +1, with 0 values indicating random previsions. According to Castro *et al.* (2019), models with TSS > 0.5 are considered satisfactory to evaluate ensemble models.

### 3.2.5 Araucaria's current distribution, its bioclimatic niche, projected distribution under both land-use and climate change scenarios

We previously set an evaluation quality threshold (minimum score of 0.6 or 60% according to AUC) to: (i) remove inaccurate models (i.e. predictions < 0.6); (ii) build the ensemble model; (iii) test and evaluate the ensemble model forecasting capacity to correctly predict species presence-absence; and (iv) make binary transformation following the committee averaging method, where the agreement of at least three out of five algorithms predicting the species occurrence indicated the conversion to binary maps (Thuiller *et al.* 2009). The predictive ability of the ensemble model was based on committee averaging, which sets the agreement among the five selected algorithms used in the SDM. We set “votes” to indicate the prediction of selected algorithms used in the SDM to predict or not Araucaria current distribution. The “vote” tallies resulted in six outputs: 1 or 100% (where 5 algorithms predicted the species occurrence), $\frac{4}{5}$ or 80%, $\frac{3}{5}$ or 60 and 0 (no accordance among algorithms). The current Species Distribution Area (SDAc) was defined as the area where the species was predicted to be present by a majority of algorithms (at least three out of five). We could then calculate the current SDAc for Araucaria species in km². Also, using 1000 random points sampled in the SDAc, we calculated the frequency, mean values, and 95% quantiles for the selected climatic variables used in the SDM to describe Araucaria bioclimatic niche.

Future ensemble forecasting combines the predictions of SDMs with GCMs, producing multiple distribution maps (Porfirio *et al.* 2014). We explored the range of projections, creating the same “votes” as for the current distribution (i.e., committee averaging method). We combined climatic data from the three different GCMs (NorESM1-M, GISS-E2-R, and HadGEM2-ES) with the five algorithms previously selected (ANN, GAM, GLM, Maxent, and RF) for the SDM. We thus obtained 16 possible “votes” (i.e., $1, \frac{14}{15}, \frac{13}{15}, \frac{12}{15} \ldots, \frac{2}{15}, \frac{1}{15}, 0$). The areas where most predictions indicated Araucaria’s presence in the future (i.e. > 50% of the combined models) we defined as a suitable area for the species’ future occurrence: the SDAf. These projections were calculated for the year 2085, under both RCPs (4.5 and 8.5), and two novel dispersal hypotheses: Full-Dispersal and Zero-Dispersal (see Vieilledent *et al.* 2013). The Full-Dispersal scenario considers the possibility for Araucaria to colonize new climatically favorable sites outside the current species’ projected distribution. The Zero-Dispersal hypothesis considers the impossibility for Araucaria to naturally colonize new climatically favorable sites outside the current species’ projected distribution. Finally, we converted all suitable projected areas in the present and under future climate change scenarios to binary maps (i.e. 0 for species absence and 1 for species presence). We overlapped these projected binary maps with climatically suitable conditions for Araucaria with the land-use map generated by the combination of three land-use sub-categories. We extracted land-use occurrence within Araucaria distribution maps to create a more realistic output of Araucaria distribution in the present and under future climatic scenarios.

### 3.2.6 Effectiveness of the protected area network and connectivity of *Araucaria* projected occurrence

To evaluate the protected areas' effectiveness (sensu CHAPE *et al.* 2005) and the connectivity of Araucaria remnant areas within the Mixed and Dense Forests, we first overlapped land-use binary maps within the protected areas polygons. We selected the three main categories of Brazilian protected areas — Sustainable Use ("Uso Sustentável"), Strictly Protected ("*Proteção Integral*"), and Private Reserves of Natural Heritage ("*Reserva Particular do Patrimônio Natural*"), from the "*SOS Mata Atlântica*" and "*Protected Planet*" websites (http://mapas.sosma.org.br/ and https://www.protectedplanet.net/en, respectively). Second, we calculated the area (in km$^2$) occupied by Araucaria inside and outside protected areas leaning on land-use data. Third, to calculate the connectivity of Araucaria projected populations we used the graph theory, where we defined a centroid in the center of current and future binary maps distanced ~12 km from each other with arcs connecting different centroids. The centroids were connected if the distance was inferior or equal to 0.15° (we assumed that *Araucaria* projected remnants are only connected to the neighboring grid cells in the height direction; sensu VIEILLEDENT *et al.* 2013). Connectivity was defined as the sum of the arcs connecting each nearest node. The sum of the total number of connected arcs between nodes is a direct measure of network connectivity. This measure allows interpreting how *Araucaria* remnant projected populations could be connected throughout its natural distribution in the present or under climate change scenarios (MATISZIW; MURRAY, 2009; VIEILLEDENT *et al.*, 2013), within and outside protected areas, besides considering the land-use change.

All computations involving the SDM were made using "BIOMOD 2" software (THUILLER *et al.* 2009) and generated using R environment (R CORE TEAM, 2020). We used R spatial library: "*sp*", "*maptools*", and "*raster*" to convert continuous maps to binary maps. To compute Araucaria connectivity, we used the package "*spatgraph*" also under R environment. All maps were built with latitude/longitude relative to the coordinate reference system WGS 84 datum.

## 3.3 RESULTS

### 3.3.1 Model's performance

Araucaria's potential distribution was supported by accurate model predictions and high statistic results evaluating the ensemble modelling and committee averaging predictions (Table S1). From the ensemble modelling before committee averaging, we obtained the mean value of the Area Under the Curve from 55 models (AUC = 0.788). The committee averaging performance was also backed by satisfactory statistics results (TSS > 0.556, Sensitivity > 0.88, and Specificity > 0.67). All performance indices showed that the five algorithms (ANN, GAM, GLM, Maxent, Random Forest) selected for the SDM can be used to predict *Araucaria*'s bioclimatic niche and species distribution. The variables selected to perform the SDM indicated the annual mean temperature and temperature seasonality were the two main variables explaining species distribution (Table S2).

### 3.3.2 Current species distribution area and its bioclimatic niche

The current occurrence area (SDAc) calculated for Araucaria was 135,468 km² with no land-use. This climatically suitable area lost another 20% of its extent considering land-use change, resulting in 108,174 km² of climatically suitable areas. The SDAc mainly covers the (i) Santa Catarina's state highlands (southeast Mixed Forest region, in the surroundings of *São Joaquim* National Park) and the state's central region (surroundings of *Araucária* National Park); (ii) the Paraná's state Plateau (Environmental Protection Areas of *Campos Gerais* and *Serra da Esperança* and *Palmas* Wildlife Refuge), and the state's northeast region (surroundings of Curitiba municipality along the *Guaricana* and *Saint-Hilaire* National Parks); and (iii) the "*Campos*" Highlands at Rio Grande do Sul state, in both natural-forested (within the Araucaria Mixed Forest) and natural non-forested areas, where two major protected areas encompass the predicted occurrence area: *Aparados da Serra* and *Serra Geral* National Parks (Fig. 2). Another Araucaria remnant occurs at the Mantiqueira Hills region and the surrounding areas of *Serra da Bocaina* and *Itatiaia* National Parks, along the border of São Paulo, Minas Gerais, and Rio de Janeiro states. The bioclimatic niche (Table S3) of Araucaria indicates that the species is adapted to areas where the seasonality of the temperature varies from 25.69 to 32.58°C; the mean annual temperature ranges from 14.1 to 17.8°C; and mean diurnal temperature averages 10.9°C. The species occurs circa 645 m above sea level, ranging from 5m until 1653m. The annual precipitation average was 1701 mm.y$^{-1}$.

### 3.3.3 Araucaria vulnerability to climate change and protected area network effectiveness

All future climatic scenarios (RCP 4.5 and 8.5, Full and Zero-Dispersal hypothesis in 2085) were pessimistic for the species. Projections indicated a range contraction of climatically suitable areas for Araucaria from 65% to 88% when compared to the current occurrence area with land-use (i.e. 108,174 km²). Furthermore, future climatic suitable areas shifted to more elevated areas (i.e. from 1056m to 1142m). Under the Zero-Dispersal hypothesis and RCP 8.5, the future suitable area is expected to be reduced by 88% (i.e. only 15,766 km² of climatically suitable areas). Assuming land-use and future climate change scenarios, it is expected that climatically suitable areas will reach no more than 12,000 km², primarily at more elevated regions (from 645m to 1142.5m in 2085, under RCP 8.5 and Zero-Dispersal hypothesis; see Table S4 for a complete description of the upward elevational shift for the species).

Also, protected areas do not effectively encompass Araucaria distribution (Fig. 3). Current projections showed that only 7500 km² (or 7%) are covered by protected area network, despite the 108,174 km² of climatically suitable areas for Araucaria occurrence in the present (see Table 1 for a complete comparison of Araucaria projections encompassed or not by protected areas). Finally, projections for 2085 under RCP 8.5 showed that only 11,993 km² will be climatically suitable areas for Araucaria. However, only 11% of this projected occurrence area will be covered by the existing protected area network (i.e. 1352 km²)

### 3.3.4 The connectivity projected for Araucaria distribution and potential refuge areas

Along the 108,174 km² predicted to be climatically suitable for Araucaria in the present assuming land-use change, we identified 715 arcs connecting 744 adjacent nodes (Fig. 4). Also, 202 arcs are connected within protected areas, whilst another 513 are distributed mainly at the three Brazilian southern states and through elevated areas at Mantiqueira and Bocaina hills, in the border region of Minas Gerais, São Paulo, and Rio de Janeiro states. Consequently, projected occurrence in the present indicates the connection between protected and unprotected Araucaria remnants populations. Future scenarios in 2085 indicated connectivity loss from 58% (298 connecting arcs – RCP 4.5) to 79% (144 connecting arcs – RCP 8.5) compared to current connectivity (Table 2). The most pessimistic climate change scenario (Zero-Dispersal hypothesis and RCP 8.5) indicated only 36 connected arcs within the current protected area network (Fig. 4); and another 108 arcs outside areas protected by Brazilian legislation.

Additionally, this scenario revealed that Araucaria's projected occurrence will be mainly connected through Santa Catarina and Rio Grande do Sul states. Protected areas such as *São Joaquim* (SC); *Aparados da Serra* (RS) and Serra Geral National Parks (RS) will be key regions to connect potential refuge areas for Araucaria in the future. The central region of Santa Catarina state could also be prioritized as a key-spot for Araucaria future protection, where *Araucária* National Park (SC) and *Palmas* Wildlife Refuge (PR) protected areas might connect future projected remnants. Future optimistic scenarios (Full-Dispersal hypothesis and RCP 4.5) showed that *Itatiaia* and *Serra da Bocaina* National Parks, at Mantiqueira hills region, could be also relevant refuge areas for *Araucaria* in the future.

## 3.4 DISCUSSION

Araucaria will be threatened by climate change in the long-term future. The species will not be effectively covered by the existing protected area network and remnant subpopulations will be poorly connected. Two different regions could embrace a *hopespot* (REZENDE *et al.* 2018) for Araucaria future conservation as climatic refuge areas. In southern Brazil, key-areas could connect remnant populations with major protected areas: (i) in Santa Catarina central and southeastern regions (surroundings of *São Joaquim* National Park and *Serra da Francisca* Environmental Protection Area); (ii) Paraná central region along with the Environmental Protection Areas of *Campos Gerais* and *Serra da Esperança*, besides the *Palmas* Wildlife Refuge; (iii) Rio Grande do Sul northern region could also connect unprotected remnant patches in the surroundings of *Aparados da Serra* and *Serra Geral* National Parks. The second refuge occurs through the Mantiqueira Hills (alongside the states' border of Rio de Janeiro, São Paulo, and Minas Gerais), near *Itatiaia* and *Serra da Bocaina* National Parks.

Our predictive models indicated Araucaria range contraction upwards as the species climatic suitable niche is favorable under milder temperatures. This is particularly important because the species is associated with constant moist and cool conditions with no dry season (NEVES *et al.* 2017). Consequently, we also recommend the creation of new protected areas in these climatically refuge areas (i.e. 1000m above sea level). Araucaria's current distribution along the Mixed and surrounding Dense Ombrophilous Forests allows the connectivity between potential remnant populations and existing protected area network (Fig. 4), an optimistic appraisal that has not been foreseen in this study.

Protected areas within the Mixed and Dense Ombrophilous Forests are concentrated especially in eastern regions of the states of Paraná, Santa Catarina, Rio Grande do Sul, and São

Paulo states (Fig. 1). These protected areas interconnect both the Mixed Forest and the Dense Ombrophilous Forest as part of conservation efforts focused on the coastal Atlantic Forest domain. However, less than 15% of the current Araucaria distribution area is encompassed by protected areas, especially in the southern inland of the Atlantic Forest, i.e. the Mixed Forest (Fig. 3). As the current patches of projected remnant populations in the present still allow species connectivity in the landscape (Fig. 4), we could affirm that the existing protected area network might connect remnant populations through the landscape, despite not being effectively covered by protected areas (sensu CHAPE *et al.* 2005).

Climatically suitable regions in the future, nevertheless, will not be effectively covered by the existing protected area network. Therefore, it is paramount that conservation strategies should be prioritized by reinforcing the creation and maintenance of the protected area network. Interestingly, the proportional increase of protected patches under climate change scenarios may be explained because Araucaria future projections showed range contraction to more elevate areas within already existing protected area network (Fig. 3; Table 2). Castro *et al.* (2019) and Marchioro *et al.* (2019) showed that projected distribution under climate change of Araucaria was also inefficiently covered by protected areas, especially "*Integral Protection*" category of protected areas. We added another step to Araucaria conservation indicating where and which protected areas could connect future species' projected distribution (Fig. 3; Table 2). We also identified that the upward elevational pattern might occur especially at Santa Catarina's highlands, Rio Grande do Sul's grasslands, and the central plateau of Paraná state. These regions should also be prioritized for conservation efforts as refuge areas, potential ecological corridors, or climatic key-areas to create new protected areas. Also, specific protected areas, such as *São Joaquim (*SC); *Campos Gerais* (PR); *Aparados da Serra* (RS); *Serra Geral* (RS/SC); *Itatiaia* (RJ), *Serra da Bocaina* (RJ/SP) National Parks ("*Integral Protection*" category) are essential to integrate conservation strategies aiming to reduce anthropic threats to the species, such as deforestation, logging, habitat loss, and climate change. These actions would also benefit the maintenance of genetic diversity among subpopulations (CARNAVAL *et al.* 2009). For species with low dispersal potential — such as Araucaria, with dispersal ranges from 35 m to 291 m, and averaging 92m (BITTENCOURT; SEBBENN 2007) — preserving adjacent areas climatically or environmentally stable over time could be a relevant strategy (OLIVEIRA *et al.* 2015), especially when climate change may shift the species' range outside existing protected areas (HANNAH *et al.* 2007).

### 3.4.1 Uncertainty in SDMs and strategies to improve the modelling approach

Any modelling exercise involves uncertainty (ARAÚJO *et al.* 2019). Despite the arbitrary choice of algorithms to perform the SDM, there is no “silver bullet” in correlative SDM algorithms, which means that there is no uniquely better algorithm to specifically perform an SDM (QIAO *et al.* 2015). The SDM generated in this study disregarded biological aspects of Araucaria; such, as gene flow (STEFENON *et al.* 2007), phenotypic plasticity (REIS *et al.* 2018), or ecological interactions with local fauna (IOB; VIEIRA 2008; BOGONI *et al.* 2020b), and human-groups (REIS *et al.* 2014; TAGLIARI; PERONI 2018; SÜHS *et al.* 2018). These are adaptive mechanisms that confer resilience to species under climate change (CATEN *et al.* 2017). Adaptive mechanisms, however, are challenging to add to predictive models (FODEN *et al.* 2019). The “Zero-Dispersal” and “Full-Dispersal” hypotheses were a strategy to improve our correlative SDM (DORMANN *et al.* 2012), as we could infer about species capacity to occupy or not newly climatic suitable areas. Connectivity computation was also an approach to enhance ecological implications using an SDM (VIEILLEDENT *et al.* 2013). We also added land-use as a proxy to infer about habitat change aiming to improve the reliability of our models, once we add to our predictive occurrence maps the influence of urban structures, forest plantations, and agriculture and pasture mosaics (MARCHIORO *et al.* 2020). Our study considered three classes of protected areas: Integral Protection, Sustainable Use, and Private Reserves of Natural Heritage. We did not include Indigenous Lands, or private conservation areas according to Brazilian environmental legislation: Permanent Preservation Areas and Legal Reserves, which may contribute to enhancing species’ connectivity (RYLANDS; BRANDON 2005) and protection. Legal Reserves in Brazil encompass one-third of Brazilian protected areas (METZGER *et al.* 2019). We also suggest that further studies could target the importance of Legal Reserves as a strategy to enhance protected areas' effectiveness for Araucaria.

### 3.4.2 Conservation strategies and study implications

Our results were consistent when compared to previous studies in specific aspects: (i) analogous priority conservation areas identified in 2085 within the Mixed and Dense Forests; (ii) similarity in the identification of climatically suitable and suitable areas in the future for Araucaria, especially at Santa Catarina and Rio Grande do Sul highlands, Paraná central region, besides Mantiqueira and Bocaina hills (CASTRO *et al.* 2019; WILSON *et al.* 2019;

MARCHIORO *et al.* 2020); (iii) ineffectiveness of protected area network in preserving Araucaria in the present and under future climate change scenarios (CASTRO *et al.* 2019; MARCHIORO *et al.* 2020) The novelty showed in our study indicates that Araucaria future populations will be isolated, poorly protected, and unconnected within what once was a majestic occurrence area through the Mixed and Dense Forests. Major protected areas that encompass Araucaria potential distribution (Table 2) are not connected along the landscape, an unprecedented appraisal over Araucaria conservation assessment. Our results indicate the necessity of new protected areas and the identification of climatic refuge areas for the species. The combination of refuge area identification with the species connectivity potential could generate prolific improvements in species conservation. From a perspective of conservation assessment for the relict Araucaria, we recommend that the combination of these recent studies about Araucaria vulnerability to climate change (CASTRO *et al.* 2019; WILSON *et al.* 2019; MARCHIORO *et al.* 2020) combined with our main result about the importance of connectivity between remnant occurrence patches and protected area network. This might boost Araucaria conservation in the short and long-term. As an ecological keystone and umbrella species, by safeguarding Araucaria we protect the socioecological system and its vast associated biodiversity both in southern and southeast Brazil (BOGONI *et al.* 2020), potentially promoting forest expansion (ROBINSON *et al.* 2018) and resilience to anthropic disturbances (TAGLIARI *et al.* 2021).

We recommend integrated conservation measures, such as the creation, expansion, and identification of ecological corridors and refuge areas, as well as the maintenance and expansion of protected area networks, along with collaborative management initiatives with local human groups, stakeholders, researchers, and decision-makers. This integrative scenario could enable *Araucaria*'s connectivity, resilience, maintenance, and conservation in a fragmented, disturbed, and vulnerable ecosystem.

## 3.5 DECLARATION

**-Fundings:** Coordenação de Aperfeiçoamento de Pessoal de Nível Superior — CAPES — Financial Code 001 (Ph.D. scholarship for MMT and JA – 88882.438725/2019; 88882.438727/2019-01 respectively); Conselho Nacional de Desenvolvimento Científico e Tecnológico — CNPq — for productivity scholarship for NP (Process 310443/2015-6) and TCLS (Process 88882.316559/2019-01).

**-Conflict of interest/Competing interests:** The authors declare no conflict of interest.

**-Availability of data and material:** The R script to reproduce entirely the results of the study is available on the GitHub digital repository (see git masemuta/*Araucaria*_sdm).

**-Authors contribution:** MMT: Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization. GV: Methodology, Software, Formal Analysis, Data Curation, Writing – Review & Editing. JA: Writing – Review & Editing, Visualization. TCLS: Methodology, Validation, Formal Analysis, Writing – Review & Editing. NP: Conceptualization, Resources, Writing – Original Draft, Writing – Review & Editing, Supervision, Funding acquisition.

**-Ethics approval:** Not applicable.

-**Consent to participate:** Not applicable.

**-Consent for publication:** Not applicable.

## 3.6 REFERENCES

Adan N, Atchison J, Reis MS, Peroni N (2016) Local Knowledge, Use and Management of Ethnovarieties of *Araucaria angustifolia* (Bert.) Ktze. in the Plateau of Santa Catarina, Brazil. Econ Bot 70:353–364. doi: 10.1007/s12231-016-9361-z

Anderson-Teixeira KJ, Miller AD, Mohan JE, et al (2013) Altered dynamics of forest recovery under a changing climate. Glob Chang Biol 19:2001–2021. doi: 10.1111/gcb.12194

Araújo MB, Anderson RP, Barbosa AM, et al (2019) Standards for distribution models in biodiversity assessments

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–47. doi: 10.1016/j.tree.2006.09.010

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 327–338. doi: 10.1111/j.2041-210X.2011.00172.x

Bellard C, Leclerc C, Leroy B, et al (2014) Vulnerability of biodiversity hotspots to global change. Glob Ecol Biogeogr 23:1376–1386. doi: 10.1111/geb.12228

Bittencourt JVM, Sebbenn AM (2007) Patterns of pollen and seed dispersal in a small, fragmented population of the wind-pollinated tree *Araucaria angustifolia* in southern Brazil. Heredity (Edinb) 99:580–591. doi: 10.1038/sj.hdy.6801019

Bogoni JA, Batista GO, Graipel ME, Peroni N (2020a) Good times, bad times: Resource pulses influence mammal diversity in meridional Brazilian highlands. Sci Total Environ 734:139473. doi: 10.1016/j.scitotenv.2020.139473

Bogoni JA, Muniz-Tagliari M, Peroni N, Peres CA (2020b) Testing the keystone plant resource role of a flagship subtropical tree species (*Araucaria angustifolia*) in the Brazilian Atlantic Forest. Ecol Indic 118:106778. doi: 10.1016/j.ecolind.2020.106778

Breiman L (2001) Random forests. Mach Learn 45:5–32. doi: 10.1023/A:1010933404324

Carnaval AC, Hickerson MJ, Haddad CFB, et al (2009) Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot. Science (80- ) 323:785–789. doi: 10.1126/SCIENCE.1166955

Castro MB, Barbosa ACMC, Pompeu PV, et al (2019) Will the emblematic southern conifer *Araucaria angustifolia* survive to climate change in Brazil? Biodivers Conserv 29:591–607. doi: 10.1007/s10531-019-01900-x

Caten C Ten, Lima-Ribeiro M de S, da Silva NJ, et al (2017) Evaluating the Effectiveness of Brazilian Protected Areas Under Climate Change. Trop Conserv Sci 10:194008291772202. doi: 10.1177/1940082917722027

Chape S, Harrison J, Spalding M, Lysenko I (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philos Trans R Soc Lond B Biol Sci 360:443–55. doi: 10.1098/rstb.2004.1592

Chen I-C, Hill JK, Ohlemüller R, et al (2011) Rapid range shifts of species associated with high levels of climate warming. Science (80- ) 333:1024–1026. doi: 10.1126/science.1206432

de Morais Pereira J, Corá Segat J, Baretta D, et al (2017) Soil Macrofauna as a Soil Quality Indicator in Native and replanted *Araucaria angustifolia* Forests. Artic Rev Bras Cienc Solo 41:160261. doi: 10.1590/18069657rbcs20160261

Dormann CF, Schymanski SJ, Cabral J, et al (2012) Correlation and process in species distribution models: Bridging a dichotomy. J Biogeogr 39:2119–2131. doi: 10.1111/j.1365-2699.2011.02659.x

Duarte LDS, Dos-Santo MMG, Hartz SM, Pillar VD (2006) Role of nurse plants in *Araucaria* Forest expansion over grassland in south Brazil. Austral Ecol 31:520–528. doi: 10.1111/j.1442-9993.2006.01602.x

Elith J, Graham CH (2009) Do they? How do they? Why do they differ? on finding reasons for differing performances of species distribution models. Ecography (Cop) 32:66–77. doi: 10.1111/j.1600-0587.2008.05505.x

Ferro VG, Lemes P, Melo AS, Loyola R (2014) The reduced effectiveness of protected areas under climate change threatens atlantic forest tiger moths. PLoS One 9:. doi: 10.1371/journal.pone.0107792

Foden WB, Young BE, Akçakaya HR, et al (2019) Climate change vulnerability assessment of species. Wiley Interdiscip Rev Clim Chang 10:e551. doi: 10.1002/wcc.551

Fonseca CR, Ganade G, Baldissera R, et al (2009) Towards an ecologically-sustainable forestry in the Atlantic Forest. doi: 10.1016/j.biocon.2009.02.017

Fourcade Y, Besnard AG, Secondi J (2018) Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. Glob Ecol Biogeogr 27:245–256. doi: 10.1111/geb.12684

Garcia RA, Cabeza M, Rahbek C, Araújo MB (2014) Multiple dimensions of climate change and their implications for biodiversity. Science 344:1247579. doi: 10.1126/science.1247579

GBIF (2021) GBIF: Global Biodiversity Information Facility. Occurrence download. doi.org/10.15468/dd.nezhn5

Gray CL, Hill SLL, Newbold T, et al (2016) Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nat Commun 7:1–7. doi: 10.1038/ncomms12306

Hannah L, Midgley G, Andelman S, et al (2007) Protected area needs in a changing climate

Hijmans RJ (2012) Cross-validation of species distribution models : removing spatial sorting bias and calibration with a null model. Ecology 93:679–688. doi: 10.1890/11-0826.1

Hijmans RJ, Cameron SE, Parra JL, et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. doi: 10.1002/joc.1276

Iob G, Vieira EM (2008) Seed predation of *Araucaria angustifolia* (*Araucaria*ceae) in the Brazilian *Araucaria* Forest: Influence of deposition site and comparative role of small and "large" mammals. Plant Ecol 198:185–196. doi: 10.1007/s11258-007-9394-6

Joly CA, Metzger JP, Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest : ecological findings and conservation initiatives. New Phytol 459–473. doi: 10.1111/nph.12989

Knutti R, Masson D, Gettelman A (2013) Climate model genealogy: Generation CMIP5 and how we got there. Geophys Res Lett 40:1194–1199. doi: 10.1002/grl.50256

Lauterjung MB, Bernardi AP, Montagna T, et al (2018) Phylogeography of Brazilian pine ( *Araucaria angustifolia* ): integrative evidence for pre-Columbian anthropogenic dispersal

Liu C, White M, Newell G (2011) Measuring and comparing the accuracy of species distribution models with presence-absence data. Ecography (Cop) 34:232–243. doi: 10.1111/j.1600-0587.2010.06354.x

Marchioro CA, Santos KL, Siminski A (2020) Present and future of the critically endangered *Araucaria angustifolia* due to climate change and habitat loss. For An Int J For Res 93:401–410. doi: 10.1093/forestry/cpz066

Matisziw TC, Murray AT (2009) Connectivity change in habitat networks. Landsc Ecol 24:89–100. doi: 10.1007/s10980-008-9282-z

Mecke R, Galileo MHM, Engels W (2001) New records of insects associated with *Araucaria* trees: Phytophagous coleoptera and hymenoptera and their natural enemies. Stud Neotrop Fauna Environ 36:113–124. doi: 10.1076/snfe.36.2.113.2132

Mello AJM, Peroni N (2015) Cultural landscapes of the *Araucaria* Forests in the northern plateau of Santa Catarina, Brazil. J Ethnobiol Ethnomed 11:51. doi: 10.1186/s13002-015-0039-x

Metzger JP (2009) Conservation issues in the Brazilian Atlantic forest. Biol Conserv 142:1138–1140. doi: 10.1016/J.BIOCON.2008.10.012

Metzger JP, Bustamante MMC, Ferreira J, et al (2019) Why Brazil needs its Legal Reserves. Perspect Ecol Conserv 17:91–103. doi: 10.1016/j.pecon.2019.07.002

Monzón J, Moyer-Horner L, Palamar MB (2011) Climate Change and Species Range Dynamics in Protected Areas. Bioscience 61:752–761. doi: 10.1525/bio.2011.61.10.5

Moreira M, Zucchi MI, Gomes JE, et al (2016) *Araucaria angustifolia* aboveground roots presented high arbuscular mycorrhizal fungal colonization and diversity in the Brazilian Atlantic Forest. Pedosphere 26:561–566. doi: 10.1016/S1002-0160(15)60065-0

Neves DM, Dexter KG, Pennington RT, et al (2017) Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. Divers Distrib 23:898–909. doi: 10.1111/ddi.12581

Oliveira G de, Lima-Ribeiro MS, Terribile LC, et al (2015) Conservation biogeography of the Cerrado's wild edible plants under climate change: Linking biotic stability with agricultural expansion. Am J Bot 102:870–877. doi: 10.3732/ajb.1400352

Oliveira U, Soares-Filho BS, Paglia AP, et al (2017) Biodiversity conservation gaps in the Brazilian protected areas. Sci Rep 7:9141. doi: 10.1038/s41598-017-08707-2

Parmesan CN (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:636–637. doi: 10.2307/annurev.ecolsys.37.091305.30000024

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 6:231–259. doi: 10.1016/j.ecolmodel.2005.03.026

Porfirio LL, Harris RMB, Lefroy EC, et al (2014) Improving the Use of Species Distribution Models in Conservation Planning and Management under Climate Change. PLoS One 9:e113749. doi: 10.1371/journal.pone.0113749

Qiao H, Soberón J, Peterson AT (2015) No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. Methods Ecol Evol 6:1126–1136. doi: 10.1111/2041-210X.12397

Quantum GIS Development Team (2018) Quantum GIS Geographic Information System. Open Source Geospatial 527 Foundation Project. http://qgis.osgeo.org

Quinteiro MM da C, Alexandre B da R, Magalhães LMS (2019) Brazilian Pine (*Araucaria angustifolia* (Bertol.) Kuntze) Ethnoecology in the Mantiqueira Atlantic Forest. Floresta e Ambient 26:1–7. doi: 10.1590/2179-8087.018516

R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical 532 Computing, Vienna, Austria. http://www.R-project.org/

Reis MS, Ladio A, Peroni N (2014) Landscapes with *Araucaria* in South America: Evidence for a cultural dimension. Ecol Soc 19:. doi: 10.5751/ES-06163-190243

Reis MS, Montagna T, Mattos AG, et al (2018) Domesticated Landscapes in *Araucaria* Forests, Southern Brazil: A Multispecies Local Conservation-by-Use System. Front Ecol Evol 6:11. doi: 10.3389/fevo.2018.00011

Rezende CL, Scarano FR, Assad ED, et al (2018) From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspect Ecol Conserv. doi: 10.1016/J.PECON.2018.10.002

Riahi K, Rao S, Krey V, et al (2011) RCP 8.5-A scenario of comparatively high greenhouse gas emissions. Clim Change 109:33–57. doi: 10.1007/s10584-011-0149-y

Robinson M, De Souza JG, Maezumi SY, et al (2018) Uncoupling human and climate drivers of late Holocene vegetation change in southern Brazil. Sci Rep 8:7800. doi: 10.1038/s41598-018-24429-5

Roderjan CV, Galvão F, Kuniyoshi YS, Hatschbach GG (2002) As Unidades Fitogeográficas do Estado do Paraná. Ciência Ambient 24:76–92

Rodrigues ASL, Pilgrim JD, Lamoreux JF, et al (2006) The value of the IUCN Red List for conservation. Trends Ecol Evol 21:71–76. doi: 10.1016/j.tree.2005.10.010

Rylands AB, Brandon K (2005) Brazilian Protected Areas. Conserv Biol 19:612–618. doi: 10.1111/j.1523-1739.2005.00711.x

Scarano FR, Ceotto P (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers Conserv 24:2319–2331. doi: 10.1007/s10531-015-0972-y

Schneider LCA, Silva MT da, Agostinetto L, Siegloch AE (2018) Deforestation in Mixed Ombrophilous Forest in the Serrana Region of Santa Catarina. Rev Árvore 42:. doi: 10.1590/1806-90882018000200006

Souza AF (2020) A review of the structure and dynamics of *Araucaria* mixed forests in southern Brazil and northern Argentina. New Zeal J Bot 0:1–53. doi: 10.1080/0028825X.2020.1810712

Souza CM, Z. Shimbo J, Rosa MR, et al (2020) Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. Remote Sens 12:2735. doi: 10.3390/rs12172735

Stefenon VM, Gailing O, Finkeldey R (2007) Genetic structure of *Araucaria angustifolia* (*Araucaria*ceae) populations in Brazil: Implications for the in situ conservation of genetic resources. Plant Biol 9:516–525. doi: 10.1055/s-2007-964974

Sühs RB, Giehl ELH, Peroni N (2018) Interaction of land management and *Araucaria* trees in the maintenance of landscape diversity in the highlands of southern Brazil. PLoS One

13:e0206805. doi: 10.1371/journal.pone.0206805

Tagliari MM, Levis C, Flores BM, et al (2021) Collaborative management as a way to enhance *Araucaria* Forest resilience. Perspect Ecol Conserv. doi: 10.1016/J.PECON.2021.03.002

Tagliari MM, Peroni N (2018) Local varieties of *Araucaria angustifolia* (Bertol.) Kuntze (Pinales : *Araucaria*ceae) in southern Brazil: A brief discussion about landscape domestication. Biotemas 31:59–68

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD - A platform for ensemble forecasting of species distributions. Ecography (Cop) 369–373. doi: 10.1111/j.1600-0587.2008.05742.x

van Vuuren DP, Edmonds J, Kainuma M, et al (2011) The representative concentration pathways: An overview. Clim Change 109:5–31. doi: 10.1007/s10584-011-0148-z

Varela S, Lima-Ribeiro MS, Terribile LC (2015) A Short Guide to the Climatic Variables of the Last Glacial Maximum for Biogeographers. PLoS One 10:e0129037. doi: 10.1371/JOURNAL.PONE.0129037

Vibrans AC, McRoberts RE, Moser P, Nicoletti AL (2013) Using satellite image-based maps and ground inventory data to estimate the area of the remaining Atlantic forest in the Brazilian state of Santa Catarina. Remote Sens Environ 130:87–95. doi: 10.1016/j.rse.2012.10.023

Vieilledent G, Cornu C, Cuní Sanchez A, et al (2013) Vulnerability of baobab species to climate change and effectiveness of the protected area network in Madagascar: Towards new conservation priorities. Biol Conserv 166:11–22. doi: 10.1016/j.biocon.2013.06.007

Watson JEM, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. Nature 515:67–73. doi: 10.1038/nature13947

Wilson OJ, Walters RJ, Mayle FE, et al (2019) Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered *Araucaria* tree. Glob Chang Biol 25:4339–4351. doi: 10.1111/gcb.14755

Wrege MS, Sousa VA De, Fritzsons E, et al (2016) Predicting Current and Future Geographical Distribution of *Araucaria* in Brazil for Fundamental Niche Modeling. Environ Ecol Res 4:269–279. doi: 10.13189/eer.2016.040506

Zhang L, Liu S, Sun P, et al (2015) Consensus Forecasting of Species Distributions: The Effects of Niche Model Performance and Niche Properties. PLoS One 10:e0120056. doi: 10.1371/journal.pone.0120056

## 3.7 FIGURES

Figure 1. The study area. 1. The Brazilian Atlantic Rainforest biome with the Mixed Ombrophilous Forest (green) and Dense Ombrophilous Forest (blue). The red border represents the three Brazilian southern states where the original Araucaria Forest extent was mainly distributed: Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS). The blue and yellow borders represent respectively the São Paulo (SP) and Rio de Janeiro (RJ) states where relict Araucaria populations remain at higher elevations through the Mantiqueira Hills. 2. The elevational gradient through the Mixed and Dense Ombrophilous Forests. White dots show occurrence points of *A. angustifolia* with complete environmental/climatic data in 1km² grid cells. Green polygons indicate the distribution of Brazilian protected areas.

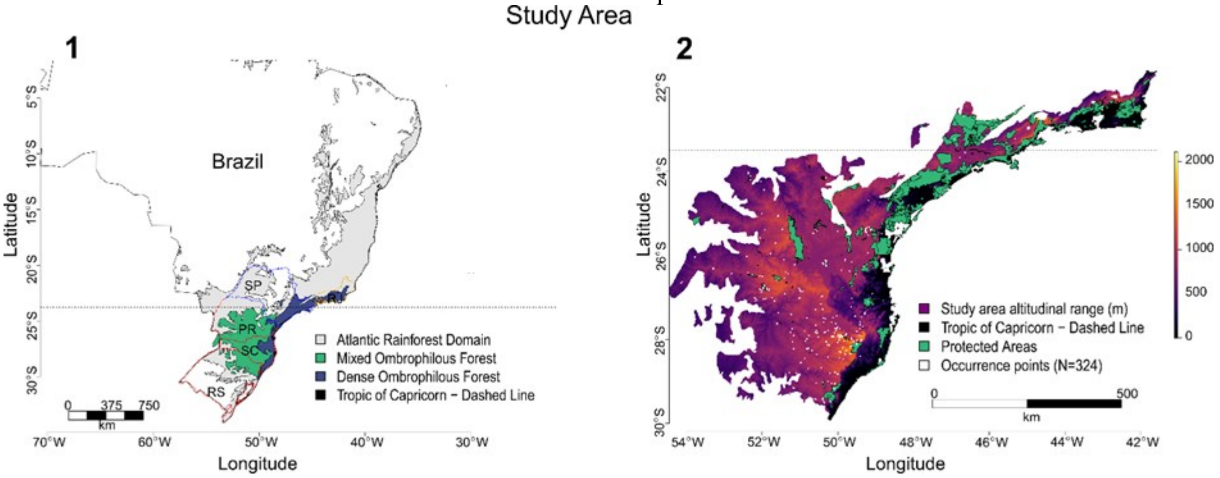


Figure 2. The *Araucaria angustifolia* (Araucaria) current predicted distribution. 1. From three votes (light blue) up to five votes (dark blue) suggest according to committee averaging method indicated species presence. Other color shaded areas (votes 2 and 1) represent incertitude among algorithms; 0 vote (yellow) shows that no algorithm predicted species' potential occurrence. The species distribution area was calculated over the agreement of at least 3 votes, totalizing 135,468 km². 2. The current binary (presence and absence) occurrence under land-use for Araucaria. Land-use reduced suitable occurrence areas up to 20% (i.e. 108,174 km²).

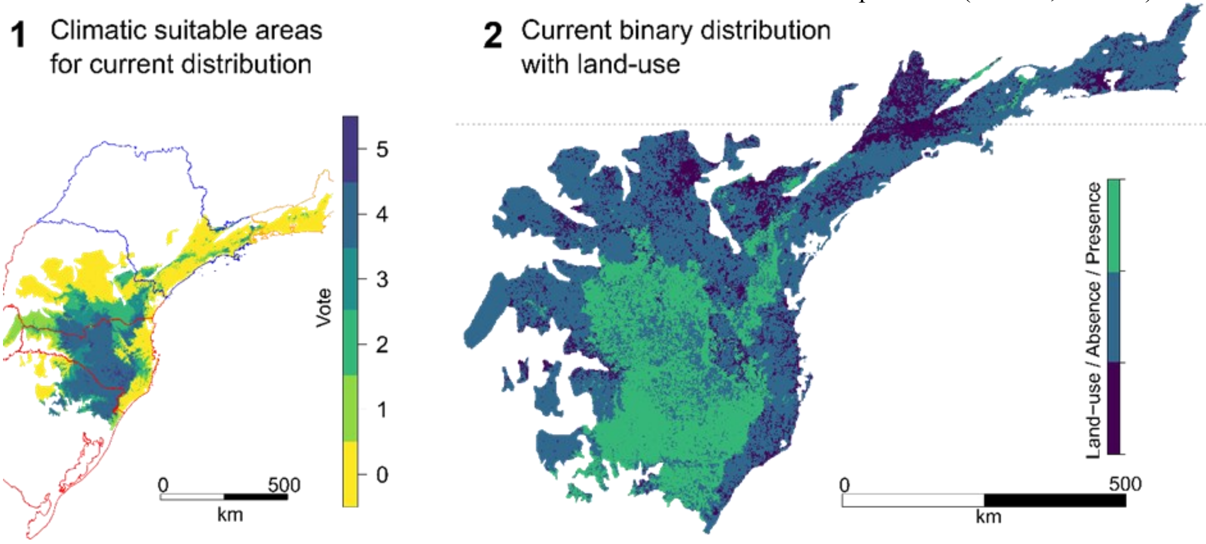
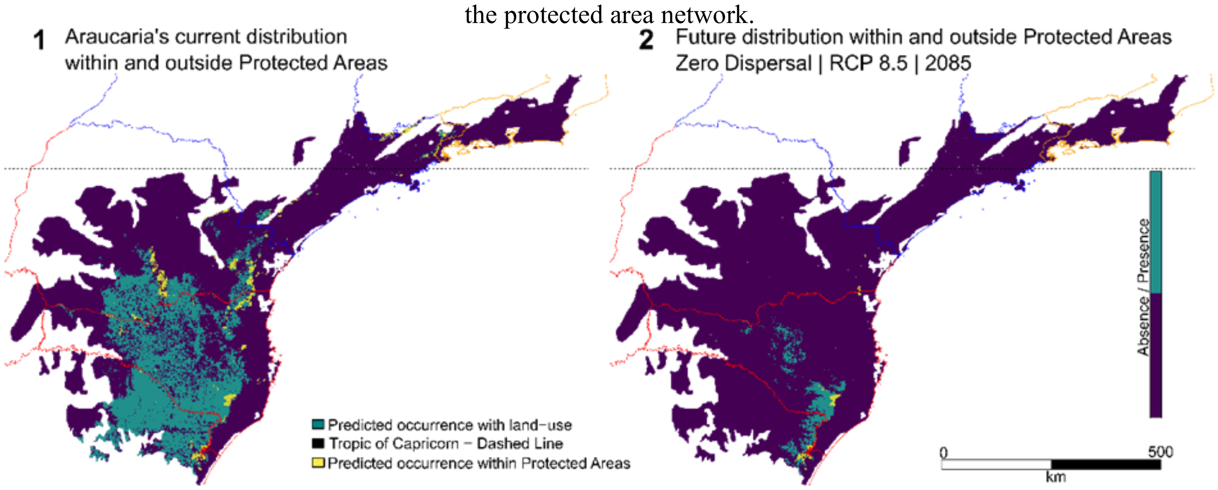


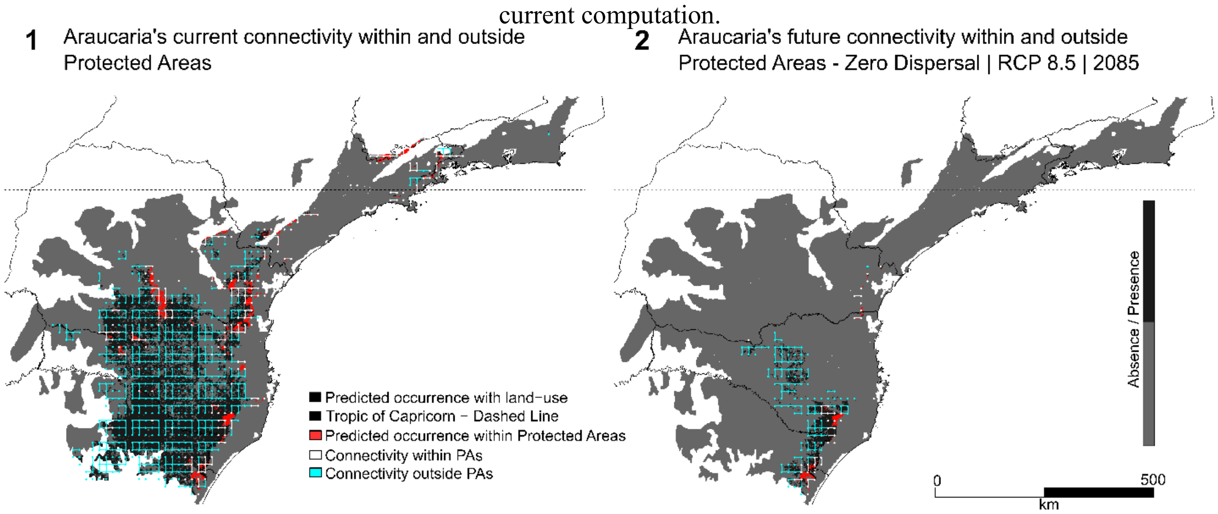
Figure 3. Predictive scenarios for Araucaria distribution encompassed or not by existing protected area network (i.e., current distribution and under climate change: Zero-Dispersal hypotheses in 2085 and RCP 8.5) with land-use change. 1. From 108,174 km² climatically suitable for *Araucaria* occurrence (species presence in blue), only 7500 km² are encompassed by protected areas (yellow-green). 2. The future predictive scenario in 2085 (Zero-Dispersal hypothesis and RCP 8.5) indicates that few existing protected areas throughout the Mixed and Dense Forests will encompass species occurrence. These remnant areas covered by existing protected areas are mostly distributed at Santa Catarina highlands (São Joaquim National Park) and the “Campos” ecosystem region, at Rio Grande do Sul state. In this worst-case scenario, only 1353 km² (i.e. 11%) of 11993 km² will be encompassed by the protected area network.



1 Araucaria's current distribution within and outside Protected Areas

2 Future distribution within and outside Protected Areas Zero Dispersal | RCP 8.5 | 2085

Figure 4. The Araucaria projected connectivity at the present and under climate change (RCP 8.5, Zero-Dispersal hypothesis). We overlapped predicted connectivity over Araucaria occurrence area (presence/absence binary maps). We set a node where models indicated Araucaria presence and arcs connecting adjacent nodes (gray, turquoise, and white segments). The sum of the arcs is the result of computed connectivity (C). 1. The Araucaria current connectivity outside protected areas was C= 513, while C= 202 within the protected area network (C=715 throughout the entire extent). Current connectivity through the Mixed and Dense Forests indicates an optimistic scenario despite land-use change (i.e. habitat change). 2. Connectivity scenario for 2085 — RCP 8.5 — Zero-Dispersal was predicted to decrease by 79% (C= 144, where C=36 within protected areas). Future connectivity reduced from 58.32% (RCP 4.5/Full-Dispersal) until 79% (RCP 8.5/Zero-Dispersal) compared to current computation.



1 Araucaria's current connectivity within and outside Protected Areas

2 Araucaria's future connectivity within and outside Protected Areas - Zero Dispersal | RCP 8.5 | 2085

## 3.8 TABLES

Table 1. The effectiveness of protected area network for Araucaria under current and future (2085) climate and land-use change: RCP 4.5 and 8.5; Full and Zero-Dispersal hypotheses. We calculated the area (km²) within the protected area network according to the SDM. The results indicated that protected areas poorly encompass projected outputs. For current distribution, more than 100,000 km² are climatically suitable (despite land-use change) for Araucaria occurrence, however, only 7500 km² lies within protected areas. As climate change will reduce the species range until 2085 (between 11,993 to 36,365 km²), only 7 to 11% of these predicted occurrence areas will be encompassed by the protected area network.

| **Species** | **Year** | **RCP** | **Dispersal Scenario** | **Suitable area presuming land-use change (km²)** | **Area within protected area network (km²)** | **Percentage of projected occurrence area within protected areas according to area calculated with land-use (%)** |
|---|---|---|---|---|---|---|
| ***Araucaria angustifolia*** | **Present** | NA | NA | 108,174 | 7500 | 7 |
| | **2085** | 4.5 | Full | 36,365 | 2443 | 7 |
| | | 4.5 | Zero | 36,240 | 2361 | 7 |
| | | 8.5 | Full | 11,993 | 1352 | 11 |
| | | 8.5 | Zero | 11,993 | 1352 | 11 |

Table 2. Araucaria's connectivity under current baseline and climate change scenarios assuming land-use change. Connectivity will decrease from 58.32 % (RCP 4.5/Full-Dispersal) to almost 80 % (RCP 8.5/Zero-Dispersal) in 2085. These future scenarios show that Araucaria remnant populations might remain isolated at higher elevations, uncovered by current protected area (PA) network, and unconnected with other subpopulations throughout the Mixed and Dense Forests.

| **Species** | **RCP (2085)** | **Dispersal Scenario (2085)** | **Total connectivity \| Outside PA \| Within PA** | **Connectivity loss compared to current baseline (%)** | **Remnant projected populations remain connected?** |
|---|---|---|---|---|---|
| ***Araucaria angustifolia*** | Current scenario | Current scenario | 715/513/212 | NA | Possible. Through the entire southern states and more elevated areas at eastern regions of Mantiqueira and Bocaina Hills. |
| | 4.5 | Full | 298/221/77 | -58.32 | Partially. Through southern states; specific regions at Mantiqueira Hills, Serra da Bocaina and Itatiaia National Parks. |
| | 4.5 | Zero | 295/221/74 | -58.74 | |
| | 8.5 | Full | 144/108/36 | -79.86 | Poorly. Isolated remnant populations at Santa Catarina (São Joaquim National Park) and Rio Grande do Sul states (Serra Geral, Aparados da Serra National Parks). |
| | 8.5 | Zero | 144/108/36 | -79.86 | |

## 3.9 SUPPORTING INFORMATION

# Relict populations of *Araucaria angustifolia* will be isolated, poorly protected, and unconnected under climate and land-use change in Brazil

Mario M. Tagliari, Ghislain Vieilledent, Jonatas Alves, Thiago C. L. Silveira, Nivaldo Peroni

Figure S1. Three strategies to select bioclimatic variables for the Species Distribution Modelling. (left) The main strategy to select our climatic variables was the correlation graph, where we selected “Annual Mean Temperature (°C)” – bio01_val; “Mean Diurnal Range (Mean of monthly (max temp - min temp °C))” – bio02_val. We excluded “altitude” because it will not change in the future. (middle) Factor analysis: we selected “Annual Mean Temperature (°C)” – bio1; “Temperature seasonality (°C)” – bio4. (right) Principal Component Analysis (PCA): we selected “Temperature seasonality (°C)” – bio4; “Annual Mean Precipitation (mm.y-1)” – bio12.

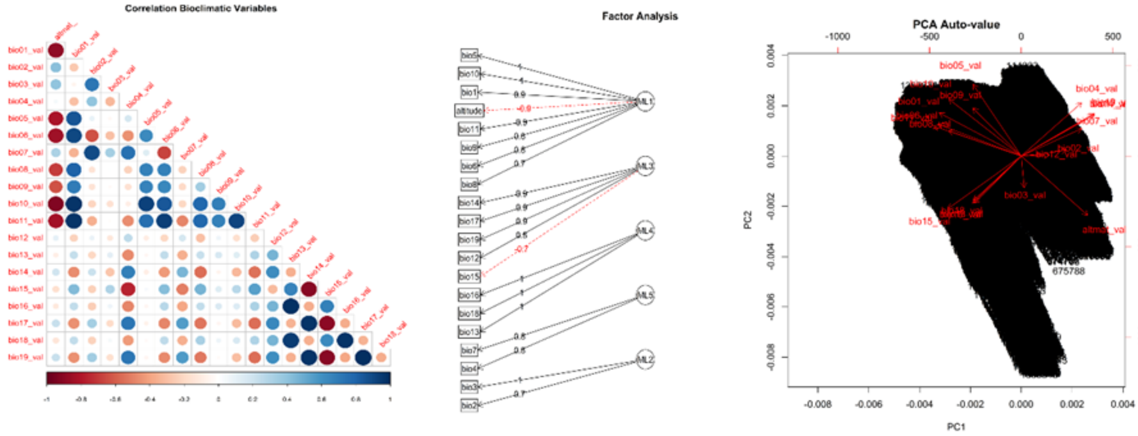


Table S1. Predictive performance of the ensemble model prior and based on committee averaging for Araucaria. Predictive performance before the binary conversion was evaluated by the Area Under de Curve (AUC) specifying a fixed threshold of 0.6 or 60%, where algorithms predicting Araucaria occurrence with values < 0.6 or 60% did not account for the committee averaging. The AUC was evaluated over the continuous prediction of Araucaria distribution after 10 model runs with 70% training and 30% testing data and 1 full dataset run (11 model runs X 5 selected algorithms). The mean AUC value was 0.788 (among 55 model runs), indicating very high predictive capacity. The True Skills Statistic (TSS), Sensitivity, and Specificity (all threshold-dependent) were selected to evaluate the statistical performance of the SDM algorithms: ANN, GAM, GLM, Maxent, and RF. All indexes' values were satisfactory to forecast *Araucaria* distribution, i.e. > 0.5 for TSS; > 0.65 for Sensitivity and Specificity.

| Species | Algorithms (ANN, GAM, GLM, Maxent, RF) | Area Under the receive operation Curve (AUC)[a] | True Skill Statistics (TSS) | Sensitivity (Sen) | Specificity (Spe) |
|---|---|---|---|---|---|
| *Araucaria angustifolia* | Ensemble | 0.788 | 0.556 | 0.883 | 0.673 |

[a] before committee averaging.

Table S2. Relative variable importance table showing which abiotic variables selected in the SDM were most relevant explaining potential Araucaria distribution in the present and future. Each algorithm used in the SDM presented an importance ranking value. The ranking is defined by the biggest importance value weighted amongst all five algorithms. Temperature-related variables (i.e. Annual Mean Temperature, Temperature Seasonality, and Mean Diurnal Range — °C) were the main variables explaining Araucaria projected distribution. Annual Precipitation (mm) was the fourth most important variable.

| **Species** | **Environmental variables** | **ANN** | **Maxent** | **Random Forest** | **GLM** | **GAM** | **Ranking** |
|---|---|---|---|---|---|---|---|
| *Araucaria angustifolia* | Annual Mean Temperature | 0.669 | 0.901 | 0.803 | 0.752 | 0.557 | 1 |
| | Mean Diurnal Range | 0.132 | 0.092 | 0.419 | 0.103 | 0.243 | 3 |
| | Temperature Seasonality | 0.414 | 0.095 | 0.387 | 0.138 | 0.220 | 2 |
| | Annual Precipitation | 0.263 | 0 | 0.385 | 0.002 | 0.074 | 4 |

Table S3. Bioclimatic niche calculated according to the Araucaria current distribution within the Mixed and Dense Forests. We computed the mean and the confidence interval (2.5 to 97.5%) values among all variables. The model confirmed the already known adaptation of Araucaria to lower temperatures (16.2°C), as well as the low mean diurnal range: 12°C. The altitude distribution varied from 5m to 1653m. Despite Araucaria's adaptation to more elevated areas, the species occurs in transitional ecosystems, like the Dense Ombrophilous Forest and the Mixed Ombrophilous Forest. As part of the Atlantic Forest biome, the Mixed and Dense Forests have an elevated annual precipitation regime, indicating why the species' average precipitation is > 1700 mm.y$^{-1}$.

| Species | Confidence interval | Annual Mean Temperature (°C) | Mean diurnal range (°C) | Temperature seasonality (°C standard deviation x 100) | Mean Annual Precipitation (mm.y$^{-1}$) | Altitude (m) |
|---|---|---|---|---|---|---|
| *Araucaria angustifolia* | Mean | 16.2 | 10.9 | 29.67 | 1701 | 645 |
| | 2.5% | 14.1 | 14.1 | 25.69 | 1419 | 5 |
| | 97.5% | 17.8 | 17.8 | 32.58 | 2072 | 1653 |

Table S4. The vulnerability of *Araucaria angustifolia* to climate change under different scenarios: RCP 4.5 and 8.5; Full and Zero-Dispersal hypotheses; year 2085; with or without land-use change. We calculated the Percentage of Area Change (%) compared to the actual Species Distribution Area (SDAc). The last column compares mean altitudinal (m) change in the future with current mean altitudinal optimal for Araucaria. As a subtropical species, Araucaria showed a common pattern to shift its centroid towards higher elevations, to tracking milder temperatures. This upward range contraction is explained because Annual Mean Temperature (°C) and Temperature seasonality were the main climatic variables explaining Araucaria projected distribution.

| Species | Present Area (km²) — SDAc Suitable/ With land-use | RCP | Year | Dispersal Hypothesis | Area Future (km²) — SDAf Suitable/ With land-use | Percentage of Area Change (%) – Suitable/ Land-use | Current elevation (mean/m) | Future elevation shift (mean/m) |
|---|---|---|---|---|---|---|---|---|
| *Araucaria angustifolia* | 135,468/ 108,174 | 4.5 | 2085 | Full | 47,683/ 36,365 | -65/-66 | 645 | 1056 |
| | | 4.5 | | Zero | 47,558/ 36,240 | -65/-66.5 | | 1056 |
| | | 8.5 | | Full | 15,767/ 11,993 | -88/-89 | | 1142.5 |
| | | 8.5 | | Zero | 15,766/ 11,993 | -88/-89 | | 1142.5 |

# 4 CAPÍTULO III

## Collaborative management as a way to enhance Araucaria Forest resilience

(Manejo colaborativo como uma alternativa para aumentar a resiliência da Mata de Araucárias)

Artigo publicado no periódico *Perspectives in Ecology and Conservation* | ISSN: 2530-0644
https://doi.org/10.1016/j.pecon.2021.03.002
Área de avaliação: Biodiversidade
Classificação A2 (Quadriênio 2017-2020).

Parque Municipal Mozart Rocha Loures, Clevelândia, PR.

Fonte: Foto de Mário Tagliari, 2021.

# Collaborative management as a way to enhance Araucaria Forest resilience

Mario M. Tagliari[1,2], Carolina Levis[1], Bernardo M. Flores[1], Graziela D. Blanco[1], Carolina T. Freitas[3], Juliano A. Bogoni[1,4,5], Ghislain Vieilledent[2], Nivaldo Peroni[1]

[1]Programa de Pós-graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil

[2]CIRAD, UMR AMAP, F-34398 Montpellier, France. AMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.

[3]Divisão de Sensoriamento Remoto, Coordenação de Observação da Terra, Instituto Nacional de Pesquisas Espaciais, São José dos Campos, SP, Brazil

[4]School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

[5]Universidade de São Paulo, Escola Superior de Agricultura "Luiz de Queiroz", Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre (LEMaC), Piracicaba, São Paulo, Brazil

# ABSTRACT

People and nature interact since millennia in forests worldwide, but current management strategies addressing these ecosystems often exclude local people from the decision-making process. This *top-down* approach is the cornerstone of conservation initiatives, particularly in highly threatened and fragmented forested ecosystems. In contrast, collaborative management involving the participation of local communities has increasingly contributed to conservation efforts globally. Here we ask how collaborative management would contribute to the conservation of a threatened, culturally important, and keystone tree species. We address this question in the Araucaria Forest System (AFS) in southern Brazil, where the main conservation strategy has been *top-down* based on restrictive use. Throughout the entire distribution of AFS, we interviewed 97 smallholders about how they use and manage *Araucaria angustifolia* trees (Araucaria). We integrated their Traditional Ecological Knowledge (TEK) with a literature review about the conservation status of Araucaria Forests to analyze potential outcomes of two alternative conservation models: *top-down* with restrictive use, and *bottom-up* with collaborative management. We identified the feedback mechanisms in each model, and how they dampen or self-reinforced critical processes for AFS resilience. Our models showed that a *top-down* strategy maintains forest cover resilient to illegal logging but at the cost of losing TEK (undermining socio-ecological resilience) and forest resilience to other external disturbances, such as climate change. Alternatively, a *bottom-up* approach based on successful collaborative management schemes may increase the general resilience of AFS, while preserving TEK, thus contributing to maintaining the entire social-ecological system. Our findings indicate how it is paramount to maintain TEK to conserve AFS in the long term through collaborative management. By including local actors in the governance of AFS, its resilience is reinforced, promoting forest expansion, maintenance of TEK, and participatory conservation.

**Keywords** Araucaria Forest System, Cultural keystone species, Ecological Keystone Species, Ethnoecology, Mixed Ombrophilous Forest, Participatory conservation, Resilience-thinking.

## 4.1 INTRODUCTION

In the human-in-nature perspective, Social-Ecological Systems (hereafter SES) are the integration of human societies with ecosystems promoting reciprocal feedbacks, interdependence, and resilience (Folke *et al.*, 2010). The resilience of SES depends on their ability to adapt and remain within a stability domain in the face of disturbances and external stressors, i.e. it does not move beyond thresholds to an alternative state of equilibrium. The adaptability of SES enhances its resilience because it allows the system to adjust itself in the face of adversities (Berkes *et al.*, 2000). Forests worldwide are perfect examples of SES given the long-term interaction between forests, plants, and peoples. In the largest conserved block of tropical forest in the world – the Amazon forest, for instance, multiple human management practices over millennia increased edible plant diversity and abundance within forest patches, particularly near to archaeological sites, contributing to enhancing food security and production (Levis *et al.*, 2018).

One of the most emblematic SES of the subtropical Atlantic Forest is the Araucaria Forest System (hereafter AFS), also known as Araucaria Mixed Forest (Fig. 1). First, because of its dominant species, the candelabra-aspect tree *Araucaria angustifolia* (Bertol.) Kuntze, popularly known as Araucaria, has a keystone role in ecosystem functioning, especially due to its nut-like seed, known as 'pinhão', which structures the associate vertebrate assemblage spatio-temporally (Bogoni *et al.*, 2020; Oliveira-Filho *et al.*, 2015). Second, because of its ancient connection with Indigenous peoples and local communities (IPLCs; Reis *et al.*, 2014; Robinson *et al.*, 2018). The Araucaria was and still is widely used by local and indigenous groups due to the consumption of pinhão (Robinson *et al.*, 2018), with high caloric content that helps coping with the winter seasons (Mello and Peroni, 2015). Araucaria seeds are part of intense traditional use, management, and commerce by smallholders as well as pinhão extractors across different regions of Southern and Southeastern Brazil (Adan *et al.*, 2016; Mello and Peroni, 2015; Reis *et al.*, 2014; Quinteiro *et al.*, 2019; Tagliari and Peroni, 2018; Zechini *et al.*, 2018). The comprehension that certain species are crucial to maintaining distinct cultures, such as smallholders or indigenous groups, was the basis to create the term "Cultural Keystone Species" (Garibaldi and Turner, 2004). Here we use a similar term "culturally important species", following Freitas *et al.* (2020), which considers the species overriding role in people's culture, although not necessarily indispensable for the survival of a specific culture. However, if a culturally important species is extinct locally or has suffered a population decline, it will strictly influence local peoples' subsistence and spirituality (Freitas *et al.*, 2020), as well as the transmission of Traditional Ecological Knowledge (Berkes, 2009). Yet, given the intense commercial exploitation of *A. angustifolia* during the 20th century due to its high-quality wood (Wendling and Zanette, 2017), the species is currently classified as “Critically Endangered” according to the International Union for Conservation of Nature (IUCN, Thomas, 2013). Since then, the Brazilian legislation forbids any forms of Araucaria logging and stimulates the creation and maintenance of *top-down* protective strategies. As a result, Strictly Protected areas are the cornerstone of conservation strategies related to Araucaria Forest Systems, which often exclude local and indigenous peoples from participating in biodiversity conservation (Zechini *et al.*, 2018).

Protected Areas (PA) are well-known refuges for biodiversity and ecosystems, particularly in the Atlantic Forest, where most of the system persists in fragments surrounded by densely inhabited urban and rural areas (Scarano and Ceotto, 2015; Pacheco *et al.*, 2018; Metzger *et al.*, 2019). Although Protected Areas encompass only 4% to 6% of the current Araucaria Forest extent (Castro *et al.*, 2019; Ribeiro *et al.*, 2009), studies evaluating their effectiveness for Araucaria conservation (Castro *et al.*, 2019) did not consider another major category: Legal Reserves – a special private PA. These compulsory private PAs host almost one-third of all remaining native vegetation in the Atlantic Forest (Metzger *et al.*, 2019). Most of the native Araucaria Forest fragments occur within small farms (Bittencourt and Sebbenn, 2009). Consequently, it is undeniable that local smallholders also contribute to preserving, willingly or unwillingly, the Araucaria Forests. However, previous ethnoecological surveys have suggested that *top-down* strategies (i.e. maintenance and creation of Strictly Public Protected Areas and Private Protected Areas) may negatively impact the interactions between smallholders and Araucaria trees (Adan *et al.*, 2016; Tagliari and Peroni, 2018). For instance, because removing Araucaria trees is illegal, some landowners do not depend on Araucaria’s resources, and thus are prone to actively prevent *Araucaria*’s natural regeneration by removing its seedlings from their properties before they reach maturity (Adan *et al.*, 2016; Mello and Peroni, 2015; Quinteiro *et al.*, 2019; Tagliari and Peroni, 2018). In this case, livestock farming (e.g. cattle), pasture or crop production for subsistence, such as corn or manioc, usually compete with Araucaria’s natural regeneration, creating a human-plant barrier (Adan *et al.*, 2016; Tagliari and Peroni, 2018), where some landowners state that they lose the rights to use their lands because of the protected species (Quinteiro *et al.*, 2019).

The Araucaria case is therefore a conservation dilemma: people and natural resources interact since millennia, but current management strategies often exclude local people from the decision-making process. *Top-down* strategies prevent local engagement in Araucaria Forest conservation. Furthermore, the contribution of *top-down* conservation strategies to the long-term conservation of nature, individually or globally, still lacks effectiveness (Rodrigues and Cazalis, 2020), especially regarding potential limitations to the protected area per se, such as socio-ecological resilience or climate change impacts (Ferro *et al.*, 2014). In contrast, *bottom-up* strategies, developed together with local human groups through sharing decisions between governments, institutions and local resource users are more likely to produce benefits for the social-ecological system as a whole, besides strengthening ecosystem resilience (Folke *et al.*, 2010; Bennett *et al.*, 2016).

From the human-influenced expansion of Araucaria Forests during the past two millennia (Robinson *et al.*, 2018) to the current highly productive systems – such as the "*faxinais*" – underneath Araucaria canopies, combined with *Ilex paraguariensis*, locally known as "*yerba-mate*", a traditional tea-like beverage (Reis *et al.*, 2018), humans are part of the Araucaria Forest System (Reis *et al.*, 2014). The maintenance of traditional practices constitutes a generational body of knowledge, beliefs, and practices, known as Traditional Ecological Knowledge (TEK; sensu Berkes, 2009), which is fundamental for the persistence of social-ecological systems (Folke *et al.*, 2005). In practice, local societies that manage ecosystems based on TEK contribute to maintaining culturally important species as well as human cultures resilient by a positive feedback mechanism (Cámara-Leret *et al.*, 2019), and by doing so, this process also maintains the ecosystem resilient, particularly if management addresses a keystone species such as Araucaria (Bogoni *et al.*, 2020). Consequently, a crucial step to maintaining the Araucaria Forest System resilient is by managing the feedbacks within its system (Biggs *et al.*, 2012; Musavengane, 2019; and see Fig. 1 comparing the Araucaria ecological and socio-ecological system).

Feedbacks are interactions in which the resulting effect either reinforces (positive) or dampens (negative) change (DeAngelis *et al.*, 1986), influencing ecosystem dynamics. For instance, when trees establish in a fire-prone savanna landscape, they reduce fire spread, favoring forest expansion (van Nes *et al.* 2018). Particularly, the positive feedbacks, which self-reinforce changes, are capable of triggering cascading effects that push entire ecosystems to alternative states (Estes *et al.*, 2011; Scheffer *et al.*, 2001). Feedbacks depict the ecological processes that promote or degrade ecosystem resilience and functioning; and hence are the key mechanisms to be incorporated in ecosystem management (Briske *et al.*, 2006). Both positive and negative feedbacks play major roles in the self-organization of social-ecological systems. Therefore, to manage resilience it is necessary to understand the most important feedbacks in the system, especially in vulnerable and threatened ecosystems, such as Araucaria Forests

(Briske *et al.*, 2006) where local peoples with deep ecological knowledge are likely to be critical partners.

Collaborative management (co-management) implies a participatory decision-making process in which the regulation of a natural resource is shared between users and other actors, such as national, and subnational governments, Non-Governmental Organizations (NGOs), and/or local cooperatives (Berkes and Davidson-Hunt, 2006). Garibaldi and Turner (2004) argue that if local people identify themselves with a certain species, they will have a strong desire to preserve or restore it. Preserving a culturally important species, therefore, may guarantee the participation of different actors in species' conservation programs, and consequently benefit both the species, local people, and its surrounding ecosystem (Cristancho and Vining, 2004; Garibaldi and Turner, 2004; Noble *et al.*, 2016). Although studies addressing co-management schemes of culturally important species remain scarce in the literature due to the lack of ecological, social, and economic quantitative data, this *bottom-up* approach seems promising to effectively engage local people into conservation actions (Freitas *et al.*, 2020). Furthermore, co-management may be part of resilience-thinking because it incorporates some of its main principles, according to Stockholm Resilience Centre (SRC, 2013), such as the management of feedbacks and the participation of locals in the governance of the social-ecological system.

Applying resilience-thinking to local or regional conservation issues is still a great challenge because decision-makers are usually attached to traditional conservation strategies. In the case of Araucaria Forest Systems, where the main conservation strategy is focused on a *top-down* conservation model with restrictive use, uncertainties still exist whether a collaborative management scheme could contribute to improving conservation outcomes. Here we address this dilemma in a broad scale study to obtain detailed information on the state of the Araucaria Forest System and understand how both *top-down* and *bottom-up* conservation strategies may affect the resilience of this system, including its cultural and ecological dimensions. First, based on a comprehensive literature review, we analyze feedbacks and the resulting dynamics of two alternative conservation models: (1) *top-down* under restrictive use and (2) *bottom-up* with co-management schemes. Second, based on evidence from 97 semi-structured interviews with smallholders across the Araucaria Forest, we explored the risks and benefits of implementing both models. By presenting the key interactions and feedbacks that could strengthen local engagement for Araucaria conservation, we expect to provide a critical perspective for managing and enhancing Araucaria Forest System resilience.

## 4.2 METHODS

### 4.2.1 Study area

The study was conducted in southern Brazil, across the entire extent of the Araucaria Forest ecoregion (Fig. 2) and covering four environments: Alluvial - on old terraces associated with the river system; Sub-montane - constituting disjunctions at altitudes below 400 m; Montane - located approximately between 400 and 1000 m of altitude; and High Montane - comprising altitudes above 1000 m (IBGE, 2021). The highland climate, where the escarpment rises ~1000 m from the Atlantic Forest coastal plain, is humid mesothermic; temperature range between 15-20°C; and mean annual rainfall of 1500-2000 mm (Robinson *et al.*, 2018). At its northeastern limit, the ecoregion experiences a tropical climate, and persists only at specific cold temperatures spots at higher altitudes, such as Mantiqueira hills, at the High Rio Preto Microbasin (Castro *et al.*, 2019; Quinteiro *et al.*, 2019).

### 4.2.2 Araucaria policies and legislation

Several categories of protected areas exist in Brazil: Conservation Units, which are divided into Strictly Protected Areas and Sustainable Use Areas, and are managed by federal, state, or municipal administration, or through partnerships with the private sector (De Moura *et al.*, 2009); Permanent Preservation Areas and Legal Reserves (private protected areas within private properties); and Indigenous Lands (Pacheco *et al.*, 2018). According to the Brazilian National System of Conservation Units (Law n° 9.985/2000), the Sustainable Use category is divided into seven sub-categories, of which two could be specially targeted to TEK holders in the *Araucaria* Forest System: Sustainable Development Reserves and Extractive Reserves. Both types of protected areas aim to safeguard the livelihoods and cultures of traditional social groups, as well as to conserve nature and its biodiversity (De Moura *et al.*, 2009). Also, Extractive Reserves require some level of community organization and cooperation.

However, only 10.6 % of the Atlantic Forest (thus including the AFS) is encompassed by Conservation Units, mostly of Sustainable Use (75%). Furthermore, from the 75% of Sustainable Use Conservation Units created within the Atlantic Forest, only 0.45% and 0.62% are classified as Sustainable Development Reserves and Extractive Reserves, respectively (Pacheco *et al.*, 2018). As a result, few protected areas in the AFS recognize the importance of traditional peoples. Also, Sustainable Use Conservation Units are managed by the state governments, contrary to Strictly Protected Areas – managed by Federal government –. Indigenous Lands, which cover only 0.72% of the AFS area (Pacheco *et al.*, 2018), are administered by the Federal Indian Agency – FUNAI. Finally, almost one-third of Atlantic Forest's remaining native vegetation occurs within Legal Reserves and Permanent Preservation Areas, in private properties (Metzger *et al.*, 2019). Consequently, most of the native Araucaria Forest occurs within small farms (Bittencourt and Sebbenn, 2009) and it is inspected by municipal, state, and federal agencies. Farmers who use and manage Araucaria's resources are usually low-income smallholders who do not receive any financial return for conserving forested areas (Orellana and Vanclay, 2018). The lack of political incentives for Araucaria Forest's active management has led to illegal land-use practices within Legal Reserves (Orellana and Vanclay, 2018).

The Brazilian legislation prohibits any type of management of Araucaria timber (Lei da Mata Atlântica or Atlantic Forest Law n° 11.428/2006; CONAMA Resolution n° 278/2001). However, the Paraná State recently approved a new Law n° 20.223/2020 (Paraná, 2020), which regulates the planting and exploitation of *Araucaria angustifolia*, aiming to stimulate timber management programs. This new law defines and authorizes timber exploitation in private properties beyond restricted areas (e.g. Legal Reserves) and areas where illegal deforestation previously occurred within the Atlantic Forest. Yet, by promoting only timber exploitation, a new market is created for Araucaria, possibly stimulating local populations under TEK systems to abandon their ancient practices. This alternative economic activity benefits landowners but may undermine the resilience of the social-ecological system in the long-term. We highlight that legislation should also promote, in this sense, the maintenance of Araucaria Forest stands ("*Floresta em Pé*") beyond Legal Reserves as potential areas for co-management initiatives via Payment for Environmental Services (Tagliari *et al.*, 2019). Sustainable pinhão production and Araucaria Forest reforestation are some of the existing projects under the possibilities of Payment for Environmental Services (see Tagliari *et al.*, 2019).

### 4.2.3 The Traditional Ecological Knowledge holders in the context of the study

Within the AFS different actors use, manage, and explore Araucaria resources as opposing to other social groups who do not use them. Despite human management since Pre-Columbian times, where ethnic groups cultivated pinhão for subsistence and religiousness (Reis *et al.*, 2014), during the 20th century, a combination of agriculture expansion, urbanization, and logging changed abruptly the AFS (Rezende *et al.*, 2018; Ribeiro *et al.*, 2009). Logging was especially relevant to decimate 97% of Araucaria remnant populations since the beginning of the 20th century (Enright and Hill, 1995). This exploratory scenario culminated in several restrictive measures, such as logging prohibition, to protect the 'Critically Endangered' species for the IUCN Red List (Thomas *et al.*, 2013).

In the AFS, many social groups use and manage Araucaria resources, but other social groups do not use or manage them. The latter relies mainly on livestock, agriculture, and farming systems for commerce and subsistence, while smallholders who use Araucaria Forest Systems depend economically on pinhão extraction and other associated crops (e.g., tobacco and yerba-mate) for their livelihoods (Adan *et al.*, 2016; Quinteiro *et al.*, 2019; Tagliari and Peroni, 2018). This interaction between traditional smallholders and AFS usually surpasses more than one generation, because they were born and raised in the same family's properties (Adan *et al.*, 2016), where they might learn the processes of community organization and cooperation (Reis *et al.*, 2018). We thus defined the specific group of smallholders and pinhão extractors distributed across Southern and Southeastern Brazil as Traditional Ecological Knowledge holders in the context of the study. This attribute indicates knowledge, use, and dependency on Araucaria management. We proceeded with the application of the semi-structured questionnaire with TEK holders. Potential participants were indicated by informal conversations with smallholders and pinhão extractors in each municipality and with environmental specialists (such as municipalities or State environments bureaus, professors, and universities). We applied the snowball technique (Bernard, 2006) to follow the semi-structured interviews, where participants at the end of the interview recommended people directly involved in Araucaria management. We recognize that indigenous peoples, such as Southern-Jê and Guarani, have shaped remnant forest composition in Southern Brazil (Cruz *et al.*, 2020), and are also important TEK holders. However, due to ethical aspects and legal authorization we did not include indigenous peoples in our study.

### 4.2.4 Data collection from ethnoecological interviews and the literature

We conducted two strategies for data collection from the study area: fieldwork and a comprehensive literature review. To quantitatively assess the aspects of Araucaria co-management with local smallholders and *Araucaria* nut-like seeds extractors, we first identified key-regions in Southern and Southeastern Brazil where pinhão use, trade, and management are commonly described (e.g. regional pinhão parties, such as "*Festa do Pinhão*" at Lages and Cunha municipalities; informal pinhão trade along estate highways; and published literature).

We thus conducted 97 semi-structured interviews with key-informants in four Brazilian States: Paraná, Santa Catarina, Rio Grande do Sul, and São Paulo (surroundings of Mantiqueira hills at Cunha municipality), covering 14 municipalities between March 2018 and January 2019 (Fig. 2). Prior to the application of the questionnaire to the participants, we obtained interviewees' consent following the code of ethics of the International Society of Ethnobiology. Our study was approved by the ethics committee of the Federal University of Santa Catarina (CAEE: 86394518.0.0000.0121). The semi-structured interview protocol addressed three main topics: (i) historical management and socioeconomic factors; (ii) the Araucaria ecology and ethnoecology aspects; (iii) interviewees' perspectives about climate change threats for Araucaria (see Table 1 and Table S1). To assess the local knowledge and state-of-the-art of Araucaria co-management for this study, we selected specific open-ended questions through the questionnaire such as (i) "What is the importance of pinhão to your property?"; (ii) "What are the causes behind the expansion/retraction in Araucaria's population?"; (iii) "How much pinhão (kg) has been gathered in your property on average?"; (iv) "How many ethnovarieties of *Araucaria* can you identify in the landscape?"; (v) What are the differences in size, color, taste, ripening period of the ethnovarieties? (vi) "Do you practice any management during pinhão gathering?". Finally, we compiled this data to produce a theoretical framework that could support potential collaborative management arrangements. Pilot interviews preceded data collection to refine the semi-structured questionnaire in January and February 2018.

The comprehensive literature review was performed by using "Web of Science" search engine, following Bogoni *et al.* (2020) and Montaño-Centellas *et al.* (2020). We searched for specific terms in the abstracts of articles published between 2010 and -2020: "*Araucaria**" and "*angustifolia**" and "*conservation**" or "*cultural**". Both terms "*conservation*" and "*cultural*" were defined because they are commonly employed in scientific publications targeting Araucaria conservation and ethnoecological studies. We found 70 scientific peer-reviewed articles (Table S2) and included a few non-indexed references, such as Ph.D. theses. First, we cross-checked the literature review information with our fieldwork data. Second, we used the selected peer-reviewed articles to propose a schematic framework (Table S3) based on two alternative conservation models.

### 4.2.5 *Top-down* versus *bottom-up* conservation schemes for the Araucaria Forest System

To create the alternative conservation models, we followed the framework of complex adaptive systems, which understands that social-ecological systems are driven by external factors, such as policies and climate change, as well as by internal feedbacks (Berkes *et al.*, 2000; Folke *et al.*, 2010). We first identified '*Forest Cover'* as the main state variable defining the ecosystem from the conservation and a more holistic perspective. State variables are meant to represent the overall state of a system and may indicate the existence of alternative stable states (Folke *et al.* 2010). We then defined two variables representing drivers under a *top-down* conceptual framework: '*Deforestation and resource overexploitation*' and '*Forest Protection'*. For the *bottom-up* conceptual framework, we used a second state variable '*Traditional Ecological Knowledge - TEK*', and '*Collaborative management*' as a driver. These variables were previously identified as the most important for AFS dynamics in our literature review and represent critical elements in each conservation model (Table S3). For instance, one of the main goals of protected areas is halting biodiversity loss, such as deforestation (Rodrigues and Cazalis, 2020). In Brazil, both federal and state governments are responsible for *top-down* conservation models, especially in the form of Protected Areas, such as Strictly Protected and Sustainable Use Conservation Units, or Legal Reserves (Metzger *et al.*, 2019; Pacheco *et al.*, 2018). In contrast, we defined '*TEK'* as another state variable under a *bottom-up* conservation model because Araucaria can be classified as a Culturally Important Species that depend on '*TEK'* to persist (Adan *et al.*, 2016; Reis *et al.*, 2014; Tagliari and Peroni, 2018; Quinteiro *et al.*, 2019). Both conceptual models suggest that alternative feedback loops produce alternative dynamics of Araucaria Forest Systems. Following these two models, we propose the main threats, strategies, and actors involved, as well as the benefits and risks of *bottom-up* and *top-down* conservation strategies (inspired by Freitas *et al.*, 2020). Finally, also based on the published literature and field data from this study that indicates the *bottom-up* scheme as the most promising for maintaining AFS in the future, we evaluate the possibilities for implementing collaborative managements that contribute to strengthening environmental governance in the region.

## 4.3 RESULTS

### 4.3.1 Socio-economic benefits and co-management possibilities for Araucaria resources

According to our interviews, local smallholders and pinhão extractors are involved in the extraction of Araucaria seeds (pinhão), for at least 3.5 generations (mean = 3.8 generations, where each generation represents 25 years on average). There are family groups who have been living in the same region for 130-150 years (35 family groups or 36 %). This long interaction between the participants with Araucaria's resources brings large socio-economic benefits to local families. Among the 97 participants, 63 (65%) told that somehow pinhão trade influences their monthly incomes, from R$ 1000 to R$ 2500 per month, i.e. US$ 490 to US$ 1235 at the time, in 2018 (WBI, 2020) or ~1 to 2.3 Brazilian minimum wages in 2018. Furthermore, 17 participants among those 63 who benefited from trade affirmed that at least 50% of their annual gross income comes from pinhão trade. Pinhão trade is among the three main sources of income for 30% of all participants. Livestock and other crops were commonly cited by smallholders as alternative income sources, together with pinhão trade, such as beans, corn, yerba mate, and tobacco. The amount of pinhão gathered per season by the participants was classified in three categories: (i) up to 1000 kg (40% or 39 participants); (ii) from 1000 to 10,000 kg (47.5% or 46 participants); and (iii) above 10,000 kg (11.5% or 11 participants). For most participants, however, the extractivism of Araucaria seeds did not stand in practice as part of a co-management scheme, despite involving local management and commerce. Only one smallholder declared that the pinhão trade in his propriety was certified by an NGO under a co-management scheme. The same participant is also granted with one project involving Payment for Environmental Services (PES) to conserve Araucaria remnants in areas beyond the Legal Reserve within his property. Four participants use their properties for tourism purposes involving Araucaria (i.e. ecotourism). Among these four interviewees, two of them have co-management partnerships with international stakeholders and NGOs to promote sustainable tourism in the Araucaria Forest region.

### 4.3.2 Traditional Ecological Knowledge about Araucaria management and ethnovarieties

Sixty-one participants (63%) said that Araucaria Forest cover around the property (if applicable) expanded in the last decades due to: (i) the creation of Protected Areas (N=33); (ii) restrictive legislation (N=18), consequently sawmills' interdiction for using native and threatened species (N=5); (iii) community participation in reforestation (N=9); and (iv) increased dispersal by local fauna (N= 6). The remaining 35 participants informed that Araucaria Forest cover has been decreasing, mainly due to: (i) seedling suppression, known as "*roçadas*" (N=22); or (ii) illegal logging (N=18). We also found interviewees describing negative impacts from (iii) pesticides (N=1); (iv) severe legislation (N=1); and (v) ecological competition with Pinus sp. (N=1). We identified 23 local names for pinhão types (ethnovarieties) based on 320 citations from all participants. These ethnovarieties were described by local people (i.e. smallholders and/or pinhão extractors) according to the ripening periods of pinhão seeds produced by female Araucarias. The five most-cited local varieties were: (i) "*Macaco*" (N=81 citations); (ii) "*Cajuvá*" (N= 80 citations); (iii) "*Comum*" (N= 48 citations); (iv) "*Do Cedo*" (N= 31 citations); and (v) "*25 de Março*" (N= 16 citations). Most participants cited three ethnovarieties (52.5%) and ~25% of them mentioned four different ethnovarieties. Ethnovarieties described by the participants were said to develop in different moments during the year indicating pinhão production throughout the entire year.

### 4.3.3 Socio-ecological benefits and risks of both alternative models for Araucaria Forest Systems

The benefits and risks of adopting a *top-down* or *bottom-up* strategy for Araucaria Forest System involve different ecological, social, economic, and cultural dimensions according to the interviews and the literature review (Fig. 3; Table 1). *Top-down* conservation models promote benefits towards the target species (in this case Araucaria) and its surrounding fauna and flora; the biodiversity maintenance; and provides ecosystem services, such as provisioning (food with pinhão production); support (pollination; nutrient cycling); regulation (carbon sequestration; alternative food resource for Araucaria Forest fauna); and cultural (heritage value, regional symbols, ecotourism). Biodiversity and ecosystem services may be indirectly enhanced by this model, thus favoring human well-being. However, restrictive *top-down* models (such as Strictly Protected areas or excessive restrictive legislation) may create: (i) barriers between human groups and the target preservation priority; (ii) the loss of TEK and socio-ecological resilience; (iii) fragility to external stressors, such as climate change.

The most promising benefits of *bottom-up* co-management are: (i) sustainable pinhão trade; (ii) sustainable tourism; (iii) Payment for Environmental Services programs; (iv) potential conservation of Araucaria Forest remnants within rural properties; and (v) possible recovery and expansion of Araucaria Forests. By incorporating these initiatives with local people, they may also stimulate local engagement in surveillance, conservation, and maintenance of biodiversity. These benefits are interconnected between local groups and Araucaria Forest, enhancing the long-term resilience and conservation of the Araucaria Forest System. The risks of adopting *bottom-up* co-management schemes for Araucaria Forest Systems may be related to: (i) psychological barriers between local people and environmental agencies due to the memory of historical excessive enforcement – an example is a practice known as '*roçadas'*, which consists in the removal of Araucaria juveniles to avoid future legal restrictions on land use (Adan *et al.*, 2016) –; (ii) the potential overexploitation of Araucaria resources within private areas, such as illegal cutting, timber exploitation, and deforestation (Orellana and Vanclay, 2018); and (iii) possible poor communication between local people, stakeholders, and environmental agencies (Freitas *et al.*, 2020). However, negative co-management experiences are more likely to be corrected by positive innovations from local peoples, since their TEK and the intrinsic body of knowledge through generations might allow them to maintain feedbacks stronger, responding faster to external changes, enhancing adaptability, and transformability of the system (as shown by Berkes *et al.*, 2000).

### 4.3.4 Two alternative models of Araucaria Forest conservation: *top-down* with restrictive use, and *bottom-up* with co-management schemes

Two alternative conservation models of Araucaria SES showed different feedbacks and dynamics (Fig. 4; Table S3). The *top-down* restrictive scheme contributed to increasing forest resilience to human disturbances. This happens because '*deforestation'* and '*resource overexploitation*' lead to more enforcement and '*forest protection*' (restrictive measures) by managers to maintain '*forest cover'*. With more forest cover, resource overexploitation is expected to decrease, relative to the overall forest abundance, reducing the perceptions of overexploitation by managers, and leading to less restrictive measures. In this sense, we identified that restrictive measures are created as a response to human disturbances (i.e. deforestation or resource overexploitation), resulting in a negative feedback loop that dampens forest loss (see Fig. 4) and partly maintains the conservation purpose. The *top-down* scheme, however, might not guarantee resilience for the entire system to other types of disturbances, such as extreme weather events due to climate change, mainly because the loss of traditional management may reduce the functional diversity of Araucaria populations (Table 1; Adan *et al.*, 2016), and consequently the forests' adaptive capacity in the face of unexpected events (Elmqvist *et al.*, 2003). Hence, the *top-down* scheme completely disrupts the historical human-plant interaction of the AFS that made this system resilient for millennia. In contrast, the *bottom-up* conservation scheme showed a distinct feedback loop (Fig. 4). In this case, a self-reinforcing (positive) feedback loop emerged in the system, because '*Traditional Ecological Knowledge (TEK)*' provides opportunities for '*collaborative management*', which allows '*forest cover*' to persist and potentially expand. With more forest cover, TEK is expected to expand as well, promoting co-management that enhances the general ecological resilience of the forest (to all sorts of unexpected disturbances), because local management enhances the functional diversity of Araucaria populations (Table 1; Adan *et al.*, 2016). The positive feedback loop we identified has therefore the potential to strengthen the ecological resilience of the whole Araucaria SES and to promote the system's expansion beyond its current limits.

## 4.4 DISCUSSION

### 4.4.1 Socio-economic benefits and co-management possibilities for Araucaria resources

Our findings reveal that Araucaria Forest Systems in southern South America might be losing resilience due to a long-term *top-down* restrictive management scheme that makes the system less adapted to all sorts of disturbances. Partly because this social-ecological system depends on TEK, which is currently being lost as restrictive measures disrupt an ancient human-nature interaction. However, our study reveals an alternative perspective on how to maintain the general resilience of Araucaria Forest Systems by stimulating TEK production through a collaborative management scheme. We have shown that *bottom-up* co-management may self-reinforce and benefit the resilience of Araucaria forests and thus provide a possible solution for the conservation dilemma that has been threatening this ecosystem. Co-management initiatives may effectively incorporate the principles of resilience-thinking: management of feedbacks; maintenance of ecological diversity; and broad participation of different actors (Folke *et al.*, 2005, 2010). Strengthening local actors and their roles in governance is particularly effective when compared to restrictive and exclusionary conservation strategies, such as Strictly Protected Areas with excessive *top-down* enforcement. We believe our findings offer an opportunity to generate optimistic *bottom-up* pathways towards an efficient, inclusive, and well-articulated conservation strategy that could self-reinforces the resilience of the Araucaria Forest System. By shifting from a *top-down* to a *bottom-up* co-management scheme that includes local actors together with existing institutions in the governance process, the AFS could develop transformability and adaptability, further enhancing its social-ecological resilience (see Folke *et al.*, 2005, 2010; Biggs *et al.*, 2012; Bennet *et al.*, 2016). Because similar ecosystems with culturally important plant species are also undergoing the same conservation dilemma, we believe that our findings could be useful in other contexts. Such innovative and collaborative systems could potentially develop to become another global *brightspot* example, where the natural and cultural capitals are preserved by *bottom-up* arrangements, inspiring societies worldwide (Bennett *et al.*, 2016).

Although the *top-down* strategy has proven useful to maintain Araucaria forests resilient to logging and other human degrading activities via a negative feedback loop (Fig. 4), this strategy has not been sufficient to maintain the entire system in the long run. Since the historical logging overexploitation in the 19th century, and later, the inclusion of Araucaria as "Critically Endangered" by IUCN (Thomas *et al.*, 2013), the creation/maintenance of *top-down* Protected Areas became the cornerstone of its conservation (Zechini *et al.* 2018). Protected Areas aim to curb anthropogenic disturbances in natural ecosystems and halt the loss of biodiversity (Geldmann *et al.*, 2019; Wiens *et al.*, 2011), but might fail to prevent the extinction of several species in the long-term due to climate change (Ferro *et al.*, 2014), as well to other anthropogenic disturbances (e.g., invasive species; poaching; land use; loss of genetic diversity; Laurance, 2013); and to potentially promote socio-economic benefits (given poor governance or regional conflicts; Laurance *et al.*, 2012). In southern Brazil, traditional land management systems protect the genetic diversity of Araucaria populations, thus contributing to the species conservation and the safeguarding of the SES (Reis *et al.*, 2014; Mello and Peroni, 2015; Adan *et al.*, 2016; Zechini *et al.*, 2018). As a result, *top-down* conservation strategies are insufficient to conserve a cultural landscape (Mello and Peroni, 2015) because it reduces the systems' adaptive capacity, as well as the participation of different actors in environmental governance; all requisites for social-ecological resilience (Folke *et al.*, 2010; de Vos *et al.*, 2016; Musavengane, 2019).

The feedback dynamics of a *bottom-up* co-management strategy has the potential to enhance the systemic resilience of AFS as well as other Social-Ecological Systems, because it promotes adaptability through TEK production (Berkes *et al.*, 2000), and because it recognizes that transformability into participatory governance is necessary, as human-nature has shaped Araucaria Forest landscapes over millennia (Reis *et al.*, 2014). Moreover, it enhances connectivity, because different actors are connected in the system (e.g. NGOs; stakeholders; local groups; governments). Also, it retains functional redundancy, i.e. if one actor is removed from the system the system itself remains resilient to the disturbance because of the different players with the same functions. We also found support for the notion that a *bottom-up* co-management strategy can enhance the resilience of AFS not only to human disturbances but also to different kinds of threats, such as extreme weather events (Folke *et al.*, 2010). One reason is that co-management increases the functional diversity of Araucaria tree populations, especially due to use and management (Adan *et al.*, 2016; Tagliari and Peroni, 2018; Quinteiro *et al.*, 2019), and consequently the adaptive capacity of the forest to unexpected disturbances (Elmqvist *et al.*, 2003). As a result, co-management generates a positive feedback loop that strengthens forest resilience as well as sociocultural resilience. The Araucaria Forest is an example of a self-reinforcing system, where in the past human-plant interaction was responsible for the forest expansion beyond its climatic niche (Robinson *et al.*, 2018).

Sühs *et al.* (2018) showed that the maintenance of Araucaria mature trees together with traditional land management promotes Araucaria Forest expansion, sapling species richness and abundance, together with the preservation of grasslands in southern Brazil. The authors argue that a maximal regional diversity of the plant communities can be achieved by a balance between preserved forest areas and traditional management practices (Sühs *et al.*, 2018). Reis *et al.* (2018) also showed that management systems within the Araucaria Forest, such as the "*caívas*" and "*faxinais*", maintain landscapes with productive forest fragments, thus favoring *Araucaria* conservation and human well-being. Furthermore, this system highly depends on the cultural and economic valuation of pinhão (Reis *et al.*, 2018). The opportunity to increase profits from Araucaria remnants could assure the long-term sustainability of co-management initiatives (Pomeroy and Berkes, 1997). The broader participation of different actors in environmental governance is within the basis of co-management initiatives (see Freitas *et al.*, 2020). Hence, co-management initiatives targeting the *Araucaria angustifolia* can represent a valuable solution for the ongoing conservation dilemma.

## 4.5 CONCLUSION

### 4.5.1 Re-evaluating the Araucaria conservation dilemma

Our *bottom-up* conceptual model was directly linked to a specific social group: the smallholders along the AFS, who possibly encompass the majority of AFS native remnants under their Legal Reserves protected areas (Bittencourt and Sebbenn, 2009; Metzger *et al.*, 2019). Other social groups still influence and manage this system, such as indigenous peoples, who were co-responsible for the transformation and expansion of the system in the past (Robinson *et al.*, 2018), and remain as essential partners for developing a co-management scheme. Although we could not incorporate indigenous peoples in our analysis, they also apply to our conceptual model as major TEK holders. It is important to recognize that the AFS is also composed of a mosaic of landowners, agricultural enterprises, timber and cellulose companies, where native remnants are still protected by *top-down* management, such as in Strictly Protection Conservation Units and Legal Reserves. Therefore, our conceptual models are not mutually exclusive, and both *top-down* and *bottom-up* strategies may co-occur within AFS and contribute to maintaining native forest remnants resilient in the face of global changes.

Araucaria Forest Systems are a heritage, left by past indigenous societies that once lived in the region (Reis *et al.*, 2014; Robinson *et al.*, 2018), and that now represents a valuable asset for local human populations (Mello and Peroni, 2015; Adan *et al.*, 2016; Tagliari and Peroni, 2018; Quinteiro *et al.*, 2019). Our findings indicate that this heritage might be at risk in the long-term for future generations. The collaborative management strategy between local peoples and other institutions interested in the conservation of these ancient and endemic forests is necessary as an alternative strategy to maintain this socio-ecological system. However, legal aspects may remove local people from decision-making and potentially produce antagonistic actions due to restrictive conservation measures, such as seedling suppression (Adan *et al.*, 2016; Tagliari and Peroni 2018; Quinteiro *et al.*, 2019) or timber illegal exploitation (Schneider *et al.*, 2018). This problematic may engender what is known as the 'Environmental Psychologic Barrier', where local people tend to avoid effective action to improve/conserve their surrounding environment, even if they perceive that these actions bring biodiversity losses and negative impacts to their lives, such as loss of life quality and food security (Tam and Chan, 2017). Still, other co-management initiatives of culturally important species in Brazil showed positive outcomes by maintaining the plant-human interaction, such as those involving *Hevea brasiliensis* and *Bertholletia excelsa* ("*rubber tree*" and "*Brazil nut tree*", respectively) in the Brazilian Amazon, and *Rumohra adiantiformis* ("*samambaia-preta*") in southern Brazil (De Souza *et al.*, 2006; Gomes *et al.*, 2018). Co-management programs with these species largely contributed to maintaining the economic livelihoods and Traditional Ecological Knowledge of local smallholders and people from indigenous and local communities (e.g. indigenous people, "*ribeirinhos*", and/or "*caiçaras*"; De Souza *et al.*, 2006; Gomes *et al.*, 2018). Similarly, the conservation of the Araucaria Forest System depends on maintaining TEK and promoting collaborative management initiatives, because *bottom-up* conservation strategies are more likely to produce the transformations that the system needs to persist in the uncertain future. By incorporating all actors of this socio-ecological system, resilience is reinforced towards expansion, maintenance of TEK, and participatory systemic socio-ecological conservation.

## Acknowledgments

MMT thanks all local people interviewed between 2018 and 2019 who contributed with their knowledge about Araucaria, the cultural landscape, and the challenges smallholders face in Brazil. The authors would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/Brazil; Finance Code 001) for the Ph.D. scholarship for MMT and GDB. CL thanks CAPES for the post-doctoral fellowship (nº 88887.474568/2020). NP thanks CNPq for the productivity scholarship (Process 310443/2015-6). CTF thanks the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for the post-doctoral fellowship (Process nº 2019/15550-2). JAB is supported by the São Paulo Research Foundation (FAPESP) postdoctoral fellowship grants 2018-05970-1 and 2019-11901-5. This study is dedicated to Estelamaris and Patrick.

### Conflict of interest

The authors declare no conflict of interest.

### Author's contribution

MMT conceived the main idea, drafted the manuscript, analyzed interviews' data, and did the main literature review. GDB drafted the manuscript and did the literature review. CL contributed to the literature review and developed the main structure of the article. BF brought valuable insights that transformed the purpose of this study. CF reviewed the early versions, suggested main changes in the structure of the manuscript. JB contributed to the draft evaluation, improved the interview questions, and analyzed the data. GV contributed with the early versions of the manuscript and insights about potential knowledge-gaps. NP contributed to draft development, literature review, insights about knowledge-gaps, improved the interview questions, reviewed the early versions, and project financing. All authors contributed critically to the drafts and gave final approval for publication.

### Data availability statement

This manuscript is part of an ongoing Ph.D. thesis. The information gathered in the ethnoecological surveys will not be able to share until the publication of another specific chapter. However, as a manuscript based on the literature review (already published elsewhere) and complemented with the ethnoecological information used in the questionnaire (see details in Supplementary File Tables S1, S2, S3), the readers may find the core information used in this manuscript.

## 4.6 REFERENCES

Adan, N., Atchison, J., Reis, M.S., Peroni, N., 2016. Local Knowledge, Use and Management of Ethnovarieties of *Araucaria angustifolia* (Bert.) Ktze. in the Plateau of Santa Catarina, Brazil. Econ. Bot. 70, 353–364. https://doi.org/10.1007/s12231-016-9361-z

Bennett, E.M., Solan, M., Biggs, R., McPhearson, T., Norström, A. V., Olsson, P., Pereira, L., Peterson, G.D., Raudsepp-Hearne, C., Biermann, F., Carpenter, S.R., Ellis, E.C., Hichert, T., Galaz, V., Lahsen, M., Milkoreit, M., Martin López, B., Nicholas, K.A., Preiser, R., Vince, G., Vervoort, J.M., Xu, J., 2016. Bright spots: seeds of a good Anthropocene. Front. Ecol. Environ. 14, 441–448. https://doi.org/10.1002/fee.1309

Berkes, F., 2009. Evolution of co-management: Role of knowledge generation, bridging organizations and social learning. J. Environ. Manage. 90, 1692–1702. https://doi.org/10.1016/j.jenvman.2008.12.001

Berkes, F., Davidson-Hunt, I.J., 2006. Biodiversity, traditional management systems, and cultural landscapes: Examples from the boreal forest of Canada. Int. Soc. Sci. J. 58, 35–47. https://doi.org/10.1111/j.1468-2451.2006.00605.x

Berkes, F., Colding, J., Folke, C., 2000. Rediscovery of Traditional Ecological Knowledge as Adaptive Management. Ecol. Appl. 10, 1251–1262

Bernard, H.R., 2006. Research Methods in Anthropology: Qualitative and Quantitative Approaches, Library. https://doi.org/10.1525/aa.2000.102.1.183

Biggs, R., Schlüter, M., Biggs, D., Bohensky, E.L., Burnsilver, S., Cundill, G., Dakos, V., Daw, T.M., Evans, L.S., Kotschy, K., Leitch, A.M., Meek, C., Quinlan, A., Raudsepp-Hearne, C., Robards, M.D., Schoon, M.L., Schultz, L., West, P.C., 2012. Toward principles for enhancing the resilience of ecosystem services. Annu. Rev. Environ. Resour. 37, 421–448. https://doi.org/10.1146/annurev-environ-051211-123836

Bittencourt, J.V.M., Sebbenn, A.M., 2009. Genetic effects of forest fragmentation in high-density *Araucaria angustifolia* populations in Southern Brazil. Tree Genet. Genomes 5, 573–582. https://doi.org/10.1007/s11295-009-0210-4

Bogoni, J.A., Muniz-Tagliari, M., Peroni, N., Peres, C.A., 2020. Testing the keystone plant resource role of a flagship subtropical tree species (*Araucaria angustifolia*) in the Brazilian Atlantic Forest. Ecol. Indic. 118, 106778. https://doi.org/10.1016/j.ecolind.2020.106778

BRASIL. (2006). Lei nº 11.428, de 22 de dezembro de 2006. Dispõe sobre a utilização e proteção da vegetação nativa do Bioma Mata Atlântica, e dá outras providências. República Federativa do Brasil, Brasília.

BRASIL. (2000). Lei nº 9.985, de 18 de julho de 2000. Institui o Sistema Nacional de Unidades de Conservação da natureza, e dá outras providências. República Federativa do Brasil, Brasília.

Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2006. A unified framework for assessment and application of ecological thresholds. Rangel. Ecol. Manag. 59, 225–236.

https://doi.org/10.2111/05-115R.1

Cámara-Leret, R., Fortuna, M.A., Bascompte, J., 2019. Indigenous knowledge networks in the face of global change. Proc. Natl. Acad. Sci. 116(20), 9913–9918

Castro, M.B., Barbosa, A.C.M.C., Pompeu, P.V., Eisenlohr, P. V., de Assis Pereira, G., Apgaua, D.M.G., Pires-Oliveira, J.C., Barbosa, J.P.R.A.D., Fontes, M.A.L., dos Santos, R.M., Tng, D.Y.P., 2019. Will the emblematic southern conifer *Araucaria angustifolia* survive to climate change in Brazil? Biodivers. Conserv. 29, 591–607. https://doi.org/10.1007/s10531-019-01900-x

Cristancho, S., Vining, J., 2004. Culturally Defined Keystone Species. Hum. Ecol. Rev. 11, 153–164

CONAMA – Conselho Nacional do Meio Ambiente. Resolução nº 278, de 24 de maio de 2001. Dispõe sobre o corte e a exploração de espécies ameaçadas de extinção da flora da Mata Atlântica. Brasília: DOU de 18/07/2001.

Cruz, A.P., Giehl, E.L.H., Levis, C., Machado, J.S., Bueno, L., Peroni, N., 2020. Pre-colonial Amerindian legacies in forest composition of southern Brazil. PLoS One 15, 1–18. https://doi.org/10.1371/journal.pone.0235819

DeAngelis, D. L., Post, W.M., Travis, C.C. 1986. Positive Feedback in Natural Systems. Berlin Heidelberg: Springer-Verlag

De Moura, R.L., Minte-Vera, C.V., Curado, I.B., Francini-Filho, R.B., Rodrigues, H.D.C.L., Dutra, G.F., Alves, D.C., Souto, F.J.B., 2009. Challenges and Prospects of Fisheries Co-Management under a Marine Extractive Reserve Framework in Northeastern Brazil. Coast. Manag. 37, 617–632. https://doi.org/10.1080/08920750903194165

De Souza, G.C., Kubo, R., Guimarães, L., Elisabetsky, E., 2006. An ethnobiological assessment of *Rumohra adiantiformis* (samambaia-preta) extractivism in Southern Brazil. Biodivers. Conserv. 15, 2737–2746. https://doi.org/10.1007/s10531-005-0309-3

de Vos, A., Cumming, G.S., Cumming, D.H.M., Ament, J.M., Baum, J., Clements, H.S., Grewar, J.D., Maciejewski, K., Moore, C., 2016. Pathogens, disease, and the social-ecological resilience of protected areas. Ecol. Soc. 21. https://doi.org/10.5751/ES-07984-210120

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. Front. Ecol. Environ. 1(9), 488-494

Enright, N.J. Hill, R.S. 1995. Ecology of the southern conifers. Melbourne University Press, 1995.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S. a, Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D. a, 2011. Trophic downgrading of planet Earth. Science 333, 301–306. https://doi.org/10.1126/science.1205106

Ferro, V.G., Lemes, P., Melo, A.S., Loyola, R., 2014. The reduced effectiveness of protected areas under climate change threatens Atlantic Forest tiger moths. PLoS One 9. https://doi.org/10.1371/journal.pone.0107792

Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Chapin, T., Rockstrom., J., 2010. Resilience thinking: integrating resilience, adaptability and transformability. Ecology and Society 15(4): Nat. Nanotechnol. 15, 20. https://doi.org/10.1038/nnano.2011.191

Folke, C., Hahn, T., Olsson, P., Norberg, J., 2005. Adaptive governance of social-ecological systems. Annu. Rev. Environ. Resour. 30, 441–473. https://doi.org/10.1146/annurev.energy.30.050504.144511

Freitas, C.T. de, Macedo Lopes, P.F., Campos-Silva, J.V., Noble, M.M., Dyball, R., Peres, C.A., 2020. Co-management of culturally important species: A tool to promote biodiversity conservation and human well-being. People Nat. 2, 61–81. https://doi.org/10.1002/pan3.10064

Garibaldi, A., Turner, N., 2004. Cultural keystone species: Implications for ecological conservation and restoration. Ecol. Soc. 9, 1. https://doi.org/10.1146/annurev-pharmtox-061008-103038

Geldmann, J., Manica, A., Burgess, N.D., Coad, L., Balmford, A., 2019. A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. Proc. Natl. Acad. Sci. U. S. A. 116, 23209–23215. https://doi.org/10.1073/pnas.1908221116

Gomes, C.V.A., Alencar, A., Vadjunec, J.M., Pacheco, L.M., 2018. Extractive Reserves in the Brazilian Amazon thirty years after Chico Mendes: Social movement achievements, territorial expansion and continuing struggles. Desenvolv. e Meio Ambient. 48, 74–98. https://doi.org/10.5380/dma.v48i0.58830

IBGE. Instituto Brasileiro de Geografia e Estatística, 2012.Manuais técnicos em geociências. Divulga os procedimentos metodológicos utilizados nos estudos e pesquisas de geociências. Rio de Janeiro.

Kelly, C., Ferrara, A., Wilson, G.A., Ripullone, F., Nolè, A., Harmer, N., Salvati, L., 2015. Community resilience and land degradation in forest and shrubland socio-ecological systems: Evidence from Gorgoglione, Basilicata, Italy. Land use policy 46, 11–20. https://doi.org/10.1016/j.landusepol.2015.01.026

Laurance, W.F., 2013. Does research help to safeguard protected areas? Trends Ecol. Evol. 28, 261–266. https://doi.org/10.1016/j.tree.2013.01.017

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., ..., Zamzani, F., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–294. https://doi.org/10.1038/nature11318

Levis, C., Flores, B.M., Moreira, P.A., Luize, B.G., Alves, R.P., Franco-Moraes, J., Lins, J., Konings, E., Peña-Claros, M., Bongers, F., Costa, F.R.C., Clement, C.R., 2018. How People Domesticated Amazonian Forests. Front. Ecol. Evol. 5.

https://doi.org/10.3389/fevo.2017.00171

Mello, A.J.M., Peroni, N., 2015. Cultural landscapes of the *Araucaria* Forests in the northern plateau of Santa Catarina, Brazil. J. Ethnobiol. Ethnomed. 11, 51. https://doi.org/10.1186/s13002-015-0039-x

Metzger, J.P., Bustamante, M.M.C., Ferreira, J., Fernandes, G.W., Librán-Embid, F., Pillar, V.D., Prist, P.R., Rodrigues, R.R., Vieira, I.C.G., Overbeck, G.E., 2019. Why Brazil needs its Legal Reserves. Perspect. Ecol. Conserv. 17, 91–103. https://doi.org/10.1016/j.pecon.2019.07.002

Montaño-Centellas, F.A., McCain, C., Loiselle, B.A., 2020. Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients. Glob. Ecol. Biogeogr. 29, 232–245. https://doi.org/10.1111/geb.13021

Musavengane, R., 2019. Using the systemic-resilience thinking approach to enhance participatory collaborative management of natural resources in tribal communities: Toward inclusive land reform-led outdoor tourism. J. Outdoor Recreat. Tour. 25, 45–56. https://doi.org/10.1016/j.jort.2018.12.002

Noble, M., Duncan, P., Perry, D., Prosper, K., Rose, D., Schnierer, S., Tipa, G., Williams, E., Woods, R., Pittock, J., 2016. Culturally significant fisheries: Keystones for management of freshwater social-ecological systems. Ecol. Soc. 21. https://doi.org/10.5751/ES-08353-210222

Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P. V., Neves, D.R.M., 2015. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. J. Plant Ecol. 8, 242–260. https://doi.org/10.1093/JPE/RTT058

Orellana, E., Vanclay, J.K., 2018. Could native *Araucaria* forests be managed for timber production on small farms in southern Brazil? For. Ecol. Manage. 430, 1–9. https://doi.org/10.1016/j.foreco.2018.07.057

Pacheco, A.A., Neves, A.C.O., Fernandes, G.W., 2018. Uneven conservation efforts compromise Brazil to meet the Target 11 of Convention on Biological Diversity. Perspect. Ecol. Conserv. 16, 43–48. https://doi.org/10.1016/j.pecon.2017.12.001

Paraná Official Diary, n°. 10.694. Law 20.223 (26th May 2020). Diário Oficial do Estado do Paraná. Lei 20.223. de 20 de maio de 2020.

Pomeroy, R.S., Berkes, F., 1997. Two to tango: The role of government in fisheries co-management. Mar. Policy 21, 465–480. https://doi.org/10.1016/S0308-597X(97)00017-1

Quinteiro, M.M. da C., Alexandre, B. da R., Magalhães, L.M.S., 2019. Brazilian Pine (*Araucaria angustifolia* (Bertol.) Kuntze) Ethnoecology in the Mantiqueira Atlantic Forest. Floresta e Ambient. 26, 1–7. https://doi.org/10.1590/2179-8087.018516

Reis, M.S., Ladio, A., Peroni, N., 2014. Landscapes with *Araucaria* in South America: Evidence for a cultural dimension. Ecol. Soc. 19. https://doi.org/10.5751/ES-06163-190243

Reis, M.S., Montagna, T., Mattos, A.G., Filippon, S., Ladio, A.H., Marques, A. da C., Zechini, A.A., Peroni, N., Mantovani, A., 2018. Domesticated Landscapes in *Araucaria* Forests, Southern Brazil: A Multispecies Local Conservation-by-Use System. Front. Ecol. Evol. 6, 11. https://doi.org/10.3389/fevo.2018.00011

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.B.N., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotpot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspect. Ecol. Conserv. 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Robinson, M., De Souza, J.G., Maezumi, S.Y., Cárdenas, M., Pessenda, L., Prufer, K., Corteletti, R., Scunderlick, D., Mayle, F.E., De Blasis, P., Iriarte, J., 2018. Uncoupling human and climate drivers of late Holocene vegetation change in southern Brazil. Sci. Rep. 8, 7800. https://doi.org/10.1038/s41598-018-24429-5

Rodrigues, A.S.L., Cazalis, V., 2020. The multifaceted challenge of evaluating protected area effectiveness. Nat. Commun. 11, 1–4. https://doi.org/10.1038/s41467-020-18989-2

Scarano, F.R., Ceotto, P., 2015. Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers. Conserv. 24, 2319–2331. https://doi.org/10.1007/s10531-015-0972-y

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596. https://doi.org/10.1038/35098000

Schneider, L.C.A., Silva, M.T. da, Agostinetto, L., Siegloch, A.E., 2018. Deforestation in Mixed Ombrophilous Forest in the Serrana Region of Santa Catarina. Rev. Árvore 42. https://doi.org/10.1590/1806-90882018000200006

Staal, A., Flores, B.M., Aguiar, A.P.D., Bosmans, J.H.C., Fetzer, I., Tuinenburg, O.A., 2020. Feedback between drought and deforestation in the Amazon. Environ. Res. Lett. 15, 044024. https://doi.org/10.1088/1748-9326/ab738e

Stockholm Resilience Centre, SRC., 2013. What is Resilience? An introduction to social-ecological research. Stockholm.

Sühs, R.B., Giehl, E.L.H., Peroni, N., 2018. Interaction of land management and *Araucaria* trees in the maintenance of landscape diversity in the highlands of southern Brazil. PLoS One 13, e0206805. https://doi.org/10.1371/journal.pone.0206805

Tagliari, M.M., Moreira, V.A., Peroni, N., 2019. Analysis of programs of payment for environmental services in southern Brazil: identifying strategies for the conservation of *Araucaria angustifolia*. Desenvolv. e Meio Ambient. 50, 216–233.

Tagliari, M.M., Peroni, N., 2018. Local varieties of *Araucaria angustifolia* (Bertol.) Kuntze

(Pinales : *Araucaria*ceae) in southern Brazil: A brief discussion about landscape domestication. Biotemas 31, 59–68

Tam, K.P., Chan, H.W., 2017. Environmental concern has a weaker association with pro-environmental behavior in some societies than others: A cross-cultural psychology perspective. J. Environ. Psychol. 53, 213–223. https://doi.org/10.1016/j.jenvp.2017.09.001

Thomas, P. 2013. *Araucaria angustifolia*. The IUCN Red List of Threatened Species 2013: e.T32975A2829141. https://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T32975A2829141.en. Downloaded on 18 May 2020

Van Nes, E.H., Staal, A., Hantson, S., Holmgren, M., Pueyo, S., Bernardi, R. E., Flores, B.F, Xu, C., Scheffer, M. 2018. Fire forbids fifty-fifty forest. PloS One, 13, e0191027. https://doi.org/10.1371/journal.pone.0191027

WBI. World Bank Indicator, accessed May 2020 <https://data.worldbank.org/indicator/)>.

Wendling, I., Zanette, F., 2017. Araucária: particularidades, propagação e manejo de plantios., Embrapa Florestas.

Wiens, J.A., Seavy, N.E., Jongsomjit, D., 2011. Protected areas in climate space: What will the future bring? Biol. Conserv. 144, 2119–2125. https://doi.org/10.1016/j.biocon.2011.05.002

Zechini, A.A., Lauterjung, M.B., Candido-Ribeiro, R., Montagna, T., Bernardi, A.P., Hoeltgebaum, M.P., Mantovani, A., dos Reis, M.S., 2018. Genetic Conservation of Brazilian Pine (*Araucaria angustifolia*) Through Traditional Land Use. Econ. Bot. 72, 166–179. https://doi.org/10.1007/s12231-018-9414-6

## 4.7 FIGURES

Fig. 1. Scheme of the Araucaria Forest System (adapted from Bogoni *et al.*, 2020). 1. The Araucaria ecological system. The Araucaria (candelabra tree) and the typical ecological system under its canopy, such as *Ocotea sp*. – "Canela"; *Ilex paraguariensis* – "*erva-mate*"; *Dicksonia sellowiana* – "*xaxim*"; and *Acca sellowiana* – "*goiabeira-serrana*"; and representative fauna, such as the *Mazama gouazoubira* – "*veado campeiro*"; *Puma concolor* – "*cougar*"; *Dasyprocta azarae* – "*cutia*"; and *Cyanocorax caeruleus* – "*azure Jay bird*". 2. The Araucaria socio-ecological system. We represented the current scenario of Araucaria remnants, especially in southern Brazil, where local groups (smallholders; indigenous peoples) continue to manage the system since pre-Columbian times.

Fig. 2. (a) The Atlantic Forest (dark gray) with the *Araucaria* Forest ecoregion (green) showing the three Brazilian states which mainly encompass the ecoregion: Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS); (b) The Araucaria Forest altitude map and the distribution of Conservation Units: Strictly (yellow) and Sustainable Use Protected Areas (green); black dots represent the occurrence of 97 ethnoecological interviews in this study. We highlight that three interviews occurred at São Paulo state (beyond the Araucaria Forest ecoregion) at Cunha municipality.

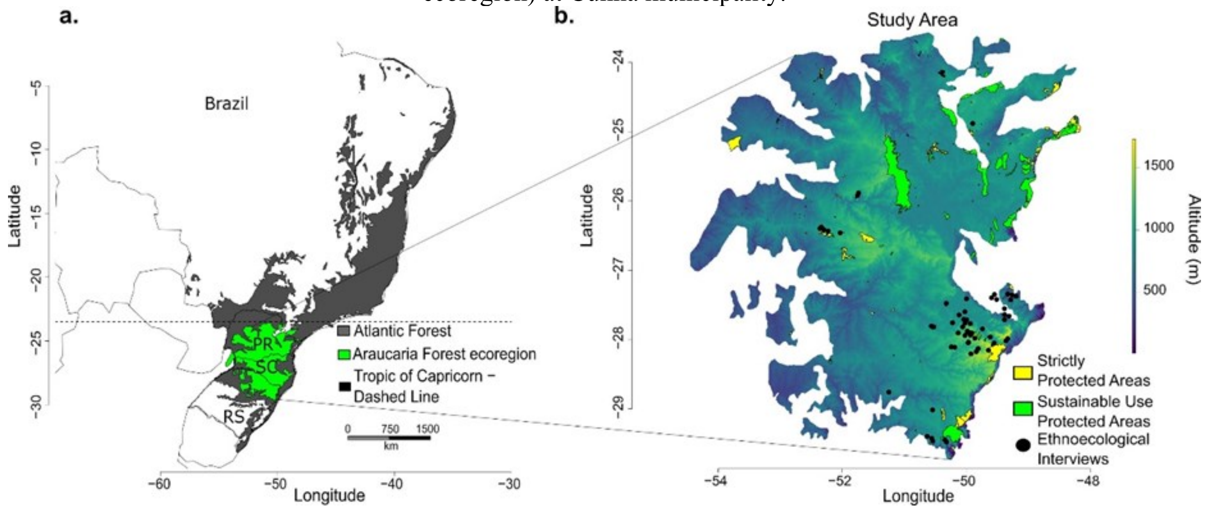


Fig. 3. Flow chart of benefits and risks (inspired by Freitas *et al.*, 2020) of distinct conservation strategies. Arrows represent the expected outcomes of every step in the flow charts. 1. *Top-down* strategies for *Araucaria angustifolia* (Araucaria) preservation. As the main conservation strategy, *top-down* policies, such as the maintenance or creation of Strictly Protected, neglect the historical human-plant interaction in the Araucaria Forest System. These policies (1) maintain the ecological resilience of the forest ecosystem and provide ecosystem services (indirect benefits for human groups), but (2) may fail due to barriers upon traditional people who use, manage, and promote the socio-ecological resilience of the system, leading to the loss of TEK; increases in overexploitation and deforestation pressures; and reduced resilience to external stressors, such as climate change, pathogens, and invasive species. 2. *Bottom-up* conservation initiatives for Araucaria as a Cultural Important Species (CIS) under co-management. Because Araucaria is a culturally important species for local people, (1) they will likely feel stimulated to engage in co-management initiatives focusing on this species; (2) we should consequently expect high compliance and local surveillance local people; (3) this human-plant interaction which will likely favor the conservation of Araucaria populations and (4) benefit other species co-existing in the Araucaria Forest, and the ecosystem as a whole. There are both benefits and risks that could be expected from this co-management approach. The risks (5) of this initiative may be related to the potential fragile arrangement between local people and institutions (e.g. environmental agencies, Non-Governmental Organizations, private sector and/or stakeholders); inadequate surveillance of the co-management initiative; and/or the excessive institutional enforcement. Another risk is the increase of illegal cutting (i.e. resources' overexploitation, juveniles' suppression, and/or non-sustainable timber production). Such negative consequences (6) will possibly affect ecological (i.e. ecosystem degradation), economic (i.e. less pinhão commerce, loss of payments or compensations for environmental services; less ecotourism), and cultural (detachment from local people, loss of traditional knowledge) aspects. A potential way to circumvent those problems (e.g. increased deforestation) could be (7) alternative co-management initiatives targeting forest recovery or recuperation of degraded areas (dashed arrow). The positive scenario (8), however, could bring ecological (maintenance of the ecosystem); economic (via Payment for Environmental Services, sustainable pinhão commerce, ecotourism); social and cultural benefits (i.e. local engagement; maintenance of the Traditional Ecological Knowledge of Araucaria and its ethnovarieties, and *Araucaria* resources' management). All of these positive consequences are interconnected (9) and could finally allow a more resilient and cyclical stable state (10) of the entire eco-socio-economic system of Araucaria Forests, besides acting as an alternative to the mainstream conservation strategy (i.e. the maintenance of exclusionary Protected Areas via *top-down* policies).

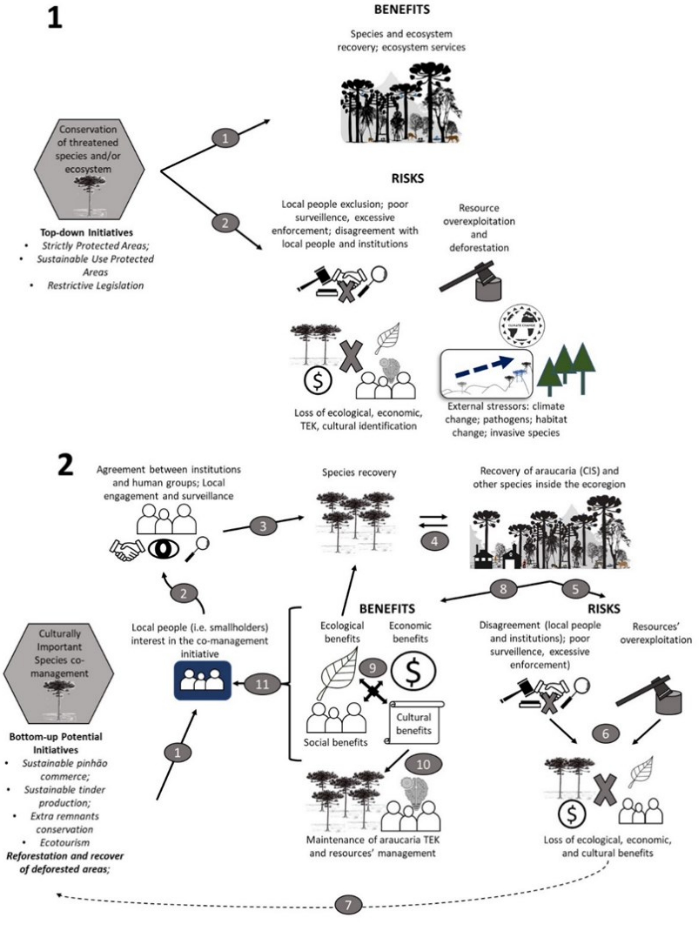
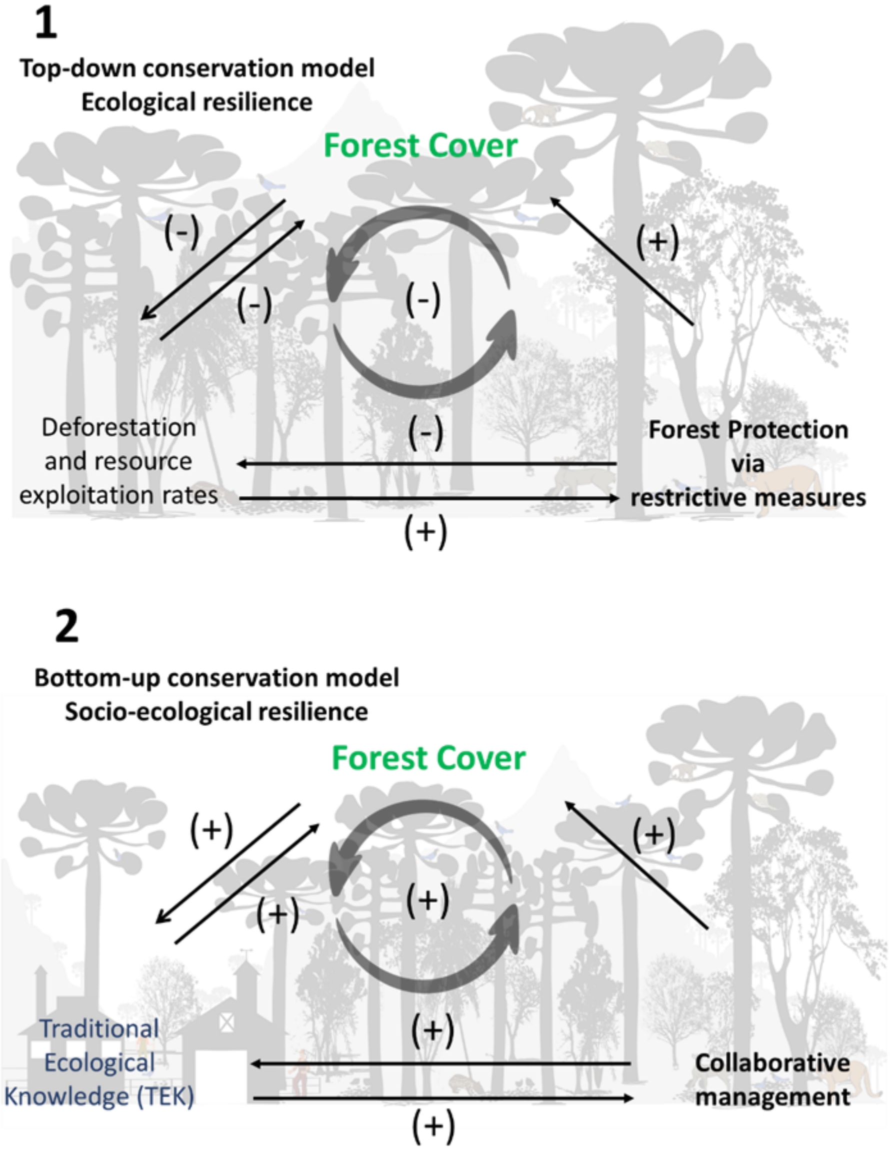


Fig. 4. The schematic *top-down* and *bottom-up* conservation models of Araucaria Forest systems are self-organized in contrasting ways, with different feedbacks. Solid lines represent positive/negative effects. Cycle schemes (gray shaded) represent the feedback loop, its direction (i.e. counter-clockwise) and its result: negative/buffer effect or positive/self-reinforcing state. 1. Schematic representation of the interactions involved in *top-down* policies, such as Strictly Protected Areas. This scheme improves only a portion of the target ecosystem, neglecting potential socio-ecological interactions (i.e. local people). This classical conservationist approach creates a buffer feedback, i.e. it sustains the current state. Excessive resource exploitation or deforestation generates protective measures that benefit forest cover. However, a forest protected by *top-down* measures may not completely avoid these disturbances (e.g. deforestation and overexploitation) and might not contribute to other external stressors, such as climate change. They also reduce the benefits for local peoples, who are virtually excluded from the system. 2. Schematic representation of the interactions produced by *bottom-up* policies. Independently from restrictive measures, this schematic socio-ecological system indicates an increase in the system's resilience, due to a self-reinforcing mechanism that promotes *Araucaria* forest expansion. Hence, by incorporating TEK and co-management initiatives, this scheme increases the general resilience of the social-ecological system. Note: our conceptual model is not mutually exclusive, both *top-down* and *bottom-up* strategies co-occur within AFS and contribute to maintaining native forest remnants.



## 4.8 TABLES

Table 1. Collaborative management of *Araucaria angustifolia* and its main challenges for implementation, considering: (i) Implications; (ii) potential benefits: cultural, ecological, social-economic, and institutional arrangements, as well as potential risks; and (iii) the literature review and interviews' data to sustain our model assumptions (inspired by Freitas *et al.*, 2020). Co-management for Araucaria considers mostly the use, management, and consumption of its nut-like seed, although other management systems exist, such as legal timber production, reforestation, maintenance of private native remnants, and payment for environmental services. We used information available in the literature to characterize the Araucaria co-management framework. Here, we describe in detail the risks and benefits of the Araucaria co-management.

**_ARAUCARIA ANGUSTIFOLIA_ CO-MANAGEMENT**

| Implications | Potential benefits | Reference |
|---|---|---|
| **Cultural** | | |
| Participants' engagement (local people) | Increase | This study (questions A3; A3a; A7a; B2; B4; see Table S1) |
| Community involvement | Increase | This study (questions A3a; A7a; see Table S1); Adan *et al.*, 2016 |
| Societal recognition and outreach | Increase | Freitas *et al.*, 2020 |
| Strengthening of cultural values and Traditional Ecological Knowledge | Increase | Reis *et al.*, 2014; Mello and Peroni, 2015; Adan *et al.*, 2016; Tagliari and Peroni 2018 |
| Maintenance of Araucaria ethnovarieties | Increase | This study (questions B4; B5; B6; B13; B14b; B14c; B15; see Table S1); Adan *et al.*, 2016; Tagliari and Peroni 2018; Quinteiro *et al.*, 2019 |
| **Ecological** | | |
| Species abundance | Increase | This study (questions A7; A7a; B1; B13; B13b; see Table S1); Sühs *et al.*, 2018 |

| | | |
|---|---|---|
| Araucaria Forest ecosystem conservation and recovery | Increase general resilience to human and natural disturbances | Folke *et al.*, 2010 |
| Ecological interactions | Increase | Bogoni *et al.*, 2020 |
| Nut-like seed production | Increase | This study (questions A3; A3a; B2; see Table S1); Robinson *et al.*, 2018 |
| Connectivity between Araucaria's remnant populations | Maintenance of *Araucaria* remnants through different Protected Areas | Tagliari *et al.*, in review |
| Species' genetic diversity | Increase | Adan *et al.*, 2016 |
| Contribution to food security | Increase | This study (questions A3a; B2. B3; see Table S1); Reis *et al.*, 2018 |
| **Social-economic** | | |
| Societal recognition and outreach | Increase | Reis *et al.*, 2014 |
| Stakeholders' participation | Possible | Tagliari *et al.*, 2019 |
| Possibility of financial self-sustainability | Possible | Tagliari *et al.*, 2019 |
| Income distribution within the community | Increase | This study (questions A3; A3a; A7a; see Table S1) |
| 'Conservation-by-use' possibility | Possible | Reis *et al.*, 2018 |
| Historical commercial overpressure | Possible | Ribeiro *et al.*, 2009; Mello and Peroni, 2015; Schneider *et al.*, 2018 |
| Value for sustainable Araucaria resources use | Possible | Tagliari *et al.*, 2019 |

| | | |
|---|---|---|
| **Opportunities for institutional arrangements** | | |
| Surveillance/enforcement | Possibly increase | Freitas *et al.*, 2020 |
| Payment for Environmental Services as a compensation strategy | Possible | Tagliari *et al.*, 2019 |
| Main stimuli to local engagement | Cultural/moral/ethic aspects; financial compensation | This study (questions A3a; A7a; see Table S1); Tagliari *et al.*, 2019 |
| Rules focusing on habitat protection | Increase[2] | See footnote |
| Legal permission to trade the target species | There is no legal permission[3] | See footnote |
| Co-management with the consent of environmental agencies (such as timber production quotas for smallholders use and management) | Possible | Orellana and Vanclay, 2018 |
| Financial compensation for supporting Araucaria's remnants besides Legal Reserves and Permanent Preservation Areas | Increase | Tagliari *et al.*, 2019 |
| **Potential risks** | | |
| Reduced inspection of environmental agencies | Possible | Freitas *et al.*, 2020 |
| Historical commercial overpressure | High | Ribeiro *et al.*, 2009; Mello and Peroni, 2015; Schneider *et al.*, 2018 |
| Current illegal harvest pressure | High | Adan *et al.*, 2016; Schneider *et* |

| | |
|---|---|
| (i.e. deforestation and logging) | *al.*, 2018; Tagliari and Peroni 2018; Quinteiro *et al.*, 2019 |

---

[1] Southern Brazilian States created their specific laws for the beginnings of pinhão commerce (i.e. Rio Grande do Sul starts from April 15th; Santa Catarina and Paraná from April 1st). This decision period is due to the maintenance of local fauna, especially the parrots "Papagaio-charão" and "Papagaio-do-peito-roxo" (*Amazona petrei* and *Amazona vinacea*, respectively), besides small rodents as "cutia" (*Dasyprocta azarae*), and mammals as "veado" (*Mazama gouazoubira*; Iob and Vieira, 2008). Once the extraction season begins no laws regulate the amount of pinhão (kg or tonnes) collected during the season period.

[2] Mata Atlântica Law n° 11.428/2006 – prohibits native species management in natural forests. CONAMA Resolution N° 278/2001.

[3] According to Brazilian legislation, Araucaria native populations are prohibited for timber harvesting once the species is 'Critically Endangered' (Thomas, 2013). However, planted Araucaria harvesting following a management plan registered and approved by environmental agencies is allowed, but bureaucracy and lack of flexibility prevent this management plan (Wandling and Zanette, 2017).

## 4.9 APPENDIX A. SUPPLEMENTARY DATA

### Co-management as a way to enhance Araucaria Forest resilience

Mario M. Tagliari, Carolina Levis, Bernardo M. Flores, Graziela D. Blanco, Carolina T. Freitas, Juliano A. Bogoni, Ghislain Vieilledent, Nivaldo Peroni

Table 1: Ethnoecological questionnaire. We applied a semi-structured questionnaire with open-ended questions. This feature allowed us to collect cultural, ecological, and socio-economic information with TEK holders in the *Araucaria* Forest System and thus describe potential benefits and risks of collaborative management strategies under a theoretical framework.

---

Universidade Federal de Santa Catarina
Programa de Pós-Graduação em Ecologia
Laboratório de Ecologia Humana e Etnobotânica

Interview script; Co-orientation: Dr.; Orientation: Prof. Dr.

CAEE: 86394518.0.0000.0121

---

Identification
Interview N°

---

Researcher___________________________ Municipality________________
Community_____________________________________

Georeference ______________S__________________N_____________A

Data _______________

Interviewee _______________________________________________________

Age _________________ Gender: ( ) M ( ) F

Occupation _________________________ Property area(ha): __________

Main activity ________________________
Residence time____________
How many family generations live in the region? ____________

---

PART A (*ARAUCARIA* FOREST)

---

A1. Are there *Araucaria* remnants in your property?

A2. Do you know the size of your remnant areas inside your property?
Small (until 10% ) _____
Medium (between 10 to 50% ) _____
Big (> 50%) _____

A3. Is there pinhão gathering/extraction/commerce in your property?
Yes _____ No _____

If the previous question was affirmative

A3a. What is the importance of pinhão in your property?

A4. Is there more male *Araucaria* than female? Why?

A6. Do you know the reason for this difference?

( ) absence of male / pollination ( ) / timber exploration ( )

slash and burn (agriculture) ( ) / dispersers' absence ()

changing climate ( ). Any other??

A7. Did *Araucaria* population increase from past to current moment? ( ) Yes( ) No

A7a. If there was an increase, describe the main causes

( ) Protected Areas ( ) Community participation ( )

fauna dispersion ( ) *Araucaria* management

other:

A7b. If any increase was identified, describe the causes:
( ) Illegal cutting / ( ) Seedling suppression / ( ) Cattle /
other:

---

---

PART B (*ARAUCARIA*, LANDSCAPE AND RESOURCES' USE)

---

B1. What are the best conditions for *Araucaria* development?

( ) water (riverbeds) ( ) deep and fertile soil

( ) fields ( ) difficult to access and shaded areas (e.g. valleys)

( ) cold regularly and intense () there is no specific condition (born anywhere)

other:

B2. What are the ideal conditions to produce pine nuts?

B2. On average, what is the production of pine nuts on your property (in kg) annually?

B3. On average, what is the consumption of pine nuts (in kg) annually on your property?

B4. How many different ethnovarieties of *Araucaria* do you identify in the landscape of your property?

B5. Which ethnovarieties of *Araucaria* do you know?

B6. What is the difference between each of the ethnovarieties you know?

B7. Do you identify the types of *Araucaria* by plant or pine nuts? Or both?

If types are identified, what differentiates them from each other?

B8. What types of pine nuts / plants are most common on your property?

B9. Which *Araucaria* ethnovarieties are commonly identified and which ethnovarieties are rare through the landscape?

B10. What is the season of maturation of the types of pine nuts that you know throughout the year?

B11. How long ethnovarieties occur throughout the year?

B12. Which of these “areas” (landscape units) do you have on the property?

( ) fields / crops ( ) pine / eucalyptus ( ) wintering ( ) orchard ( ) Legal Reserve ( ) APP

B13. Do you use management techniques for *Araucaria*?
If yes:

B13b.
( ) pasture fires, how often?
( ) mowing, what frequency?
Other:

B14b. Do you manage trees / select types?
( ) selects *Araucaria* types
Other:

B14c Do you handle the types of pine cones, and consequently, the type of pine nuts?

Describe the management you perform:
( ) Selects pinion types
Other:

B15. What are the characteristics of the ethnovarieties that you identify on your property regarding:
Tree shape:

Pinion shape and color?

Preferred location of types in the landscape (e.g. hillside, falls, near water bodies, etc.)

B16. Is it possible to identify the ethnovarieties of male *Araucaria*? If so, describe the characteristics of these types:

PART C (SPATIAL AND FUTURE PERSPECTIVES)

C1. If there is a temperature increase (get warmer) in the future, where will we find more *Araucaria*s?

( ) at higher areas ( ) in areas closer to rivers

( ) on slopes and valleys ( ) cooler areas in general

( ) there will be no change in the areas where they currently occur

other_____________________________________________________________________

___________

C2. Has there been a change in any climatic factor over time? For example (more or less rain, more or less cold winters, more or less strong summers, etc.). If so, how does it affect the *Araucaria* population?

C3. Has the production of pine nuts been affected over time?
If the answer is yes:

C3a. Were there more pine nuts in the past than today? Why?

C4. What is your opinion on climate change in the distribution of *Araucaria* types in the landscape?

Table 2: Results of the literature review using the search engine Web of Science. We searched specific terms from studies' abstracts: *Araucaria**, *angustifolia**, and conservation* or cultural. We obtained 70 studies from Web of Science main collection.

| **Source** | **Title** |
|---|---|
| Costa *et al.* (2020) | Understanding bark thickness variations for *Araucaria angustifolia* in southern Brazil |
| Das Neves Brandes *et al.* (2020) | Endangered species account for 10% of Brazil's documented timber trade |
| Marchioro *et al.* (2020) | Present and future of the critically endangered *Araucaria angustifolia* due to climate change and habitat loss |
| Latorre *et al.* (2020) | Daily, seasonal, and interannual variability of airborne pollen of *Araucaria angustifolia* growing in the subtropical area of Argentina |
| De Souza *et al.* (2020) | Genetic diversity and biogeographic determinants of population structure in *Araucaria angustifolia* (Bert.) O. Ktze |
| Hess *et al.* (2020) | Height-to-diameter ratios with temporal and dendro/morphometric variables for Brazilian pine in south Brazil |
| Roik *et al.* (2020) | Above ground Biomass and Organic Carbon of Native *Araucaria angustifolia* (Bertol.) Kuntze |
| Pereira *et al.* (2020) | Edaphic fauna and its relations with chemical, physical and microbiological attributes in *Araucaria* forest |
| Wilston *et al.* (2019) | Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered *Araucaria* tree |
| Montagna *et al.* (2019) | Guidelines for seed collection of *Araucaria angustifolia* (Bertol.) Kuntze: A genetic, demographic and geographic approach |
| Tagliari *et al.* (2019) | Analysis of programs of payment for environmental services in southern Brazil: identifying strategies for the conservation of *Araucaria angustifolia* |
| Gaidino *et al.* (2019) | Novel and Conserved miRNAs Among Brazilian Pine and Other Gymnosperms |
| Lauterjung *et al.* (2019) | Temporal changes in population genetics of six threatened Brazilian plant species in a fragmented landscape |
| Stefenon *et al.* (2019) | Phylogeography of plastid DNA sequences suggests post-glacial southward demographic expansion and the |

| | |
|---|---|
| | existence of several glacial refugia for *Araucaria angustifolia* |
| Furlanetto *et al.* (2019) | Cold stress on *Araucaria angustifolia* embryogenic cells results in oxidative stress and induces adaptation: implications for conservation and propagation |
| Araldi *et al.* (2019) | Reserve metabolism of stored and germinated *Araucaria angustifolia* seeds |
| Suhs *et al.* (2019) | Species diversity, community structure and ecological traits of trees in an upper montane forest, southern Brazil |
| Souza *et al.* (2019) | Forests of the Iguacu National Park: Structure, Composition, and Richness |
| Quinteiro *et al.* (2019) | Brazilian Pine (*Araucaria angustifolia* (Bertol.) Kuntze Ethnoecology in the Mantiqueira Atlantic Forest |
| Inza *et al.* (2018) | Genetic variability of *Araucaria angustifolia* in the Argentinean Parana Forest and implications for management and conservation |
| Zechini *et al.* (2018) | Genetic Conservation of Brazilian Pine (*Araucaria angustifolia*) Through Traditional Land Use |
| Lauterjung *et al.* (2018) | Phylogeography of Brazilian pine (*Araucaria angustifolia*): integrative evidence for pre-Columbian anthropogenic dispersal |
| Santana *et al.* (2018) | Structure, diversity and heterogeneity of an Upper Montane Mixed Umbrophylous Forest in its extreme northern distribution (Minas Gerais state) |
| Reis *et al.* (2018) | Domesticated Landscapes in *Araucaria* Forests, Southern Brazil: A Multispecies Local Conservation-by-Use System |
| Dalzochio *et al.* (2018) | Effect of tree plantations on the functional composition of Odonata species in the highlands of southern Brazil |
| Schneider *et al.* (2018) | Deforestation in Mixed Ombrophilous Forest in the serrana region of Santa Catarina |
| Fritzsons *et al.* (2017) | Climatic factors for limiting *Araucaria* distribution in Sao Paulo state |

| | |
|---|---|
| De Souza *et al.* (2017) | Phytosociology of tree vegetation in Iguacu National Park |
| Aimi *et al.* (2017) | Horizontal structure and influence of soil characteristics on distribution in Floresta Ombrofila Mista |
| Pereira *et al.* (2017) | Soil Macrofauna as a Soil Quality Indicator in Native and replanted *Araucaria angustifolia* Forests |
| Da Silva *et al.* (2017) | New records of rare dematiaceous conidial fungi on *Araucaria angustifolia* from Brazil |
| Adan *et al.* (2016) | Local Knowledge, Use and Management of Ethnovarieties of *Araucaria angustifolia* (Bert.) Ktze. in the Plateau of Santa Catarina, Brazil |
| Renner *et al.* (2016) | Man-made lakes form species-rich dragonfly communities in the Brazilian Atlantic Forest (Odonata) |
| Ariotti *et al.* (2016) | Tree and arborescent composition in an urban forest fragment in the municipality of Serio, Rio Grande do Sul State, Brazil |
| Paludo *et al.* (2016) | The size of *Araucaria angustifolia* (Bertol.) Kuntze Entering into reproductive stages as a basis for seed management projects |
| Lacerda, A.E.B (2016) | Conservation strategies for *Araucaria* Forests in Southern Brazil: assessing current and alternative approaches |
| Shibata el al., (2016) | Early harvest increases post-harvest physiological quality of *Araucaria angustifolia* (*Araucaria*ceae) seeds |
| Fraga *et al.* (2016) | DNA methylation and proteome profiles of *Araucaria angustifolia* (Bertol.) Kuntze embryogenic cultures as affected by plant growth regulators supplementation |
| Shibata *et al.* (2016) | Physiological and physical quality of local *Araucaria angustifolia* seed variety |
| Medina-Macedo *et al.* (2016) | Using genetic diversity and mating system parameters estimated from genetic markers to determine strategies for the conservation of *Araucaria angustifolia* (Bert.) O. Kuntze (*Araucaria*ceae) |
| Guerra *et al.* (2016) | Fundamentals, advances and applications of somatic embryogenesis in selected Brazilian native species |
| Prudente *et al.* (2016) | Cryopreservation of shoot tips excised from zygotic embryos of *Araucaria angustifolia* (Bertol.) Kuntze |

| | |
|---|---|
| Behling *et al.* (2016) | Late Holocene Vegetation History and Early Evidence of *Araucaria angustifolia* in Cacapava do Sul in the Lowland Region of Rio Grande do Sul State, Southern Brazil |
| Garcia *et al.* (2016) | Biochemical changes in *Araucaria angustifolia* (*Araucaria*ceae) zygotic embryos during the storage |
| Araldi *et al.* (2015) | Establishment of post-harvest early-developmental categories for viability maintenance of *Araucaria angustifolia* seeds |
| Mello *et al.* (2015) | Cultural landscapes of the *Araucaria* Forests in the northern plateau of Santa Catarina, Brazil |
| Rezende *et al.* (2015) | Restricted geographic distribution of tree species calls for urgent conservation efforts in the Subtropical Atlantic Forest |
| Martinkoski *et al.* (2015) | Climate influence in diameter growth of *Araucaria angustifolia*: literature review |
| Liebsch *et al.* (2015) | First record of Eucalyptus spp. Bark-stripping by brown-capuchin monkeys (Sapajusnigritus, PRIMATES: CEBIDAE) |
| Elbl *et al.* (2015) | Comparative transcriptome analysis of early somatic embryo formation and seed development in Brazilian pine, *Araucaria angustifolia* (Bertol.) Kuntze |
| Medina-macedo *et al.* (2015) | High levels of genetic diversity through pollen flow of the coniferous *Araucaria angustifolia*: a landscape level study in Southern Brazil |
| Negrini *et al.* (2015) | Floristic-structural heterogeneity of the tree component in a system of forest fragments in the southernplateau of Santa Catarina, Brazil |
| Kuhn *et al.* (2014) | Reproductive biology of the "Brazilian pine" (*Araucaria angustifolia* - *Araucaria*ceae): Development of microspores and microgametophytes |
| Jo *et al.* (2014) | Proteomic analysis and polyamines, ethylene and reactive oxygen species levels of *Araucaria angustifolia* (Brazilian pine) embryogenic cultures with different embryogenic potential |

| | |
|---|---|
| Reis *et al.* (2014) | Landscapes with *Araucaria* in South America: evidence for a cultural dimension |
| Rezende *et al.* (2013) | Vascular flora of Serra da Pedra Branca, Caldas, Minas Gerais and floristic relationships with altitude areas of Southeastern Region of Brazil |
| Sant'anna *et al.* (2013) | Realized pollen and seed dispersal within a continuous population of the dioecious coniferous Brazilian pine [*Araucaria angustifolia* (Bertol.) Kuntze] |
| Danner *et al.* (2013) | Impact of monoecy in the genetic structure of a predominately dioecious conifer species, *Araucaria angustifolia* (Bert.) O. Kuntze |
| Pereira *et al.* (2013) | Relationships between microbial activity and soil physical and chemical properties in native and reforested *Araucaria angustifolia* forests in the state of Sao Paulo, Brazil |
| Cenci *et al.* (2013) | Composition of the tree flora in the botanical garden of Bento Goncalves, Rio Grande do Sul, Brazil |
| Carvalho *et al.* (2012) | Chemical and biochemical properties of *Araucaria angustifolia* (bert.) ktze. forest soils in the state of Sao Paulo |
| Souza *et al.* (2012) | Native forest management in subtropical South America: long-term effects of logging and multiple-use on forest structure and diversity |
| Ferreira *et al.* (2012) | Genetic analysis of 50-year old Brazilian pine (*Araucaria angustifolia*) plantations: implications for conservation planning |
| Schloegl *et al.* (2012) | Gene expression during early somatic embryogenesis in Brazilian pine (*Araucaria angustifolia* (Bert) O. Ktze) |
| Zanette *et al.* (2011) | Grafting of *Araucaria angustifolia* (Bertol.) Kuntze through the four seasons of the year |
| Moreira *et al.* (2011) | Genetic diversity and mating system of bracatinga (Mimosa scabrella) in a re-emergent agroforestry system in southern Brazil |

| | |
|---|---|
| Melo *et al.* (2011) | First records of *Araucaria* Tit-Spine tail in the city of Sao Paulo |
| Vibrans *et al.* (2011) | Structure of mixed ombrophyllous forests with *Araucaria angustifolia* (*Araucaria*ceae) under external stress in Southern Brazil |
| Emer and Fonseca (2011) | *Araucaria* Forest conservation: mechanisms providing resistance to invasion by exotic timber trees |
| Patreze and Tsai (2010) | Intrapopulational genetic diversity of *Araucaria angustifolia* (Bertol.) Kuntze is different when assessed on the basis of chloroplast or nuclear markers |

Table 3: Interactions used to create the schematic *top-down* and *bottom-up* conservation models of *Araucaria* Forest System. Using the literature review and collected field data we propose these interactions. Each model presents a specific state that represents important elements and processes of the system. Based on these interactions, we could create networks to understand how the *Araucaria* Forest System may respond depending on positive or negative feedback loops.

| **System state variables and critical processes (à + / positive interaction; à - / negative interaction)** | **References** |
|---|---|
| *Top-down conceptual framework* | |
| Forest Cover reduces (à -) Deforestation and resource overexploitation rates | Enright and Hill, 1995 ; Folke *et al.*, 2010 ; Kelly *et al.*, 2015 |
| Deforestation and resource exploitation rates increase (à +) Forest Protection via restrictive measures | Ribeiro *et al.*, 2009 ; Mello and Peroni, 2015; Rezende *et al.*, 2018 ; Schneider *et al.*, 2018 ; Robinson *et al.*, 2018 ; Castro *et al.*, 2019 ; Wilson *et al.*, 2019 |
| Forest Protection via restrictive measures increases (à +) Forest Cover | Lei da Mata Atlântica n° 11.428/2006 ; CONAMA Resolution n° 278/2001 ; Thomas, 2013; Pacheco *et al.*, 2018 ; Schneider *et al.*, 2018 ; Metzger *et al.*, 2019 ; Wilson *et al.*, 2019 ; Rodrigues and Cazales, 2020 |
| Forest Protection via restrictive measures decreases (à -) Deforestation and resource exploitation rates | Ribeiro *et al.*, 2009 ; Schneider *et al.*, 2018 ; Rodrigues and Cazales, 2020 |
| Deforestation and resource exploitation rates decrease (à -) Forest Cover | Pacheco *et al.*, 2018 ; Schneider *et al.*, 2018 ;Metzger *et al.*, 2019 ; Rodrigues and Cazales, 2020 |
| *Bottom-up conceptual framework* | |
| Forest Cover increases (à +) Traditional Ecological Knowledge | Reis *et al.*, 2014 ; Mello and Peroni, 2015 ; Adan *et al.*, 2016 ; Reis *et al.*, 2018 ; Tagliari and Peroni 2018 ; Quinteiro *et al.*, 2019; this study |
| Traditional Ecological Knowledge increases (à +) Collaborative-management | Reis *et al.*, 2018 ; Tagliari and Peroni, 2019 ; Freitas *et al.*, 2020 ; this study |

| | |
|---|---|
| Collaborative-management increases (à +) Forest Cover | De Souza *et al.*, 2016 ; Gomes *et al.*, 2018 ; Musavengane *et al.*, 2019 ; Freitas *et al.*, 2020 |
| Collaborative-management increases (à +) Traditional Ecological Knowledge | Freitas *et al.*, 2020 ; this study |
| Traditional Ecological Knowledge increases (à +) Forest Cover | Folke *et al.*, 2010 ; Mello and Peroni, 2015 ; Robinson *et al.*, 2018 ; Sühs *et al.*, 2018 |

# 5 CAPÍTULO IV

## Disrupting a socioecological system: how Traditional Ecological Knowledge could be the key to preserve Araucaria Forest in Brazil under climate change?

(Disrupção de um sistema socioecológico: como o Conhecimento Ecológico Tradicional pode ser a chave para preservar a Mata de Araucárias brasileira sob o efeito das mudanças climáticas)

Artigo para ser submetido no periódico *Ambio* (ISSN: 1654-7209)
Área de avaliação: Biodiversidade
Classificação A1 (Quadriênio 2017-2020).

Região dos faxinais paranaenses, em Guarapuava – PR. A importância da mata de araucárias para grupos humanos faxinelenses é fundamental tanto para a mata quanto para as pessoas.

Fonte: Foto de Mário Tagliari, 2018.

# Disrupting a socioecological system: how Traditional Ecological Knowledge could be the key to preserve Araucaria Forest in Brazil under climate change?

Mario M. Tagliari[1,2*], Juliano A. Bogoni[1,3], Graziela D. Blanco[1], Aline P. Cruz[1], Nivaldo Peroni[1]

[1] Programa de Pós-graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil

[2] Faculdade Municipal do Meio Ambiente, Clevelândia, Brazil

[3] Universidade de São Paulo (USP), Escola Superior de Agricultura “Luiz de Queiroz” (ESALQ), Departamento de Ciências Florestais, Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre (LEMaC), Piracicaba, SP 13418-900, Brazil

Correspondence
* Mario M Tagliari
mario.tagliari@posgrad.ufsc.br

# ABSTRACT

Socioecological systems (SES) hinge on human groups and ecosystems, promoting interdependence and resilience to disturbances. Climate change effects propagate from organism to biomes, likely influencing SESs. In southern Brazil, Araucaria Forest is a typical SES due to the historical interaction between humans and its forests. We thus aimed to evaluate empirically how climate change could disrupt this system by interviewed 97 smallholders and assessed their Traditional Ecological Knowledge (TEK). We evaluated and measured: (i) socioeconomic impact of Araucaria's nut-like seed (pinhão) trade; (ii) ethnoecological knowledge about climate change; (iii) provided an ecosystem services network. We projected these empiric data with a projected loss of 50-70% of the Araucaria Forest to quantify the risks of climate change. We found evidence that to avoid the disruption of the Araucaria Forests is paramount to value TEK holders and promote non-mutually exclusive measures in an integrative response.

**Keywords** Araucaria Forest System; Climate change; Ecosystem Services Network; Ethnoecology; Mixed Ombrophilous Forest; Pinhão management

## 5.1 INTRODUCTION

Climate change effects have been described throughout all ecosystems (Malhi *et al.* 2020), from organism to biome levels (Parmesan 2006), affecting from organism's genetics (e.g. allelic diversity) to biomes integrity, such as the ecological resilience to disturbances (Bellard *et al.* 2012). These threats also impinge on Socio-Ecological Systems (hereafter SES), which consists in the integration of local human groups with ecosystems promoting reciprocal feedbacks, interdependence, and resilience (Folke *et al.* 2010). These local human groups commonly rely on the interaction with natural assets and could be represented in Brazil by indigenous people, local communities (e.g. "*ribeirinhos*"; "*caiçaras*"), or even small landowners (De Souza *et al.* 2006; Fatorić and Chelleri 2012; Gomes *et al.* 2018; Tagliari *et al.* 2021). These groups are characterized to hold the Traditional Ecological Knowledge (hereafter TEK): a long-term experience, based on observation, use, and management of natural resources, which offers a basis for ecosystems' adaptation and resilience to environmental disturbances, such as climate change (Ladio 2017).

The ecosystems under continuing interaction between plants and peoples are examples of SES. For instance, enduring human-plant interactions in the Neotropics contributed to enhancing plant domestication and food security across both the Amazon (Levis *et al.* 2018) and *Araucaria* Forest in southern Brazil (Cruz *et al.* 2020). Precisely, the *Araucaria* Forest, also known as *Araucaria* Mixed Forest, is an emblematic SES of the subtropical Atlantic Forest region (Tagliari *et al.* 2021). The main plant species of this ecosystem is the candelabra-aspect tree *Araucaria angustifolia* (Bertol.) Kuntze, popularly known as *Araucaria*, a 'Critically Endangered' species — according to the International Union of Conservation of Nature — which was almost depleted owing to extensive and illegal logging from early to late 20th century (Thomas 2013). The species has an ecological keystone role in the ecosystem's functioning owing to its nut-like seed, known as pinhão. The nutritious pinhão structures the associate vertebrate consumers spatiotemporally (Oliveira-Filho *et al.* 2015; Bogoni *et al.* 2020b). Furthermore, the species is also valuable due to the ancient connection with Indigenous peoples and local communities (Reis *et al.*, 2014; Robinson *et al.*, 2018), who still use and manage pinhão (Adan *et al.* 2016; Quinteiro *et al.* 2019). Forest management strategies by human groups since the last 1400 years expanded the *Araucaria* Forest beyond its natural boundaries, with landscape modifications visible in present days (Robinson *et al.* 2018; Cruz *et al.* 2020). Currently, the traditional management systems by local smallholders: (i) maintain forest fragments productive (Mello and Peroni 2015); (ii) promote ecosystem services (Tagliari *et al.* 2019) and temporal food security to local fauna and human groups (Adan *et al.* 2016; Bogoni *et al.* 2020b); (iii) preserve cultural, social, and economic dynamics in this SES (Zechini *et al.* 2018; Tagliari *et al.* 2021); and (iv) maintain the functional diversity of *Araucaria*, especially due to pinhões ethnovarieties identification thanks to TEK holders (Adan *et al.* 2016; Tagliari and Peroni 2018; Quinteiro *et al.* 2019). These traditional systems under TEK holders also boost positive feedbacks which might expand *Araucaria* Forest (Tagliari *et al.* 2021). Consequently, *Araucaria* is also classified as a "Cultural Keystone Species" (Garibaldi and Turner 2004), once it portrays a cultural and socio-ecological role in southern Brazil (Reis *et al.* 2014; Adan *et al.* 2016; Quinteiro *et al.* 2019). Further, it brings solid arguments that the entire ecosystem behaves as a socioecological system (Tagliari *et al.* 2021).

However, chronic deforestation, agriculture expansion, and more recently, climate change (Orellana and Vanclay 2018; Castro *et al.* 2019; Wilson *et al.* 2019; Marchioro *et al.* 2020), have been dampening *Araucaria* conservation and the SES resilience. To halt biodiversity losses the creation of protected areas is a cornerstone strategy (Geldmann *et al.* 2013). The *Araucaria* Forest remnants, although, are still poorly encompassed by the existing protected area network, as recent studies showed that less than 10% of the species' projected distribution falls within an existing protected area rather in the present or under future climate change scenarios (Castro *et al.* 2019; Wilson *et al.* 2019; Marchioro *et al.* 2020; Tagliari *et al.* in review). From almost 1500 BP until late 19th century, *Araucaria* Forest's natural extent covered an estimated area of 200,000 km² spanning over Brazil, Argentina, and Paraguay (Nodari 2016). Due to deforestation no more than 30% of native remnants remain preserved (Rezende *et al.* 2018). Moreover, future climate change predictions indicated losses of climatically suitable areas ranging from 60% to 96.5% compared to the species' current distribution (Castro *et al.* 2019; Wilson *et al.* 2019; Marchioro *et al.* 2020). Despite these studies showed the species' vulnerability to climate change, they all failed to properly indicate what is at stake if climate change disrupts this SES by showing potential losses in ecological, social, and economic aspects. Also, these studies do not consider the historical human-plant interaction and the possibilities to increase resilience to anthropic disturbances (Tagliari *et al.* 2021).

We aimed to answer this knowledge gap by approaching one of the main actors behind the SES resilience in the *Araucaria* Forest: the local smallholders. First, because of their TEK leaning on *Araucaria* use and management (Mello and Peroni 2015; Adan *et al.* 2016; Quinteiro *et al.* 2019), which promote resilience to climate disturbances and functional diversity (Ladio 2017; Tagliari *et al.* 2021). Second, Brazilian Legislation has a specific protected area category within private areas, the "*Reservas Legais*" (Legal Reserves), a compulsory protected area that hosts almost one-third of all remaining native vegetation of the Atlantic Forest (Metzger *et al.* 2019). Consequently, TEK holders preserve the majority of *Araucaria* native remnants because, in southern Brazil, 20% of private properties must be retained to native vegetation (Orellana and Vanclay 2018). Third, communities of poor small farmers might be the most vulnerable group due to global environmental changes (Pyhälä *et al.* 2016).

We thus propose to depict which aspects within the *Araucaria* Forest SES might be at risk due to climate change, looking at a social, economic, ecologic, ethnoecological, and ecosystem services framework. Further, we aimed to describe how TEK holders could increase *Araucaria* Forest's resilience to climate change. To achieve this framework, we interviewed 97 smallholders throughout the *Araucaria* Forest. By assessing their TEK, we aimed to systematically describe why this specific human group might be critical to safeguard the whole *Araucaria* SES, maintaining its preservation, ecosystem services, *Araucaria*s' functional diversity (intraspecific diversity), socio-ecological interactions, and resilience to disturbances, especially contributing to avoid its disruption to climate change.

## 5.2 METHODS

### 5.2.1 Study area

The study was conducted through the extent of the *Araucaria* Forest where we still find the interaction between human groups with *Araucaria* species (Fig. 1). We also revisited areas where this human-plant interaction was previously described (see Adan *et al.* 2016; Tagliari and Peroni 2018; Quinteiro *et al.* 2019). Historically, the extent of the *Araucaria* Forest is distributed at highlands plateaus along altitudes above 500 m (De Souza *et al.*, 2009), especially in Southern Brazil (states of Paraná, Santa Catarina, and Rio Grande do Sul) and relict occurrence patches in Southeastern Brazil, through the borders of the States of São Paulo, Minas Gerais, and Rio de Janeiro (Quinteiro *et al.* 2019; Tagliari *et al.* 2021).

### 5.2.2 Traditional Ecological Knowledge in the *Araucaria* Forest System in a nutshell

Different human groups interacted with *Araucaria* Forest through time. Use and management date back to Pre-Columbian times, where paleoindigenous ethnic groups cultivated pinhão (*Araucaria* nut-like seed) for subsistence or religiousness (Reis; Ladio; Peroni, 2014). Their historical footprint changed the *Araucaria* landscape, where archeological data indicated human-made influence over past forest expansion (Cruz *et al.*, 2020; Robinson *et al.*, 2018). Currently, human groups (i.e. indigenous people and local smallholders) still rely on *Araucaria* Forest resources, especially due to the use and management of pinhão and other plant species, such as *Ilex paraguariensis*, known as *yerba-mate*, a tea-like beverage (Reis; Ladio; Peroni, 2014), or *Acca sellowiana*, known as *goiabeira-serrana* (Bogoni; Graipel; Peroni, 2018).

This long-lasting interaction created productive forest management systems that promote the 'conservation-by-use' (REIS *et al.*, 2018), as well as benefits for human groups, such as (i) economic: pinhão trade; (ii) social: cultural identification; (iii) subsistence: food security; and (iv) socioecological: environmental services, ecological resilience, and functional diversity of pinhões (Mello and Peroni 2015; Adan *et al.* 2016; Reis *et al.* 2018; Zechini *et al.* 2018; Quinteiro *et al.* 2019; Tagliari *et al.* 2021). The functional diversity of pinhões (ethnovarieties) is well-described in the literature as an example of TEK by local smallholders (Adan *et al.*, 2016; Quinteiro; Alexandre; Magalhães, 2019; Tagliari; Peroni, 2018).

The identification of different ethnovarieties shows aspects of how intricated is this human-plant relationship, indicating food security spatiotemporally, economic dependence (Adan *et al.*, 2016; Quinteiro; Alexandre; Magalhães, 2019; Tagliari *et al.*, 2021), and knowledge about *Araucaria* phenology, distribution, threats, uses, or management aspects (Adan *et al.*, 2016; Bogoni *et al.*, 2020; Quinteiro; Alexandre; Magalhães, 2019; REIS *et al.*, 2018; Tagliari *et al.*, 2021; Tagliari; Peroni, 2018). We thus used this human group (i.e. local smallholders and pinhão extractors) to proceed with the application of a semi-structured questionnaire. We used the snowball technique (Bernard, 2006) to follow the semi-structured interviews, where participants recommended people directly involved in *Araucaria* management at the end of the interview. We aimed to include indigenous peoples as TEK holders, such as Southern-Jê and Guarani groups, who have shaped forest composition in Southern Brazil (Cruz *et al.*, 2020), however, ethical limitations and legal aspects did not allow us to include them in our study.

### 5.2.3 Socioeconomic data

We defined two distinct strategies to compile socioeconomic data. First, leaning on our semi-structured interviews we collected information about interviewees' gender, age, profession, main crops cultivated, time living in the property, how much pinhão trade boost family incomes, and the amount of pinhão (in kg) collected in each property. Second, we use the Brazilian System of Automate Recuperation – SIDRA – (https://sidra.ibge.gov.br/home/ipca15/brasil), a public and open-access database from the Brazilian Institute of Geography and Statistics (Instituto Brasileiro de Geografia e Estatística) to collect several economic indicators and their historical series. We collected two pinhão historical series between 2010-2019: (i) the amount of pinhão collected per year (tonnes); and (ii) the economic value of pinhão annual trade (see here https://sidra.ibge.gov.br/tabela/289#resultado).

### 5.2.4 Ethnoecological knowledge under an ecosystem services approach

To collect ethnoecological data we also used our semi-structured interviews. We collected information about the use, management, and knowledge of *Araucaria* and its pinhões ethnovarieties. Leaning on smallholders' TEK we collected evidence of (i) pinhão ethnovarieties ripening period, abundance, size, color; (ii) the different pinhão ethnovarieties known by each smallholder; (iii) the reproductive phenology and seed production of *Araucaria* trees due to pinhão maturation throughout the year; (iv) interviewees perception about the potential impact of climate change over the *Araucaria* Forest, especially *Araucaria* species. Leaning on these pieces of information we created a framework to describe two aspects of *Araucaria* ethnoecology: (i) the ecosystem's services provided by *Araucaria* use and management, targeting four potential ecosystem services: provision; regulation; cultural; and support (following Bogoni *et al.* 2020a); (ii) how pinhão ethnovarieties use and management confer *Araucaria* functional diversity; socioecological food security; and smallholders well-being under climate change.

To generate the ecosystem services framework — defined by the Millennium Ecosystem Assessment (MEA) as the "benefits people obtain from ecosystems, promoting human well-being" (Millennium Ecosystem Assessment 2005) —, we created a binary matrix of n smallholders by m ecosystem services suggested. The total number of ecosystem services perceived by an interviewee about *Araucaria* use and management was given by the sum of all ecosystem services perceived, following Machado *et al.* (2019). According to the Millennium Ecosystem Assessment (2005) the ecosystem services that affect people well-being are described as (i) provision (resource for human groups, seed predation, seed dispersal, phytodemographic dynamics); (ii) regulation (climate regulation, disease control, insect pest control, natural disasters control), (iii) cultural (e.g. ethnocultural identity, ecotourism, aesthetics, education); and (iv) support (e.g. nutrient cycling, soil formation, primary production, oxygen), following Bogoni *et al.* (2020a) to select the specific categories of each ecosystem service. We cross-checked the interviewees' perceptions of ecosystem services with the already published literature to indicate real or potential ecosystem services provided by the AFS.

### 5.2.5 Quantifying AFS disruption under climate change

To estimate the potential losses due to climate change over the *Araucaria* Forest System we selected the latest peer-reviewed studies that have shown the impacts of future climate change over *Araucaria* forest (Table 1). We combined the studies' projections for 2070 (Castro *et al.* 2019; Wilson *et al.* 2019; Marchioro *et al.* 2020; Tagliari *et al.* in review) over the potential losses of climatically suitable areas (ΔS loss) for *Araucaria* in the future under two climate scenarios –Representative Concentration Pathways (RCP) 4.5 and 8.5 – to propose a baseline of "climate change loss". These three studies selected both RCPs 4.5 and 8.5 because it became a common practice of species modelling approaches once they represent an optimistic (RCP 4.5) or a pessimistic (RCP 8.5) CO2 emission scenario (Riahi *et al.* 2011; Thomson *et al.* 2011). We thus counted all six projections of area loss and divided them by the total amount of projections (n projections) to indicate a value that represents the potential area loss of the *Araucaria* Forest System due to climate change (see Equation 1).

$$\sum RCP\ 4.5\ \Delta S\ loss + \sum RCP\ 8.5\ \Delta S\ loss \Big/ n\ projections \tag{1}$$

We thus defined the average loss of climatically suitable areas to evaluate how climate change could dampen *Araucaria* Forest's resilience in the future. Thus, we evaluated the potential losses of the entire system looking at the socioeconomic, ethnoecological, and ecosystem services aspects described above.

To quantify the AFS disruption under climate change scenarios, we analyzed the matrices of adjacency of ecosystem services (i.e. the original and the matrices with penalization due to climate change, following Bogoni *et al.* 2020a) via ecological networks (Boccaletti *et al.* 2006). For each network (i.e. original, and under climate changes scenarios) we obtained: (1) interviewed degree (Id); (2) ecosystem services degree (ESd); (4) connectance (C); (5) nestedness (N); and (6) modularity (M). The average degree (i.e. □Id and □ESd) describes the average number of interactions by interviewed and the putative ecosystem services in the network (Boccaletti *et al.* 2006). Connectance (C) represents the proportion of interactions (i.e. interviewed opinion vs. ES) observed regarding the total possible interactions (Boccaletti *et al.* 2006). Modularity (M) quantifies the tendency of the nodes (interviewed–ESs) to form groups of vertices more connected to each other than to the other components of the network (Boccaletti *et al.* 2006). Nestedness (N, based on NODF criteria) indicates a hierarchical pattern of interactions interviewed-ES, in which the interactions of the less connected interviewed-ES form a subset of the interactions of the most connected, representing a structural fitting (Almeida-Neto *et al.* 2008). We compared the metrics between the original adjacency matrix and climate change regimes, where any numerical change of the metrics will suggest a loss of robustness or stability of the network of services provided by SES.

## 5.3 RESULTS

### 5.3.1 The potential loss of *Araucaria* Forest due to climate change

According to the three peer-reviewed studies showing the impacts of potential area loss of *Araucaria* Forest due to climate change, we identified that until 2070, climate change will shrink the *Araucaria* Forest system area up to 68.37%. The RCP 8.5 — leaning on most pessimistic climate previsions — indicates a suitable area loss up to 80%, while the RCP 4.5 – an optimistic climate projection — pointed out a potential suitable area loss up to 56% comparing to the current *Araucaria* Forest extent (Table 1). Furthermore, no more than 10% of the projected distribution of *Araucaria* Forest (i.e. currently or in the future) will be encompassed by existing Protected Areas according to these studies, which only considered Brazilian Full Protection and Sustainable Use Protected Areas (*Proteção Integral* and *Áreas de Uso Sustentável*, respectively). These climatically suitable areas might be also encompassed by private Protected Areas, such as Legal Reserves and Permanent Preservation Areas (*Reserva Legal* and *Área de Preservação Permanente*), besides Indigenous Territories. Finally, it is expected that the remaining forest will be restrained at more elevated areas, indicating an upslope niche contracting pattern.

### 5.3.2 Traditional Ecological Knowledge about pinhão and climate change

According to smallholders, we identified 23 local pinhão ethnovarieties based on 320 citations from all participants throughout southern and southeastern Brazil. These ethnovarieties were described by local people (i.e. smallholders and/or pinhão extractors) due to pinhão ripening periods by female *Araucaria*s. The cluster dendrogram showed that among the 23 ethnovarieties described by interviewees, seven represented properly the differences or similarities according to the descriptions (i.e. color, shape, ripening period, size, taste), especially: (i) Macaco; (ii) 25 de Março; (iii) São José; (iv) Cajuvá; (v) Comum; and (vi) Do Cedo; (vii) Do Tarde (Fig. S1). The most-cited pinhão ethnovarieties were: (i) Macaco (N=81 citations); (ii) Cajuvá (N= 80 citations); (iii) Comum (N= 48 citations); (iv) Do Cedo (N= 31 citations); and (v) 25 de Março (N= 16 citations). Participants cited, on average, three ethnovarieties (52.5%) and another 25% described four different ethnovarieties. The main ethnovarieties described by the participants were said to develop in different moments during the year indicating pinhão production throughout the year, especially from March until December (Fig. 2). The ethnovarieties "Do cedo" and "Cajuvá" were classified as the most abundant, which confirms that pinhão peak production occurs between March until July. The "Macaco" ethnovariety is the rarest by 67% of interviewees (n = 65). We also identified a completely different identification of pinhão according to the regions. Usually, along the Paraná, Santa Catarina and Rio Grande do Sul states, the "Cajuvá", "Macaco", "Do Cedo", and "Do Tarde" ethnovarieties are commonly described. However, at Cunha municipality (Mantiqueira Hills region) the most described ethnovarieties were "Caiano" and "Roxo".

Interviewees were also demanded to describe how they perceive the effects of climate change in the *Araucaria* Forest. Only eight interviewees did not answer about the effect of climate change on the *Araucaria* Forest, while 91.75% (n = 89) believe that somehow climate will impact the ecosystem. The increasing temperatures, whiter winters, and frost reduction were the main aspects described by interviewees as the consequences of climate change for 74.15% (n = 66). The climate unpredictability, such as anomalous or unstable winter and summer seasons, was also described as the main changes perceived throughout the landscape (46% or n = 41). We also asked whether the *Araucaria* tree would be affected by climate change. Among the 89 interviewees, 36 (40.4%) did not indicate that *Araucaria* species will be affected by climate change, while those who suggested the climate change influence over *Araucaria* species (53 interviewees), 50.1% (n = 27) believes that the species will move to colder areas and 35.8% (n = 19) states the species will move to higher elevations (see Fig. 4 for a complete description about smallholders and pinhão extractors perception).

### 5.3.3 Socioeconomic benefits of pinhão extractivism

The pinhão extractivism and trade have been an alternative economic resource for smallholders' families for at least 3.5 generations, where 65% of the 97 interviewees declared that pinhão trade contributes to their monthly income from R$ 1000 to R$ 2.500 (i.e. 1 to 2.3 Brazilian minimum wage in 2018), or US$ 253.8 to US$ 633.9 in 2019 (i.e. US$ 1 = R$ 3.94), according to the World Bank Indicator (https://data.worldbank.org/indicator/PA.NUS.FCRF?locations=BR). For 30% of the interviewees, the pinhão trade is their main annual income. Typical crops such as yerba-mate, tobacco, corn, and beans are alternative income resources with pinhão extractivism. The pinhão extraction is mainly man-made for 95% (n = 92). Women usually contribute to pinhão gathering underneath *Araucaria* trees. Family groups might collect up to 10,000 kg of pinhão per year (11.5% or 11 people). Another 50% (n = 46) commonly collects from 1,000 to 10,000 kg per year. The pinhão trade has been increasing its economic value between 2010-2019 (Table 02). The three southern Brazilian states: Paraná, Santa Catarina, and Rio Grande do Sul, extract, on average, 7.736.000 kg of pinhão per year. This amount contributes to US$ 3.803.245, on average, per year in Brazil's southern region (Table 03). In southeastern Brazil, São Paulo and Minas Gerais states also benefit from pinhão trade. Minas Gerais has been increasing pinhão extractivism, collecting 1.126.000 kg per year, totalizing US$ 855.983,77 per year (Table 3). Unless São Paulo state, both the amount collected per year of pinhão and the monetary value of this nut-like seed in the market increased (Fig. 3).

### 5.3.4 Ecosystem Services perceptions by TEK holders

The TEK holders' perceptions were grouped into 19 ecosystem services assigned to: (i) provision (resource for human-groups; seed predation and dispersion; genetic resource; phytodemographic dynamic); (ii) regulation (climate regulation; disease control; insect control; biological control; natural disaster control; pollination); (iii) cultural (ecotourism; ethnocultural identity; aesthetic; education); and (iv) support (soil formation; oxygen and nutrient cycling; primary production). TEK holders identify at least one up to 14 ecosystem services (mean 3.94), among the 4 assigned services. The assigned services (i.e. provision, regulation, cultural, and support were identified almost three times (mean 2.84) per TEK holder. The most perceived ecosystem services were: (i) resource for human-groups, due to pinhão use and trade (n = 96); (ii) ethnocultural identity, because of the ethnovarieties knowledge and description (n = 76);

(iii) climate regulation, thanks to their perception about *Araucaria* phenology and potential climate change impacts on the ecosystem (n = 75); (iv) phytodemographic dynamics, as a consequence of *Araucaria* occurrence in the landscape and its climatic niche (n = 40); (v) and aesthetic given the interaction of people with the environment based on human perceptions and judgments (n=24) (see Fig. 5 for a complete description of all perceived ecosystem services).

The metrics evaluating the ecosystem services scenarios in the present and under future projections (2050 and 2070) indicated a decrease in every metric evaluated (Fig. 5). The average services degree according to our 97 interviews originally was □ESdOriginal = 22.95. Assuming a random loss of 50% of the ecosystem services in 2050, the potential services might be reduced to to □ESd2050 = 11.84. Under a potential loss of 70% of the ecosystem services perceived by TEK holders, ecosystem services might be □ESd2070 = 6.95. The other network metrics (i.e. connectance; modularity; and nestedness) also reflect these projected losses. Connectance, originally was Coriginal = 0.24, decreasing to C2050 = 0.12 (50.0% reduction), and to C2070 = 0.07 (70.8% reduction). Modularity, increased towards future: MOriginal = 0.24; M2050 = 0.35; and M2070 = 0.48. Finally, nestedness of our ecosystem services network might decrease as well: NOriginal = 72.5 in the present; N2050 = 32.6 in 2050 (55.0% reduction); and N2070 = 12.8 in 2070 (82.5% contraction; Fig. 5).

## 5.4 DISCUSSION

### 5.4.1 The potential losses of *Araucaria* Forest due to climate change and its impacts in a holistic perspective

Using the most recent studies about the effects of climate change over *Araucaria angustifolia* and consequently, to the entire SES of the *Araucaria* Forest in Brazil, we showed the main socio-economic, ethnoecological, and ecological aspects that might be at risk in the medium- (2050) and long-term (2070) climate change. We found under an ethnoecological approach that smallholders and pinhão extractors who use, manage, differentiate pinhão ethnovarieties, and trade *Araucaria*'s pinhão, provide several ecosystem services, socioeconomic benefits, and potential resilience to disturbances, such as climate change. By undermining this vulnerable group to global change, the entire SES might be doomed. Furthermore, it is paramount to quantitatively understand the effects of biodiversity loss on human well-being under the science of ecosystem services (BOGONI; PERES; FERRAZ, 2020), and we provide a valuable contribution using an ecological (BOGONI *et al.*, 2020) and cultural (sensu Garibaldi and Turner 2004) keystone species as the main proxy in the SES of the *Araucaria* Forest.

### 5.4.2 *Araucaria* ethnovarieties as an ecological keystone resource

Besides its umbrella and nurse effect, which structures, increase sapling richness, and promote plant species diversity, regeneration, and development under its canopy in a non-trophic landscape contribution (Reis *et al.*, 2018; Sühs; Giehl; Peroni, 2018), the *Araucaria* species has pivotal importance in maintaining fauna community and diversity. Thanks to its resource availability — pinhão — the *Araucaria* provides to local fauna: (i) low temporal redundancy (i.e. few other plant resources available during pinhão availability); (ii) low consumer specificity (i.e. pinhão is usually consumed by different species); (iii) high resource reliability (i.e. the staggering availability of pinhão throughout the year); and (iv) resource abundance (i.e. high production of *Araucaria* nut-like seed). Consequently, *Araucaria* structures the associate consumers spatiotemporally (Bogoni *et al.*, 2020), such as mammals (*Dasyprocta azarae, Delomys dorsalis, Oligoryzomys nigripes, Procyon cancrivorus, Tayassu pecari*) and birds (*Amazona vinaceae*, *A. pretrei*, *Cyanocorax caeruleus*, and *C. chrysops* (Iob; Vieira, 2008; Montagna *et al.*, 2019).

By identifying the pinhão ethnovarieties and their peak production throughout the year, which is mainly comprised between March and December, we also suggest that both keystone plant resource aspects (i) high resource reliability and (ii) resource abundance characteristics might be a consequence of the historical species' domestication process with human-groups. The pinhão ethnovariety described as "Macaco", on one hand, is usually described as the "rarest" and "smaller" variety, but it occurs throughout the entire year (Adan *et al.*, 2016; Tagliari; Peroni, 2018). The most abundant variety ("Cajuvá"), on the other hand, is commonly described as the "biggest" or "taster" pinhão (Adan *et al.*, 2016; Tagliari; Peroni, 2018). We believe that both *Araucaria* reproductive phenology and ethnovarieties characteristics are a consequence of the domestication process and the use of *Araucaria* resources since pre-colonial Amerindians from human groups (Cruz *et al.*, 2020), benefiting and structuring both fauna and flora in the AFS.

The historical forest management in the AFS region for the past 1400 years expanded this forest beyond its natural extent in areas with elevated demography since the pre-colonial period (Robinson *et al.*, 2018). We advocate that the current use and knowledge of *Araucaria* ethnovarieties still shape and maintain this ecosystem productive and preserved under a landscape domestication perspective (Reis *et al.*, 2018), where management practices, the species demographic structure, and its genetic diversity reinforce this concept (Reis *et al.*, 2018). Assuming that climate change might drastically reduce *Araucaria* distribution until 2070 (Castro *et al.*, 2019; Marchioro; Santos; Siminski, 2020; Wilson *et al.*, 2019), we might expect that this effect would ruin critical ecological interactions, as well collapsing the actual human-plant interaction.

### 5.4.3 Socioeconomic impact and ecosystem services declines

The actual human-plant interaction brings economic profits not only to local smallholders and pinhão extractors but to an entire network until the final consumers (Vieira-da-Silva; Miguel, 2017). The SIDRA historical series of pinhão trade and consumption (see Tables 1; 2) only accounts for the pinhão traded at the Brazilian CEASAS (State Supply Centers). However, there is an "informal" market of pinhão trade before arriving at the CEASAS which is not calculated in the historical series. This informal market is mostly linked to local landowners and pinhão sellers along Brazilian State highways supplying internal markets in smaller cities, mainly in highlands of southern Brazil and specific regions at Mantiqueira hills in the southeastern portion of the country (Adan *et al.* 2016; Tagliari and Peroni 2018; Quinteiro *et al.* 2019). Despite the vertiginous increase in pinhão value per year in Brazil (Fig. 3b), which indicates an appreciation of pinhão consumption, the amount collected per year (Fig. 3a) reveals that pinhão harvesting might be already reaching its limit. The uncontrolled pinhão harvesting is made by smallholders and pinhão extractors exclusively via extractivism. However, uncontrolled pinhão harvesting might be dangerous because there is a critical intensity threshold between 60 to 85% (Fichino; Pivello; Santos, 2017). By exceeding this threshold, uncontrolled pinhão harvesting might prevent in both short- and long-term: *Araucaria* regeneration; limitation and reduction of ecosystem services, such as provision (pinhão provisioning), support (primary production), and regulation (carbon sequestration) (Fichino; Pivello; Santos, 2017).

The very few regulations about pinhão harvesting are limited to the beginning of the season extraction (usually from 1st April in Paraná and Santa Catarina states; or 15th April in Rio Grande do Sul; we found no information for São Paulo and Minas Gerais states). However, the majority of extractors usually gather and trade pinhão for financial subsistence and food security, and not to guarantee the species conservation, ecosystem maintenance, or sustainable harvesting (Adan *et al.*, 2016; Quinteiro; Alexandre; Magalhães, 2019; Tagliari *et al.*, 2021; Tagliari; Peroni, 2018). The lack of environmental incentives, especially via Payment for

Ecosystem Services (Tagliari; Moreira; Peroni, 2019), promote, especially for landowners, antagonistic conservation practices, such as the *Araucaria* seedling suppression (Quinteiro; Alexandre; Magalhães, 2019; Schneider *et al.*, 2018; Tagliari; Peroni, 2018). It is widely documented the claim of TEK holders to create a mechanism for valuing their interactions and indirect consequences by preserving *Araucaria* (Adan *et al.*, 2016; Quinteiro; Alexandre; Magalhães, 2019; Tagliari; Peroni, 2018), even though this socioeconomic and ecological interaction in the highly fragmented relics of the *Araucaria* Forest promotes: gene flow (Zechini *et al.*, 2018); genetic diversity (Montagna *et al.*, 2019); intraspecific diversity for *Araucaria* populations (Adan *et al.*, 2016; Mello; Peroni, 2015; Quinteiro; Alexandre; Magalhães, 2019; Reis *et al.*, 2018); maintenance of productive forest remnants via "conservation-by-use" (Reis *et al.*, 2018); and the maintenance or even the expansion of the entire socio-ecological system via positive feedbacks (Tagliari *et al.*, 2021).

Due to climate change, however, TEK holders might be even more vulnerable due to their dependency on climatic conditions (Holland *et al.*, 2017). In the AFS, TEK holders usually live under food insecurity, poverty, and precarious conditions, reinforcing their vulnerability and priority to aidance efforts. The imminent impacts of climate change within the AFS, especially over *A. angustifolia* (Castro *et al.*, 2019; Marchioro; Santos; Siminski, 2020; Wilson *et al.*, 2019), and the potential cascading effect to the entire socio-ecological system will impact one of the major contributors to the maintenance of this SES. However, this existing human group also promotes adaptive capacity to reinforce the SES resilience and to reduce its general vulnerability (sensu Holland *et al.* 2017; Tagliari *et al.* 2021). We might witness a combination of threats acting both in short- and long-terms along the *Araucaria* Forest: unsustainable harvesting; precarious socioeconomic conditions of TEK holders; the imminent impact of climate change.

Under climate change, we revealed that the ES provided by *Araucaria* Forest will undermine and thus compromise human well-being. For instance, the presumed ecosystem services degree can decline by 69.7% from 2070s. The ecological network of ES perception by the small landowners based on their TEK also could be threatened due to climate change in all their metrics. Declines in connectance and nestedness — on average of 65% — can indicate that the proportion of links small-landowners recognizing the ESs in the future will decay by at least a half. A similar pattern in the nestedness was found, ensuring the decline of both intraindividual perception of ES and the perception of ES as a group. The increase in modularity can indicate dense connections within the nodes in every cluster in 2070 but with a sparse connection between different notes, i.e. the perception of ES could be shared by sub-groups of people, but not shared by the group as a whole. Empirical evidence indicates a similar pattern in declines of ES and network re-arranges due to mammal defaunation scenarios (Bogoni *et al.* 2020b). Given that the ecological network is a tool to understand, depict and predict the ecosystem functioning, the species interactions, and the ecological functions (Boccaletti *et al.* 2006), the SES of *Araucaria* Forest may disrupt to climate change.

### 5.4.4 Food security and sociocultural interconnection with the Araucaria Forest System

Climate change future projections and the potential reduction of *Araucaria* distribution indicates a major concern for local communities and their food security. *Araucaria*'s pinhão is a nutrient-rich food resource containing several minerals (e.g. potassium, phosphorus, and manganese; Barbosa *et al.* 2019). As a typical regional resource, which guarantees both economic and dietary security of local human groups, by strengthening traditional use and management of local food resources we also might preserve local keystone species (Tagliari *et al.* 2021). Also, it values the maintenance and aesthetic connection of peoples' cultures, and how human groups perceive and incorporate the sense of belonging with the surrounding environment (Tam and Chan, 2007). Consequently, as climate change might disrupt the *Araucaria* socioecological system, there is a necessity to implement strategies to safeguard and preserve this cultural ecosystem (Tam; Chan, 2017).

## 5.5 CONCLUSION

### 5.5.1 Araucaria Forest contributions to people and people contribution to *Araucaria* Forest: the pathway to promote resilience to climate change

Several aspects must be considered to avoid the imminent impact of climate change on the *Araucaria* Forest system. The first one is the cornerstone of conservation: Protected Areas (Rodrigues; Cazalis, 2020). Within the *Araucaria* Forest extent, only 10.3% of the more than 1.118.000 km$^2$ is encompassed by these areas (Indigenous Territories cover only 0.72% or 8.050 km$^2$), where 25% is classified as Strict Protected areas and another 75% as Sustainable Use areas (Pacheco; Neves; Fernandes, 2018). Within the Sustainable Use areas, two categories could potentially benefit TEK holders of the *Araucaria* Forest: the Sustainable Development Reserves (RDS) and Extractive Reserves (RESEX). However, considering the 75% of

Sustainable Use areas, only 1.07% is classified as RDS or RESEX, while 72% is classified as Environmental Protection Area (Pacheco; Neves; Fernandes, 2018), which does not benefit local peoples. This might be a consequence of the Legal Reserves (a private Protected Area) which host another one-third of the remaining remnants of the Atlantic Forest within private properties, such as smallholders' properties. Concerning the *Araucaria* species, only 5 to 10% of its predicted suitable areas in the future (i.e. which are expected to be reduced by =~70% in 2070) will be encompassed by the existing network of protection (Castro *et al.*, 2019; Marchioro; Santos; Siminski, 2020). These suitable areas will be found at more elevated, moister, and colder areas (Bergamin *et al.*, 2019; Castro *et al.*, 2019; Marchioro; Santos; Siminski, 2020; Wilson *et al.*, 2019), as TEK holders also described in this study (Fig. 04). Consequently, the first conservation priority as a response to climate change is the identification of these potential areas and the necessity to implement new Protected Areas, as well as the creation of both RESEX and RDS Sustainable Use areas.

The second major aspect is targeting the main actors of this Socioecological System: TEK holders. Different potential strategies must be implemented to value this human-plant interaction under the Payment for Ecosystem Services framework: (i) conservation of forest stands beyond the minimum legally required; (ii) the valuation of the pinhão supply chain; (iii) the maintenance of pinhão ethnovarieties; (iv) the mensuration of the ecosystem services provided by remnant areas; (v) the restoration of degraded areas; (vi) food security for vulnerable social groups (see Tagliari *et al.* 2019 for an evaluation of different Payment for Ecosystem Services programs in Southern Brazil). Also, recent studies shed a light on the possibility of sustainable timber exploitation as a strategy to engage local people (Montagna *et al.*, 2019; Orellana; Vanclay, 2018). Hence, by valuing these actors, *Araucaria* intraspecific and functional diversity is boosted, and, consequently, promote resilience and adaptive capacity to climate change, besides creating positive feedback between TEK holders and the entire socioecological system (Elmqvist *et al.*, 2003; Holland *et al.*, 2017; Tagliari *et al.*, 2021). Also, by preserving *Araucaria* remnants via TEK holders we find a win-win strategy because there is a possibility to engage more local groups in environmental governance and shorten the distance of actions that degrade the surrounding environment thanks to restrictive measures that usually exclude local groups (Orellana; Vanclay, 2018; Tagliari *et al.*, 2021; Tam; Chan, 2017; Zechini *et al.*, 2018). Notwithstanding, the ecosystem services perception of TEK holders indicates a profound knowledge and commitment with the *Araucaria* Forest, providing ecosystem services, such as regulation, provision, and cultural services.

We do not expect to treat TEK holders as a new panacea to fight against climate change. However, especially for socio-ecological systems worldwide, there is a necessity to implement holistic, integrative, and non-mutually exclusive conservation measures, from *top-down* (such as restrictive legislation or Strict Use Protected Areas) to *bottom-up* strategies (such as collaborative-management, Payment for Ecosystem Services, or Sustainable Use Protected areas). By considering this integrative scenario, we might reinforce resilience and adaptive capacity to anthropic disturbances of the *Araucaria* Forest. Otherwise, if we do not seek an integrative response, we might follow the disruption of an extreme and valuable socioecological system to climate change.

## Acknowledgements

This manuscript is the result of 8 years of listening, learning, and discussing with local smallholders and pinhão extractors of southern and southeastern Brazil. We hope our research might impact stakeholders and politicians to recognize this vulnerable traditional group as a cultural heritage in Brazil. The authors like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/Brazil; Finance Code 001) for the Ph.D. scholarship for MMT, JAB, GDB, and APC. JAB is supported by the São Paulo Research Foundation (FAPESP) postdoctoral fellowship grants 2018-05970-1 and 2019-11901-5. NP thanks CNPq for the productivity scholarship (Process 310443/2015-6).

## Author information

### Affiliations

Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, ECZ/CCB/UFSC, Campus Trindade s/n, Florianópolis, SC, 88010-970, Brazil: Mário M. Tagliari, Juliano A. Bogoni, Graziela D. Blanco, Aline P. Cruz, Nivaldo Peroni

Faculdade Municipal do Meio Ambiente, Clevelândia: Mário M. Tagliari

Universidade de São Paulo, Escola Superior de Agricultura “Luiz de Queiroz”, Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre (LEMaC), Piracicaba, São Paulo, Brazil: Juliano A. Bogoni

### Contributions

MMT conceived the research; all authors reviewed the literature; MMT and JAB wrote the original draft with major contributions of GDB, APC, and NP; all authors edited and approved the manuscript.

### Corresponding author

Correspondence to Mario M. Tagliari (mario.tagliari@posgrad.ufsc.br; mario.tagliari@famapr.edu.br | +55 46 9 9979 7651

### Ethics declarations

The authors declared no competing interest.

## 5.6 REFERENCES

Adan, N., J. Atchison, M. S. Reis, and N. Peroni. 2016. Local Knowledge, Use and Management of Ethnovarieties of *Araucaria angustifolia* (Bert.) Ktze. in the Plateau of Santa Catarina, Brazil. Economic Botany 70: 353–364. doi:10.1007/s12231-016-9361-z.

Assessement, M. E., ed. 2005. Ecosystems and Human Well-being: health synthesis. World Health Organization. Vol. 18. Geneva.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15: 365–377. doi:10.1111/j.1461-0248.2011.01736.x.

Bergamin, R. S., V. Debastiani, D. C. Joner, P. Lemes, T. Guimarães, R. D. Loyola, and S. C. Müller. 2019. Loss of suitable climatic areas for *Araucaria* forests over time. Plant Ecology and Diversity 12. Taylor and Francis Ltd.: 115–126. doi:10.1080/17550874.2019.1618408.
Bernard, H. R. 2006. Research Methods in Anthropology: Qualitative and Quantitative Approaches. Library. Vol. 4th. doi:10.1525/aa.2000.102.1.183.

Bogoni, J. A., M. E. Graipel, and N. Peroni. 2018. The ecological footprint of *Acca sellowiana* domestication maintains the residual vertebrate diversity in threatened highlands of Atlantic Forest. Edited by Manu E Saunders. PLOS ONE 13. Public Library of Science: e0195199. doi:10.1371/journal.pone.0195199.

Bogoni, J. A., C. A. Peres, and K. M. P. M. B. Ferraz. 2020a. Effects of mammal defaunation on natural ecosystem services and human well being throughout the entire Neotropical realm. Ecosystem Services 45. Elsevier B.V.: 101173. doi:10.1016/j.ecoser.2020.101173.

Bogoni, J. A., M. Muniz-Tagliari, N. Peroni, and C. A. Peres. 2020b. Testing the keystone plant resource role of a flagship subtropical tree species (*Araucaria angustifolia*) in the Brazilian Atlantic Forest. Ecological Indicators 118. Elsevier: 106778. doi:10.1016/j.ecolind.2020.106778.

Castro, M. B., A. C. M. C. Barbosa, P. V. Pompeu, P. V. Eisenlohr, G. de Assis Pereira, D. M. G. Apgaua, J. C. Pires-Oliveira, J. P. R. A. D. Barbosa, *et al.* 2019. Will the emblematic southern conifer *Araucaria angustifolia* survive to climate change in Brazil? Biodiversity and Conservation 29. Springer Netherlands: 591–607. doi:10.1007/s10531-019-01900-x.

Cruz, A. P., E. L. H. Giehl, C. Levis, J. S. MacHado, L. Bueno, and N. Peroni. 2020. Pre-colonial Amerindian legacies in forest composition of southern Brazil. PLoS ONE 15: 1–18. doi:10.1371/journal.pone.0235819.

Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment. doi:10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2.

Fatorić, S., and L. Chelleri. 2012. Vulnerability to the effects of climate change and adaptation: The case of the Spanish Ebro Delta. Ocean and Coastal Management 60. Elsevier: 1–10. doi:10.1016/j.ocecoaman.2011.12.015.

Fichino, B. S., V. R. Pivello, and R. F. Santos. 2017. Trade-offs among ecosystem services under different pinion harvesting intensities in brazilian *Araucaria* forests. International Journal of Biodiversity Science, Ecosystem Services and Management. doi:10.1080/21513732.2016.1275811.

Folke, C., S. R. Carpenter, B. Walker, M. Scheffer, T. Chapin, and J. Rockstrom. 2010. Resilience thinking: integrating resilience, adaptability and transformability. Ecology and Society 15(4): Nature Nanotechnology 15: 20. doi:10.1038/nnano.2011.191.

Garibaldi, A., and N. Turner. 2004. Cultural keystone species: Implications for ecological conservation and restoration. Ecology and Society 9: 1. doi:10.1146/annurev-pharmtox-061008-103038.

Geldmann, J., M. Barnes, L. Coad, I. D. Craigie, M. Hockings, and N. D. Burgess. 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biological Conservation 161. Elsevier Ltd: 230–238. doi:10.1016/j.biocon.2013.02.018.
Gomes, V. H. F., S. D. IJff, N. Raes, I. L. Amaral, R. P. Salomão, L. de Souza Coelho, F. D. de Almeida Matos, C. V. Castilho, *et al.* 2018. Species Distribution Modelling: Contrasting presence-only models with plot abundance data. Scientific Reports 8. Nature Publishing Group: 1003. doi:10.1038/s41598-017-18927-1.

Holland, M. B., S. Z. Shamer, P. Imbach, J. C. Zamora, C. Medellin Moreno, E. J. L. Hidalgo, C. I. Donatti, M. R. Martínez-Rodríguez, *et al.* 2017. Mapping adaptive capacity and smallholder agriculture: applying expert knowledge at the landscape scale. Climatic Change 141. Climatic Change: 139–153. doi:10.1007/s10584-016-1810-2.

Iob, G., and E. M. Vieira. 2008. Seed predation of *Araucaria angustifolia* (*Araucaria*ceae) in the Brazilian *Araucaria* Forest: Influence of deposition site and comparative role of small and "large" mammals. Plant Ecology 198: 185–196. doi:10.1007/s11258-007-9394-6.

Ladio, A. H. 2017. A Conceptual Approach to Unveil Traditional Homegardens as Fields of Social Practice. Ethnobiology and Conservation 6: 1–8. doi:10.15451/ec2017.

Levis, C., B. M. Flores, P. A. Moreira, B. G. Luize, R. P. Alves, J. Franco-Moraes, J. Lins, E. Konings, *et al.* 2018. How People Domesticated Amazonian Forests. Frontiers in Ecology and Evolution 5. doi:10.3389/fevo.2017.00171.

Machado, A. M. da S., F. G. Daura-Jorge, D. F. Herbst, P. C. Simões-Lopes, S. N. Ingram, P. V. de Castilho, and N. Peroni. 2019. Artisanal fishers' perceptions of the ecosystem services derived from a dolphin-human cooperative fishing interaction in southern Brazil. Ocean and Coastal Management 173. Elsevier: 148–156. doi:10.1016/j.ocecoaman.2019.03.003.

Malhi, Y., J. Franklin, N. Seddon, M. Solan, M. G. Turner, C. B. Field, and N. Knowlton. 2020. Climate change and ecosystems: Threats, opportunities and solutions. Philosophical Transactions of the Royal Society B: Biological Sciences 375. doi:10.1098/rstb.2019.0104.

Marchioro, C. A., K. L. Santos, and A. Siminski. 2020. Present and future of the critically endangered *Araucaria angustifolia* due to climate change and habitat loss. Forestry: An International Journal of Forest Research 93: 401–410. doi:10.1093/forestry/cpz066.

Mello, A. J. M., and N. Peroni. 2015. Cultural landscapes of the *Araucaria* Forests in the northern plateau of Santa Catarina, Brazil. Journal of ethnobiology and ethnomedicine 11. Journal of Ethnobiology and Ethnomedicine: 51. doi:10.1186/s13002-015-0039-x.

Metzger, J. P., M. M. C. Bustamante, J. Ferreira, G. W. Fernandes, F. Librán-Embid, V. D. Pillar, P. R. Prist, R. R. Rodrigues, *et al.* 2019. Why Brazil needs its Legal Reserves. Perspectives in Ecology and Conservation 17. Associacao Brasileira de Ciencia Ecologica e Conservacao: 91–103. doi:10.1016/j.pecon.2019.07.002.

Montagna, T., M. B. Lauterjung, N. C. F. da Costa, A. P. Bernardi, R. Candido-Ribeiro, and M. S. dos Reis. 2019. Guidelines for seed collection of *Araucaria angustifolia* (Bertol.) Kuntze: A genetic, demographic and geographic approach. Forest Ecology and Management 438. Elsevier: 10–17. doi:10.1016/j.foreco.2019.02.006.

Nodari, E. 2016. Historia de la devastación del bosque de *Araucaria* en el sur del Brasil. Revista internacional de ciencias sociales 55: 75–85.

Oliveira-Filho, A. T., J. C. Budke, J. A. Jarenkow, P. V. Eisenlohr, and D. R. M. Neves. 2015. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. Journal of Plant Ecology 8. Oxford Academic: 242–260. doi:10.1093/JPE/RTT058.

Orellana, E., and J. K. Vanclay. 2018. Could native *Araucaria* forests be managed for timber production on small farms in southern Brazil? Forest Ecology and Management 430. Elsevier: 1–9. doi:10.1016/j.foreco.2018.07.057.

Pacheco, A. A., A. C. O. Neves, and G. W. Fernandes. 2018. Uneven conservation efforts compromise Brazil to meet the Target 11 of Convention on Biological Diversity. Perspectives in Ecology and Conservation 16. Associação Brasileira de Ciência Ecológica e Conservação: 43–48. doi:10.1016/j.pecon.2017.12.001.

Parmesan, C. N. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics 37: 636–637. doi:10.2307/annurev.ecolsys.37.091305.30000024.

Pyhälä, A., Á. Fernández-Llamazares, H. Lehvävirta, A. Byg, I. Ruiz-Mallén, M. Salpeteur, and T. F. Thornton. 2016. Global environmental change: Local perceptions, understandings, and explanations. Ecology and Society 21. doi:10.5751/ES-08482-210325.

Quinteiro, M. M. da C., B. da R. Alexandre, and L. M. S. Magalhães. 2019. Brazilian Pine (*Araucaria angustifolia* (Bertol.) Kuntze) Ethnoecology in the Mantiqueira Atlantic Forest. Floresta e Ambiente 26: 1–7. doi:10.1590/2179-8087.018516.

Reis, M. S., A. Ladio, and N. Peroni. 2014. Landscapes with *Araucaria* in South America: Evidence for a cultural dimension. Ecology and Society 19. doi:10.5751/ES-06163-190243.

Reis, M. S., T. Montagna, A. G. Mattos, S. Filippon, A. H. Ladio, A. da C. Marques, A. A. Zechini, N. Peroni, *et al.* 2018. Domesticated Landscapes in *Araucaria* Forests, Southern Brazil: A Multispecies Local Conservation-by-Use System. Frontiers in Ecology and Evolution 6. Frontiers: 11. doi:10.3389/fevo.2018.00011.

Rezende, C. L., F. R. Scarano, E. D. Assad, C. A. Joly, J. P. Metzger, B. B. N. Strassburg, M. Tabarelli, G. A. Fonseca, *et al.* 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation. Elsevier. doi:10.1016/J.PECON.2018.10.002.

Riahi, K., S. Rao, V. Krey, C. Cho, V. Chirkov, G. Fischer, G. Kindermann, N. Nakicenovic, *et al.* 2011. RCP 8.5-A scenario of comparatively high greenhouse gas emissions. Climatic Change 109: 33–57. doi:10.1007/s10584-011-0149-y.

Robinson, M., J. G. De Souza, S. Y. Maezumi, M. Cárdenas, L. Pessenda, K. Prufer, R. Corteletti, D. Scunderlick, *et al.* 2018. Uncoupling human and climate drivers of late Holocene vegetation change in southern Brazil. Scientific Reports 8. Nature Publishing Group: 7800. doi:10.1038/s41598-018-24429-5.

Rodrigues, A. S. L., and V. Cazalis. 2020. The multifaceted challenge of evaluating protected area effectiveness. Nature Communications 11. Springer US: 1–4. doi:10.1038/s41467-020-18989-2.

Schneider, L. C. A., M. T. da Silva, L. Agostinetto, and A. E. Siegloch. 2018. Deforestation in Mixed Ombrophilous Forest in the Serrana Region of Santa Catarina. Revista Árvore 42. Sociedade de Investigações Florestais. doi:10.1590/1806-90882018000200006.

De Souza, G. C., R. Kubo, L. Guimarães, and E. Elisabetsky. 2006. An ethnobiological assessment of *Rumohra adiantiformis* (samambaia-preta) extractivism in Southern Brazil. Biodiversity and Conservation 15: 2737–2746. doi:10.1007/s10531-005-0309-3.

de Souza, M. I. F., F. Salgueiro, M. Carnavale-Bottino, D. B. Félix, M. Alves-Ferreira, J. V. M. Bittencourt, and R. Margis. 2009. Patterns of genetic diversity in southern and southeastern *Araucaria angustifolia* (Bert.) O. Kuntze relict populations. Genetics and Molecular Biology 32: 546–556. doi:10.1590/S1415-47572009005000052.

Sühs, R. B., E. L. H. Giehl, and N. Peroni. 2018. Interaction of land management and *Araucaria* trees in the maintenance of landscape diversity in the highlands of southern Brazil. Edited by Suzannah Rutherford. PLOS ONE 13. Public Library of Science: e0206805. doi:10.1371/journal.pone.0206805.

Tagliari, M. M., and N. Peroni. 2018. Local varieties of *Araucaria angustifolia* (Bertol.) Kuntze (Pinales : *Araucaria*ceae) in southern Brazil: A brief discussion about landscape domestication. Biotemas 31: 59–68.

Tagliari, M. M., V. A. Moreira, and N. Peroni. 2019. Analysis of programs of payment for environmental services in southern Brazil: identifying strategies for the conservation of *Araucaria angustifolia*. Desenvolvimento e Meio Ambiente 50: 216–233.

Tagliari, M. M., C. Levis, B. M. Flores, G. D. Blanco, C. T. de Freitas, J. A. Bogoni, G. Vieilledent, and N. Peroni. 2021. Collaborative management as a way to enhance *Araucaria* Forest resilience. Perspectives in Ecology and Conservation. Elsevier. doi:10.1016/J.PECON.2021.03.002.

Tam, K. P., and H. W. Chan. 2017. Environmental concern has a weaker association with pro-environmental behavior in some societies than others: A cross-cultural psychology perspective. Journal of Environmental Psychology 53. Elsevier Ltd: 213–223. doi:10.1016/j.jenvp.2017.09.001.

Thomas, P. 2013. *Araucaria angustifolia*, parana pine. The IUCN Red List of Threatened Species: 2013. Vol. 8235. doi:10.2305/IUCN.UK.2013-1.RLTS.T32975A2829141.en.

Thomson, A. M., K. V. Calvin, S. J. Smith, G. P. Kyle, A. Volke, P. Patel, S. Delgado-Arias, B. Bond-Lamberty, *et al.* 2011. RCP4.5: A pathway for stabilization of radiative forcing by 2100. Climatic Change 109: 77–94. doi:10.1007/s10584-011-0151-4.

Vieira-da-Silva, C., and L. de A. Miguel. 2017. Os canais de comercialização do pinhão e seus agentes, em São Francisco de Paula, Rs. Floresta 47: 489–500. doi:10.5380/rf.v47i4.49570.

Wilson, O. J., R. J. Walters, F. E. Mayle, D. V. Lingner, and A. C. Vibrans. 2019. Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered *Araucaria* tree. Global Change Biology 25: 4339–4351. doi:10.1111/gcb.14755.

Zechini, A. A., M. B. Lauterjung, R. Candido-Ribeiro, T. Montagna, A. P. Bernardi, M. P. Hoeltgebaum, A. Mantovani, and M. S. dos Reis. 2018. Genetic Conservation of Brazilian Pine (*Araucaria angustifolia*) Through Traditional Land Use. Economic Botany 72: 166–179. doi:10.1007/s12231-018-9414-6.

## 5.7 FIGURES

Figure 1. (a) The Atlantic Forest (dark gray) with the *Araucaria* Forest ecoregion (green) showing the three Brazilian states which mainly encompass the ecoregion: Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS); (b) The *Araucaria* Forest altitude map and the distribution of Conservation Units: Strictly (yellow) and Sustainable Use Protected Areas (green); black dots represent the occurrence of 97 ethnoecological interviews in this study. We highlight that three interviews occurred at São Paulo state (beyond the *Araucaria* Forest ecoregion) at Cunha municipality.

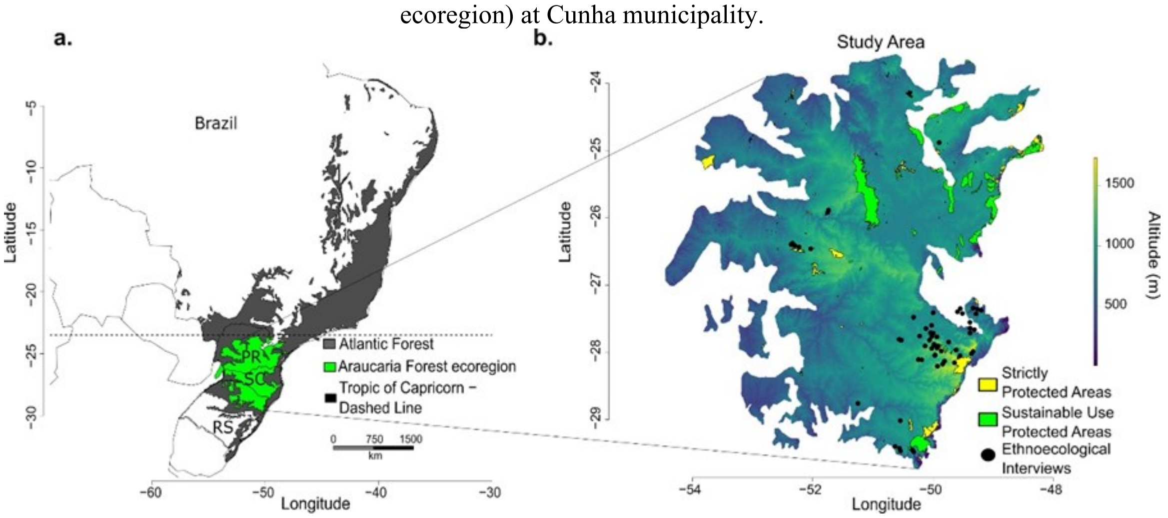


Figure 2. The reproductive phenology of the main pinhão ethnovarieties throughout the year. The very first ethnovarieties peak production start in March ("25 de Março", "Do Cedo", "São José" until April. The two most cited ethnovarieties – "Cajuvá" and "Macaco" – peak production start in May until July and from August until December. The pinhão production according to all varieties (yellow square) occurs between Mars until December.

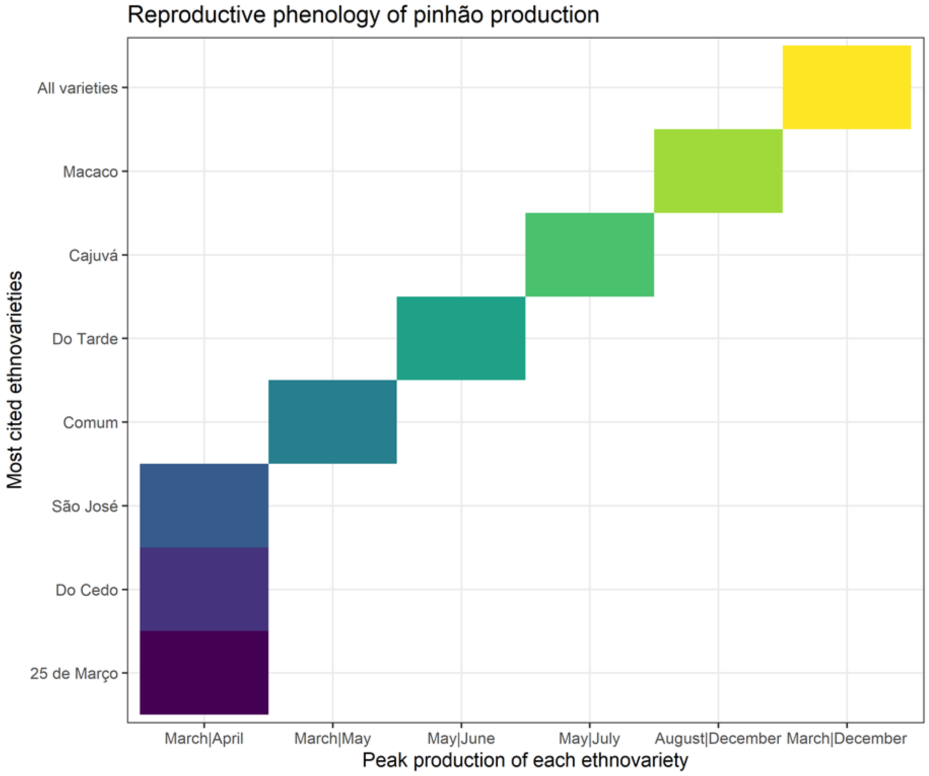


Figure 3. The pinhão harvesting (kg) and (b) pinhão trade (R$) according to the time-series between 2010-2019. Pinhão harvesting indicate that all states collecting pinhão might have reached the limit in this extraction activity. However, the economic value indicates an increase since 2010 and a potential cap for the valuation of pinhão trade for the next years.

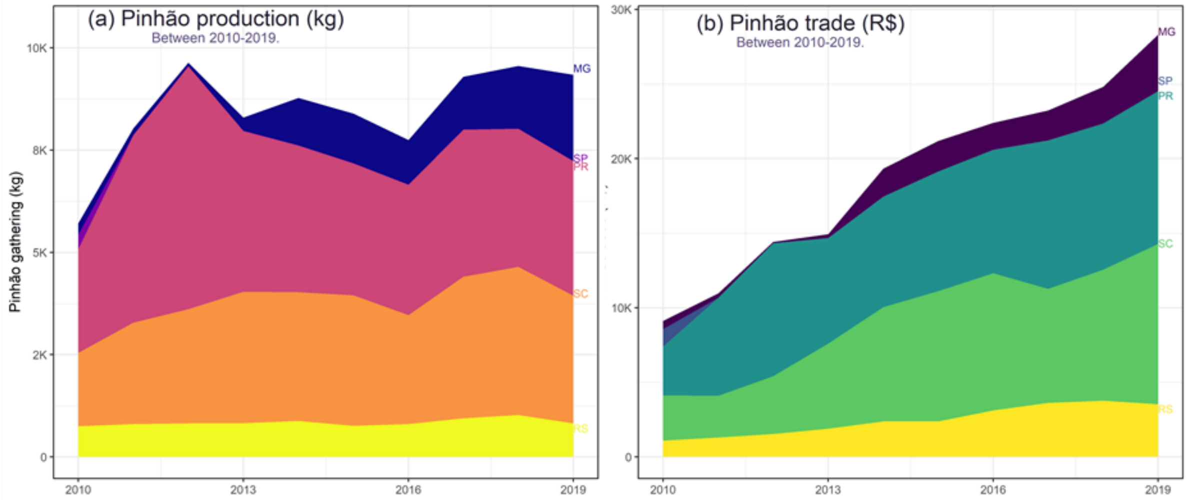


Figure 4. (a) The perceptions of TEK holders about the effect of climate change on *Araucaria* species and how this emblematic tree might respond to this disturbance. Semi-structured interviews indicate that TEK holders believe that due to climate change, *Araucaria* might move to more elevated, colder, and moister areas.

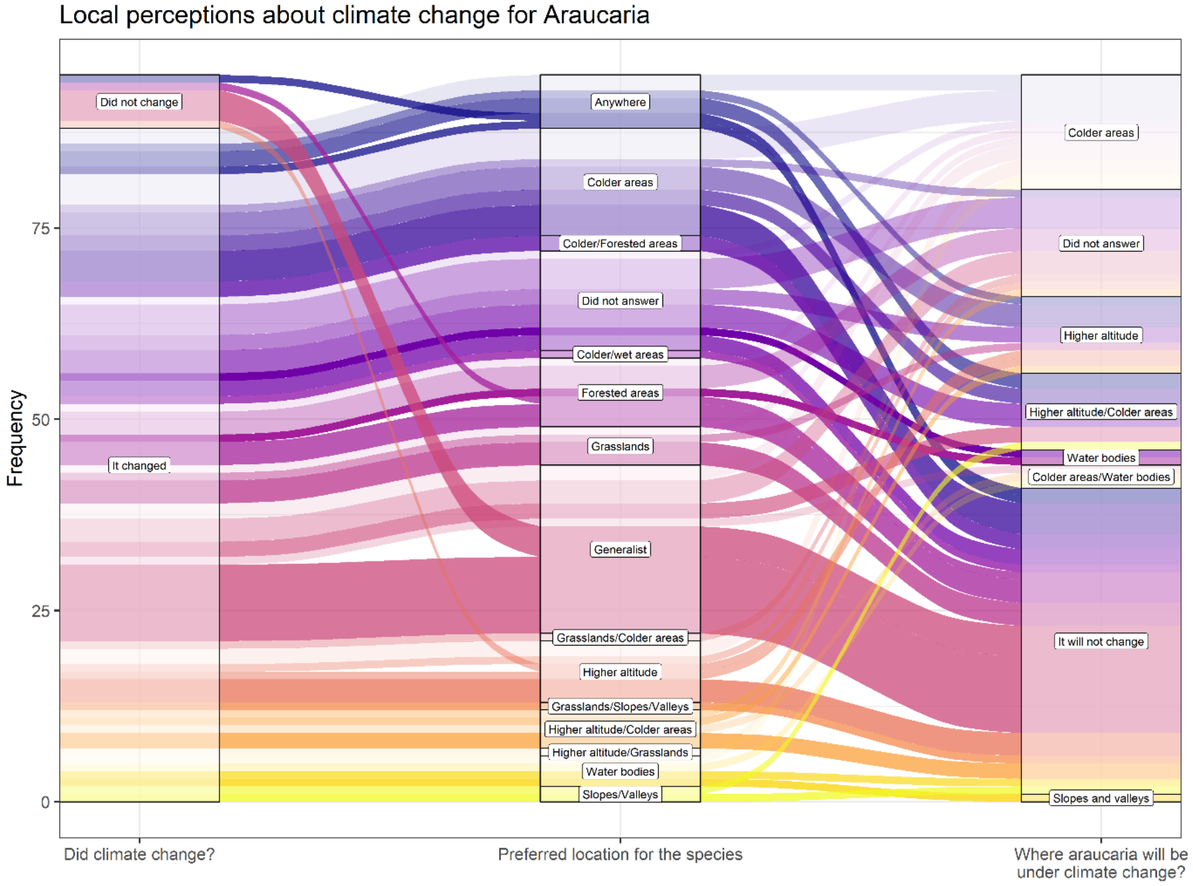
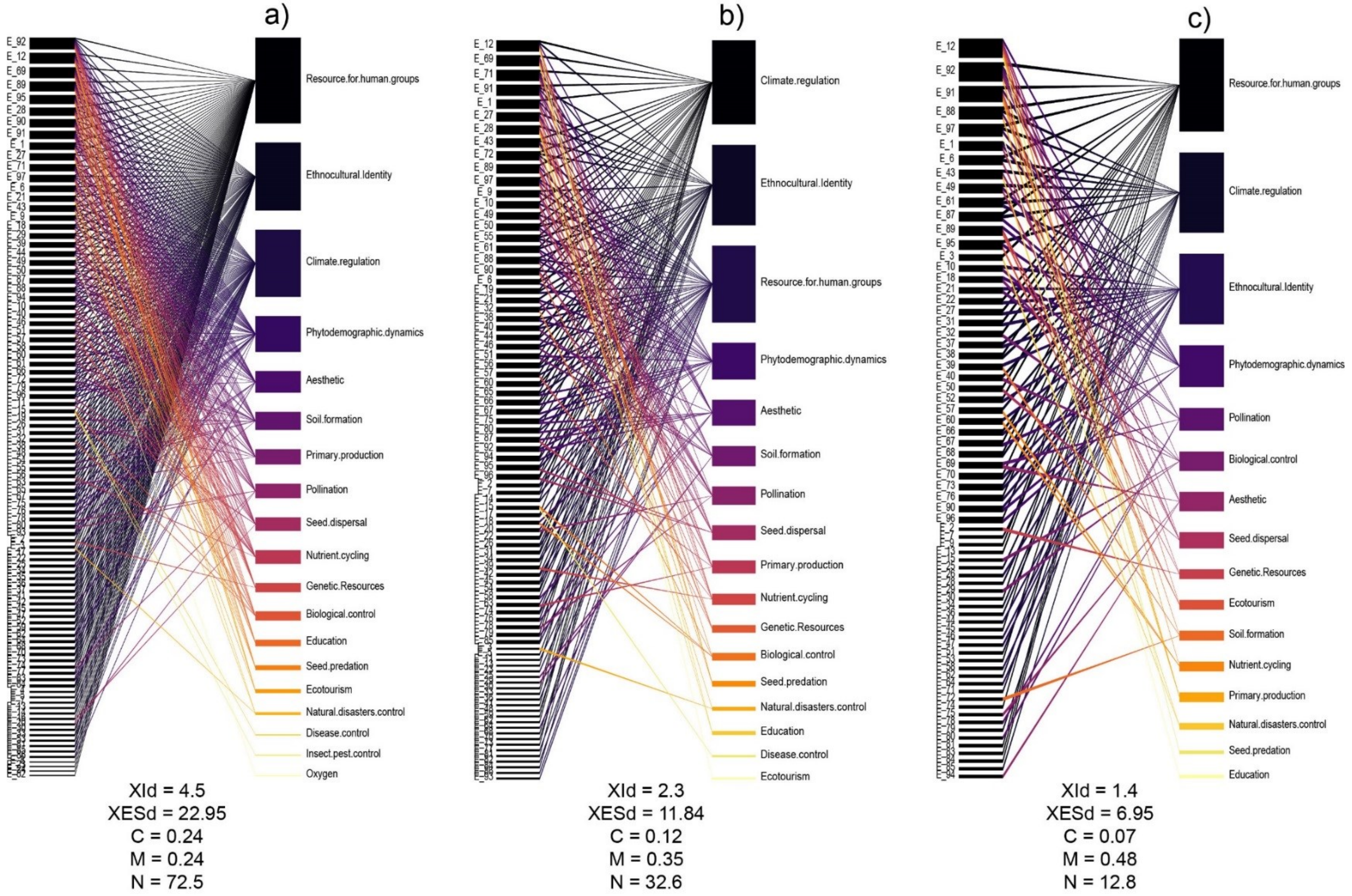


Figure 5. (a) The perceptions of TEK holders about the ecosystem services provided by the *Araucaria* Forest. We represented all answers among the four main ecosystem services that affect people well-being: (i) provision (resource for human-groups, seed predation, seed dispersal, phytodemographic dynamics); (ii) regulation (climate regulation, disease control, insect pest control, natural disasters control), (iii) cultural (e.g. ethnocultural identity, ecotourism, aesthetics, education); and (iv) support (e.g. nutrient cycling, soil formation, primary production, oxygen), following Bogoni *et al.* (2020a) to select the specific categories of each ecosystem service. To model the potential loss of ecosystem services' perception due to climate change, we combined the outputs of the most recent peer-reviewed studies that estimated the potential area loss for *Araucaria* in 2050 (b) and 2070 (c).



## 5.8 TABLES

Table 1. References selected to estimate the potential threat of climate change over the *Araucaria* Forest System. We selected only peer-reviewed studies that calculated under the Species Distribution Modelling approach the potential loss of climatically suitable areas for *Araucaria* in 2070. The Representative Concentration Pathways (RCPs) are $CO_2$ emission scenarios, where RCP 4.5 is an optimistic scenario that considers the increase mean of 1.4-1.8°C until the late-twenty first century, whereas the RCP 8.5 is a realistic and pessimistic scenario which mean temperatures are expected to increase by 3.7 °C until the late-twenty first century (IPCC, 2013).

| **Reference** | **Climatically suitable area loss in 2070 compared to current predictions (%)** | | | |
|---|---|---|---|---|
| **Climate scenario** | **RCP 4.5** | **RCP 8.5** | **RCP 4.5** | **RCP 8.5** |
| *Years* | *2050* | *2050* | *2070* | *2070* |
| Wilson *et al.* 2019 | NA | NA | 85.33 | 96.5 |
| Castro *et al.* 2019 | NA | NA | 27.7 | 60 |
| Marchioro *et al.* 2020 | 45 | 53 | 53 | 77 |
| Tagliari *et al.* 2021 | NA | NA | 66.5 | 89 |
| Projected loss (mean) | – | | 56.13% | 80.62% |
| Projected average loss | 49% | | 68.37% | |

Table 2. The amount of pinhão harvesting collected per year (kg * 1000) in the Brazilian states registered at the CEASAS (State Supply Centers).

| **Pinhão harvest between 2010-2019 (kg x $10^3$)** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Brazilian States* | *2010* | *2011* | *2012* | *2013* | *2014* | *2015* | *2016* | *2017* | *2018* | *2019* |
| **Minas Gerais** | 276 | 164 | 87 | 323 | 1162 | 1213 | 1090 | 1288 | 1535 | 2108 |
| **São Paulo** | 355 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 5 |
| **Paraná** | 2536 | 4581 | 5932 | 3924 | 3582 | 3220 | 3183 | 3596 | 3373 | 3290 |
| **Santa Catarina** | 1799 | 2476 | 2790 | 3213 | 3147 | 3192 | 2663 | 3456 | 3621 | 3120 |
| **Rio Grande do Sul** | 749 | 806 | 823 | 828 | 881 | 762 | 805 | 947 | 1025 | 819 |

Source: IBGE - Produção da Extração Vegetal e da Silvicultura

Table 3. The economic value of pinhão harvesting collected per year (US$ * 1000) in the Brazilian states registered at the CEASAS (State Supply Centers).

| **Pinhão harvest between 2010-2019 (US$ x 10³)** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Brazilian States* | *2010* | *2011* | *2012* | *2013* | *2014* | *2015* | *2016* | *2017* | *2018* | *2019* |
| **Minas Gerais** | 137 | 73 | 20 | 65 | 471 | 517 | 457 | 505 | 622 | 955 |
| **São Paulo** | 297 | 2 | 4 | 4 | 4 | 4 | 5 | 5 | 6 | 6 |
| **Paraná** | 831 | 1666 | 2259 | 1790 | 1881 | 2034 | 2097 | 2524 | 2505 | 2598 |
| **Santa Catarina** | 771 | 707 | 983 | 1449 | 1943 | 2216 | 2335 | 1870 | 2231 | 2729 |
| **Rio Grande do Sul** | 278 | 333 | 393 | 482 | 606 | 606 | 793 | 922 | 957 | 897 |

Source: IBGE - Produção da Extração Vegetal e da Silvicultura.

## 5.9 SUPPLEMENTARY SOURCES

Figure S1. The cluster dendogram created to identify the main pinhão ethnovarieties described in this study. To create de dendogram we select seven pinhão characteristics collected in the semi-structured interviews: (i) number of citations; (ii) most abundant ethnovariety; (iii) the rarest ethnovariety; (iv) beginning (which month) of ethnovariety production; (v) the end (which month) of ethnovariety production; (vi) where the ethnovariety is found; and (vii) the color of the ethnovariety.

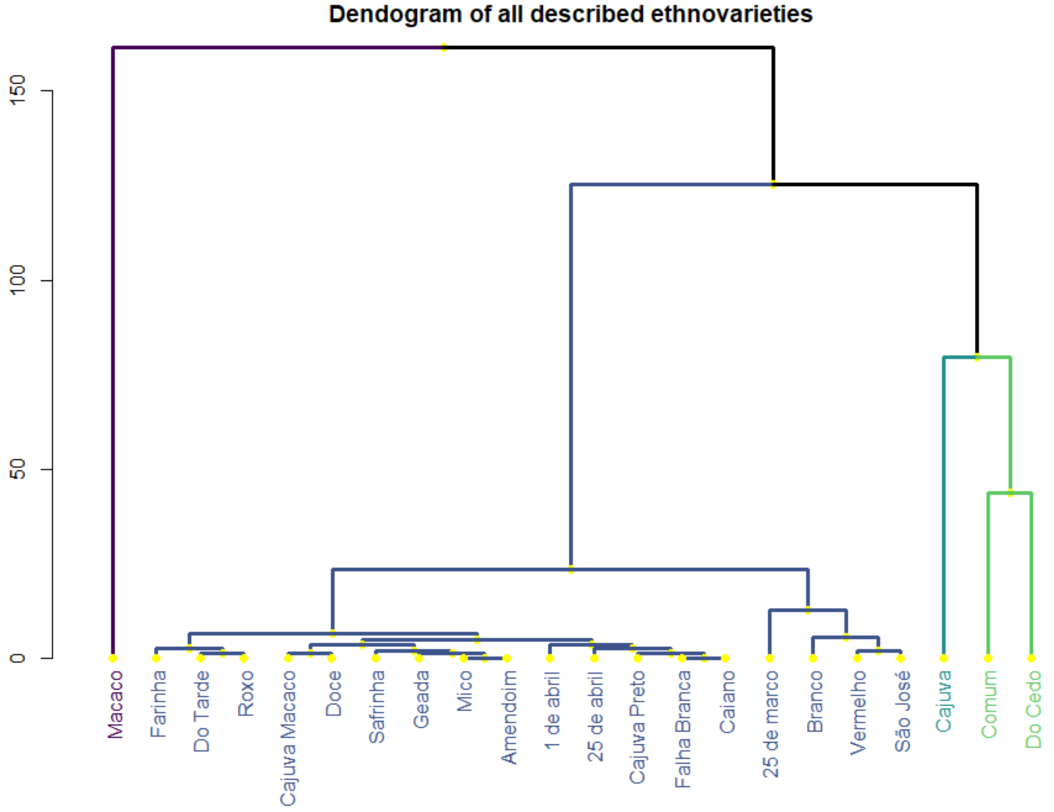


Table 1: Ethnoecological questionnaire. We applied a semi-structured questionnaire with open-ended questions. This feature allowed us to collect cultural, ecological, and socio-economic information with TEK holders in the *Araucaria* Forest System and thus describe potential benefits and risks of collaborative management strategies under a theoretical framework.

Universidade Federal de Santa Catarina
Programa de Pós-Graduação em Ecologia
Laboratório de Ecologia Humana e Etnobotânica

Interview script; Co-orientation: Dr.; Orientation: Prof. Dr.

CAEE: 86394518.0.0000.0121

Identification
Interview N°

Researcher__________________________ Municipality________________
Community____________________________________

Georeference ______________S__________________N____________A

Data _______________

Interviewee _____________________________________________________

Age _________________ Gender: ( ) M ( ) F

Occupation ________________________ Property area(ha): __________

Main activity _______________________
Residence time____________
How many family generations live in the region? ____________

PART A (*ARAUCARIA* FOREST)

A1. Are there *Araucaria* remnants in your property?

A2. Do you know the size of your remnant areas inside your property?
Small (until 10% ) _____
Medium (between 10 to 50% ) _____
Big (> 50%) _____

A3. Is there pinhão gathering/extraction/commerce in your property?
Yes _____ No _____

If the previous question was affirmative

A3a. What is the importance of pinhão in your property?

A4. Is there more male *Araucaria* than female? Why?

A6. Do you know the reason for this difference?

( ) absence of male / pollination ( ) / timber exploration ( )

slash and burn (agriculture) ( ) / dispersers' absence ()

changing climate ( ). Any other??

A7. Did *Araucaria* population increase from past to current moment? ( ) Yes( ) No

A7a. If there was an increase, describe the main causes

( ) Protected Areas ( ) Community participation ( )

fauna dispersion ( ) *Araucaria* management

other:

A7b. If any increase was identified, describe the causes:
( ) Illegal cutting / ( ) Seedling suppression / ( ) Cattle /
other:

---

## PART B (*ARAUCARIA*, LANDSCAPE AND RESOURCES' USE)

---

B1. What are the best conditions for *Araucaria* development?

( ) water (riverbeds) ( ) deep and fertile soil

( ) fields ( ) difficult to access and shaded areas (e.g. valleys)

( ) cold regularly and intense () there is no specific condition (born anywhere) other:

B2. What are the ideal conditions to produce pine nuts?

B2. On average, what is the production of pine nuts on your property (in kg) annually?

B3. On average, what is the consumption of pine nuts (in kg) annually on your property?

B4. How many different ethnovarieties of *Araucaria* do you identify in the landscape of your property?

B5. Which ethnovarieties of *Araucaria* do you know?

B6. What is the difference between each of the ethnovarieties you know?

B7. Do you identify the types of *Araucaria* by plant or pine nuts? Or both?

If types are identified, what differentiates them from each other?

B8. What types of pine nuts / plants are most common on your property?

B9. Which *Araucaria* ethnovarieties are commonly identified and which ethnovarieties are rare through the landscape?

B10. What is the season of maturation of the types of pine nuts that you know throughout the year?

B11. How long ethnovarieties occur throughout the year?

B12. Which of these “areas” (landscape units) do you have on the property?

( ) fields / crops ( ) pine / eucalyptus ( ) wintering ( ) orchard ( ) Legal Reserve ( ) APP

B13. Do you use management techniques for *Araucaria*?

If yes:

B13b.

( ) pasture fires, how often?

( ) mowing, what frequency?

Other:

B14b. Do you manage trees / select types?

( ) selects *Araucaria* types

Other:

B14c Do you handle the types of pine cones, and consequently, the type of pine nuts?

Describe the management you perform:

( ) Selects pinion types

Other:

B15. What are the characteristics of the ethnovarieties that you identify on your property regarding:

Tree shape:

Pinion shape and color?

Preferred location of types in the landscape (e.g. hillside, falls, near water bodies, etc.)

B16. Is it possible to identify the ethnovarieties of male *Araucaria*? If so, describe the characteristics of these types:

---

PART C (SPATIAL AND FUTURE PERSPECTIVES)

---

C1. If there is a temperature increase (get warmer) in the future, where will we find more *Araucaria*s?

( ) at higher areas ( ) in areas closer to rivers

( ) on slopes and valleys ( ) cooler areas in general

( ) there will be no change in the areas where they currently occur

other_________________________________________________________________
_____________

C2. Has there been a change in any climatic factor over time? For example (more or less rain, more or less cold winters, more or less strong summers, etc.). If so, how does it affect the *Araucaria* population?

C3. Has the production of pine nuts been affected over time?
If the answer is yes:
C3a. Were there more pine nuts in the past than today? Why?

C4. What is your opinion on climate change in the distribution of *Araucaria* types in the landscape?

---

# 6 DISCUSSÃO GERAL

A presente tese buscou avaliar, usando Modelagens Ecológicas de Nicho (MEN) e levantamentos in situ do conhecimento de povos tradicionais, os efeitos e as distintas implicações das mudanças climáticas sobre duas espécies-chave, tanto para a estruturação de comunidades e ecossistemas quanto da manutenção de sistemas socioecológicos. O principal objetivo foi alcançado, conforme explicitado nos resultados descritos e discutidos em cada um dos Capítulos de que se compõe este projeto de pesquisa. Observando os objetivos específicos, contudo, pode-se compreender que, embora existam em literatura dados bastante robustos e conclusivos sobre os efeitos deletérios que as mudanças climáticas e as alterações dos parâmetros abióticos possam exercer sobre espécies-chave, estes não seguem estritamente os padrões preditos para as espécies avaliadas. Por isto, vale reforçar a importância do alinhamento entre os instrumentos matemáticos, tais como os MEN juntamente com as inferências coletadas em campo, os conhecimentos de povos tradicionais e os estudos sobre a fenologia das espécies focais, para a implementação de estratégias mais eficazes à conservação das mesmas e interpretações das distintas implicações espaço-temporais.

Os dois primeiros Capítulos deste manuscrito trouxeram a aplicação de uma ferramenta cada vez mais reconhecida e valorizada em estudos ecológicos, as modelagens de nicho. Estas foram realizadas com base em dados históricos e levantamentos em campo da distribuição de espécies-chave, sendo a *A. angustifolia* representante das florestas ombrófilas mistas no Brasil e *Adansonia* spp., incluindo as seis espécies endêmicas do gênero, como as ocorrentes em Madagascar. Ambas as fitofisionomias possuem particularidades e distinções entre elas, que permitem por si só inferências específicas, tanto sobre a relevância quanto os enviesamentos que a aplicação de modelagens de nicho pode representar na interpretação dos resultados preditivos das mudanças climáticas sobre a distribuição das mesmas em seus nichos fundamentais e realizados. Entretanto, cabe também ressaltar que tais limitações das modelagens, como será discutido sequencialmente, também representam um fator analítico relevante para a gestão integrativa e medidas mais eficazes de conservação de sistemas naturais.

No caso específico das modelagens realizadas para as espécies de *Adansonia*, os resultados demonstraram divergências entre as proposições já realizadas em relação aos padrões de migração de espécies temperadas e tropicais diante dos efeitos das mudanças climáticas. Como já observado para outras espécies florestais, aquelas que são evolutivamente adaptadas a condições temperadas tenderão à dispersão e migração em gradiente latitudinal, em direção aos polos, e em gradiente altitudinal para áreas mais elevadas. Estes ambientes, em um cenário futuro, tenderão à tropicalização, ainda que mantendo características de habitat mais similares às atuais condições climáticas das zonas temperadas. Ao observarmos que algumas espécies endêmicas de baobás não seguem este padrão, também nos foi possível a inferência de um sentido oposto de tendência dispersiva e migratória, em direção às áreas mais próximas à linha do Equador.

A partir destes resultados de MEN novas teorias foram propostas para tal cenário, que consideraram a biologia das espécies e do gênero, e mesmo o planejamento na realização das modelagens. Conforme os dados apresentados, a MEN feita para as espécies de Madagascar indica um potencial de expansão de áreas propícias para a colonização em menores latitudes. Ao inserirmos variáveis aquém das relacionadas com as variações das temperaturas (mínimas, médias e máximas), tais como precipitações médias, déficit hídrico e sazonalidade das temperaturas, estes parâmetros demonstraram grande relevância no poder preditivo e explicativo das diferenças obtidas para os padrões migratórios esperados. De acordo com a biologia das espécies, uma vez que espécies com tolerâncias mais estritas às condições climáticas em zonas temperadas, estas poderão encontrar maior estabilidade ambiental em áreas de menor latitude, favorecendo sua ocupação nestas áreas específicas.

Apesar dos parâmetros abióticos, e das implicações fisiológicas de tais condições de habitat para o sucesso de sobrevivência das espécies analisadas de *Adansonia*, também há que se considerar outros fatores ambientais e culturais como medidas para conservação eficaz das espécies endêmicas. Ao considerar-se a área insular de Madagascar, observa-se que as áreas propícias à conservação das espécies de baobás serão ainda mais restritas, o que influencia diretamente nos esforços de delimitação de áreas prioritárias ao manejo e conservação. Ademais, nota-se que as áreas mais ao norte do país, onde o nicho climático do gênero mostra-se mais favorável em cenários futuros de mudanças climáticas para as espécies mais vulneráveis, também representam algumas das áreas mais intensamente modificadas por usos humanos, com manejo inadequado de solo, uso intensivo de áreas florestais para agricultura e remoção de cobertura florestal. Todas estas alterações na paisagem podem significar um efeito de fragmentação ainda maior nos remanescentes florestais de baobás, comprometendo a viabilidade reprodutiva e o sucesso de colonização. Sendo assim, as modelagens de nicho para as espécies de baobás demonstram que outros fatores ambientais também devem ser inclusos em análises mais abrangentes de redistribuição populacional, de forma que a ecologia e a ecofisiologia da espécie sejam também relevantes na seleção de áreas prioritárias à conservação, em detrimento de padrões bem estabelecidos em literatura, que não podem ser tomados como únicos e absolutos para mitigar o efeito das mudanças climáticas em espécies potencialmente ameaçadas de extinção em seu habitat natural. Estas ponderações e considerações são fundamentais para estudos futuros e modelagem de outras espécies florestais ocorrentes nas latitudes tropicais e temperadas, de forma a verificar a efetividade e aplicabilidade de padrões migratórios estabelecidos como reais para espécies de relevância ecológica à conservação sistêmica.

Em oposição, as modelagens aplicadas para a distribuição de *A. angustifolia* foram exploradas com outro viés de análise. Esta espécie tem fundamental importância sociocultural, e como ressaltado, desempenha um papel histórico na construção social e formação das paisagens da região sul do país, especialmente a região serrana do estado de Santa Catarina, dos campos de altitude no Rio Grande do Sul, no planalto central paranaense e nas poucas manchas remanescentes de altitute na área da Serra da Mantiqueira, nos estados de Minas Gerais e São Paulo. Foram aplicados modelos ecológicos de nicho, explorando justamente o viés dos efeitos das mudanças climáticas, com ênfase nas variações em temperaturas, sobre a sua distribuição e áreas prioritárias à conservação. Estes resultados evidenciaram a concordância com os atuais modelos e padrões esperados para a distribuição florestal de espécies temperadas, com um deslocamento de áreas de habitat adequadas em maiores altitudes e latitudes. Neste caso, a temperatura média anual é fundamental para a espécie, o que é determinante para adequabilidade de habitat, devido à fenologia da espécie em análise.

Este cenário também está alinhado com as expectativas de perda de áreas de cobertura vegetal e distribuição da espécie diante dos cenários previstos para as mudanças climáticas. Especificamente, os dados de modelagem corroboraram a contração de áreas adequadas para a ocorrência da espécie, além da fragmentação destes habitats a zonas restritas, onde os parâmetros abióticos possam suportar as populações. A fragmentação populacional é um dos fatores contributivos para a perda de variabilidade genética, o que aumenta o risco de vulnerabilidade frente aos distúrbios ambientais, sejam eles fatores abióticos ou bióticos, tais como competição, doenças e invasões por espécies exóticas/alóctones. Por isto, a conservação de tais áreas não é em si uma seguridade para a manutenção da dinâmica populacional ou da preservação da espécie-chave, uma vez que outros fatores, tais como a conectividade, devem ser prioritariamente considerados no delineamento de estratégias de manejo e conservação.

No caso das araucárias no Brasil, estratégias de conservação relacionadas ao estabelecimento de Unidades de Conservação vêm sendo propostas. Entretanto, conforme o presente estudo aponta, estas unidades não se mostrarão efetivas em cenários futuros de predição das mudanças climáticas. Isto porque as áreas destinadas à conservação da araucária não se mostram pertinentes dentro das modelagens de adequabilidade de habitat, uma vez que: i) não oferecem o adequado dimensionamento ou inclusão de áreas onde, futuramente, a espécie terá maior probabilidade de ocorrência e sobrevivência; e ii) considerando as atuais áreas destinadas à conservação, a conectividade entre os remanescentes florestais e em especial, as manchas de habitat adequado, não serão afetivas para manutenção de fluxo gênico.

Pautado nestes resultados, o presente estudo evidenciou, a partir do embasamento e mapeamento das áreas de distribuição de araucária, que os efeitos das mudanças climáticas em escala continental serão diferentes daqueles esperados para um país insular. Igualmente, os efeitos das mudanças no clima, incluindo tanto o aumento médio das temperaturas, bem como as alterações nos regimes de chuvas e secas, exercem uma pressão abiótica que se torna forçante de migração da espécie para áreas mais favoráveis ao seu desenvolvimento. Assegurar, portanto, que estas áreas recebam adequados esforços de manejo e restauração é prioritário para a conservação.

Nesta dimensão, a araucária tem uma importância sociocultural fundamental, sobretudo no sul do país. A partir do manejo, através do extrativismo de agricultores familiares e coletores de pinhão, muitas comunidades mantém tradições e culturas, desde a identificação e sensação de pertencimento, até mesmo na identidade cultural de inúmeros municípios, além de sustentar uma cadeia produtiva inteira pelo comércio do pinhão. Consequentemente, demonstra que a araucária é um elemento chave não apenas na estruturação e composição de uma fitofisionomia, mas de uma paisagem cultural moldada historicamente. Por esta razão, a avaliação dos efeitos que as mudanças climáticas podem exercer sobre essa fitofisionomia, e sobretudo, sobre esta paisagem sociocultural, não poderia estar dissociada de tais atores, que são agentes modificadores e utilitários dos recursos naturais. A partir da identificação deste contexto, foram propostos e delineados dois estudos, que trataram, respectivamente, de abordagens distintas que avaliam facetas das mudanças climáticas e quais fatores podem gerar resiliência ao iminente impacto das mudanças climáticas. No terceiro Capítulo, avaliamos os atuais modelos de gestão de unidades de conservação em relação à resiliência do sistema de Floresta de Araucárias, enquanto o quarto Capítulo avaliou na relação entre os serviços ecossistêmicos deste ambiente e a contribuição do conhecimento tradicional para o manejo e conservação, mostrando que sem o conhecimento tradicional as mudanças climáticas podem ruir este sistema socioecológico.

Conforme apresentado no referencial teórico da presente tese, as Unidades de Conservação se subdividem em diferentes categorias, de acordo com o seu objeto de conservação e estratégia de manejo. Entre aquelas onde é possível exercer atividades de extrativismo e/ou manejo sustentável dos recursos naturais, estão as áreas de cobertura de araucária, onde podem ser implementadas ações correlatas com os conhecimentos tradicionais para a preservação dos remanescentes florestais. Este fato é reforçado pelos resultados das análises de modelos aplicadas, onde os modelos tradicionais de conservação foram confrontados com cenários alternativos de estratégias de manejo e restauração para prover maior resiliência frente a distúrbios climáticos.

Neste trabalho, observou-se que a implementação de Unidades de Conservação estritamente para a preservação, sem nenhum tipo de manejo ou interferência humana, não se mostra como o sistema mais eficaz para a fitofisionomia em análise. Estas unidades estão sujeitas a outras interferências, igualmente deletérias e prejudiciais à conservação das espécies deste sistema. Entre tais distúrbios, majoritariamente relacionados com atividades antrópicas em nível local, estão a introdução de espécies exóticas com potencial invasor, patógenos e supressão de populações de dispersores naturais, tais como aves e mamíferos. Como discussão adicional aos dados, apresento a viabilidade de tal estratégia frente à redução das taxas de desmatamento e supressão vegetal como justificativa para a sua implementação. Teoricamente, a manutenção das áreas de cobertura poderia exercer um efeito de tamponamento (*buffer*) sobre os impactos e estressores diversos, já que a população poderia manter sua dinâmica, recolonizando e migrando a partir de manchas mais adensadas para áreas de campos. Em especial no caso das araucárias, foi constatado que a área sob a sua copa proporciona microambientes favoráveis ao recrutamento de diversas espécies vegetais, o que viabiliza a expansão da floresta (DUARTE *et al.*, 2006). Isto porque, com a presença de espécies lenhosas e produtoras de frutos, como as Myrtaceae, são atrativas a dispersores zoocóricos, que facilitam a dispersão da araucária e a sua colonização nas bordas da floresta, avançando sobre as áreas de campo (DUARTE *et al.*, 2006).

Entretanto, a realidade atual das Unidades de Conservação não permite um cenário promissor ou mesmo seguro com relação a esta proteção, uma vez que áreas destinadas à conservação integral são ainda alvo de exploração madeireira ilegal, o que adiciona um fator de perturbação ao sistema. Ademais, como observado nos resultados da modelagem, as Unidades de Conservação estritas não promovem um aumento na resiliência da araucária frente às mudanças climáticas, uma vez que possíveis supressões na cobertura vegetal ou mesmo a presença de outros distúrbios reduzem a viabilidade de expansão da floresta e a manutenção da dinâmica de suas populações.

Outro fator preocupante realçado com os presentes resultados diz respeito à efetividade das atuais Unidades de Conservação. Como observado nas modelagens e cenários preditivos dos efeitos das mudanças climáticas sobre a distribuição da espécie, a araucária terá seu espaço de nicho e disponibilidade de habitat restritos às áreas de altitude e zonas de maiores latitudes (veja dados no Capítulo III). Entretanto, como foi correlacionado, as atuais Unidades de Conservação compreendem uma área inferior a 15% dos remanescentes da Floresta de Araucárias, o que coloca em risco a proteção da espécie, não priorizando a delimitação de tais áreas de conservação a ambientes com adequabilidade de habitat.

Ainda considerando a contração predita para a década de 2070, de acordo com as mudanças no clima e nas variáveis abióticas locais por elas influenciadas, os remanescentes de araucárias não contarão com áreas destinadas à conservação que sejam adequadas à sua preservação. Adicionalmente, como estes remanescentes tenderão a ocupar áreas de maior altitude, espera-se que o efeito da fragmentação de habitat e a consequente constituição de metapopulações seja responsável por uma maior pressão sobre a espécie, levando-a ao declínio populacional e mesmo à extinção local e/ou regional. Conforme estudos em nível populacional clássicos na ecologia, metapopulações que apresentem baixa conectividade entre si, não viabilizando a troca gênica e/ou estrutura para a progressão e expansão de suas populações, tendem a contrair-se ao longo do tempo, sendo mais vulneráveis a efeitos estocásticos e distúrbios (BULL *et al.*, 2007).

Por outro lado, o modelo que incorpora o fator de manejo sustentável, a partir dos conhecimentos tradicionais das comunidades relacionadas à araucária, mostra um cenário mais promissor em relação à manutenção da floresta, bem como a resiliência frente a distúrbios. A partir do manejo colaborativo, observa-se a viabilidade de estágios alternativos no equilíbrio dinâmico do ecossistema. Os estágios alternativos, como compreendido e descrito em literatura, são fundamentais para uma maior resiliência ambiental frente a diferentes distúrbios (BEISNER; HAYDON; CUDDINGTON, 2003). Isto porque proporcionam tanto estados transitórios, quando dos processos de sucessão ecológica, quanto constituírem estados intermediários e diversos da dinâmica original do ambiente. Estes estados intermediários são ecologicamente relevantes, uma vez que oportunizam uma maior resiliência aos distúrbios, consistindo em rearranjos em estrutura na comunidade que permitem o reestabelecimento da dinâmica populacional ao longo do tempo (BEISNER; HAYDON; CUDDINGTON, 2003).

Ao identificar a importância e relevância do conhecimento tradicional para a manutenção sistêmica da Floresta de Araucária, também era preciso mensurar os benefícios - ou seja, os serviços ecossistêmicos - que a floresta representa no estabelecimento e manutenção das comunidades tradicionais e quais os riscos caso perdidos. Apesar de atualmente restrita em relação à sua área de cobertura original, os remanescentes da Floresta de Araucária distribuemse entre o Sudeste e Sul do Brasil, sendo nesta última região a sua maior área de conservação e cobertura. Ainda assim, pequenos produtores agrícolas e comunidades tradicionais dos três estados do Sul, além de São Paulo e Minas Gerais, são intimamente ligados com o extrativismo da araucária, com a sua renda familiar dependente da comercialização do pinhão. Estes produtores detêm profundo conhecimento a respeito das variedades de pinhões, e das melhores estratégias de colheita e manejo florestal, que seguramente são norteadores altamente relevantes para o estabelecimento de políticas públicas focadas na conservação florestal.

Como avaliado e descrito presentemente, os MEN demonstraram a contração das áreas de ocorrência de araucárias (Capítulos II e III), o que trará uma implicação direta na perda dos serviços ecossistêmicos relacionados com este sistema. Não apenas a desestruturação da comunidade biológica, mas também de toda a estrutura sociocultural e das tradições comunitárias em torno da colheita do pinhão, bem como dos conhecimentos tradicionais relacionados ao funcionamento sistêmico. Este fato demonstra que a relação humana com a paisagem de araucárias trata-se de uma via de mão dupla para que as iniciativas de conservação sejam efetivas. Não apenas o homem depende do recurso, seja por fatores econômicos e culturais, como o conhecimento sobre a biologia da espécie, as variedades de pinhão e estratégias de manejo e colheita são decisivas para preservação das araucárias.

O conhecimento tradicional sobre esta espécie-chave é o responsável pela modificação da paisagem nas áreas de ocorrência da araucária. Pela dependência dos recursos oriundos da coleta das semenstes, o manejo da araucária vem sendo transmitido por gerações a partir dos povos originários, que já utilizavam as sementes como recurso alimentar-energético. Estes conhecimentos, ao serem partilhados, constituem uma unidade cultural que estrutura um sistema socioecológico, através do qual a conservação da araucária é promovida graças ao manejo sustentável. Sendo assim, a manutenção da unidade social e cultural tendo a araucária como espécie-focal da conservação é fundamental para acessar e promover o manejo cooperativo. Sem ele, a resiliência das araucárias frente aos estressores climáticos, tanto em escala regional quanto local, terão um efeito muito mais severo sobre a expansão e manutenção das populações em seu habitat. O manejo humano, através da reintrodução da espécie e também do monitoramento, é fator decisivo na conservação das Florestas de Araucárias nas paisagens montanas do sul e sudeste brasileiros.

# 7 CONCLUSÃO

A presente tese cumpriu seu objetivo no tocante à compreensão dos efeitos das mudanças climáticas nos padrões de distribuição de espécies-chave para a conservação da biodiversidade. Através das Modelagens Ecológicas de Nicho (MENs), foi possível observar que os efeitos das mudanças climáticas atuarão de forma diferenciada sobre os padrões de distribuição de *A. angustifolia* e as espécies malgaches do gênero *Adansonia*. Também refletem que, ao considerarmos diferentes escalas espaciais, os parâmetros abióticos exercerão diferentes pressões ecofisiológicas, como reflexo direto da adequabilidade de habitat, modificando as áreas propícias à distribuição das espécies. Sendo assim, torna-se imprescindível a análise holística e integrativa destes fatores na modelagem de nicho, de forma a identificar áreas prioritárias à conservação e ao manejo sustentável das espécies-chave para a estruturação de comunidades. A partir do conhecimento da biologia e de sua integração com os fatores preditivos das mudanças climáticas, o direcionamento para tomada de decisão referente às estratégias de conservação poderá alcançar resultados mais efetivos na conservação destas espécies.

Nos presentes resultados, também foi possível identificar o papel imprescindível que o conhecimento tradicional apresenta para a conservação de sistemas socioecológicos. Através de modelos de gestão participativos e com a aplicação de manejo sustentável, pautado nos conhecimentos tradicionais, a conservação da araucária, como modelo analítico de sistema socioecológico, mostra-se mais favorável, comparativamente a um cenário onde as áreas protetivas sejam destinadas à conservação estrita da espécie.

Por fim, é possível inferir que as modelagens de nicho, ainda que não sejam determinísticas, possuem papel fundamental no delineamento de políticas públicas de conservação. Através da observação conjunta entre as modelagens matemáticas e o conhecimento de povos tradicionais, é possível traçar projetos mais eficazes, cooperativos e integrativos, que permitam não apenas a conservação ambiental, mas a manutenção sociocultural que aproxima os povos tradicionais de seu ambiente, pelo reconhecimento e identificação com a paisagem e seus recursos, além de fornecer subsídios para a resiliência socioecológica frente a distintos distúrbios.

# 8 REFERÊNCIAS

ADAN, N.; ATCHISON, J.; REIS, M. S.; PERONI, N. Local knowledge, use and management of ethnovarieties of *Araucaria angustifolia* (Bert.) Ktze. in the Plateau of Santa Catarina, Brazil. **Economic Botany**, v. 70, n. 4, p. 353–364, 2016.

ANDERSON-TEIXEIRA, Kristina J.; MILLER, Adam D.; MOHAN, Jacqueline E.; HUDIBURG, Tara W.; DUVAL, Benjamin D.; DELUCIA, Evan H. Altered dynamics of forest recovery under a changing climate. **Global Change Biology**, v. 19, n. 7, p. 2001–2021, 1 Jul. 2013. DOI: 10.1111/gcb.12194.

ARAÚJO, Miguel B.; ANDERSON, Robert P; BARBOSA, A Márcia; BEALE, Colin M; DORMANN, Carsten F; EARLY, Regan; GARCIA, Raquel A; GUISAN, Antoine; MAIORANO, Luigi; NAIMI, Babak; O'HARA, Robert B; ZIMMERMANN, Niklaus E; RAHBEK, Carsten. **Standards for distribution models in biodiversity assessments**. 2019. Available at: http://advances.sciencemag.org/. Acesso em: 6 Jan. 2020.

BAUM, David A. The comparative pollination and floral biology of baobabs (*Adansonia*-Bombacaceae). **Annal Missouri Botanical Garden**, v. 82, n. 2, p. 322–348, 1995.

BEISNER, B. E.; HAYDON, D. T.; CUDDINGTON, K. Alternative stable states in ecology. **Frontiers in Ecology and the Environment**, v. 1, n. 7, p. 376–382, 2003.

BELLARD, Céline; BERTELSMEIER, Cleo; LEADLEY, Paul; THUILLER, Wilfried; COURCHAMP, Franck. Impacts of climate change on the future of biodiversity. **Ecology Letters**, v. 15, n. 4, p. 365–377, 2012.

BERGAMIN, Rodrigo S.; DEBASTIANI, Vanderlei; JONER, Daiany C.; LEMES, Priscila; GUIMARÃES, Taís; LOYOLA, Rafael D.; MÜLLER, Sandra C. Loss of suitable climatic areas for Araucaria forests over time. **Plant Ecology and Diversity**, v. 12, n. 2, p. 115–126, 4 Mar. 2019. DOI 10.1080/17550874.2019.1618408.

BERKES, Fikret; COLDING, Johan; FOLKE, Carl. Rediscovery of traditional ecological knowledge as adaptive management. **Ecological Applications**, v. 10, n. 5, p. 1251–1262, 2000.

BITENCOURT, Ana Luisa Vietti; KRAUSPENHAR, Patrícia Maria. Possible prehistoric anthropogenic effect on. **Revista Brasileira de Paleontologia**, v. 9, n. 1, p. 109–116, 2006.

BOGONI, Juliano André; GRAIPEL, Maurício Eduardo; PERONI, Nivaldo. The ecological footprint of *Acca sellowiana* domestication maintains the residual vertebrate diversity in threatened highlands of Atlantic Forest. **PLOS ONE**, vol. 13, no. 4, p. e0195199, 4 Apr. 2018. DOI 10.1371/journal.pone.0195199.

BOGONI, Juliano André; PERES, Carlos A.; FERRAZ, Katia M.P.M.B. Effects of mammal defaunation on natural ecosystem services and human well being throughout the entire Neotropical realm. **Ecosystem Services**, v. 45, p. 101173, 1 Oct. 2020. DOI: https://doi.org/10.1016/j.ecoser.2020.101173.

BRASIL. **Lei nº 9.985, de 18 de julho de 2000**. Regulamenta o art. 225, § 1o, incisos I, II, III e VII da Constituição Federal, institui o Sistema Nacional de Unidades de Conservação da Natureza e dá outras providências. Disponível em: http://www.planalto.gov.br/ccivil_03/leis/L9985.htm. Acesso em: 15 Jun. 2021.

BRODIE, Jedediah; POST, Eric; LAURANCE, William F. Climate change and tropical biodiversity: A new focus. **Trends in Ecology and Evolution**, v. 27, n. 3, p. 145–150, 2012. DOI 10.1016/j.tree.2011.09.008.

BULL, James C; PICKUP, Nicola J; PICKETT, Brian; HASSELL, Michael P; BONSALL, Michael B. Metapopulation extinction risk is increased by environmental stochasticity and assemblage complexity. **Proceedings of the Royal Society B: Biological Sciences**, v. 274, n. 1606, p. 87–96, 7 Jan. 2007. DOI 10.1098/rspb.2006.3691.

CASTRO, Monik Begname; BARBOSA, Ana Carolina Maioli Campos; POMPEU, Patrícia Vieira; EISENLOHR, Pedro V.; DE ASSIS PEREIRA, Gabriel; APGAUA, Deborah Mattos Guimarães; PIRES-OLIVEIRA, João Carlos; BARBOSA, João Paulo Rodrigues Alves Delfino; FONTES, Marco Aurélio Leite; DOS SANTOS, Rubens Manoel; TNG, David Yue Phin. Will the emblematic southern conifer *Araucaria angustifolia* survive to climate change in Brazil? **Biodiversity and Conservation**, v. 29, n. 2, p. 591–607, 2019.

CATEN, Cléber Ten; LIMA-RIBEIRO, Matheus de Souza; DA SILVA, Nelson Jorge; MORENO, Ana Karolina; TERRIBILE, Levi Carina. Evaluating the Effectiveness of Brazilian Protected Areas Under Climate Change. **Tropical Conservation Science**, vol. 10, p. 194008291772202, 2017. https://doi.org/10.1177/1940082917722027.

CHEN, I. Ching; SHIU, Hau Jie; BENEDICK, Suzan; HOLLOWAY, Jeremy D.; CHEY, Vun Khen; BARLOW, Henry S.; HILL, Jane K.; THOMAS, Chris D. Elevation increases in moth assemblages over 42 years on a tropical mountain. **Proceedings of the National Academy of Sciences of the United States of America**, v. 106, n. 5, p. 1479–1483, 2009.

COLWELL, R. K. *et al.* Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. **Science**, v. 322, n. 5899, p. 258–261, 10 Oct. 2008. DOI 10.1126/science.1162547.

CRIMMINS, Shawn M.; DOBROWSKI, Solomon Z.; GREENBERG, Jonathan A.; ABATZOGLOU, John T.; MYNSBERGE, Alison R. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. **Science**, v. 331, n. 6015, p. 324–327, 2011. DOI https://doi.org/10.1126/science.1199040.

CRUZ, Aline Pereira; GIEHL, Eduardo Luiz Hettwer; LEVIS, Carolina; MACHADO, Juliana Salles; BUENO, Lucas; PERONI, Nivaldo. Pre-colonial Amerindian legacies in forest composition of southern Brazil. **PLoS ONE**, v. 15, n. 7 July, p. 1–18, 2020.

DE BRUIJN, Karin; BUURMAN, Joost; MENS, Marjolein; DAHM, Ruben; KLIJN, Frans. Resilience in practice: Five principles to enable societies to cope with extreme weather events. **Environmental Science and Policy**, v. 70, p. 21–30, 2017.

DE KORT, H. *et al.* Life history, climate and biogeography interactively affect worldwide genetic diversity of plant and animal populations. **Nature Communications**, v. 12, n. 516,

2021. DOI: https://doi.org/10.1038/s41467-021-20958-2.

DE SOUZA, G. Coelho; KUBO, R.; GUIMARÃES, L.; ELISABETSKY, E. An ethnobiological assessment of *Rumohra adiantiformis* (samambaia-preta) extractivism in Southern Brazil. **Biodiversity and Conservation**, v. 15, n. 8, p. 2737–2746, 2006.

DI COLA, Valeria; BROENNIMANN, Olivier; PETITPIERRE, Blaise; BREINER, Frank T.; D'AMEN, Manuela; RANDIN, Christophe; ENGLER, Robin; POTTIER, Julien; PIO, Dorothea; DUBUIS, Anne; PELLISSIER, Loic; MATEO, Rubén G.; HORDIJK, Wim; SALAMIN, Nicolas; GUISAN, Antoine. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. **Ecography**, v. 40, n. 6, p. 774–787, 1 Jun. 2017. DOI 10.1111/ecog.02671.

DORMANN, Carsten F.; SCHYMANSKI, Stanislaus J.; CABRAL, Juliano; CHUINE, Isabelle; GRAHAM, Catherine; HARTIG, Florian; KEARNEY, Michael; MORIN, Xavier; RÖMERMANN, Christine; SCHRÖDER, Boris; SINGER, Alexander. Correlation and process in species distribution models: bridging a dichotomy. **Journal of Biogeography**, v. 39, n. 12, p. 2119–2131, 1 Dec. 2012. DOI 10.1111/j.1365-2699.2011.02659.x.

DOS SANTOS, Karine Louise; PERONI, Nivaldo; GURIES, Raymond Paul; NODARI, Rubens Onofre. Traditional knowledge and management of Feijoa (*Acca sellowiana*) in Southern Brazil. **Economic Botany**, v. 63, n. 2, p. 204–214, 2009.

DUARTE, Leandro Da S.; DOS-SANTOS, M. M. G.; HARTZ, Sandra M.; PILLAR, V. Depatta. Role of nurse plants in Araucaria Forest expansion over grassland in south Brazil. **Austral Ecology**, v. 31, n. 4, p. 520–528, 1 Jun. 2006.

DUFLOT, R.; AVON, C.; ROCHE, P.; BERGÈS, L. Combining habitat suitability models and spatial graphs for more effective landscape conservation planning: An applied methodological framework and a species case study. J**ournal for Nature Conservation,** v. 46, p. 38-47, 2018.

ELITH, Jane; FRANKLIN, Janet. Species Distribution Modeling. **Encyclopedia of Biodiversity**. Second. [*S. l.*]: Elsevier, 2013. p. 692–705. DOI 10.1016/B978-0-12-384719-5.00318-X. Disponível em: https://linkinghub.elsevier.com/retrieve/pii/B978012384719500318X. Acesso em: set. 2021.

ELITH, Jane *et al.*. Novel methods improve prediction of species' distributions from occurrence data. **Ecography**, v. 29, p. 129–151, 2006.

ELITH, Jane; KEARNEY, Michael; PHILLIPS, Steven. The art of modelling range-shifting species. **Methods in Ecology and Evolution**, v. 1, n. 4, p. 330–342, 1 Dec. 2010.

ESSER, Luíz Fernando; NEVES, Danilo M; JARENKOW, João André. Habitat-specific impacts of climate change in the Mata Atlântica biodiversity hotspot. **Diversity and Distributions**, v. 25, n. 12, p. 1846–1856, 2019.

FADRIQUE, Belén; BÁEZ, Selene; DUQUE, Álvaro; MALIZIA, Agustina; BLUNDO, Cecilia; CARILLA, Julieta; OSINAGA-ACOSTA, Oriana; MALIZIA, Lucio; SILMAN, Miles; FARFÁN-RÍOS, William; MALHI, Yadvinder; YOUNG, Kenneth R.; CUESTA C, Francisco; HOMEIER, Jurgen; PERALVO, Manuel; PINTO, Esteban; JADAN, Oswaldo; AGUIRRE, Nikolay; AGUIRRE, Zhofre; FEELEY, Kenneth J. Widespread but heterogeneous responses of Andean forests to climate change. **Nature**, v. 564, n. 7735, p. 207–212, 2018. DOI https://doi.org/10.1038/s41586-018-0715-9.

FATORIĆ, Sandra; CHELLERI, Lorenzo. Vulnerability to the effects of climate change and adaptation: The case of the Spanish Ebro Delta. **Ocean and Coastal Management**, v. 60, p. 1–10, 1 May 2012.

FEELEY, Kenneth J; SILMAN, Miles R; DUQUE, Alvaro. Where are the tropical plants? A call for better inclusion of tropical plants in studies investigating and predicting the effects of climate change. **Frontiers of Biogeography**, v. 7, n. 4, 15 Jan. 2016.

FERREIRA, Matheus Pinheiro; LOTTE, Rodolfo Georjute; D'ELIA, Francisco V.; STAMATOPOULOS, Christos; KIM, Do-Hyung; BENJAMIN, Adam R. Accurate mapping of Brazil nut trees (*Bertholletia excelsa*) in Amazonian forests using WorldView-3 satellite images and convolutional neural networks. **Ecological Informatics**, v. 63, p. 101302, 1 Jul. 2021. DOI 10.1016/j.ecoinf.2021.101302.

FERRO, Viviane G.; LEMES, Priscila; MELO, Adriano S.; LOYOLA, Rafael. The reduced effectiveness of protected areas under climate change threatens atlantic forest tiger moths. **PLoS ONE**, v. 9, n. 9, 2014.

FODEN, Wendy B. *et al*. Climate change vulnerability assessment of species. **Wiley Interdisciplinary Reviews: Climate Change**, v. 10, n. 1, p. e551, 11 Jan. 2019. DOI 10.1002/wcc.551.

FOLKE, C.; CARPENTER, S. R.; WALKER, B.; SCHEFFER, M.; CHAPIN, T.; ROCKSTROM., J. Resilience thinking: integrating resilience, adaptability and transformability. **Nature Nanotechnology**, v. 15, n. 4, p. 20, 2010.

GARCIA, Raquel A; CABEZA, Mar; RAHBEK, Carsten; ARAÚJO, Miguel B. Multiple dimensions of climate change and their implications for biodiversity. **Science (New York, N.Y.)**, v. 344, n. 6183, p. 1247579, 2 May 2014. DOI 10.1126/science.1247579.

GARIBALDI, Ann; TURNER, Nancy. Cultural keystone species: Implications for ecological conservation and restoration. **Ecology and Society**, v. 9, n. 3, p. 1, 2004. DOI https://doi.org/10.1146/annurev-pharmtox-061008-103038.

GEORGES, Damien; THUILLER, Wilfried. Multi-species distribution modeling with biomod2. **R-CRAN Project**, vol. 1, p. 11, 2013.

GODSOE, W.; JANKOWSKI, J.; HOLT, R. D.; GRAVEL, D. Integrating biogeography with contemporary niche theory. **Trends in Ecology & Evolution**, v. 32, n. 7, p. 488–499, 2017. DOI:10.1016/j.tree.2017.03.008.

GUISAN, Antoine; ZIMMERMANN, Niklaus E. Predictive habitat distribution models in ecology. **Ecological Modelling**, v. 135, n. 2–3, p. 147–186, Dec. 2000.

HARRIS, Rebecca Mary B; GROSE, Michael R.; LEE, Greg; BINDOFF, Nathaniel L.;

PORFIRIO, Luciana L.; FOX-HUGHES, Paul. Climate projections for ecologists. **Wiley Interdisciplinary Reviews: Climate Change**, v. 5, n. 5, p. 621–637, 2014.

HOFFMANN, A.A. *et al*. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples.

HUECK, K. Distribuição e Habitat Natural do Pinheiro do Paraná (*Araucaria angustifolia*). **Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. Botânica**, v. 10, p. 5, 1953. https://doi.org/10.11606/issn.2318-5988.v10i1p5-24.

IPCC, Core Writing Team; PACHAURI, R. K.; MEYER, L. A. **The IPCC Synthesis Report**. [*S. l.*: *s. n.*], 2015. https://doi.org/10.1016/S0022-0248(00)00575-3.

IPCC. Summary for Policymakers. *In*: MASSON-DELMOTTE, V. *et al.* (eds.). **Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change**. United Kingdom: Cambridge University Press. *In Press*. Disponível em: https://www.ipcc.ch/report/ar6/wg1/#FullReport. Acesso em: 02 set. 2021.

JOHNSON, S.A.; OBER, H.K.; ADAMS, D.C. Are keystone species effective umbrellas for habitat conservation? A spatially explicit approach. **Journal for Nature Conservation**, v. 37, p. 47–55, 2017. DOI:10.1016/j.jnc.2017.03.003.

JOLY, Carlos A; METZGER, Jean Paul; TABARELLI, Marcelo. Experiences from the Brazilian Atlantic Forest : ecological findings and conservation initiatives. **New Phytologist**, n. 204, p. 459–473, 2014. DOI https://doi.org/10.1111/nph.12989.

JONES, Miranda C.; DYE, Stephen R.; FERNANDES, Jose A.; FRÖLICHER, Thomas L.; PINNEGAR, John K.; WARREN, Rachel; CHEUNG, William W L. Predicting the Impact of Climate Change on Threatened Species in UK Waters. **PLoS ONE**, v. 8, n. 1, 2013.

LAENDER, Frederik de. Community and ecosystem-level effects of multipleenvironmental change drivers: Beyond null model testing. **Global Change Biology,** v. 24, p. 5021-5030, 2018. DOI: 10.1111/gcb.14382.

LAUTERJUNG, Miguel Busarello; BERNARDI, Alison Paulo; MONTAGNA, Tiago; CANDIDO-RIBEIRO, Rafael; CLÓVIS, Newton; MANTOVANI, Adelar; SEDREZ, Maurício. Phylogeography of Brazilian pine ( *Araucaria angustifolia* ): integrative evidence for pre-Columbian anthropogenic dispersal. 2018.

LEMES, Priscila; MELO, Adriano Sanches; LOYOLA, Rafael Dias. Climate change threatens protected areas of the Atlantic Forest. **Biodiversity and Conservation**, v. 23, n. 2, p. 357–368, 2014.

LENOIR, J.; GÉGOUT, J. C.; GUISAN, A.; VITTOZ, P.; WOHLGEMUTH, T.; ZIMMERMANN, N. E.; DULLINGER, S.; PAULI, H.; WILLNER, W.; SVENNING, J. C. Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. **Ecography**, v. 33, n. 2, p. 295–303, 2010.

LENOIR, J.; GÉGOUT, J. C.; MARQUET, P. A.; DE RUFFRAY, P.; BRISSE, H. A significant upward shift in plant species optimum elevation during the 20th century. **Science (New York, N.Y.)**, v. 320, p. 1768–1771, 2008.

LENOIR, J.; SVENNING, J. C. Climate-related range shifts - a global multidimensional synthesis and new research directions. **Ecography**, p. 15–28, 2015.

LEVIS, Carolina *et al*. Help restore Brazil's governance of globally important ecosystem services. **Nature Ecology and Evolution**, v. 4, n. 2, p. 172–173, 2020. DOI 10.1038/s41559-019-1093-x.

LEVIS, Carolina *et al*. How People Domesticated Amazonian Forests. **Frontiers in Ecology and Evolution**, v. 5, p. 171, 17 Jan. 2018. DOI 10.3389/fevo.2017.00171.

MALHI, Yadvinder; FRANKLIN, Janet; SEDDON, Nathalie; SOLAN, Martin; TURNER, Monica G.; FIELD, Christopher B.; KNOWLTON, Nancy. Climate change and ecosystems: Threats, opportunities and solutions. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 375, n. 1794, 2020.

MARCHIORO, Cesar A; SANTOS, Karine L; SIMINSKI, Alexandre. Present and future of the critically endangered *Araucaria angustifolia* due to climate change and habitat loss. **Forestry: An International Journal of Forest Research**, v. 93, n. 3, p. 401–410, 2020.

MARIOD, Abdalbasit Adam; SAEED MIRGHANI, Mohamed Elwathig; HUSSEIN, Ismail. *Adansonia digitata* Baobab Seed Oil. *In*: MARIOD, Abdalbasit Adam; MIRGHANI, Mohamed Elwathig Saeed; HUSSEIN, Ismail (eds.). **Unconventional Oilseeds and Oil Sources**. [*S. l.*]: Elsevier, 2017. p. 267–271. DOI 10.1016/B978-0-12-809435-8.00039-1.

MAXWELL, S.L.; BUTT, N.; MARON, M.; McAlpine, C.A.; CHAPMAN, S.; ULLMANN, A.; SEGAN, D.B.; WATSON, J.E.M. Conservation implications of ecological responses to extreme weather and climate events. **Diversity and Distributions**, v. 25, p. 613-625, 2018.

MELLO, Anna Jacinta Machado; PERONI, Nivaldo. Cultural landscapes of the Araucaria Forests in the northern plateau of Santa Catarina, Brazil. **Journal of ethnobiology and ethnomedicine**, v. 11, n. 1, p. 51, 2015. DOI 10.1186/s13002-015-0039-x.

METZGER, Jean Paul; BUSTAMANTE, Mercedes M.C.; FERREIRA, Joice; FERNANDES, Geraldo Wilson; LIBRÁN-EMBID, Felipe; PILLAR, Valério D.; PRIST, Paula R.; RODRIGUES, Ricardo Ribeiro; VIEIRA, Ima Célia G.; OVERBECK, Gerhard E. Why Brazil needs its Legal Reserves. **Perspectives in Ecology and Conservation**, v. 17, n. 3, p. 91–103, 1 Jul. 2019.

MEURANT, Margaux; GONZALEZ, Andrew; DOXA, Aggeliki; ALBERT, Cécile H. Selecting surrogate species for connectivity conservation. **Biological Conservation**, v. 227, p. 326–334, 1 Nov. 2018. DOI 10.1016/J.BIOCON.2018.09.028.

MILLS, L.S.; SOULÉ, M.L.; DOAK, D.F. The Keystone-Species concept in ecology and conservation. **BioScience**, v. 43, n. 4, p. 219–224, 1993. DOI:10.2307/1312122.

MONTAGNA, Tiago; LAUTERJUNG, Miguel Busarello; COSTA, Newton Clóvis Freitas da; BERNARDI, Alison Paulo; CANDIDO-RIBEIRO, Rafael; REIS, Maurício Sedrez dos.

Guidelines for seed collection of *Araucaria angustifolia* (Bertol.) Kuntze: A genetic, demographic and geographic approach. **Forest Ecology and Management**, v. 438, p. 10–17, 2019. DOI https://doi.org/10.1016/j.foreco.2019.02.006.

MORELLI, Toni Lyn *et al*. The fate of Madagascar's rainforest habitat. **Nature Climate Change**, v. 10, n. 1, p. 89–96, 1 Jan. 2020.

MYERS, Norman. Threatened biotas: "Hot spots" in tropical forests. **Environmentalist**, v. 8, p. 187–208, 1988. DOI: https://doi.org/10.1007/BF02240252.

NAIMI, Babak; ARAÚJO, Miguel B. sdm: a reproducible and extensible R platform for species distribution modelling. **Ecography**, v. 39, n. 4, p. 368–375, 1 Apr. 2016. DOI 10.1111/ecog.01881.

OROFINO, Gabriela Guimarães; ROQUE, Thais Vezehaci; DA FONSECA KRUEL, Viviane Stern; PERONI, Nivaldo; HANAZAKI, Natalia. Local knowledge about dugout canoes reveals connections between forests and fisheries. **Environment, Development and Sustainability**, v. 20, n. 6, p. 2773–2793, 2018. DOI 10.1007/s10668-017-0016-8.

PACHECO, André A.; NEVES, Ana Carolina O.; FERNANDES, G. Wilson. Uneven conservation efforts compromise Brazil to meet the Target 11 of Convention on Biological Diversity. **Perspectives in Ecology and Conservation**, v. 16, n. 1, p. 43–48, 2018.

PATTERSON, Trista M.; COELHO, Dana L. Ecosystem services: Foundations, opportunities, and challenges for the forest products sector. **Forest Ecology and Management**, v. 257, n. 8, p. 1637–1646, Mar. 2009. DOI 10.1016/j.foreco.2008.11.010.

PECL, Gretta T. *et al*. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. **Science**, v. 355, n. 6332, p. eaai9214, 31 Mar. 2017. DOI 10.1126/SCIENCE.AAI9214.

PERES, Carlos A. Identifying Keystone Plant Resources in Tropical Forests : The Case of Gums from Parkia P. **Journal of Tropical Ecology**, v. 16, n. 2, p. 287–317, 2000.

PIGGOTT, Jeremy J.; TOWNSEND, Colin R.; MATTHAEI, Christoph D. Reconceptualizing synergism and antagonism among multiple stressors. **Ecology and Evolution**, v. 5, n. 7, p. 1538–1547, 2015.

QUINTEIRO, Mariana Martins da Costa; ALEXANDRE, Brenda da Rocha; MAGALHÃES, Luis Mauro Sampaio. Brazilian Pine (*Araucaria angustifolia* (Bertol.) Kuntze) Ethnoecology in the Mantiqueira Atlantic Forest. **Floresta e Ambiente**, v. 26, n. 1, p. 1–7, 2019.

REID, Walter V. *et al*. **Ecosystems and human well-being**. 2005. DOI 10.1196/annals.1439.003. Disponível em: http://www.who.int/entity/globalchange/ecosystems/ecosys.pdf%5Cnhttp://www.loc.gov/catdir/toc/ecip0512/2005013229.html. Acesso em: set. 2021.

REIS, Maurício S.; LADIO, Ana; PERONI, Nivaldo. Landscapes with Araucaria in South America: Evidence for a cultural dimension. **Ecology and Society**, v. 19, n. 2, 2014. DOI https://doi.org/10.5751/ES-06163-190243.

REIS, Maurício S. *et al*. Domesticated Landscapes in Araucaria Forests, Southern Brazil: A Multispecies Local Conservation-by-Use System. **Frontiers in Ecology and Evolution**, v. 6, p. 11, 7 Feb. 2018. DOI 10.3389/fevo.2018.00011.

REZENDE, C.L.; SCARANO, F.R.; ASSAD, E.D.; JOLY, C.A.; METZGER, J.P.; STRASSBURG, B.B.N.; TABARELLI, M.; FONSECA, G.A.; MITTERMEIER, R.A. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. **Perspectives in Ecology and Conservation**, 2018. DOI 10.1016/J.PECON.2018.10.002.

RIAHI, Keywan; RAO, Shilpa; KREY, Volker; CHO, Cheolhung; CHIRKOV, Vadim; FISCHER, Guenther; KINDERMANN, Georg; NAKICENOVIC, Nebojsa; RAFAJ, Peter. RCP 8.5-A scenario of comparatively high greenhouse gas emissions. **Climatic Change**, v. 109, n. 1, p. 33–57, 2011.

RIBEIRO, Bruno R.; MARTINS, Eline; MARTINELLI, Gustavo; LOYOLA, Rafael. The effectiveness of protected areas and indigenous lands in representing threatened plant species in Brazil. **Rodriguesia**, v. 69, n. 4, p. 1539–1546, 1 Oct. 2018.

RIBEIRO, Milton Cezar; CAMARGO, Alexandre Martensen; METZGER, Jean Paul; TABARELLI, Marcelo; SCARANO, Fabio; FORTIN, Marie-Josee. The Brazilian Atlantic Forest: A Shrinking Biodiversity Hotspot. **Biodiversity Hotspots - Distribution and Protection of Conservation Priority Areas**, p. 405–434, 2011. DOI 10.1007/978-3-642-20992-5.

RIBEIRO, Milton Cezar; METZGER, Jean Paul; MARTENSEN, Alexandre Camargo; PONZONI, Flávio Jorge; HIROTA, Márcia Makiko. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, v. 142, n. 6, p. 1141–1153, 2009a. DOI 10.1016/j.biocon.2009.02.021.

RIBEIRO, Milton Cezar; METZGER, Jean Paul; MARTENSEN, Alexandre Camargo; PONZONI, Flávio Jorge; HIROTA, Márcia Makiko. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, v. 142, n. 6, p. 1141–1153, 2009b. DOI https://doi.org/10.1016/j.biocon.2009.02.021.

ROBINSON, Mark *et al*. Uncoupling human and climate drivers of late Holocene vegetation change in southern Brazil. **Scientific Reports**, v. 8, n. 1, p. 7800, 17 Dec. 2018. DOI 10.1038/s41598-018-24429-5.

RODRÍGUEZ-CASTAÑEDA, G. The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. **Global Ecology and Biogeography**, v. 22, n. 1, p. 118–130, 1 Jan. 2013. DOI 10.1111/j.1466-8238.2012.00795.x.

SANQUETTA, Carlos Roberto; MATTEI, Eloi (eds.). Perspectivas de recuperação e manejo sustentável das florestas de araucária. Curitiba: Multi-Graphic Gráfica e Editora, 2006. (Programa Ecológico de Longa Duração - PELD).

SCALES, Ivan R. Farming at the Forest Frontier: Land Use and Landscape Change in

Western Madagascar, 1896-2005. **Environment and History**, v. 17, n. 4, p. 499–524, 1 Nov. 2011. DOI 10.3197/096734011X13150366551481.

SCHRÖTER, Matthias; STUMPF, Klara H.; LOOS, Jacqueline; VAN OUDENHOVEN, Alexander P.E.; BÖHNKE-HENRICHS, Anne; ABSON, David J. Refocusing ecosystem services towards sustainability. **Ecosystem Services**, v. 25, p. 35–43, Jun. 2017. DOI 10.1016/j.ecoser.2017.03.019.

SENTINELLA, Alexander T.; WARTON, David I.; SHERWIN, William B.; OFFORD, Catherine A.; MOLES, Angela T. Tropical plants do not have narrower temperature tolerances, but are more at risk from warming because they are close to their upper thermal limits. **Global Ecology and Biogeography**, v. 29, n. 8, p. 1387–1398, 2020.

SILVA JUNIOR, Celso H.L.; PESSÔA, Ana C.M.; CARVALHO, Nathália S; REIS, João B.C.; ANDERSON, Liana O; ARAGÃO, Luiz E.O.C. The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. **Nature Ecology and Evolution**, v. 5, n. 2, p. 144–145, 2021. DOI 10.1038/s41559-020-01368-x.

SOARES-FILHO, Britaldo *et al*. Role of Brazilian Amazon protected areas in climate change mitigation. **Proceedings of the National Academy of Sciences of the United States of America**, v. 107, n. 24, p. 10821–6, 15 Jun. 2010. DOI 10.1073/pnas.0913048107.

SOBERÓN, J.; ARROYO-PEÑA, B. Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. **PLoS ONE,** v. 12, n. 4, p. e0175138, 2017. DOI: https://doi.org/ 10.1371/journal.pone.0175138.

TABARELLI, Marcelo; AGUIAR, Antonio Venceslau; RIBEIRO, Milton Cezar; METZGER, Jean Paul; PERES, Carlos A. Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. **Biological Conservation**, v. 143, n. 10, p. 2328–2340, 2010. DOI 10.1016/j.biocon.2010.02.005.

TAGLIARI, Mario M. *et al*. Collaborative management as a way to enhance Araucaria Forest resilience. **Perspectives in Ecology and Conservation**, v. 19, n. 2, p. 131–142, 2021. DOI 10.1016/j.pecon.2021.03.002.

TAGLIARI, Mário Muniz; PERONI, Nivaldo. Local varieties of *Araucaria angustifolia* (Bertol.) Kuntze (Pinales : Araucariaceae) in southern Brazil: A brief discussion about landscape domestication. **Biotemas**, v. 31, n. 3, p. 59–68, 2018.

TEWKSBURY, Joshua J.; HUEY, Raymond B.; DEUTSCH, Curtis A. Ecology: Putting the heat on tropical animals. **Science**, v. 320, n. 5881, p. 1296–1297, 2008.

VELLEND, M. Conceptual Synthesis in Community Ecology. **The Quarterly Review of Biology,** v. 85, n. 2, p. 183–206., 2010. DOI:10.1086/652373.

VIEILLEDENT, Ghislain; CORNU, Cyrille; CUNÍ SANCHEZ, Aida; LEONG POCK-TSY, Jean-Michel; DANTHU, Pascal. Vulnerability of baobab species to climate change and effectiveness of the protected area network in Madagascar: Towards new conservation priorities. **Biological Conservation**, v. 166, p. 11–22, Oct. 2013a. DOI 10.1016/j.biocon.2013.06.007.

VIEILLEDENT, Ghislain; CORNU, Cyrille; CUNÍ SANCHEZ, Aida; LEONG POCK-TSY, Jean-Michel; DANTHU, Pascal. Vulnerability of baobab species to climate change and effectiveness of the protected area network in Madagascar: Towards new conservation priorities. **Biological Conservation**, v. 166, p. 11–22, Oct. 2013b. DOI https://doi.org/10.1016/j.biocon.2013.06.007.

VIEILLEDENT, Ghislain; GRINAND, Clovis; RAKOTOMALALA, Fety A.; RANAIVOSOA, Rija; RAKOTOARIJAONA, Jean Roger; ALLNUTT, Thomas F.; ACHARD, Frédéric. Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. **Biological Conservation**, v. 222, p. 189–197, 2018. DOI 10.1016/j.biocon.2018.04.008.

VIEILLEDENT, Ghislain; GRINAND, Clovis; RAKOTOMALALA, Fety A; RANAIVOSOA, Rija; RAKOTOARIJAONA, Jean-Roger; ALLNUTT, Thomas F; ACHARD, Frédéric. Combining global tree cover loss data with historical national forest-cover maps to look at six decades of deforestation and forest fragmentation in {Madagascar}. **bioRxiv**, p. 147827, 2017. DOI 10.1101/147827.

VIOLLE, C.; REICH, P.B.; PACALA, S.W.; ENQUIST, B.J.; KATTGE, J. The emergence and promise of functional biogeography. **Proceeding of the National Academy of Sciences of the United States of America,** v. 111, n. 38, p. 13690–13696 2014.

WAEBER, P.O.; WILMÉ, L.; RAMAMONJISOA, B.; GARCIA, C.; RAKOTOMALALA, D.; RABEMANANJARA, Z.H.; KULL, C.A.; GANZHORN, J.U.; SORG, J.-P. Dry forests in Madagascar: neglected and under pressure. **International Forestry Review**, v. 17, n. 2, p. 127–148, 1 Aug. 2015. DOI 10.1505/146554815815834822.

WAN, Jun-Nan *et al.* Modeling impacts of climate change on the potential distribution of six endemic baobab species in Madagascar. **Plant Diversity**, v. 43, n. 2, p. 117–124, Apr. 2021. DOI 10.1016/j.pld.2020.07.001.

WAN, Jun-Nan *et al.* Modeling impacts of climate change on the potential distribution of six endemic baobab species in Madagascar. **Plant Diversity**, 18 Jul. 2020. DOI https://doi.org/10.1016/j.pld.2020.07.001.

WATSON, Keri B.; GALFORD, Gillian L.; SONTER, Laura J.; KOH, Insu; RICKETTS, Taylor H. Effects of human demand on conservation planning for biodiversity and ecosystem services. **Conservation Biology**, v. 33, n. 4, p. 942–952, 27 Aug. 2019. DOI 10.1111/cobi.13276.

WICKENS, Gerald E. **The Baobabs: Pachycauls of Africa, Madagascar and Australia**. [*S. l.*]: Springer Netherlands, 2008. DOI 10.1007/978-1-4020-6431-9.

WILSON, Oliver J.; WALTERS, Richard J.; MAYLE, Francis E.; LINGNER, Débora V.; VIBRANS, Alexander C. Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered Araucaria tree. **Global Change Biology**, v. 25, n. 12, p. 4339–4351, 2019. DOI https://doi.org/10.1111/gcb.14755.

YU, Huajun; XIE, Wei; YANG, Lan; DU, Anshu; ALMEIDA, Cecilia M.V.B.; WANG, Yutao. From payments for ecosystem services to eco-compensation: Conceptual change or paradigm shift? **Science of The Total Environment**, v. 700, p. 134627, Jan. 2020. DOI 10.1016/j.scitotenv.2019.134627.

ZACHOS, Frank E.; HABEL, Jan Christian. **Biodiversity Hotspots - Distribution and Protection of Conservation Priority Areas**. [*S. l.*: *s. n.*], 2011. vol. 53, . DOI 10.1007/978-3-642-20992-5.

ZONNEVELD, Maarten; KINDT, Roeland; SOLBERG, Svein Ø.; N'DANIKOU, Sognigbé; DAWSON, Ian K. Diversity and conservation of traditional African vegetables: Priorities for action. **Diversity and Distributions**, v. 27, n. 2, p. 216–232, Feb. 2021. DOI 10.1111/ddi.13188.

## 9 EXTRAS

Aqui vocês poderão encontrar as demais produções que participei ao longo de minha tese e que não foram incluídas para a avaliação:

1. **Tagliari** et al., 2019. M.M. **Tagliari**, V.A. Moreira, N. Peroni. Analysis of programs of payment for environmental services in southern Brazil: identifying strategies for the conservation of *Araucaria angustifolia*. Desenvolv. e Meio Ambient., 50 (2019), pp. 216-233.
2. **Tagliari** and Peroni, 2018. M.M. **Tagliari**, N. Peroni. Local varieties of *Araucaria angustifolia* (Bertol.) Kuntze (Pinales: Araucariaceae) in southern Brazil: A brief discussion about landscape domestication. Biotemas, 31 (2018), pp. 59-68.
3. Bogoni et al., 2020. J.A. Bogoni, M. **Muniz-Tagliari**, N. Peroni, C.A. Peres. Testing the keystone plant resource role of a flagship subtropical tree species (*Araucaria angustifolia*) in the Brazilian Atlantic Forest. Ecol. Indic., 118 (2020), Article 106778, 10.1016/j.ecolind.2020.106778.
4. *O que memes, araucárias, pinhões e conservação têm em comum?* **Tagliari**, M.; Bogoni, J.; Peres, C.; Peroni, N. Coluna. 2020. https://www.oeco.org.br/analises/o-que-memes-araucarias-pinhoes-e-conservacao-tem-em-comum/
5. Alves et al., 2020. J. Alves, A. Matthiensen, M. **Tagliari**. M. Petrucio. Climate and hydrological process explain temporal dissimilarity in the phytoplankton community and favor seasonal dominance of harmful and alien algae in a subtropical reservoir. PANAMJAS. Pan-American Journal of Aquatic Sciences.
6. Amorim et al. 2020. P.B. Amorim, M. **Tagliari**, C. Levis, B. Flores, B. Segal. Communicating science in times of pandemic, EoS 101. https://doi.org/10.1029/2020EO149200.
7. Bogoni & **Tagliari**, 2021. J. Bogoni & M. **Tagliari**. Potential distribution of piscivores across the Atlantic Forest: From bats and marsupials to large-bodied mammals under a trophic-guild viewpoint. Ecol. Info., 64 (2021), 10.1016/j.ecoinf.2021.101357
8. *Resiliência para reforçar o óbvio e a conservação das araucárias no Brasil.* **Tagliari**, M. 2021. Coluna. https://www.oeco.org.br/analises/resiliencia-para-reforcar-o-obvio-e-a-conservacao-das-araucarias-no-brasil/#comments