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Aline Pereira Cruz

Legados Ameríndios nas Florestas Subtropicais da América do Sul

Florianópolis
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Legados Ameríndios nas Florestas de Santa Catarina

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Prof.(a) Nivaldo Peroni, Dr.
Orientador

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“Deste jardim cujo eu sou jardineiro
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O meu herdeiro quem eu vou sempre cuidar(...)
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Canção de Marie Gabriella, 2018.

“No tempo antigo, seus pais e avós haviam ensinado esse trabalho a eles, que por isso foram capazes de impedir mais essa queda. [...] estou certo de que, uma vez mais, o céu tinha mesmo ameaçado de cair sobre nós. Sei que isso já ocorreu, muito longe da nossa floresta [...]. Os habitantes dessas regiões distantes foram exterminados porque não souberam segurar o céu.”

(Kopenawa, Davi, and Bruce Albert. A queda do céu: palavras de um xamã Yanomami. p. 194 2019)

RESUMO

A Mata Atlântica Subtropical é ocupada por grupos humanos desde, pelo menos, 10.000 anos atrás, com múltiplos usos e consequentes modificações do ambiente e da biota. A Teoria da Construção de Nicho indica que as modificações na paisagem deixam marcas, legados, persistentes ao longo do tempo. Contudo, as práticas culturais de um passado anterior à chegada de Europeus ainda são ignoradas como força transformadora das paisagens e da composição florestal no Brasil Subtropical. Reconhecer a interação histórica entre grupos humanos e florestas traz uma mudança de perspectiva para as estratégias de conservação, por permitir compreender os efeitos das ações humanas no passado e integrar o conhecimento milenar dos povos originários. Esses que extraíram recursos florestais, mas também enriqueceram florestas e paisagens com práticas agroflorestais. Por esse motivo, busca-se com a presente tese a compreensão de como a presença de populações do passado podem ser visualizadas na composição de espécies arbóreas atuais. Para tal, utilizamos dados multidisciplinares: presença e abundância de espécies arbóreas foram obtidas do Inventário Florístico Florestal de Santa Catarina (FlorestaSC); dados arqueológicos do Banco de Dados do Laboratório de Estudos Interdisciplinares em Arqueologia da UFSC e dados com datação da Base BRC14; dados topográficos do *Shuttle Radar Topography Mission* (SRTM), hidrológicos da Agência Nacional de Águas e Climáticos do WorldClim. No capítulo 1 a ocupação Jê-meridional e Guarani foi modelada com estratégia de modelagem de nicho, com uso da localização de sítios arqueológicos, dados hidrográficos e topográficos. Foram gerados mapas de probabilidade de ocupação para cada grupo cultural. Após, buscou-se identificar espécies arbóreas na paisagem atual que apresentavam correspondência com áreas ocupadas por grupos ameríndios Jês-meridional e/ou Guaranis com uso de uma Análise de Redundância (RDA). Encontramos 29 espécies, entre elas *Araucaria angustifolia*, *Ilex paraguariensis,* relacionadas com áreas de ocupação Jê-meridional; *Casearia sylvestris,* com ocupação Guarani (e também Jê-meridional, em análise posterior) e Arecaceaes relacionadas com ambos grupos. A espécie *C. sylvestris* é mundialmente reconhecida por suas propriedades medicinais, motivo pelo qual teve a investigação aprofundada no capítulo 2. A espécie foi utilizada para a validação de modelos de rotas Jê-meridional e Guarani. Para identificação de rotas foram gerados modelos de custo de superfície específicos para Jê-meridionais e Guaranis, com base nas características culturais de escolha de caminhos, na localização dos respectivos sítios arqueológicos, na topografia e hidrografia. Por fim, foram aplicados Modelos Generalizados Mistos para testar as relações entre a ocupação, as rotas e características climáticas, sobre a presença e abundância de *C. sylvestris*. Os resultados indicam que a espécie não está relacionada apenas com Guarani, mas também com Jê-meridional. A espécie está relacionada com rotas de ambos os grupos culturais, porém, de forma mais clara com Jê-meridional. A distribuição da espécie está fortemente relacionada com aspectos climáticos. Os resultados indicam que apesar dos impactos recentes as marcas de ações do passado são tão intensas que ainda são visíveis e que as Terras Indígenas contribuem para a manutenção de espécies de valor cultural. A contribuição da tese aqui apresentada aponta para a necessidade da valorização e da promoção das culturas dos povos indígenas para conservar a biodiversidade, foram gerados mapas de probabilidade de ocupação no passado (territórios Ameríndios), que podem ser utilizados pelos indígenas do Sul do Brasil em processos territoriais. Além disso, nossos resultados mostram não só que existem espécies associadas com a ocupação humana no passado, mas que são espécies com diversos potenciais de uso, incluindo a *C. sylvestris* com múltiplos atributos medicinais. Também apresenta um avanço na compreensão do movimento humano na arqueologia, demonstra que árvores podem ser marcadores de movimento, além de indicar 29 espécies chaves para futuras investigações em Ecologia Histórica na Mata Atlântica Subtropical. Por fim, afirmo que as descrições da cobertura original da Mata Atlântica devem ser acompanhadas de um período de referência e, sobretudo, que estamos reconhecendo a presença de povos cujas culturas estão entrelaçadas com as florestas.

Palavras-chave: Mata Atlântica; construção de nicho; grupos culturais; Ameríndios

ABSTRACT

The Subtropical Atlantic Forest has been occupied by human groups since at least 10,000 years ago, with multiple uses and consequent changes in the environment and biota. The Theory of Niche Construction indicates that changes in the landscape leave marks, legacies, persistent over time. However, cultural practices from a past prior to the arrival of Europeans are still ignored as a transforming force in landscapes and forest composition in the Brazilian Subtropical. Historical interaction between human groups and forests brings a change of perspective to conservation strategies, to allow understanding the effects of human actions in the past and integrating the ancient knowledge of the original peoples. Those who extracted forest resources, but not only that, enriched forests and landscapes with agroforestry practices. For this reason, this thesis seeks to understand how the presence of past populations can be seen in the composition of current tree species. For this purpose, we used multidisciplinary data: presence and abundance of tree species were obtained from the Floristic Forest Inventory of Santa Catarina (FlorestaSC); archaeological data from the Database of the Laboratory of Interdisciplinary Studies in Archeology (LEIA) at UFSC (Federal University of Santa Catarina) and data with temporal register from Base BRC14; topographic data from the Shuttle Radar Topography Mission (SRTM), hydrological data from the National Water Agency (ANA) and Climate of WorldClim. In chapter 1, the Jê-meridional and Guarani occupation was modeled with a niche modeling strategy, using the location of destroyed sites, hydrographic and topographic data. Occupancy probability maps were generated for each cultural group. Afterwards, an attempt was made to identify tree species in the current landscape that correspond to areas occupied by South Jes and/or Guaranis Amerindian groups using a Redundancy Analysis (RDA). We found 29 species, among them *Araucaria angustifolia, Ilex paraguariensis*, related to areas of Jê-meridional occupation; *Casearia sylvestris*, with Guarani occupation and Arecaceae related to both groups. The species *C. sylvestris* is world-renowned for its medicinal properties, which is why it has had an in-depth investigation in chapter 2. The species was used for the validation of Jê-meridional and Guarani route models. For the identification of routes, specific surface cost models were generated for Jê-meridionais and Guaranis, based on the cultural characteristics of choosing paths, on the location of the respective sunken sites, on the topography and hydrography. Finally, Mixed Generalized Models were applied to test the relationships between occupancy, routes and climatic characteristics, on the presence and abundance of *C. sylvestris.* The results indicate that the species is not only related to the Guarani, but also to the southern Jê. The species is related to the routes of both cultural groups, however, more clearly with the southern Jê. The distribution of the species is strongly related to climatic aspects. The results indicate that despite the recent impacts on the marks of past actions, they are so intense that they are still visible and also that the Indigenous Lands are highlighted for the maintenance of species of cultural value. The contribution of the thesis presented here points to the need to value and promote the cultures of indigenous peoples to conserve biodiversity, maps of probability of occupation (Amerindian territories) in the past were generated, which can be used by indigenous peoples in southern Brazil in territorial processes. Furthermore, our results show not only that there are species associated with human occupation in the past, but that they are species with diverse possibilities of use, including *C. sylvestris* with multiple medicinal attributes. It also advances the understanding of human movement in archeology and demonstrates that trees can be markers of movement and indicates 29 key species for future investigations in Historical Ecology in the Subtropical Atlantic Forest. Finally, I affirm that descriptions of the original coverage of the Atlantic Forest must be accompanied by a reference period and, above all, that we are recognizing the presence of peoples whose cultures are intertwined with the forests.

Keywords: Atlantic Forest; niche construction; cultural groups, Amerindians

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

1 INTRODUÇÃO

Em preparo para submissão à *Perspectives in Ecology and Conservation*

Embora o período de presença humana na Terra seja apenas uma fração da história das florestas, a montagem das comunidades florestais recentes conta com influência humana desde milênios. Em todo o mundo estão sendo encontrados sítios arqueológicos sob a cobertura de florestas tropicais e subtropicais que eram consideradas intocadas (ROBERTS et al, 2017), e em alguns casos com evidências de uma complexa organização social (SOUZA et al, 2016, HECKENBERGER et al, 2008).

No Brasil, a descrição da história dessas relações avançou muito na região amazônica, identificando: ocorrência de solos antropogênicos (FRASER et al, 2011), alta densidade populacional (CLEMENT, 2015), domesticação da paisagem com hiperdominância de arbóreas (LEVIS et al, 2017), urbanização (SOUZA et al, 2016, HECKENBERGER et al, 2008). Para a Mata Atlântica (M.A.), um dos hotspots mundiais de diversidade biológica (MYERS, 2000) é um conhecimento que está avançando. Na porção subtropical foram identificados adensamentos de espécies úteis, tais como butiazais (palmeira *Butia eriospatha*) (MERCEDES et al 2023), ervais (*Ilex paraguariensis*), utilizado no preparo de uma bebida tradicional denominada chimarrão, pinheirais (*Araucaria angustifolia*) (REIS et al 2018), cuja distribuição atual está relacionada com povos ameríndios (LAUTERJUNG et al; 2018; ROBINSON et al, 2018).

Há uma frase clássica para descrever o estado atual da Mata Atlântica em qualquer fitogeografia ou em sua totalidade: "... restam apenas (um valor)% da cobertura original". Mas, original desde quando? Afinal, se trata de um Domínio com histórico de retração e expansão de refúgios ao longo do quaternário (CARNAVAL & MORITZ, 2008). Nesse contexto, a história dos povos originários ou fica omitida, levando a falsa ideia de ambientes não povoados, se enquadrando no mito dos ambientes prístinos (POSEY & BALÉE, 1989; DENEVAM, 1992) ou leva a falsa ideia de que tais povos não interferiram nas dinâmicas ambientais, o que se enquadra com o mito do bom selvagem, baseado na obra de Rousseau (RAYMOND, 2007).

O fato de parte dos pesquisadores de diversas ciências, entre elas a Ecologia, a Biologia da Conservação e a Arqueologia, terem ignorado a presença humana nesses locais nos direcionou para uma lacuna em nossa história e na história do papel dos humanos na montagem das comunidades florestais. E os motivos para essa ignorância vem de uma cultura ocidentalizada, colonizada, em que o discurso preconceituoso da arqueologia imperial ainda na arqueologia moderna (NOELLI, FERREIRA, 2007; NOELLI, SOUZA, 2017). Afinal, é fato e amplamente compreendido que as terras Brasileiras já eram ocupadas por indígenas no momento da colonização. Então por que essa presença foi desconsiderada e aceitou-se a ideia de ambientes prístinos? Souza (2015) descreve uma linha invisível que separa a realidade em um universo distinto e “para além dela há apenas a inexistência, invisibilidade e ausência não dialética”. Além disso, a presença indígena é minimizada na história que foi escrita por portugueses, que tinham objetivos do que sua própria cultura considerava “avanços” para o Brasil. O uso da palavra “descobrimento” ao invés de “conquista” contribui com a continuidade do ofuscamento da presença anterior de povos indígenas nas terras brasileiras (NEVES, 1995).

As teorias da Ecologia Histórica e da Construção Cultural de Nicho guiam aqui a busca pela desconstrução da falsa dicotomia entre seres humanos e natureza, e pelo esclarecimento de que nós, humanos, fazemos parte das redes ecológicas, atuando tanto no enriquecimento quanto na degradação, e que há diferenças culturais dirigindo tais processos. Na presente tese quero reforçar a realidade invisibilizada de que a Mata Atlântica foi e é moldada por diferentes grupos culturais desde milhares de anos, sendo que há remanescentes dos povos originários, detentores de amplo conhecimento, que seguem marginalizados e ignorados. Além disso apresento novas informações sobre espécies arbóreas florestais que tem relação com a presença de povos originários, que são indicadoras de presença e movimento humano, e ainda aponto uma espécie de importância farmacêutica relacionada com a presença (e provável manejo) indígena no passado e no presente.

1.1 ECOLOGIA HISTÓRICA

O Termo Ecologia Histórica vem sendo utilizado com diferentes significados por diferentes áreas do conhecimento e mesmo dentro da Ecologia (SZABÓ, 2014). Na ecologia é por vezes utilizado como sinônimo de história evolutiva (NOGUEIRA, 2001), história de um ecossistema (CONWAY, 1948; MORENO E MONTANARI, 2008; RTHEMTULLA E MLADENOFF, 2007), de História Ambiental (SWETNAM et al., 1999). Há algo que une todos os autores: o uso do passado para entender o presente (SZABÓ, 2014).

Mas, com essa diversidade de conceitos é importante situar qual o significado de Ecologia Histórica no presente trabalho, que é a mais utilizada segundo a revisão de Szabó (2014): o entrelaçamento das ações humanas ao meio ambiente encerrando a dicotomia entre homem e natureza. Alguns autores definem a Ecologia Histórica como um *frame-work* (STAHL, 2008), como um *paradigma* (LUNT & SPOONER, 2005), mas aqui será utilizado o termo *Programa de Pesquisa,* definido por Balée em 1998 e atualizado em 2018. O Programa de Pesquisa está fundamentado na filosofia de Lakatos, para o qual um programa de pesquisa necessita de fortes postulados centrais, que no caso são:

a) humanos têm impactado quase todos os ambientes habitáveis da Terra de forma física ou material; praticamente todos os ambientes da Terra foram afetados pelo gênero *Homo*, e maiores escalas coincidem com o início da agricultura;
b) diferentes sociedades impactam os ambientes de forma distinta devido a diferenças em organização e estrutura; a natureza humana não é programada geneticamente para alterar a diversidade de espécies ou outros parâmetros ambientais;
c) a natureza humana é indiferente a diversidade de espécies; diferentes organizações sociais resultam em diferentes níveis de transformação da paisagem;
d) o fenômeno total, Ecologia Global, resulta da união de ecologias históricas do mundo, resultando em uma matriz de “Pegada Humana” realista.

Este programa de pesquisa está voltado às investigações das relações entre seres humanos e o ambiente, nas dimensões temporal e espacial, e de seus efeitos cumulativos (BALÉE, 2006, 2010) e é baseado na interpretação materialista destas relações (BALÉE, 2018). Para o mesmo autor, os princípios do programa de pesquisa são: “os ambientes com que humanos interagem estão em constante mudança; e a manutenção da diversidade natural e cultural é desejada pela sociedade”, de modo a interpretar a relação entre a cultura e o ambiente ao invés da adaptação de humanos a seus ambientes. Contraria assim o determinismo ambiental que ainda é uma teoria influente na arqueologia brasileira, o qual defende que o ambiente define a cultura e que assim, ambientes "com escassez de recursos" desenvolveria culturas "menos avançadas" (NOELLI, FERREIRA, 2007).

A Ecologia histórica busca entender como os recursos são criados e manejados, assumindo que ao invés de adaptarem-se ao ambiente, os seres humanos cocriaram o ambiente onde vivem, sendo o principal mecanismo de mudança no mundo natural e atuando de forma similar a seleção natural (ERICKSON, 2008). Com isso, contraria as ideias conservacionistas baseadas na teoria da sucessão, iniciada por Clements (1916). Nessa teoria as comunidades apresentam um estágio ideal, de equilíbrio - o clímax, e distúrbios, ainda que naturais, interrompem a situação de equilíbrio. Contudo, o avanço das descobertas científicas (oriundos de esforços de áreas diversas), têm indicado que as comunidades florestais recentes foram co-construídas por distúrbios naturais e humanos, e que não existem ambiente intocados (LEVIS et al., 2017; ROBERTS et al, 2017).

A escala temporal e o conceito de História da Ecologia Histórica se referem ao tempo de presença humana, de todos os humanos na pluralidade de paisagens que habitamos e modificamos, em que as paisagens são a dimensão espacial que é alterada pelo conhecimento e comportamento de diferentes grupos culturais (BALÉE, 2018). Assim, a paisagem e a transformação da paisagem são palavras-chave na Ecologia Histórica.

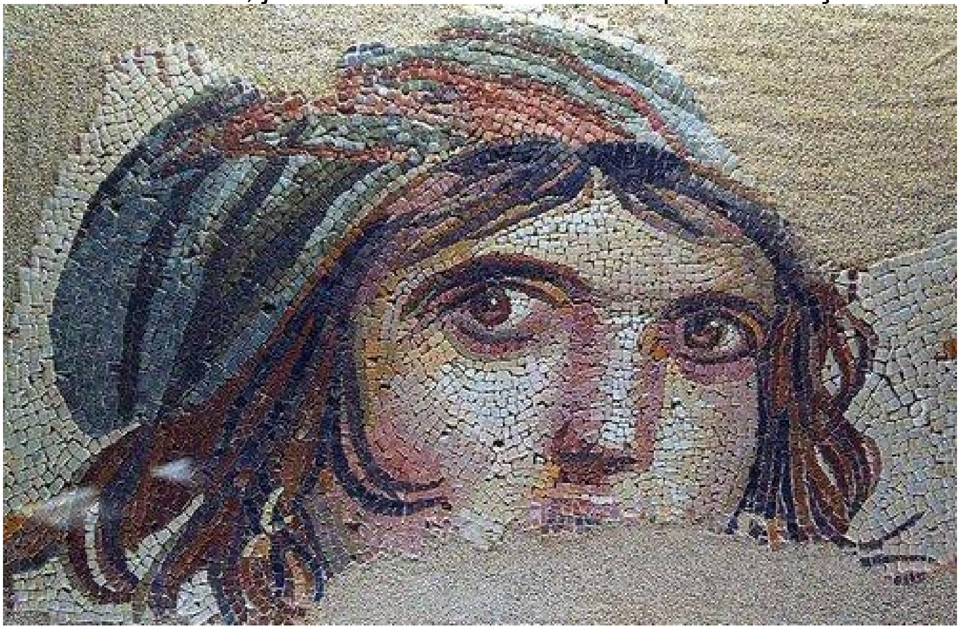
1.2 O CONCEITO DE PAISAGEM

A paisagem é um termo central na Ecologia Histórica por abranger o comportamento humano e seu gerenciamento do ambiente de entorno (BALÉE, 2006) e por ser onde as marcas do passado ficam registradas, “testemunho das vidas e trabalhos das gerações passadas que nela moraram” (INGOLD, 2000). Para Ingold (2015) as paisagens podem ser simplificadas como tramas de tear, uma malha tecida por diversos organismos, de modo que o encontro de seus caminhos forma uma estrutura de rede, as linhas constroem as formas e as superfícies. A paisagem para a Ecologia Histórica é constituída de matéria, pela natureza física da Terra e dos seres vivos que afetam as sociedades humanas (BALÉE, 2018). Trata-se de um lugar (tem dimensão espacial) onde as interações entre história e cultura (dimensão temporal) são evolutivas em si (BALÉE, 2006). A dimensão temporal das paisagens está enquadrada pelo tempo da presença humana (BALÉE, 2006, 2018). Aqui, o termo paisagem será utilizado como sinônimo de “ambiente de entorno” da área em que um determinado grupo cultural vive, o que Erickson (2008) definiu como “assentamentos e paisagens associadas”.

Além disso, “paisagem” é uma palavra utilizada por múltiplas áreas do conhecimento: geografia, ecologia, artes, história, arquitetura, urbanismo, entre outras. Em Ecologia há uma área específica destinada a esse termo, definida como Ecologia de Paisagens. A Ecologia da Paisagem traz um modelo que simplifica qualquer paisagem em um mosaico, de matriz, manchas, e corredores, conceitos que podem ser aplicados na Ecologia Histórica. A avaliação do mosaico é feita por cálculos geométricos, ou seja, de formas, o que é similar com as descrições de paisagem do antropólogo Tim Ingold. Em sua obra Ingold busca a desconstrução da dicotomia homem e natureza, assim como na Ecologia Histórica, razão pela qual utilizei pelo menos três pontos de tal área do conhecimento: 1) como os organismos percebem seu ambiente, e aqui, como humanos a percebem; 2) como as características espaciais influenciam os processos ecológicos; e 3) As análises de paisagens podem ser simplificadas considerando mosaicos formados por unidades de similaridade visual (FORMAN, 1997; METZGER, 2001). A matriz é como um plano de fundo, o que domina na paisagem. As manchas são unidades menores circundadas pela matriz. Os corredores são as estruturas alongadas que conectam diferentes áreas da paisagem, como estradas, cursos de água, pontes. Mas os corredores também podem ser barreiras. Por exemplo, um grande rio pode ser uma barreira, mas também é um corredor. A matriz, as manchas e os corredores são os elementos que definem a estrutura da paisagem e é através dessas estruturas que os fluxos ocorrem. Os corredores irão conectar manchas distantes, a matriz será mais permeável quando tiver muitas manchas e/ou manchas próximas.

Em comparação com um mosaico artístico (Figura 1), em que os desenhos são formados pela união de peças denominadas tesselas com as mesmas cores, cada conjunto de tesselas agrupado cria um padrão geométrico, isso seria a “mancha” na ecologia de paisagens.

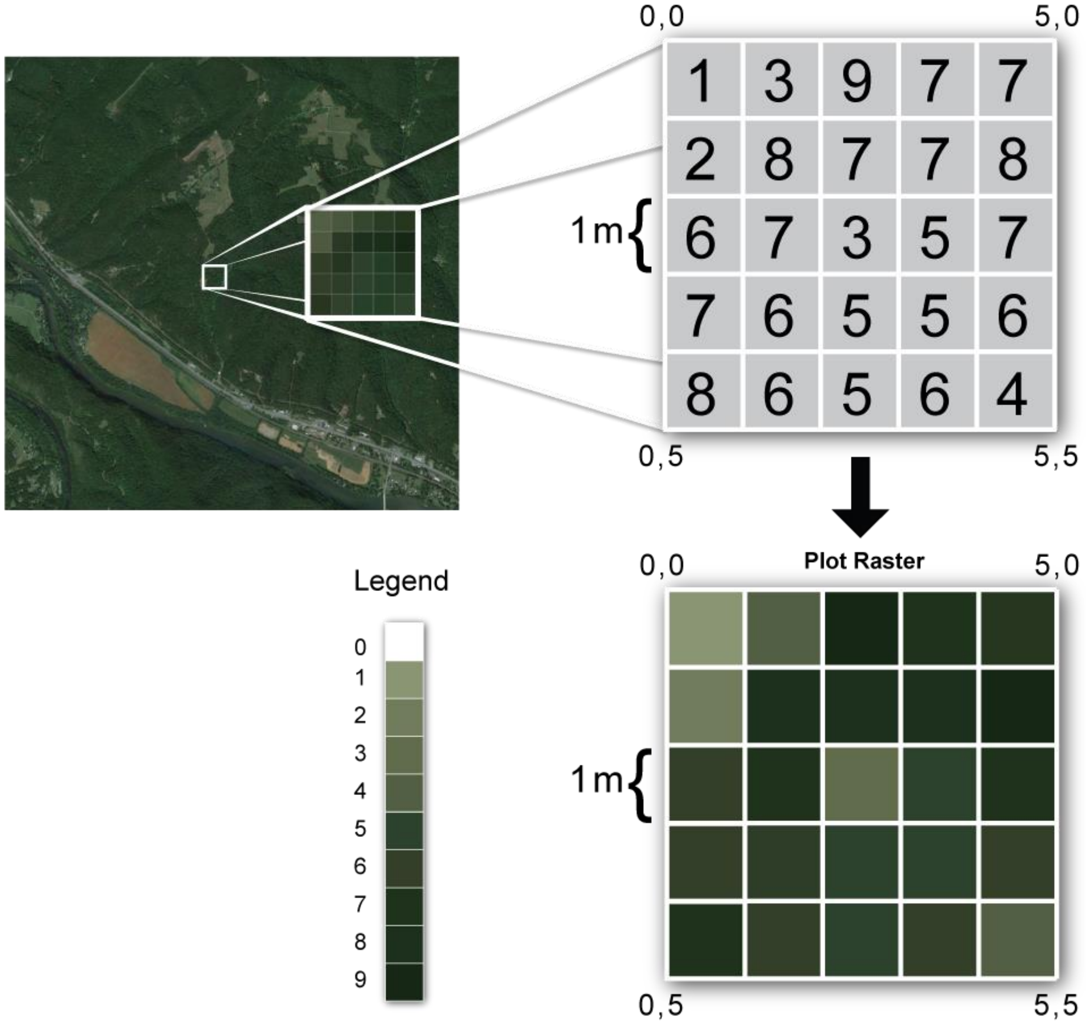
Figura 1 – “A Gypsy Girl”, mosaico do século 20 exposto em um museu na Turquia. Há um fundo bege em que faltam tesselas, esse plano de fundo seria a matriz. Os cabelos, detalhes do lenço, sobrancelhas e linhas das pálpebras, que são composições alongadas, seriam os corredores. A pele e a íris dos olhos seriam manchas, junto com as áreas mais amplas do lenço.



Fonte: Mosaic Art Gallery. https://www.mosaicartgallery.com/history-of-mosaics. Acessado em 06/08/2023.

As tesselas em uma imagem digital, tal qual uma fotografia ou imagem de satélite, seriam os pixels – as menores “unidades” que se vê com amplificação maximizada. Cada pixel tem uma cor que é formada por uma combinação numérica representando o vermelho, verde e azul. Com essa lógica das imagens digitais, aquilo que compõe a paisagem, mas que não é perceptível à visão, e pode ser representado de forma numérica, pode ser traduzido em escala de cores. Por exemplo, valores de temperatura e precipitação, valores indicativos de relevo e topografia, dados demográficos, a presença de uma determinada etnia, e demais variáveis ambientais e sociais. Afinal a paisagem não é um mero elemento visual. As paisagens são percebidas também pelos sons, cheiros, sensações, por percepções individuais, quando por humanos, percepções culturais, quando por outros organismos por fatores que podemos não compreender.

Figura 2 - Imagem de Satélite, representação matricial e colorimétrica dos pixels.



1	3	9	7	7
2	8	7	7	8
6	7	3	5	7
7	6	5	5	6
8	6	5	6	4

Fonte: Data Carpentry for Biologists (https://datacarpentry.org/semester-biology/materials/spatial-data-raster-R/) acesso em 08/06/2023.

Aqui, no Capítulo 1, onde a probabilidade de ocupação por grupos Jê-Meridionais é Guaranis foi modelada, os pixels representarão nichos de uma forma próxima ao conceito Hutchsoniano. O nicho ecológico é um conceito da Ecologia de Comunidades, uma paisagem tem muitos nichos. Nicho foi inicialmente definido por Grinnel (1917) como um lugar adequado para um organismo. Nos primórdios da elaboração desse um conceito, se relaciona com a Teoria da Seleção Natural (DARWIN, 1859), quanto a força seletiva do ambiente. Hutchinson (1957) adicionou ao conceito múltiplas camadas ambientais, e de forma metodológica é esse o conceito aqui utilizado na modelagem de probabilidade de ocupação de Jê-meridionais e Guaranis (Capítulo 1), uma simplificação da paisagem com múltiplas camadas ambientais e sociais. Cada pixel tem uma localização e uma combinação de características, que pode ser favorável ou limitante para algum organismo. Contudo, o nicho Hutchinsoniano não considera aspectos de movimento e função dos organismos. No Capítulo 2 incluímos aspectos de movimento humano, traduzido em pixels com um valor de Custo de Superfície específico para cada grupo cultural. Contudo, embora o processo de modelagem de ocupação e movimento sejam similares ao contexto de nicho Hutchinsoniano isso se limita ao método. Elton (1927) contrariou o conceito de Hutchison ao não considerar os fatores ambientais em seu conceito de nicho que é sobre redes tróficas. Posteriormente, Chase e Leibold (2003) incluíram a competição e a hipótese da "perturbação intermediária", aplicável à Ecologia Histórica (ERICSON, 2008). Recentemente, Bruno (2003) trouxe os conceitos de facilitação, oposto à competição de Chase e Leibold. Os modelos aqui sintetizam a paisagem em um **Mosaico de Nichos**, que direciona os fluxos e é transformado por eles ao longo do tempo. Mas, as teorias que norteiam a discussão são: a Teoria da Construção de Nicho (ODLING-SMEE et al., 2003) e a construção cultural de nicho (ALBUQUERQUE et. al, 2018), focados nos processos de transformação da paisagem.

1.3 PROCESSOS DE TRANSFORMAÇÃO DA PAISAGEM

Usando conceitos da Ecologia de Paisagens: a estrutura da paisagem é moldada pelos fluxos (de matéria, energia, organismos), bem como os fluxos moldam a estrutura da paisagem. O relevo, os corredores, entre outros compõe a estrutura da paisagem, e são elementos que podem facilitar ou dificultar os fluxos de matéria e energia. Por outro lado, os movimentos e fluxos por si só transformam a estrutura da paisagem. Assim há uma relação bidirecional, onde as paisagens moldam os fluxos e os fluxos moldam a paisagem (FORMAN, 1997). Dentro desse processo pode ser acoplada a Teoria da Construção de Nicho (TCN) (ODLING-SMEE et al., 2013). A TNC prevê que além do ambiente selecionar os organismos aptos às suas condições (teoria da Seleção Natural de Darwin) os organismos também são capazes de modificar o ambiente, sendo assim capazes de modificar a seleção e esse processo deixa uma assinatura, um legado ou herança ecológica (ODLING-SMEE et al., 2013). Isso torna a TCN um segundo sistema geral de herança na evolução (ODLING-SMEE et al., 2013). A Tabela 1 sintetiza as diferenças entre a teoria evolutiva padrão e a TCN.

Tabela 1 - Tabela comparativa entre a Teoria Evolutiva Padrão e a Teoria de Construção de Nicho.

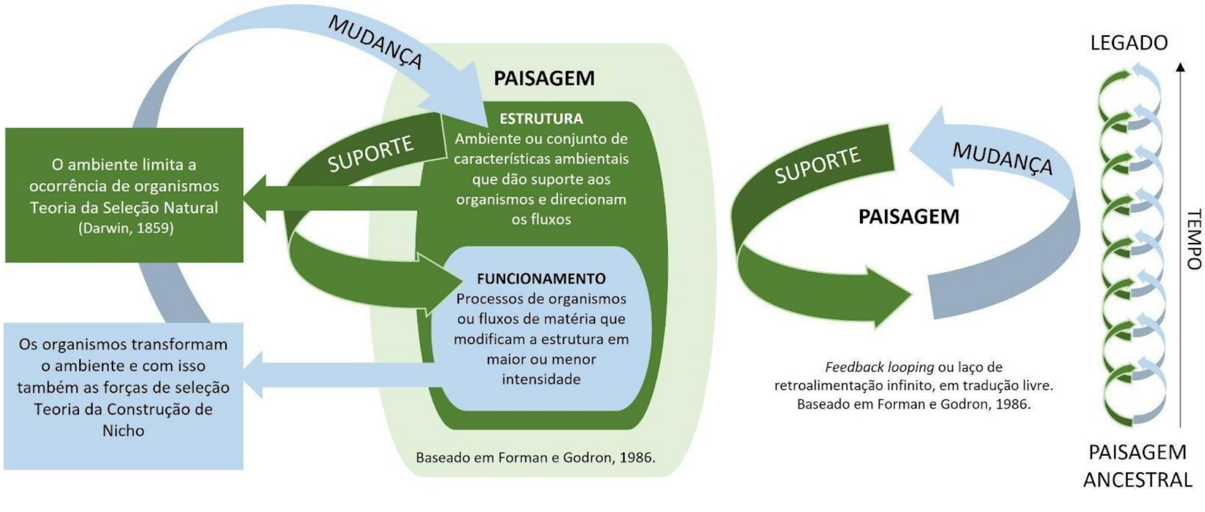
	TEORIA EVOLUTIVA PADRÃO	**TEORIA DA CONSTRUÇÃO DE NICHO**
FOCO	Evolução orgânica em resposta a ambientes.	Co-evolução de organismos e ambientes.
CAUSALIDADE	Principalmente unidirecional. Seleção autônoma por ambientes que moldam os organismos. ex.: seleção sexual, coevolução entre predador-presa.	Principalmente recíproco. Ambientes seletivos moldando organismos e organismos moldando ambientes seletivos, em relação a si mesmos ou a outros organismos.
CONSTRUÇÃO DE NICHO	Organismos reconhecidos para mudar estados ambientais, mas isso é tratado como o produto de seleção natural e raramente como um processo evolutivo em seu próprio direito. O foco é restrito às adaptações expressas fora dos corpos dos organismos.	O foco não está exclusivamente nas adaptações, mas inclui mudanças nos ambientes causadas por subprodutos de organismos (por exemplo, detritos), caracteres adquiridos (por exemplo, aprendidos), ou metabolismo coletivo ou comportamentos de vários indivíduos/espécies.
HERANÇA	Principalmente genética, embora heranças maternas, epigenéticas, citoplasmáticas e culturais sejam reconhecidas como “casos especiais”.	Herança genética e ecológica (ou seja, legados de pressões de seleção previamente modificadas pela construção de nicho). Herança genética e ecológica interagem para formar “herança de nicho”. Heranças maternas, epigenéticas, citoplasmáticas e culturais podem ser exemplos.
COMPLEMENTARIDADE ORGANISMO-AMBIENTE (ADAPTAÇÃO)	Produto da seleção natural.	As correspondências entre organismo e ambiente resultam das interações dinâmicas entre construção de nicho e seleção natural.

Fonte: Traduzido de ODLING-SMEE et al., 2013.

Assim, como os postulados da Ecologia Histórica apresentados anteriormente, a Teoria de Construção de Nicho permite analisar a integração das ações humanas na pesquisa ecológica (ALBUQUERQUE et. al, 2018). Em especial o segundo postulado “Diferentes sociedades impactam os ambientes de forma distinta devido a diferenças em organização e estrutura” inclui a importância das diferentes culturas nos processos de transformação do ambiente, de modo que foi criada uma categoria de TCN especial para humanos: a Construção Cultural de Nicho. Essa, diferencia humanos de outras espécies construtoras de nicho, por considerar que decisões influenciadas pela cultura direcionam as modificações de nicho, que vão refletir no nível da paisagem (ALBUQUERQUE, FERREIRA JÚNIOR, 2017; ALBUQUERQUE et al, 2018). Seres humanos são excelentes construtores de nicho e os impactos das modificações do passado e seus feedbacks persistem nas paisagens co-construídas entre pessoas e o ambiente, tendo implicações importantes nos padrões de diversidade e processos ecológicos (FOSTER et al., 2003; McKEY et al., 2010). Assim, humanos constroem nichos que podem beneficiar outras espécies consideradas úteis (SMITH, 2012), por meio do gerenciamento do ambiente de forma inconsciente e consciente, resultando em mudanças na ecologia da paisagem e na demografia de suas populações de plantas (CLEMENT, 1999).

As paisagens estão em constante mudança, sendo transformadas por processos abióticos e bióticos, aqueles explicados pelas teorias de construção de nicho. Há algo fixo, o lugar, que passa por transformações e conserva legados do passado. Desse modo, é possível comparar diretamente as mudanças na paisagem com a ancestralidade: ambas mantêm aspectos do passado, legados (Figura 3).

Figura 3 - Processos de geração de legados na paisagem.



Fonte: A autora.

1.4 COMO O PASSADO PODE SER INTERPRETADO NAS PAISAGENS DO PRESENTE

As informações sobre o passado então inscritas nas paisagens do presente: modificações no terreno, legados na vegetação, entre outros. As assinaturas deixadas na paisagem apontam para os grupos culturais que as deixaram, legados e assinaturas previstos na TCN.

A presença de legados persistentes ao longo do tempo é uma consequência da alta capacidade humana de modificar ambientes e a composição de espécies. As grandes extinções, por exemplo, causaram mudança pela redução da diversidade terrestre. Contudo, as ações humanas não causaram apenas a redução de espécies. Causaram também modificações em tamanhos populacionais, em traços populacionais, na área de ocorrência de espécies, entre outros. Isso pode ser explicado pelo Teoria de Construção de Nicho (ODLING-SMEE et al, 2013): a modificação que humanos causam no ambiente modificam as espécies que este ambiente poderá suportar. Desde intervenções humanas sutis, como a abertura de clareiras que pode favorecer espécies heliófilas, até a seleção e o favorecimento de espécies úteis como as frutíferas, resultam em modificações nas populações que podem ser persistentes ao longo do tempo. Diferentes formas de intervenções são exercidas por diferentes grupos culturais (ALBUQUERQUE, FERREIRA JÚNIOR, 2017; ALBUQUERQUE ET AL, 2018). Pode-se dizer que existe uma conexão entre as culturas e a diversidade local, sendo que se reconhece um padrão global de relação entre a diversidade linguística e a diversidade biológica (MAFFI, 2005).

1.5 ARQUEOLOGIA E ECOLOGIA HISTÓRICA NA MATA ATLÂNTICA SUBTROPICAL

As florestas da Mata Atlântica Subtropical (Figura 4) foram utilizadas por povos pré-colombianos, com diversas formas de ocupação, ao longo do espaço e do tempo (NOELLI, 2000; MILHEIRA, 2010; GIANNINI et al., 2010; HADLER, DIAS, BAUERMANN, 2013; IRIARTE et al., 2013; LOURDEAU, HOELTZ, VIANA, 2014; BONOMO et al., 2015; COPÉ, 2015). Os primeiros habitantes eram caçadores coletores, construtores de sambaquis, e depois vieram os Jê-meridional e Guarani (Tabela 2). Jê-meridional e Guarani são as línguas faladas pelos grupos culturais aqui estudados.

Figura 4 - Mata Atlântica com indicação de sua porção Subtropical, abaixo do trópico de Capricórnio.

Fonte: A autora.

Tabela 2 - Classificação linguística dos grupos culturais objetos do presente estudo: Jê-meridional e Guarani.

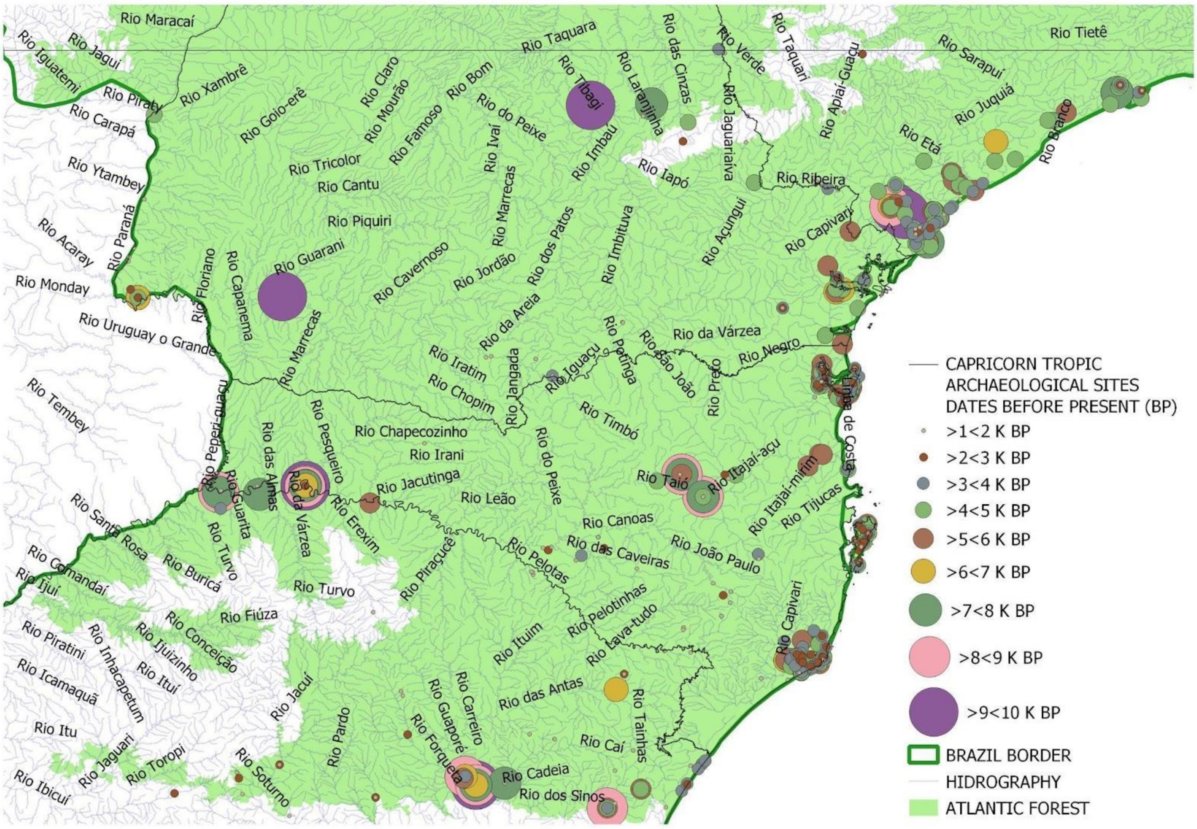
TRONCO LINGUÍSTICO	**MACRO JÊ**	**TUPI**
FAMÍLIA LINGUÍSTICA	Jê	Tupi Guarani
LÍNGUAS	Jê-meridional, que veio a se dividir em Xokleng e Kaingang	Guarani

Fonte: Línguas - Povos Indígenas no Brasil (socioambiental.org). Acesso em 08/06/2023.

Os primeiros registros arqueológicos datados com Carbono 14 (C14) na Mata Atlântica Subtropical são de cerca de 10.000 anos atrás (Figura 5) (https://brc14database.com.br), sendo que o sítio mais antigo datado por Carbono 14 é de 9.925 antes do presente (AP) e está situado onde hoje é o estado de Santa

Catarina (LOURDEAU et al., 2016). No estado de São Paulo as datas partem de 9.810 AP e se trata de um sítio da Tradição Umbu (COLLET, 1985; DIAS, JACOBUS, 2001; PENIN, 2005). A definição da Tradição Umbu é baseada na cultura material, no padrão da tecnologia lítica (HADLER, DIAS, BAUERMANN, 2013). No Rio Grande do Sul e no Paraná os sítios mais antigos são de 9.430 AP (DIAS, 2004; DIAS, 2012; HADLER, DIAS, BAUERMANN, 2013) e 9.190 AP (CHMYZ et al., 2008) respectivamente, sendo que o primeiro é um sítio da Tradição Umbu e não há descrição de grupo cultural para o segundo.

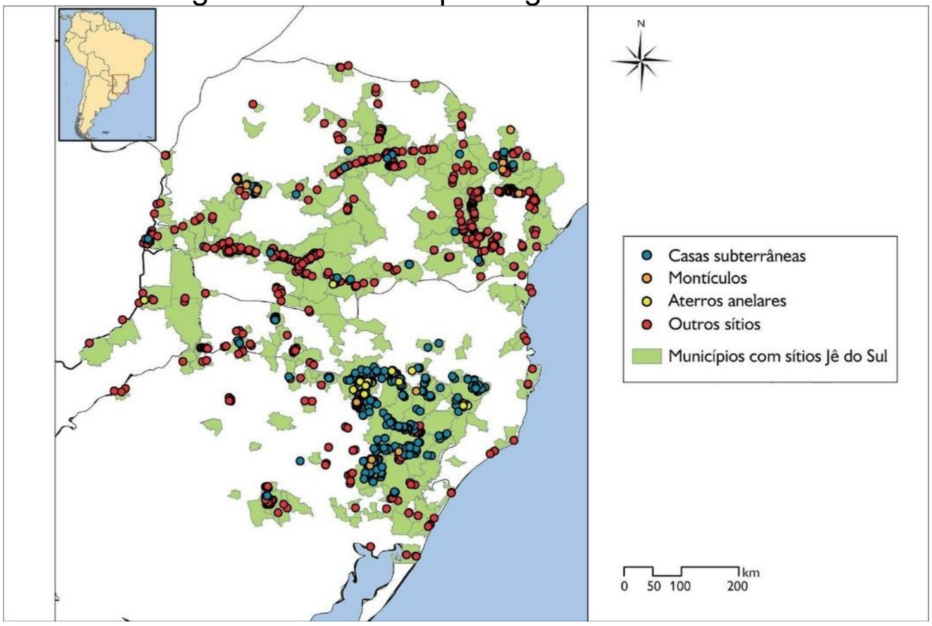
Figura 5 - Sítios arqueológicos datados por Carbono 14 na Mata Atlântica Subtropical, a partir de 1.000 anos atrás.



Fonte: autora, utilizando dados de localização e datas de sítios arqueológicos da base de dados BRC14 (https://brc14database.com.br/), o limite da Mata Atlântica foi obtido no site "http://terrabrasilis.dpi.inpe.br/", e a hidrografia foi obtida no site "https://metadados.snirh.gov.br".

O primeiro registro datado de sambaquis está no estado de São Paulo, Sambaqui Capelinha I, e data de 7.870 AP (COLLET, 1985, PENIN, 2005). No Paraná é de 6.540 AP, Sambaqui do Ramal, (PARELLADA & GOTTARDI NETO 1993; WAGNER et al. 2011) e em Santa Catarina é de 6.130 AP, Jabuticabeira II. No Rio Grande do Sul, o primeiro registro é do Sambaqui Balneário Atlantico 9, que tem data de 3.540 AP, pouco antes da chegada dos Jê-meridionais que aparecem nos registros datados 3.000 AP. Apesar das datas serem relativamente próximas, isso não é o suficiente para afirmar que a mudança se deu em função das interações entre Jê-meridionais e populações sambaquieiras, o que ainda é um tema controverso (NEVES, 1984, NOELLI, SOUZA, 2017). Há 3.000 anos atrás houve a intensificação de uma mudança climática e de cobertura vegetal, situação em que o clima na Mata Atlântica subtropical se tornava mais úmido e a vegetação passava a conter mais árvores do que herbáceas (BEHLING & PILLAR, 2007; JESKE-PIERUSCHKA, 2013). Tal mudança climática pode ter motivado a migração dos Jê-meridionais para o Sul (URBAN, 1992), sendo que vieram a ocupar muito da área de Mata Atlântica subtropical (Figura 6).

Figura 6 - Sítios arqueológicos Jê-meridionais.



Fonte: Noelli e Souza, 2017.

Na sequência, há cerca de 2.500 anos atrás, chegam os Guaranis, e ocorre em sequência um aumento populacional (NOELLI, 2000). Com isso há uma compartimentação do território entre Jê-meridionais e Guaranis, sendo que os primeiros passam a ocupar as áreas mais altas e encostas, onde desenvolvem marcadores arquitetônicos (SOUZA et al., 2016; CÁRDENAS et al., 2015), enquanto os Guaranis mantiveram seu padrão de ocupação em redes ao longo de rios e da linha da costa (BONOMO, 2015). 1.500 BP a formação de sambaquis grandes reduz drasticamente, junto com a ocupação costeira de grupos da tradição Taquara/Itararé (Jê-meridionais) (COLONESE et al, 2014).

Nota-se que a Mata Atlântica Subtropical já apresentava uma longa história de interação com humanos anterior à chegada dos europeus no Neotrópico, assim como já demonstrado para a Floresta Amazônica (CLEMENT, 2015; DeCASTRO, 2002; BALEÉ, 1994), para a transição entre Cerrado e Floresta Amazônica (POSEY, 1985) e para outras regiões da Mata Atlântica (OLIVEIRA, 2007). Ao longo dessa história, as práticas de produção de alimentos se deram predominantemente por sistemas agroflorestais. Como consequência, formam-se áreas de adensamento de espécies úteis, tais como pinheirais, butiazais, palmitais e ervais, (NOELLI, 2000). Além disso, levaram à presença de as árvores indicadoras de distúrbio, que são aquelas presentes em áreas de pousio que naturalmente ocorrem isoladas ou com poucos indivíduos, em geral apresentam um ciclo de vida longo, como as palmeiras, e são nômades biológicos transportados por humanos (BALÉE, 1994). Mas um exemplo que expressa a intensidade das relações entre humanos e os padrões de distribuição de espécies arbóreas é o da *Araucaria angustifolia*, cuja ampla distribuição tem também a influência de ações humanas, o que foi comprovado pelos trabalhos de Robinson e colaboradores (2018) e Lauterjung e colaboradores (2018). No presente trabalho apontaremos outras espécies que tem relação com processos passados de Construção Cultural de Nicho.

1.6 PREMISSAS

a) o território da Mata Atlântica Subtropical é ocupado desde pelo menos 14.000 anos atrás, com aumento populacional desde a chegada dos grupos ameríndios Jês-meridional e Guarani há cerca de 3.000 anos atrás;
b) trata-se de um ambiente com alterações antrópicas nas florestas desde os períodos supracitados;
c) grupos culturais tem sua própria forma de manejar a paisagem;
d) indígenas Jê-meridional (Xokleng e Kaingang) e Guarani estão presentes na Mata Atlântica Subtropical.

1.7 HIPÓTESES

Capítulo 1

a) A composição florística atual contém espécies relacionadas com a presença de grupos Ameríndios.
b) A composição florística apresenta diferença entre áreas ocupadas por diferentes grupos culturais no passado.

Capítulo 2

c) A *Casearia sylvestris* pode ser indicadora de caminhos e de territórios de grupos Guarani e Jês-meridional (atuais Xokleng e Kaingang) desde o período pré-colonial, visto que a espécie é utilizada por ambos os grupos, que há indícios de uso indígena em seus nomes populares (chá de bugre e guaçatonga que é uma palavra tupi-guarani).
d) A *Casearia sylvestris* pode ser indicadora de caminhos de Jê-meridional (atuais Xokleng e Kaingang) e Guarani, distribuição quase linear ao longo de rios (padrão de deslocamento Guarani) e da borda de encostas (padrão de deslocamento Jê-meridional).
e) A *Casearia sylvestris* é mais abundante onde é mais longa a duração da relação entre etnia e planta, e assim mais abundante próximo de terras indígenas.

1.8 OBJETIVO

O objetivo dessa tese é resgatar a história das relações humanas com as florestas subtropicais e de identificar os legados ameríndios na vegetação recente.

1.8.1 Objetivos Específicos

a) Identificar espécies relacionadas com a ocupação Jê-meridional e/ou Guarani no passado.
b) Testar o uso de uma espécie como indicador de rotas Ameríndias.
c) Verificar se há influência da proximidade das terras indígenas sobre a vegetação.

Se transponho as palavras de Cora Coralina

“[...]*uma mulher que fez a escalada da Montanha da Vida removendo pedras e plantando flores*[...].” (CORALINA, Cora. 2001.)

para os termos da ecologia história:

Uma mulher que construiu nichos, corredores e domesticou a paisagem.

2 CAPÍTULO 1 - PRE-COLONIAL AMERINDIAN LEGACIES IN FOREST COMPOSITION OF SOUTHERN BRAZIL

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Pre-colonial Amerindian legacies in forest composition of southern Brazil

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Abstract

Past human societies have left persistent marks on forests worldwide. However, the degree to which pre-colonial Amerindian societies have affected forest structure is still not fully understood, especially in southern Brazil. This study investigated the influence of two distinct Amerindian groups (Southern-Jê and Guarani) over tree composition of forest fragments in the State of Santa Catarina. Vegetation data was obtained from the Santa Catarina Forest and Floristic Inventory (SCFFI): a statewide systematic vegetation sampling project. Archaeological data was collated from literature reviews as well as existing databases for archaeological sites occupied by Guarani and Southern-Jê groups. Using these sites of known Amerindian occupation, and corresponding environmental variables, ecological niche models were developed for each Amerindian group, predicting potential archaeological sites occupied by these groups across southern Brazil. Maps of these potential occupation sites of pre-colonial Amerindian groups were compared with 417 corresponding floristic inventory plots. Redundancy analysis (RDA) was used to identify floristic composition patterns linked to areas with a high probability of Southern-Jê or Guarani presence. Southern-Jê and Guarani pre-colonial occupations overlapped near main rivers; however, Southern-Jê groups generally occupied elevated areas whereas Guarani occupied mostly coastal areas. We observed differences in forest composition associated with the predicted occurrence of these pre-colonial Amerindian groups. Based on these results, we argue there is a relationship between tree species distribution and pre-colonial human occupation by these two Amerindian groups.

Keywords: *Historical Ecology; Forest Composition; Archaeology; Southern-Jê; Guarani; Ecological Niche Modeling;* ***Araucaria****.*

Introduction

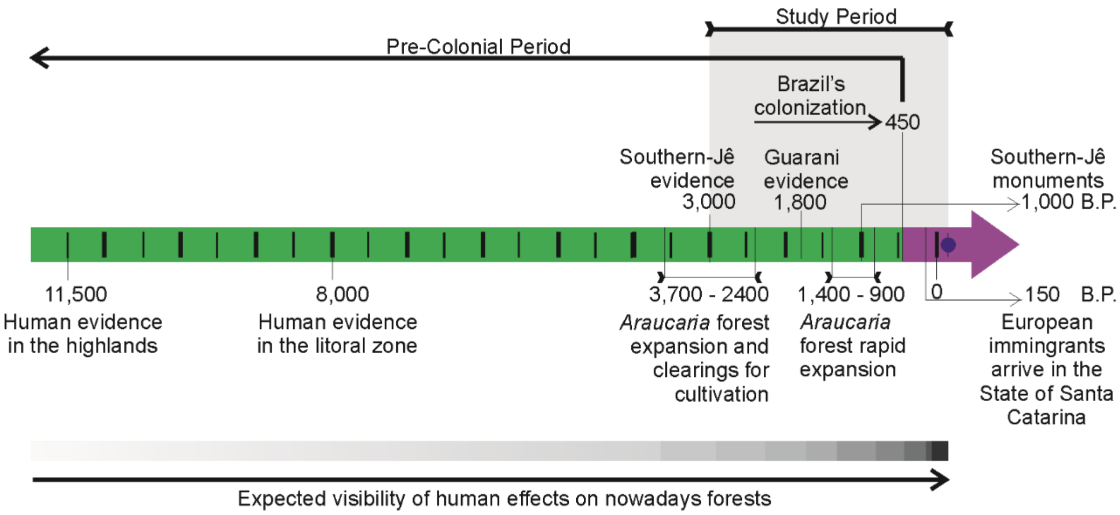
To understand species distribution, we need to consider many different aspects, both biotic and abiotic, and their interdependence, as well as the historical processes. Historical ecology research seeks to understand past human legacy on present day species composition, community assemblage, and identify positive interactions (eg. mutualism) and process associated with niche modification [1–3]. A place with the appropriate environmental characteristics for a species is how Grinell (1924)[4] defined a niche. The development of the niche concept incorporated new factors: biotic interactions were considered [5], environment was expanded to multiple layers [6], and the effect of negative biotic interactions (e.g., competition) on species niche retraction were intensely evaluated [7–9]. Subsequent evolution of the niche concept recognized that positive interactions (e.g., facilitation) were capable of widening the niche [10]; introducing the idea that some species can modify their environment, and thereby can promote changes in resource availability for another species. These species are called ecosystem engineers[11]. The most effective ecosystem engineers are species that cause the longest-lasting modifications to their environment, and have the largest population size; for example, humans [11]. Once species modify their environment, they are able to change the direction and force of selection. This bi-directional relationship between species and their environment, may affect the species' niche as well as the niches of other species [12]. The Niche Construction Theory (NCT) predicts that past bi-directional selective processes result in species composition signatures that are perpetuated over time, and can be recognized in contemporary communities, a pattern called 'legacy' [12]. Different societies placed in different contexts modify their environments in different ways [1]. The term Cultural Niche Construction (CNC) has been coined to emphasize that cultural factors drive decisions about the changes that humans promote in their environment and, consequently, to the environment available to other species [13,14]. CNC theory provides an integrative scenario to understand human legacies on natural ecosystems worldwide [14].

Recent historical, archaeological, and ethnographical studies recognize the historical influence of human activities on what has previously been considered primary, untouched, or pristine forests. Many tropical forests previously thought of as pristine were revealed to have been shaped by past human societies [15,16]. For example, recent studies have shown that Amazonian forests have been modified by indigenous populations for millennia, altering plant species distributions across the region [17,18].

The Atlantic Forest is likely no exception: the region was also occupied by Amerindians long before and continued after European arrival [19]. Archaeological studies have reconstructed the long-term human history of the region, identifying many Holocene archaeological sites in southern Brazil (at least 1704 sites already mapped in the region). This indicates that the Atlantic Forest, now drastically reduced and fragmented [20], has had a long history of human interaction.

History of human occupation in the State of Santa Catarina (Fig 7) commenced in the highlands ~ 11,500 Before Present (BP) [21] and in the littoral zone ~ 8, 000 BP [22,23]. Hunters and gatherers were the first human groups to occupy this territory [24]. Current indigenous peoples in the area belong to the Southern-Jê (Xokleng or Laklaño and Kaingang) and Guarani linguistic groups. Jê groups from Central Brazil has started their migration to Southern around 3, 000 years BP [25] [26]. Archaeological dating in southern Brazil indicates The Southern-Jê commenced occupation along highland rivers, and then moved into littoral areas [25]. Highland occupancy is a general distribution pattern of Macro-Jê linguistic groups in Brazil in the central and eastern plateaus [26]. In the southern Brazil highlands, they relied on 'pinhão' (*Araucaria angustifolia* seed) as a key food source [27,28], associated with another cultivated resources, as *Zea mays*, *Manihot esculenta*, and *Dioscorea* sp., and widespread hunting and fishing. The Guarani migration is related with Tupi expansion from Amazon. The main route for this Guarani migration from Amazon basin to southern Brazil is related to Paraná and La Plata river basin The two principal Guarani suggested centers are the Amazon and La Plata Basins [29]. The Guarani arrived in Southern Brazil only around 1800 years BP [30]. They are recognized as sealers, fishermen and farmers who followed the main rivers and the coast expansion of their territories. Contrasting both migration dynamics, Guarani groups migrated by expanding their territory, whereas the Southern-Jê migrated by leaving old territory and moving into new ones [25,26].

Figure 7 - Timeline of diachronical succession of human population events and linked changes in vegetation cover, in State of Santa Catarina.



Source: author.

The Southern-Jê and Guarani migrated to the south of Brazil to a landscape where forests were expanding and at a time of climate transition. In the highlands, *Araucaria* moist forests were expanding over what were previously grasslands. Grasslands are remnants of a drier climate, whereas forests are favored by the current climatic conditions [31]. Around 3000 years ago, forest expansion over grasslands intensified [32,33], coinciding with the arrival of the Southern-Jê people in southern Brazil [25,26]. Together with climate changes, humans may have acted as a complementary driver of forest expansion due to transportation of seeds [27,28,34,35], and maintained grasslands using fire [32,33,36]. Recent research has shown that human action was essential for these forests to reach their maximum distribution [34,35]. There are many evidence of the long-term use of *A. angustifolia* by past Amerindian societies also suggests they promoted the population expansion of this species, which is the dominant species of *Araucaria* moist forests in southern Brazil [37]. *Araucaria angustifolia* is recognized as a nurse plant, that is, its dispersion would favor the expansion of other forest species [38–40]. The role of human action in the assembly of forest communities in the pre-Colombian period as well as legacies in recent communities are still issues to be understood in the historical ecology of southern Brazil.

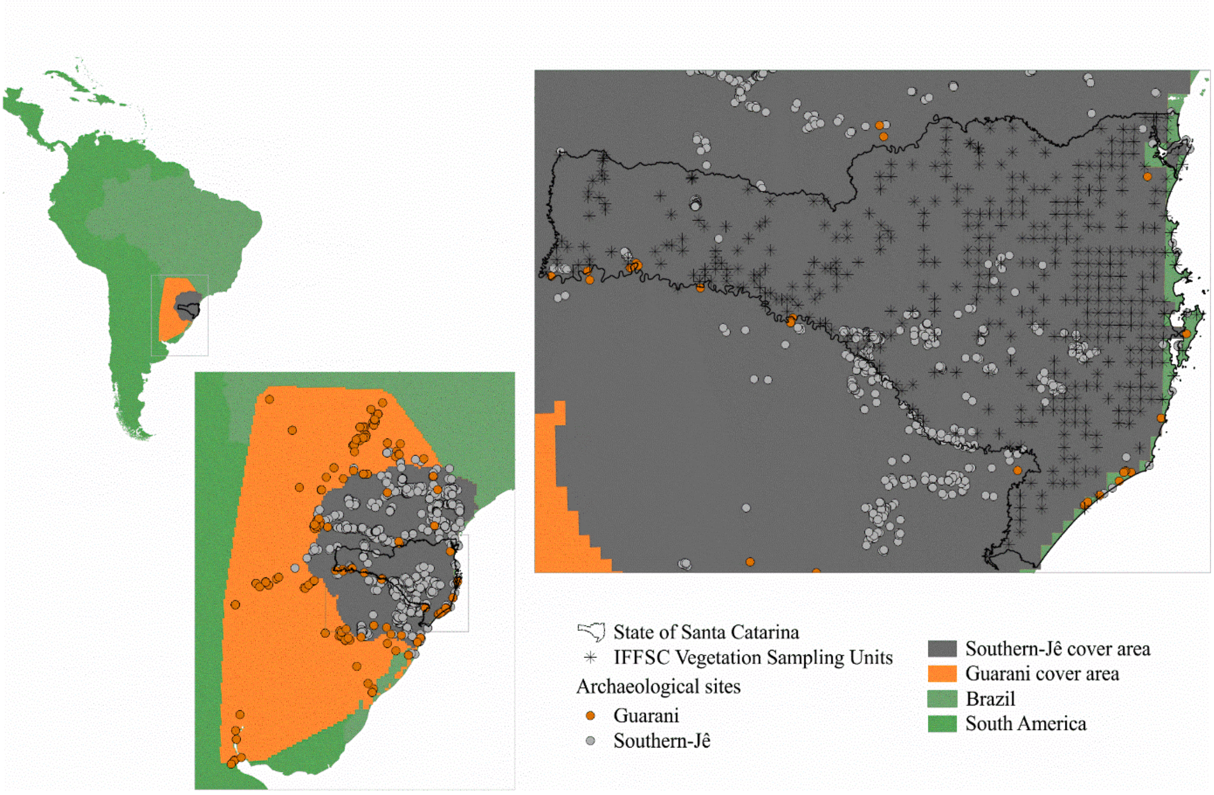
Globally, studies showing the influence of past cultural groups on species distribution patterns have intensified (see[16]); however, the long-term history of the Atlantic Forest is still poorly understood. Historical ecology studies in this region are hampered by the intensification of human occupation in recent times, which is obscuring past human legacies. This study aims to address this knowledge gap for southern Brazil. The niche modeling approach was used to understand the distribution of past Southern-Jê and Guarani Amerindian groups and then correlate this distribution with modern forest composition. Based on the premises that, (a) Southern Brazil has been occupied by humans for millennia, and (b) humans are cultural niche constructors, our hypothesis is that floristic composition differs in Southern Atlantic Forests with a high probability of past human activities, and that different cultural groups also leave differing floristic composition and abundance legacies notable yet, despite the disruption of these cultural groups and of the intense changes caused by recent populations. We suggest that humans have been shaping these forest communities for at least 10,000 years; and that some differences in floristic composition are the results of the historical process of human occupancy and cultural variability.

Materials and methods

Study area

The study area (Fig 8) covers part of the pre-colonial Southern-Jê and Guarani distribution, in the Southern portion of the Neotropical Region. Located in southern Brazil, the State of Santa Catarina (SC) was selected because floristic data has been systematically collected across the state [41], providing the opportunity to compare spatial patterns with pre-colonial occupation. The entire area of SC is in the Atlantic Forest Domain [42], one of the global hotspots for biodiversity conservation [43]. Vegetation consists of coastal scrubland, mangroves, grasslands, and forests. Variation in forest types is influenced by geomorphology and climate. The entire State is in the subtropical zone and climatic variation is related to latitudinal and altitudinal gradients. The elevation gradient induces variation in air pressure, and consequently, promotes cooling. Landforms also drive atmospheric water movement and influence rainfall regimes [44]. Temperature variability increases with distance from the coast [44]. Santa Catarina has eighteen hydrographical basins, and combined with a moderate to high annual rainfall, has substantial river resources for local populations.

Figure 8 - Map of South America highlighting the study area that comprises the State of Santa Catarina. Points indicate archaeological sites (Guarani sites in orange points and Southern-Jê sites in gray points) and stars are the floristic sample units.



Source: author.

Vegetation Data

We investigated whether there is a legacy of past human populations on present-day forest composition. Vegetation data used in this study was collected by the Santa Catarina Forest and Floristic Inventory (SCFFI), which systematically sampled shrubs and trees across the State in a grid system [41,45] (Fig 1). Each sample unit covered 4000 m² [41,45]. All forest plots except sand dunes and mangroves (a total of 417 sample units) were used to evaluate the abundance and distribution of all tree and shrub species in the study area.

Archaeological Data

Aiming to identify past human effects on forest composition, the first step was to locate archaeological sites. Archaeological sites within the study area were identified from literature reviews, as well as field data collected since 2011, by the Laboratory of Interdisciplinary Archaeology Studies at the Federal University of Santa Catarina. The literature review considered data published by Bonomo et al (2015), and Noelli and Souza (2017), covering the south of Brazil, and only used sites that were classified as Southern-Jê or Guarani. Another Southern-Jê archaeological sites were identified in LEIA database based on earthworks description. Using this data, we constructed a matrix with geographical coordinates of Southern-Jê and Guarani archaeological sites. Geographical location was the only information available for spatial analysis that could be obtained from all archaeological sites (although not always mentioned in archaeological studies). Only archaeological data with cultural attribution was used in order to identify any association between species and cultural variability. The selected archaeological sites have been occupied over the past 3,000 years.

Topographic, hydrographic and forest type data

In order to understand which landscape features most influenced past Amerindian distribution, and contributed to defining their niche, we selected variables related to human preferences for specific environments; such as, topography, hydrology [46], and river proximity [23,47]. The Height Above the Nearest Drainage (HAND) was used as a proxy for water table depth, and altitude and slope were used to define terrain (topography) [48]. Water course vectors were separated using Otto Pfafstetter's watershed coding method [49]. Coastline distance was used, assuming that the sea is a source of food and other services used by the populations [30,47,50]. Correlations between geomorphologic and hydrographic variables were evaluated. Forest types were mapped according to the classification of global terrestrial biomes [51] as follows: (1) Rain Forest (locally called "Dense Forest") on the coastal mountain range; (2) Mixed Forest (locally called "*Araucaria* Forest") on the highlands; and (3) Deciduous Forest found inland, especially in the Uruguay River basin [52].

Data Analysis

River classes area were grouped in case of collinearity (other variables did not present autocorrelation). The distance from each river class was rasterized using the Euclidean Distance function in Qgis. We also generated a Euclidean raster distance from the coastline.

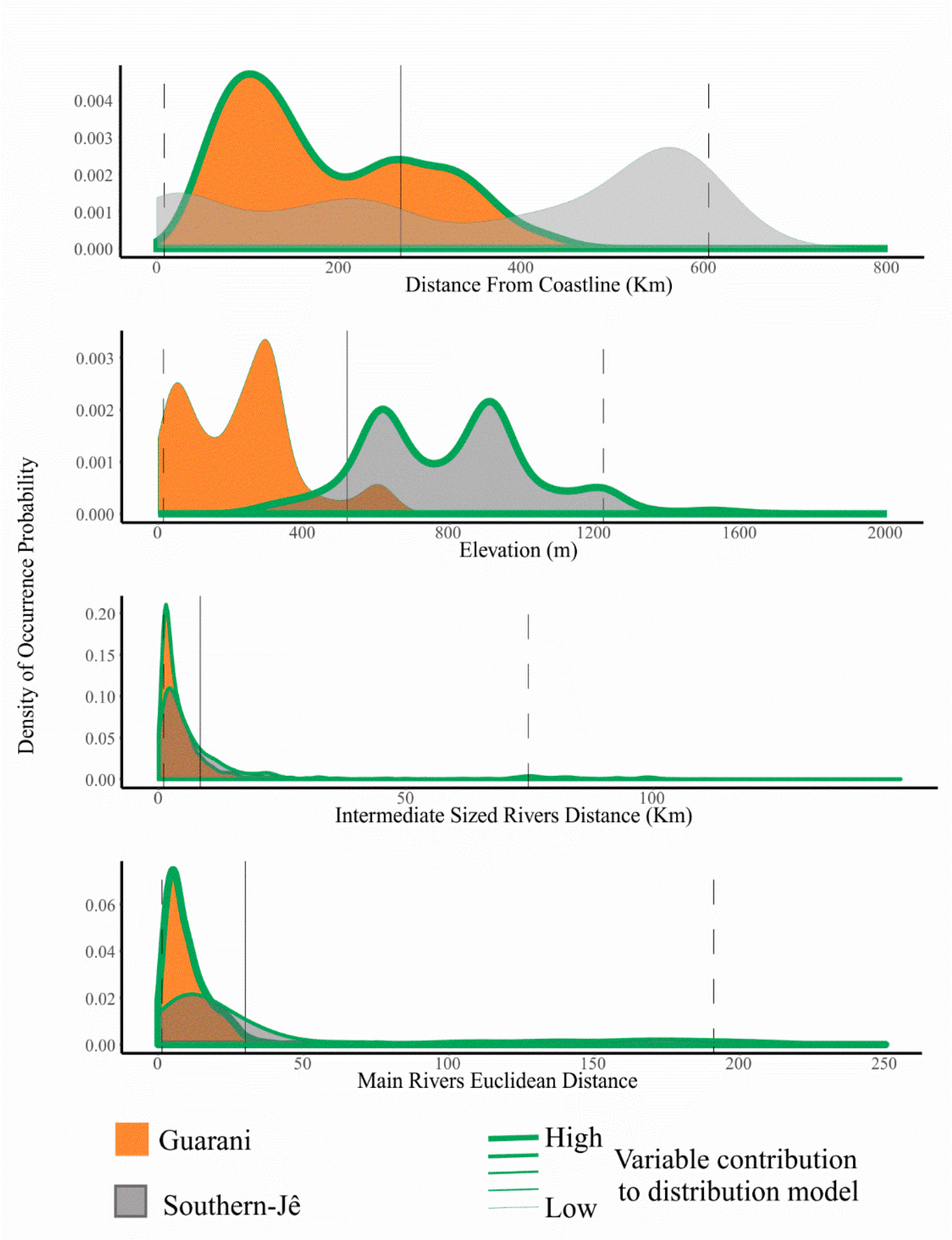
Occurrence area of each Amerindian group was defined based on the geographical distribution of Southern-Jê and Guarani archaeological sites. Occurrence area was used to limit the spatial area modeled for each cultural group. To understand the past Amerindian distribution, we developed models based on archaeological, topographic, and hydrographic data in Maxent interface (Ecological Niche Model – ENM; using the package 'ENMeval' [53]) to fit models and predictions of archaeological sites beyond sampled locations in R [53,54]. Since we only had presence-only data on the location of archeological sites and because data wasn't obtained by systematically sampling, we decided to use Maxent, Maximum Entropy Method, suited for analyzing presence-only data [55]. To further minimize sampling bias, we worked only with one archaeological site on every 10 × 10 km pixel. We used random k-fold validation with 4 k-folds, combining Features Class (FC): Linear (L), Linear and Quadratic (LQ), Hinge (H), and Linear Quadratic Hinge (LQH); and Regularization Multiplier (RM) sequence values 0.5, 4, 0.5. Models were sorted in decreasing order by the largest AUC values (Area under receiver operating Curve) and lowest overfitting, estimated by contrasting AUC values of train and test sets, and then, between top ranking models. Only one model was finally chosen by visual inspection. The chosen model was then used to generate predictive maps of the potential distribution of past Amerindian occupation. Estimates of the variables contribution to each model was expressed in terms of percent contribution and permutation importance values. Two separate maps for Southern-Jê and Guarani sites were constructed. Using these maps, the overlap of Southern-Jê and Guarani past distributions was calculated with the similarity statistic 'I' [56], where results fall between 0 and 1 (0 indicating no overlap and 1 indicating full overlap).

Vegetation sampling locations were overlaid with the maps of the potential distribution of both cultural groups. Next, we extracted the probability of each vegetation sample location falling over Southern-Jê or Guarani sites, or both. To assess the relationships between past Amerindian groups distributions and floristic composition of current forest fragments, we carried out a Redundancy Analysis (RDA), using the package 'vegan' [57] in R. The matrix of species abundances was used as the response variable and the probabilities of Southern-Jê and Guarani sites for each site were used as predictors. Forest type was added to ordination diagrams to aid interpretation but was not used as a predictor in the analysis. QGIS software was used for all geoprocessing procedures and R for multivariate analyses.

Results

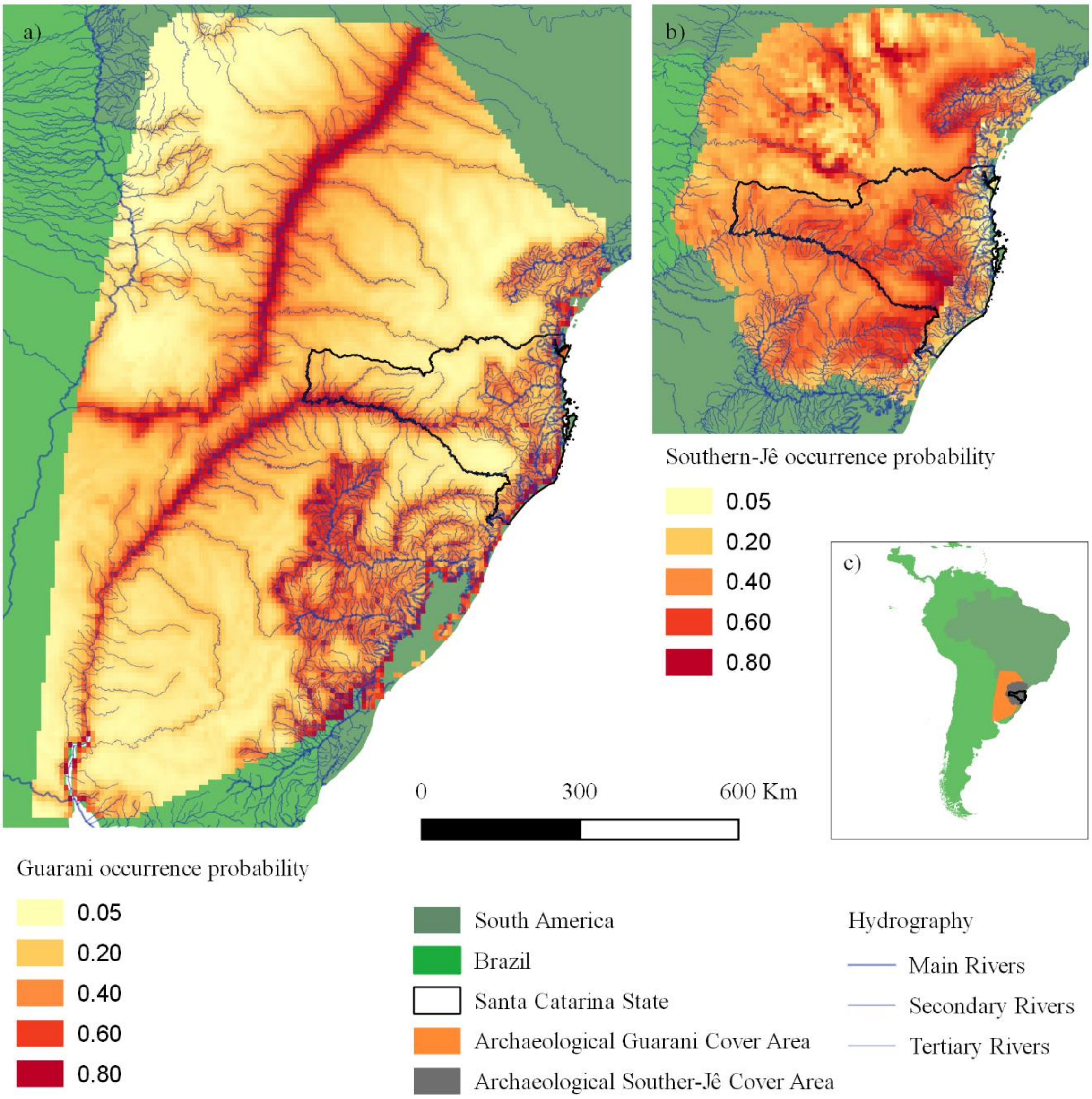
Guarani and Southern-Jê distributions were influenced by the distance to first or second order rivers (using Otto Pfafstetter's hierarchy, Fig 9). The importance of this variable was 42.2% and 40% (contribution and permutation importance values, respectively) in the Guarani model and 22% and 31.9% in the Southern-Jê model. Guarani distribution was also influenced by coastline distance (contribution: 36.9%; importance: 51.8 %), which, conversely, was the environmental variable with the lowest influence over Southern-Jê distribution (contribution: 0.2 %; permutation importance: 0.6 %). Elevation was the environmental variable with the highest influence over Southern-Jê distribution (contribution: 39.6%; permutation importance: 27.1%), being irrelevant to Guarani distribution (contribution: 1.2%; permutation importance: 5.2%). The most suitable environments for Guarani people were those with proximity to the sea or rivers, while Southern-Jê sites were mostly found in elevated areas and near rivers. The final Guarani model (Fig a) was generated with FC=H and RM= 2, showing an AUC = 0.83. The final Southern-Jê model (Fig 4b) was generated with FC=LQP and RM=4, and had an AUC = 0.71. Final images are available in S1A and S1B files.

Figure 9 - Ridgeline plot of smoothed density estimates of the probability of occurrence of Southern-Jê (gray) and Guarani (orange) archaeological sites in relation to environmental variables. Green line width indicates variable importance to the model.



Source: author.

Figure 10 - a) Map of the probability of past Guarani distribution; b) Map of the probability of past Southern-Jê distribution; c) Map without scale of South America highlighted areas showed in a and b. These maps were created with ecological niche models that presented the lowest overfitting and the highest AUC values.



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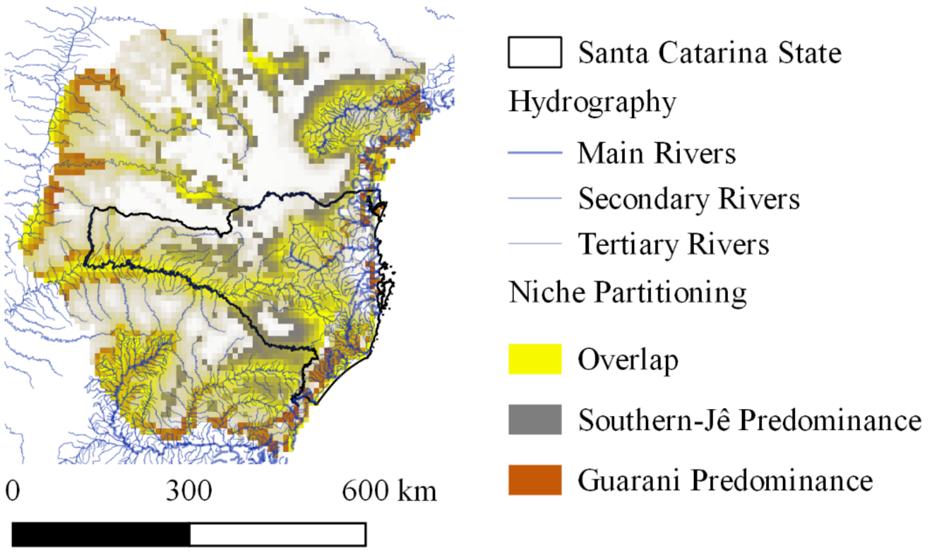
Niche overlap between past distributions of Southern-Jê and Guarani was noticeable (*I* = 0.64; Fig 5). Overlapping areas are located along the major rivers (1st and 2nd order) and along main rivers within intermediate-sized basins (3rd order, Fig 11).

Figure 11 - Spatial partitioning between archaeological Southern-Jê and Guarani distribution.



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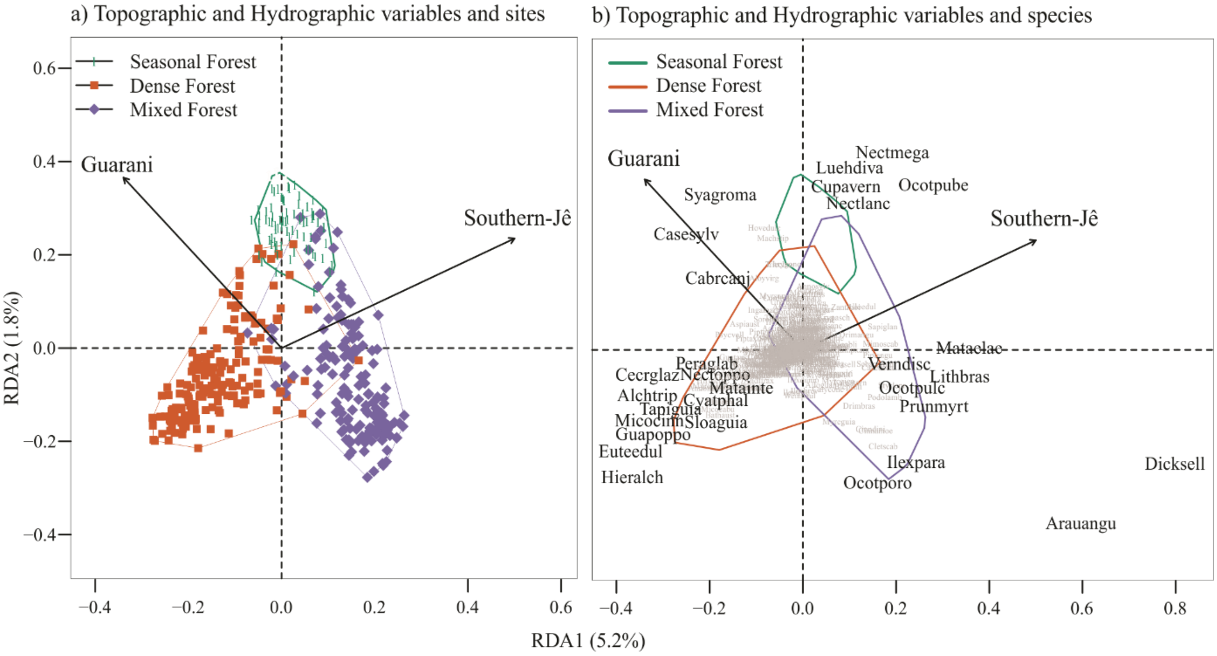
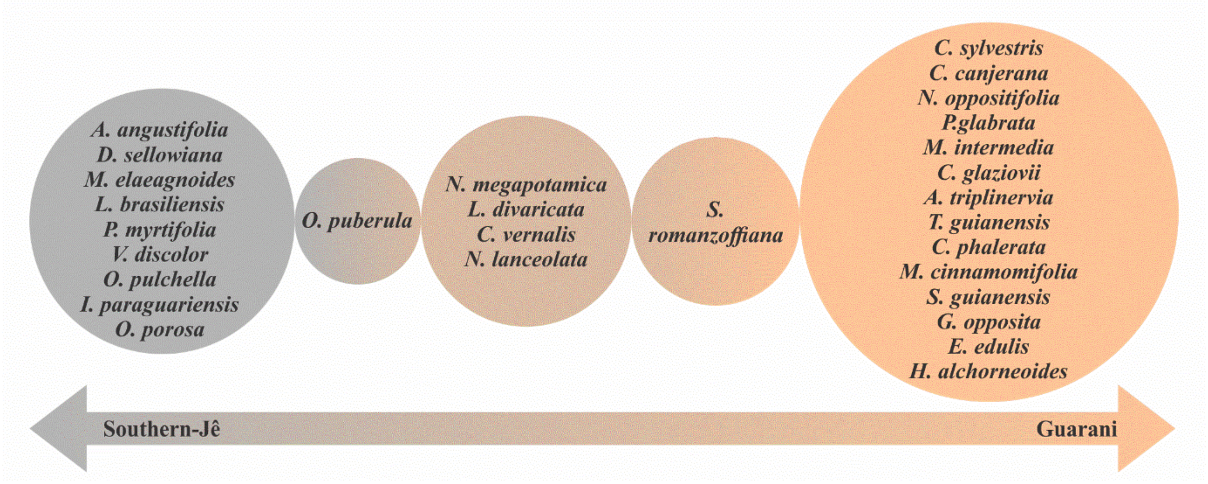
The first two axes of the Redundancy Analysis (RDA) explained 7% of the data variation (Fig 6) and show (i) directional segregation between the two cultural groups and (ii) the links between the distribution of these Amerindian groups and forest typologies. Ordination of sampling units (Fig 6a) suggest Southern-Jê sites relate with Mixed Forests and Guarani sites are more related with Rain Forests. Seasonal forests were likely used by both groups. The scores of the relation between the first axis of the RDA and the past Amerindian groups distribution was -0.57 for Guarani and 0.85 for Southern-Jê: the second axis had positive scores for both groups (Southern-Jê = 0.52 and Guarani = 0.81). RDA ordination analysis highlighted three clear groups (Fig 6): (1) species shared between the Southern-Jê and Guarani groups that are in the positive range of the second axis, (2) species related to the occurrence of the Southern-Jê group in the positive range of the first axis, and (3) species related to the Guarani presence in the negative range of both axes. Some species related to both axes, but were more strongly related to the Southern-Jê (left side of the first RDA axis) or Guarani (right side of the first RDA axis). Twenty-nine species had ordination scores higher than 0.1 or lower than –0.1 and were considered as associated with Amerindian past distribution. These 29 species were listed along a cultural gradient (Fig 7). The listed species belong to 20 families, Lauraceae (n = 6), Sapindaceae (n = 3), Anacardiaceae and Arecaceae (n = 2), with the other families represented by only one species each.

Figure 12 - The redundancy analysis of species abundance and the probability of occurrence of Southern-Jê and Guarani archaeological sites. Arrows represent maximum variation directions. a) Dots represent vegetation sampling units. b) Shows the species distribution. Polygons and colors indicate forest typologies in both figures.



Source: author.

Figure 13 - Relationship between tree species and the two past Amerindian groups (Guaraní and Southern-Jê). These species were selected because they had ordination scores higher than 0.1 or lower than –0.1 in the RDA.



Source: author.

Discussion

This study investigated the cultural legacy of pre-colonial Guarani and Southern-Jê in the present floristic composition of forest remnants. Correlation of the distribution of past Amerindian groups and forest species detected species associated with each group. Landscape compartmentalization between the geographical distribution of archaeological sites occupied by Southern-Jê and Guarani groups was identified. Landscapes suitable for Southern-Jê are generally at higher altitudes and close to water courses. Guarani settlements were more likely to be closer to the sea or large rivers. Suitable landscapes for both groups seem to overlap near the larger rivers.

The species that showed association with pre-colonial Amerindian groups could simply be associated with the landscape characteristics that predicted the distribution of these groups. Alternatively, the plant species could be attracted to human occupation or could be favored by humans, by both intentional or unintentional actions [58]. For instance, Amerindians intentionally cleared the land and used fire to produce crops, and unintentionally favored plants by interrupting seeds dormancy, like *Mimosa scabrella* [59–61], by improvement in light availability to pioneer species, like *Solanum mauritianum* [60]. In the State of Santa Catarina palynological evidence indicates that the opening of clearings for cultivation started between 3760 and 2430 B.P (Fig 1) [34]. Guarani expanded their occupation area and transplanted useful plants when they migrated, favoring fruit trees that attract fauna, and expanding the territories of species of cultural importance [62]. Amerindians transplanted cassava, beans, maize, and genipap from the Amazon to southern Brazil as part of a cyclic agroforestry production system [62]. The Southern-Jê were probably responsible for *Araucaria* forest expansion over grasslands [27,34,35]. Pre-colonial Southern-Jê and Guarani archaeology reveals evidence of agriculture [30,62,63] and pottery production [30,62–64], and both these activities require fire. Fire was used for many things (e.g., heating, cooking, ceramic preparation, and cremation) and may have involved selective extraction or gathering of species for fuel. Fuel for funeral use must reach very high temperatures, for domestic use it must be easily controllable [65]. The use of fire in rituals can also lead to the selection of woods by symbolic characteristics. Archaeological research has shown that Southern-Jê used preferred species in contexts that indicate the practice of rituals: *Araucaria angustifolia*, and *Jacaranda* sp. in a location where *Araucaria* is not available [66]. Fire use could also be unintentionally selective, driving changes in species composition, unintended by those lighting the fires. Agriculture and transplanting fruit trees are examples of intentional activities that modify species composition. Southern-Jê constructed earthworks, that were landscape modifications benefiting some species, in a similar way to the Amazon mounds earthworks[17].

We observed a distribution pattern of Southern-Jê and Guarani groups that was associated with forest types. Southern-Jê sites occur mainly in Mixed Forests (*Araucaria* forests), where many subterranean structures, earthworks, have been found. *Araucaria* forests are recognized as an important element in the social organization of the current Southern-Jê (Kaingang and Xokleng/Laklaño) [34,66]. Southern-Jê controlled their territories by managing the *Araucaria* forests [64]. Guarani sites have not been found in Mixed Forests but are common in Rain Forest areas. Both groups co-occurred in Seasonal Forests, probably because this forest type is mainly distributed along an important river (the Uruguay River). Rivers are a factor associated with both groups' distributions, including their ancestral territories. Rivers are especially important in Guarani culture, they are excellent sealers and fishermen [30]. The Southern-Jê arrived before the Guarani in southern Brazil and initially occupied coastal zones and riversides [25]. However, main rivers and the coastline were also migration routes used by the Guarani [30]. The Southern-Jê subsequently intensified the highlands occupation, and this may be due to arrival of the Guarani people [25,67], or due to ecological identity with their ancestral territories, which are highland headwaters [26].

We found a species partitioning gradient between the two cultural groups in analysis of the species distribution (Fig 7). An important point is that our analyzes do not isolate the causes of the distribution of plant species, we are considering niche construction as a process in which factors of different natures are inseparable. Many of the species listed in this gradient are cited in the ethnobotanical literature as important for Southern-Jê and Guarani. Species such *Dicksonia sellowiana* (Fig 7a) is associated with Southern-Jê groups, and cited in literature as a culturally valued species that is used to prepare a traditional drink called "Mõg" [68,69]. *Araucaria angustifolia* (Fig 7b) appears to be associated with Southern-Jê presence, and archaeological evidence exists of its use by pre-colonial Southern-Jê groups [27,70,71]. *Dicksonia sellowiana* and *A. angustifolia* are very abundant species in Mixed Forests, as are *Ilex paraguariensis* (Fig 7c) and *Matayba elaeagnoides* (Fig 7d). *I. paraguariensis* is a key cultural species, whose leaves are used to prepare a drink called "chimarrão" or "mate", that is popular in South America [72]. The practice of consumption and processing of *I. paraguariensis* leaves are culturally tran;smitted by Amerindians [72]. *M. elaeagnoides* is described as a good quality burning wood [73]. *Lithraea brasiliensis* (Fig 7e) has a popular name "bugreiro" ("bugre" with an added suffix to indicate that it is connected to, or used by, the bugre). Although this species is associated with Southern-Jê, *L. brasiliensis* was also reportedly used by Guarani for construction purposes [74]. Along the entire gradient, we observed species of the Lauraceae family, composed by the genera *Ocotea* (Figure 6f) and *Nectandra* (Fig 7g). Among these and linked with Southern-Jê distribution, the species *Ocotea porosa* is currently listed as vulnerable to extinction[75]. We observed a change in the composition of Lauraceae inside the gradient. From the species are shared by both Southern-Jê and Guarani, the genus *Ocotea* is replaced by the genus *Nectandra*. The species shared by the two cultural groups are at the center of the gradient and all of them are abundant in inland Seasonal forests. In addition, all of these shared species are cited by various cultural groups in ethnobotanical literature, reinforcing that they are species of shared cultural use and knowledge. *Luehea divaricata* (Fig 7h) is used medicinally by Laklaño (Southern-Jê) [69], Guarani [74,76,77], and regional farmers [73]. *Cupania vernalis* (Fig 7i) is used by Laklaño [69], Guarani [74,76,77] and regional nowadays farmers [73] for food, construction and artifact production. Species such as *Syagrus romanzoffiana* (Fig 7j) *and Euterpe edulis* (Fig 7k) are associated with Guarani presence, but only *S. romanzoffiana* was common to both Guarani and Southern-Jê. Both species are reportedly used by the Guarani [74] and *S. romanzoffiana* is known to be cultivated by them [62]. Arecaceae is an important family for human subsistence in the Atlantic Forests, because its species produce many fruits, and in some cases, palm heart [19]. Arecaceae phytoliths have been found in archaeological Southern-Jê pottery, which could suggest consumption and processing or may represent background vegetation [63]. *Euterpe edulis* is a very abundant species in dense forest (Rain Forest) [78], while *S. romanzoffiana* also occurs in other forest typologies [78–80]. Other species associated with Guarani presence are *Casearia sylvestris* (Fig 7l) and *Pera glabrata* (Fig 7m), both species with Amerindian references in their popular name: "bugre tea" [73,74,76] and "bugre heart"[69]respectively ("bugre" is a pejorative name for native people). *Casearia sylvestris* is a species culturally prominent for present day Guarani [76] and *P. glabrata* wood is used by Guarani for construction [74,77] and by Laklaños (Southern-Jê) for artifact production [69].

Our analysis explained only 7% of data variation; however, given the wide spectrum of environmental characteristics that may influence vegetation patterns at the landscape scale, past Amerindian cultures may be an important factor to consider. Our results indicate past Southern-Jê and Guarani distributions are another factor driving differences in present-day forest species composition.

To infer how much of the activities in the pre-colonial period may be registered in today's forest composition, it is important to consider demographic changes. We illustrate the expectation of human impact at different times (Fig 1). Although we still don't have detailed demographic estimates for the pre-colonial period in southern Brazil [24], we have estimate up 3,000 years ago [81]. The population density in the state of Santa Catarina would have been 0,15 inhab/km2 in the period between 11,000 and 7,000 years ago [81]. That density would have remained in the western portion until 3,000 years ago, but would have increased in the east reaching up to 0,75 inhab / km2 [81]. that we don’t have demographic data, but in the period between 1,800 BP and 1,400 BP the Guarani occupation began [30], there was an increase in the Southern-Jê population [34], and as a consequence of this interaction there were cultural changes [67]. In the present year, 2,020, the population density in the state of Santa Catarina varies from 0.7 inhab/km2 (in the largest portion of the territory) to 400/ inhab/km2 (in a few places) [82]. Thus, despite the collapse of the Amerindian populations, there was a population increase in the study area. That pattern contrasts with the Amazon, where there was general depopulation [58]. If on the one hand in the Amazon, populations of domesticated plant species are being lost [58], on the other hand, pre-colonial legacies are evident [18]. In State of Santa Catarina Amerindian populations have drastically reduced, just like in the Amazon, so populations of domesticated species may also be missing. However, if there was intercultural transmission of knowledge, some populations of domesticated species may have perpetuated. In general way, State of Santa Catarina population density increased and that has resulted in intense recent changes in vegetation [83]. Despite this, we have listed here 29 species related to the Southern-Jê and Guarani occupation in the pre-Colonial period. We suggest that traits of domestication of these species be investigated, because some populations of domesticated species in the pre-Colonial period may have been maintained [84], and we need more investigations in this regard.

Past Amerindian distribution

This study found that Southern-Jê and Guarani group distributions are related to different environments. Landscapes preferred by Southern-Jê were likely higher altitude and close to minor water courses, whereas Guarani settlements were more likely located near the sea. Both groups may have shared locations near large rivers.

The past distribution models generated, are an advance on broad analyses, because they reinforce, and spatialize the preferential landscape characteristics for pre-colonial Southern-Jê and Guarani groups. Maps of past Amerindian group distributions are useful for investigating spatial patterns; such as, relationships with vegetation, or landscape partitioning between cultural groups. Distribution models generated with presence data are only potentially usable when they have an AUC value above 0.75 [85]: however, for goodness of fit evaluation of models in general, AUC values above 0.7 can be considered good [86]. Evaluating AUC values in species distribution models, Elith et al (2006, [87]) observed that 64% of the best models presented AUC values above 0.75, and 14% of the best models presented AUC values between 0.7 and 0.75. In this respect, the Guarani distribution model, with a value of 0.83, can be considered adequate. The Southern-Jê model presented an AUC above 0.7, so we consider it acceptable, but understand there are caveats. Our maps explain the spatial dimension of the occupation of southern-Jê and Guarani, but the temporal dimension mixes the entire period of pre-Colonial occupation.

There was a niche overlap between both cultural groups near main rivers. This may be explained by occupation at different times, or by simultaneous occupation involving interactions between the two groups and remains to be further addressed. The Southern-Jê initially occupied diverse territories in Southern Brazil. Around the time the Guarani arrived and began to occupy areas close to large rivers and the coast the Southern-Jê were settled in the highlands. Although there are records of Southern-Jê presence in the highlands since 2000 years BP, it is only around 1000 years BP that these groups started to build their funerary earthworks [64,67]. This new architectural expression may be a way of controlling their territory, because it coincides with the arrival of Guarani groups [67]. Guarani groups expanded their occupation along the margins of major rivers and along the coastline [30]. The Jê people were distributed over the highlands in their Brazilian territory [25,26], and their pattern of migration created isolated groups, differing from the Guarani [25]. Following contact with Europeans, Amerindian populations were reduced due to territorial conflicts, diseases, political, and social disruption. There is evidence of Guarani occupation followed by subsequent Southern-Jê occupation in some locations [25], suggesting that the groups competed for the territories. Furthermore, synchronous Guarani sites inside of Southern-Jê areas have been found, suggesting fluid frontiers where these groups have interacted over time [25].

Conclusion

Although there are still many pieces of the puzzle to be put together for a complete understanding of vegetation patterns, this study is the first to assess pre-colonial cultural effects, on the contemporary forest composition, of a large extent of the Atlantic Forest. This study evaluated forests that have been seriously altered post-European colonization [83] and still detected a legacy of pre-colonial cultural groups on forest composition. Forest composition differs in landscapes previously occupied by different Amerindian groups. This difference may be due to the different ways differing cultures manage territory, indicative of Cultural Niche Construction. We conclude that long-term cultural activities may have acted with other biotic and abiotic processes to determine forest compositions in the Southern Atlantic Forest.

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Supporting Information

S1 File. R Scripts. This file contains all the codes wrote in R. (APÊNDICE A)

S1A File. ENM Guarani raster. This file can be opened using a Geographic Information System (Gis Software) or following the script provided in S1.

S1B File. ENM Southern-Jê raster. This file can be opened using a Geographic Information System (Gis Software) or following the script provided in S1.

3 CAPÍTULO 2 – HUMAN DISPERSION EVIDENCE IN THE DISTRIBUTION OF THE *CASEARIA SYLVESTRIS* SPECIES IN SOUTHERN BRAZIL

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> “é-se índio porque se foi índio –, mas também um conceito que remete ao futuro – é possível voltar a ser índio, é possível tornar-se índio. A indianidade é um projeto de futuro, não uma memória do passado.”
> Viveiros de Castro para Prisma Jurídico. Entrevista com Eduardo Viveiros de Castro p. 265. 2011.

Article

Human dispersion evidence in the distribution of the *Casearia sylvestris* species in Southern Brazil

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Abstract: Current landscapes may contain tree populations favored by past cultural groups. We investigated the *Casearia sylvestris* species to find out whether its current distribution is related to the past presence of Guarani and Meridional-Jê peoples in southern Brazil. We used data on species location, abundance and, presence, and absence; Meridional Jê and Guarani models of past occupation probability. We calculated: The cost surfaces to estimate the movement for each cultural group based on topographical, hydrological, and cultural characteristics; and the distance from individuals of *C. sylvestris* to Indigenous Areas, and we obtained current climate data. We used Generalized Linear Models to identify the effect of the variables on the presence and abundance (individuals number) of *C. sylvestris*. The abundance model explained 67% of the total data variation, and the presence model, 37%. The Meridional-Jê occupation and its less costly paths favored the species abundance and presence, as well as the distance to indigenous areas. The cost of the paths to Guarani peoples showed an inverse relationship. Phytogeographic regions provided the highest responses in the models. Our results highlight the influence possibility of the Meridional-Jê and Guarani peoples' role on ecological patterns of *C. sylvestris* and point out that the species can be used as a marker of Amerindian routes.

Keywords: Landscapes; Culture; *Casearia sylvestris*; Atlantic forest; Guarani; Meridional-Jê; Indigenous areas; Amerindians; Path markers; Past occupation.

1. Introduction

Landscapes constitute the central axis of a research program called Historical Ecology, which focuses on the spatial and temporal dimensions of human beings' relationships with their surrounding environments [1,2]. Many past human actions have left marks that can still be seen in the landscapes, such as, earth engineering, paintings, and even changes in biological diversity. Thus, landscapes are testimony of those who lived there and modified it [3]. The landscapes are inserted in a geographic space, a place, where organism, matter, and energy flows occur [4]. For Ingold, space can be defined as a mesh ("meshwork"), like a weaving, in which yarn are as the lines (in the geometric sense), which are the paths and the flows, the growth of the lines occurs by the expansion of the movement, and the interspersed lines are the meeting of paths, which form networks, and thus build the landscape [4,5]. For the author, there are still dashed lines, which are not lines, but "a succession of instants in which nothing moves or grows" [6, p.3]. In ecology, a landscape is organized in a structure that defines operating patterns, and the elements of this structure can facilitate or hinder flows. In an analogy with Ingold's proposal, there would be easier or more difficult spaces to weave lines and dots. These would be the corridors and barriers, respectively. However, the structure of a landscape is determinant for flows, but these can also modify the landscape structure, and the relationship between flows and the landscape is bidirectional [7,1].

Another fundamental bidirectional relationship for understanding human actions on the environment is in the Theory of Niche Construction, which predicts that in addition to the environment acting as a filter that selects suitable organisms (natural selection), organisms can modify the environment and, thus, change the selection exerted by the environment [8,9].

Humans are very efficient as niche builders, and it is a fact that they are not limited to landscapes [10]. We transpose and break so many geographical and ecological barriers that we have modified about 75% of the earth's surface [11]. Furthermore, we provoked changes in the distribution of species at a global level, especially in the distribution of plants, as these were continuously transported at different spatial and geographic scales [12,13]. The ability to surpass barriers through movement was fundamental to the success of humanity, motivated by the search for food, water, exchange of goods, or maintenance of social dynamics, which required displacements of different spatial scales throughout human history [3,4,14].

Building a bridge is an example of how humans break barriers [15]. It is a construction that attracts other flows, in addition to the builders. Thus, it becomes a significant place [16], attractive to a greater number of people [17]. This is because the lines or marks left in the landscape are attractive for re-occupation [18]. Other examples of marks are constructions, engravings, but there are also subtle marks, such as populations of useful plants.

Along old paths there may be persistent population densities of intentionally or unintentionally transported species. Trees can be markers of mobility [14] and also markers of management actions, such as the density of species that naturally occur isolated or with few individuals [19,20].

Examples of human groups that left tree populations as markers of movement are the Nukak and the Kayapó peoples [21,22,23]. The Nukak hunter-gatherer group movement has modified the landscape in the Colombian Amazon, creating patches and changing the species density. The Nukak move around a lot throughout the year, with short distances between camps. By always returning to the same area, they create resource patches, even orchards. The species used for food are favored by the clearings opened for the encampments, thus, the densities of useful species are formed over many years [21]. The Kayapó, on the other hand, modify the landscape on their collection trips, with walks that last from a month to a year. It would not be feasible to carry out these routes carrying food, so, over time, collected plants were transplanted near trails and camps [22,23]. In the present study, we seek to better understand the movement marks of indigenous groups in southern Brazil, where it is possible to identify evidence of species favored by their cultural practices, with indications of species connected with the meridional Jê (current Laklãnõ-Xokleng and Kaingang) and the Guarani peoples [24]. Among the species cited by Cruz et al. (2020) is *Casearia sylvestris* (Salicaceae), which presents a distribution similar to corridors that match the movement pattern of the Guarani peoples, along rivers [25], and also of meridional Jê peoples, for whom mobility networks have been described in flat and high areas in archaeological context [26] and also along the edges of walls to access symbolic sites [27,28].

The Guarani peoples correspond to one of the indigenous peoples that make up the Tupi-Guarani linguistic family. Its origin is related to a division of Proto-Tupí-Guaraní speaking groups that diverged about 4,000 years ago in the southwest Amazon, moving to the south along the lowlands of the Paraguay river basin (Paraguay, Argentina, and Southern

Brazil) [29]. Archaeological data suggest the border region between Brazil and Paraguay as a possible nucleation site for the Guarani peoples in southern Brazil around 2,500 years ago [25]. Currently, the Guarani peoples are subdivided into four groups that live in villages or in urban centers and that have different dialects and cultural practices: Mbyá, Nhandéva, Kaiowá, and Ñandeva-Mybiá. The Guarani movement is linked to the expansion of the population into new areas without abandoning old ones, forming interaction networks along water bodies or the coastline [25,30], in a process defined by Brochado (1989) as swarming. Migratory agriculture is a cultural practice of the Guarani peoples, and it is possible that one of the transported species was *Casearia sylvestris*, since it is important for this cultural group indicated by the popular name "guaçatonga," which is of Guarani origin [31,32]. Another vernacular of the species is "pau-de-lagarto," in reference to the lizards of the Teiidae Family that consume their leaves. These lizards are present in the Guarani diet and consume the leaves of *C. sylvestris*, according to oral tradition, to take advantage of the anti-ophidic properties [33].

Southern-Jê is a concept used by archaeologists and linguists to refer to indigenous peoples who are found in southern Brazil and whose language derives from the Macro-Jê linguistic trunk. Based on linguistic evidence, peoples who speak languages linked to this linguistic trunk, originating from the highlands of Central Brazil, would have migrated to the southern portion of the country from 4,000 years ago [34,35], reaching the southern states of Brazil between 3,000 and 2,000 years ago [36-39]. It is assumed that the Jê peoples went through new subdivisions, moving across Brazil along the plateaus [40,41] and possibly maintained this pattern of movement in the new occupied areas, considering the higher occupation density in the areas of plateau and mountain ranges in the south [42,43]. However, it is important to highlight that the archaeological remains associated with the southern-Jê occur in different topographic compartments, such as on the coast [41,42]. In Santa Catarina, there is evidence of paths related to the southern-Jê peoples on the flat tops of the plateau, such as those that pass through the cliff edges (locally known as "peirais") to access the most symbolic places, such as shelters, as reported by Machado [27] on access to the Gruta da Paca site: "through the upper part of the wall, locally called 'peiral'" (p. 91). High mobility networks were also identified in areas of higher altitude and flat topography [26]. The Meridional-Jê language family gave rise to the recent Xokleng and Kaingang languages [44]. Like the Guarani peoples, the Meridional-Jê peoples transplant plants in their migrations, including native trees [45], as well as practicing agroforestry management in a large territorial extension [27,28], also interacting with the *C. sylvestris* species [46,47].

C. sylvestris is a widely dispersed species, but it has some characteristics indicating that it may have some degree of domestication, such as low phytochemical and genetic variability between populations [48-51]. In addition, it has multiple medicinal uses, which include anti-ophidic, analgesic, anesthetic, antiulcer, antimicrobial, anti-inflammatory, healing, diuretic, antiseptic, antiherpetic, anti-different agents of tropical diseases (malaria, leishmaniasis, Chagas disease) and, more recently, anticancer uses [52-57], which makes it very important to the global pharmaceutical scenario. The species is used by several indigenous peoples [55], holders of traditional knowledge associated with genetic heritage. This includes the indigenous peoples of southern Brazil [47,58,59], a region where our purpose is to understand whether the millennial history of indigenous relationships in this environment has favored the species. Our hypothesis are:

1) *Casearia sylvestris* can be an indicator of paths and areas of ancient occupation by Guarani and Meridional Jê peoples (currently Laklãnõ-Xokleng and Kaingang), since the species is used by both, with indications of indigenous use in its popular names (bugre tea and guaçatonga, which is a Tupi-Guarani word).

2) *Casearia sylvestris* can be an indicator of paths used by the meridional Jê (current Xokleng and Kaingang) and Guarani peoples, with an almost linear distribution along rivers (Guarani displacement pattern) and along the edge of the perais (Jê displacement pattern).

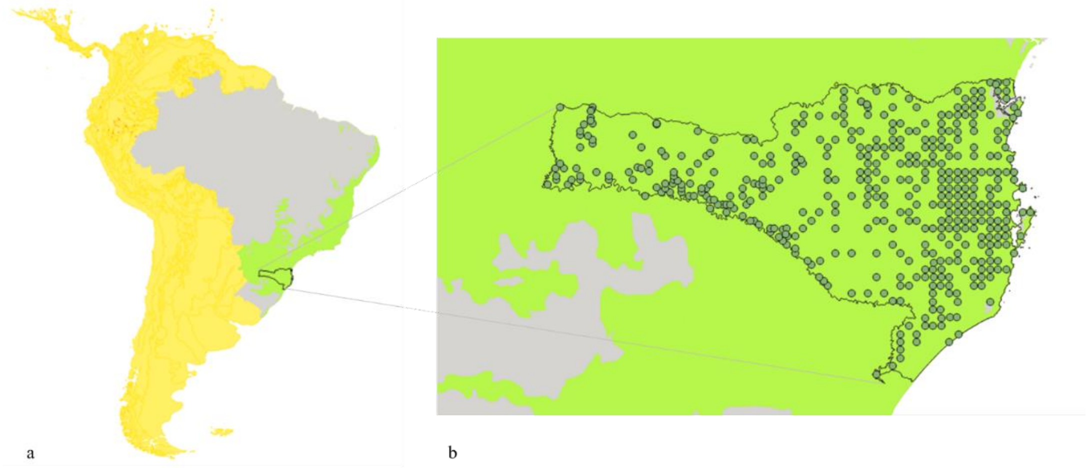
3) *Casearia sylvestris* is more abundant where the people x plant relationship is longer, and therefore it is more abundant close to indigenous lands.

2. Materials and Methods

2.1. Study Area

Santa Catarina is a Brazilian state (Figure 14a), located in the subtropical region, between the latitudesparallels 25◦57'41''S and 29◦23'55''S, and between the longitudesmeridians 48◦19'37''W and 53◦50'00''O. It is fully inserted in the Atlantic Forest Domain, a world biodiversity hotspot. The relief is formed by lowlands, mountains, and plateaus, and the altitude varies from sea level to 1,800 m. The climate is humid, and the rainfall is well distributed throughout the year. The hydrographic network is rich, evenly distributed and is divided by the Serra do Mar into two main basins: One on the Atlantic side and the other on the interior side (Plate Basin).

Figure 14 - a) Study area, state of Santa Catarina, inserted in the Atlantic Forest (green), in the Brazilian territory (grey) and in South America; b) Study area with the distribution of sampling units of vegetation.



Source: author.

2.2. *Vegetation*

We used the floristic database of FlorestaSC, which is a program of the state government of Santa Catarina (SC), focused on forestry studies, including floristic inventory. The allocation of the inventory samples covers the entire state of Santa Catarina (Figure 14b), they are distributed within a 10 km x 10 km grid, and in the Semideciduous Seasonal Forest area the grid was reduced to 5 km x 5 km, due to high fragmentation. FlorestaSC data collection records tree and shrub individuals with a diameter at breast height greater than or equal to 10 cm. and taller than 1.30 m. The data we used corresponds to the survey carried out between the years 2007 and 2010 [60]. We use raw data on the number of individuals (abundance) and presence and absence of the species *C. sylvestris.*

Geological diversity provides different environments that support different physiological-ecological systems. The phytogeographic division system used by FlorestaSC was proposed by Klein in 1978:

- The Seasonal Deciduous Forest (SDF), also known as deciduous forest, is characterized by the total loss of leaves in up to 50% of individuals in the unfavorable season, which is winter. Located in the west of the state, along the Uruguay River and its tributaries. It is the most fragmented formation in SC. There are areas of ecotones with MOF.
- The Mixed Ombrophylous Forest (MOF), also known as the *Araucaria* Forest, in reference to the conifer *Araucaria angustifolia*. From 1,000 m altitude it is called montane MOF. It connects with grasslands, SDF, and DOF.
- The Dense Ombrophylous Forest (DOF) is the characteristic formation of the Atlantic Forest Domain, presenting a closed canopy with little luminosity for the lower strata. In SC it is limited to the west by the Serra do Mar and Serra do Geral and is the least fragmented formation in the state. It presents areas of ecotone with restingas and to the West with the MOF.

2.3. *Casearia sylvestris*

Casearia sylvestris (Salicaceae) occurs in Central America and throughout South America, where it is the probable origin of the genus *Casearia* [61]. In Brazil, it occurs in the Cerrado, the Atlantic Forest, the Amazon, the Pantanal, and the Caatinga. The oldest recorded pollen of the genus *Casearia* was found in Panama about 37 million years ago and this pollen is similar to that of *C. sylvestris* [61]. In an archaeological context, the pollen of *C. sylvestris* was found in Missiones, Argentina, in a column with dates between 1932±53 BP (Erl-12105) and 1072±43 BP (Erl-12104) [62].

It is a species that, depending on the environment, can occur as a shrub, arboretum, or as a tree up to 20 m high; its flowers are hermaphrodite, pollinated by insects and with ornithochoric dispersion [63, 33]. In the review of the genus for the Neotropical Flora, Sleumer [64] distinguishes two varieties of the species: *C. sylvestris* var. sylvestris and *C. sylvestris* Sw. var. lingua (Cambess.) Eichler, based on differences in leaf morphology, conspicuity of secondary veins and preferred occurrence environment: var. tongue, in cerrados, and var. sylvestris in forest formation. However, the separation between varieties is complex due to the occurrence of morphologically intermediate individuals. Torres and Ramos [65], who studied the Flacourtiaceae family in southeastern Brazil, preferred not to adopt the separation proposed by Sleumer [64] for this reason.

Cavallari and coworkers [63] studied the genetic structure of nine populations of the species in southeastern Brazil by using microsatellite markers and found, among other aspects, that there are significant genetic differences between the varieties. Genetic analysis with a Bayesian approach grouped the 376 individuals studied into two large groups that correspond to the two varieties. That is, the genetic analysis showed great agreement with the classification based on external morphology. The authors observed that there is probably a duplication in the genome of the species, notably in var. language.

Varieties of the species occur allopatrically, due to the isolation of populations, but also in a sympatric and mixed way. The allopatric form predominates in isolated populations (natural selection), while sympatry can lead to the coexistence of different varieties of the *C. sylvestris* species with different genetic adaptations to survive in different environmental conditions, leading to greater genetic diversity; populations with intermediate individuals also occur, which may be the result of complex evolutionary processes, including the migration of different populations and the occurrence of hybridization between varieties [63].

The varieties show strong genetic and phytochemical differentiation, with the lingua variety producing more phenolic compounds and sylvestris variety producing more clerodane diterpenes [66], both with multiple medicinal applications [52-57]. The healing properties were already related to the traditional knowledge of native peoples [67, 53]. One of the first publications on the species investigated compounds for arthritis used by Native American populations [67]. Medicinal properties include: Antidote for snake venom [68-73] and, in Brazil, oral tradition points out that "Teiú" lizards use the plant as an antidote for pit viper venom [33]; the antitumor properties of casearins are widely studied [74-78,57]; in addition to properties against various agents of tropical diseases, such as anti-leishmaniasis and trypanocides [52,54], schitomicidal [79].

C. sylvestris It is used by different indigenous populations [80-84], to the extent that it is popularly known as 'bugre-tea,' a name that refers to indigenous people in the pejorative term 'bugre'; 'pau-de-lagarto', in reference to the "teiú," a lizard that consumes the leaves of *C. sylvestris* [33]; and by the indigenous Guarani name 'guaçatonga' [55]. In the southern region it is consumed by the Guarani [59], Kaingang [47], and Laklãnõ-Xokleng [58] peoples.

2.4. Settlement of the State of Santa Catarina

Archaeological evidence indicates that around 11,000 years ago, parts of the Uruguay River valley and Babitonga Bay in the state of Santa Catarina, were already occupied. The oldest site in the Uruguay Valley has continuous dating from 11,614-11,196 years cal BP (9,925±45; Gif3116/SacA40193) to 495-320 years cal BP (395±40; Gif3160/SacA44482), related to the reoccupation of the site by Guarani peoples [85]. In the

Babitonga Bay, a date obtained estimates the occupation of the region by hunter-gatherers between 11,095-10,724 years cal BP (9,600±30; Beta-496156) [86]. Around 9,000-8,000 years ago, human settlement began to expand along the Uruguay River, with the first sites appearing in the Itajaí Valley [87-89]. On the coast, later human occupation dates back to 8,000 years, indicated by the presence of shellmounds [90-92].

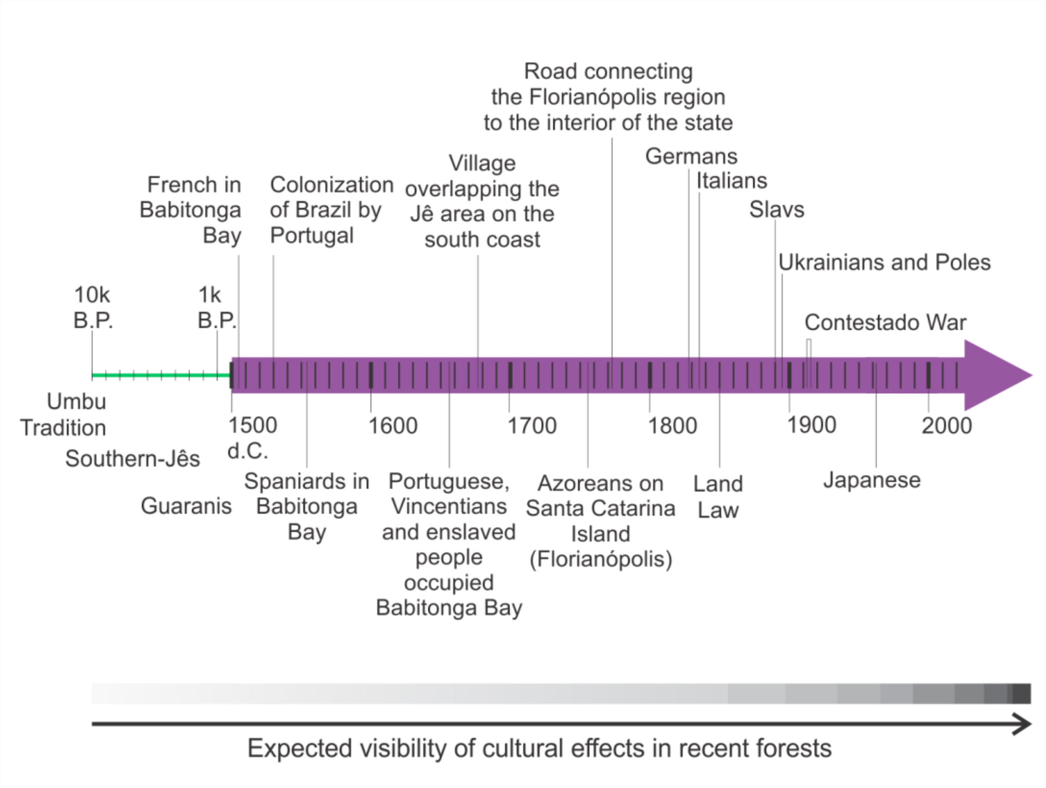
Subsequently, according to the available archaeological data, around 2,000 years cal BP ago there was a population increase in the plateau areas of Santa Catarina state, associated g with the expansion of the *Araucaria* forests and with the arrival of the southern-Jê peoples [36-39], followed by the expansion of the Guarani peoples [25]. During the same period, Bbetween 2,200 and 900 years cal BP, a series of changes took place on the coast, with the gradual reduction of active shellmounds and the beginning of the construction of late shellmounds (shallow sites), which show elements of continuity with the shellmounds [93-95]. Around 1,300 years cal BP, pottery associated with the southern-Jê peoples began to appear on the coast, raising the debate as to whether there was a movement of groups from the plateau/inland to the coast or whetherthere was an intensification of interactions between both groups [96-100]. In terms of Guarani occupation in Santa Catarina, the oldest sites are located on the southern coast, dating to 1,200 years cal BP (1040±110, TL) [101]. In the southern region of Brazil, the oldest dates on Guarani sites indicate an initial occupation between 1607-1318 years cal BP in the Paraná River area (1625±60, SI-5021) [25]. Based on this, Bonomo and coworkers [25] estimate that the oldest Guarani sites are located in the west of the state of Santa Catarina, between the Uruguay and Pelotas rivers..

It was these more recent populations, related to the southern-Jê and Guarani peoples, who initially came into contact with European populations. Before the Portuguese colonization, a French expedition landed in Babitonga Bay at 1504, on the north coast of Santa Catarina state, which was occupied by the Guarani peoples [102]. But it was in 1658 that groups of Portuguese, Vincentians (who came from what is now the state of São Paulo) occupied the region more effectively. In 1678, a meridional Jê village, in the south of the state, where the southern landmark of the Treaty of Tordesillas had been implemented, was occupied by people sent by the Portuguese Crown [102]. The Treaty of Tordesillas divided the territory between the Portuguese (to the East) and Spaniards (to the West) [102].

In 1756, five thousand Azoreans arrived at what is now the administrative headquarters of the state of Santa Catarina, in the coastal region, and in 1771 the first road was built, connecting the coast with the plateau of Lages [103], a region that was occupied by the Kaingang people. According to Zanelatto, Jung and Ozório [104], the contact between both groups probably resulted in the "incorporation" of the Kaingang people to local farms, while, on the other hand, many indigenous groups resisted the colonizing action [104].

From 1830, the arrival of the first European immigrants — especially Germans, Italians, Slavs, Ukrainians, and Poles — motivated by the distribution of land plots facilitated by foreign companies and laws to encourage immigration [105], intensified territorial conflicts with the native peoples. The events of the Santa Catarina settlement are summarized in Figure 15.

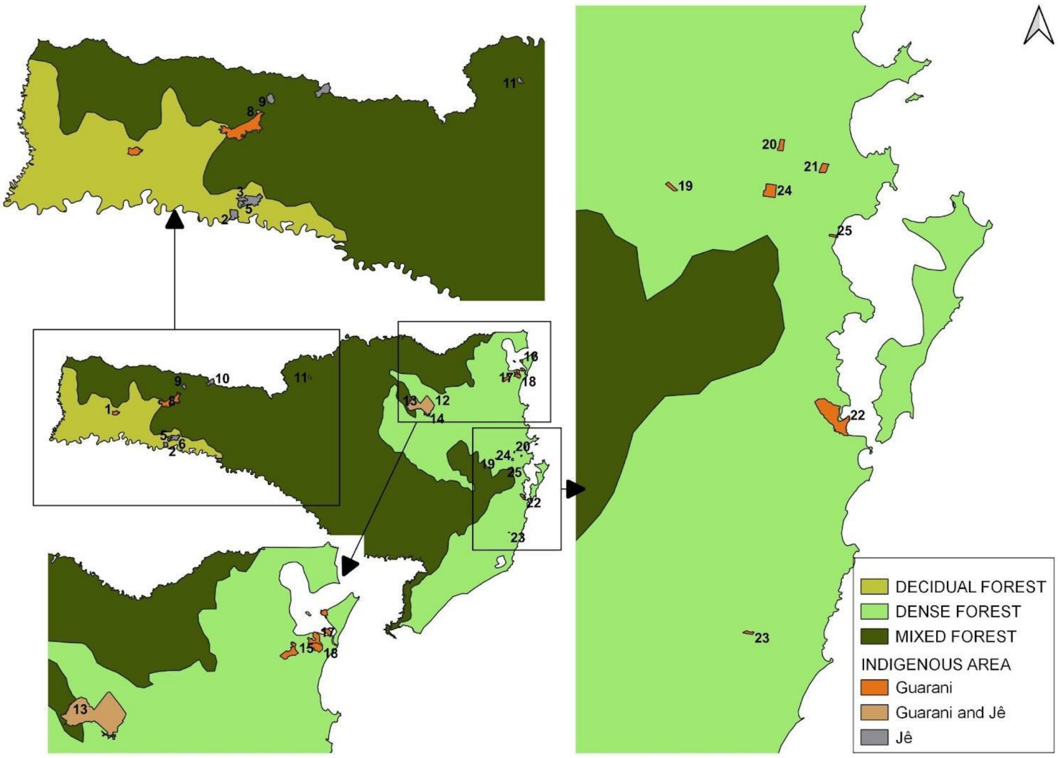
Figure 15 - Timeline of the settlement of Santa Catarina State.



Source: author.

To protect immigrants from indigenous territorial defenses, the Santa Catarina government hired armed people (militias), called *bugreiros*, to decimate and capture indigenous people [106,107]. Currently, the indigenous population of Santa Catarina is distributed in twenty-five Indigenous Lands (Figure 16) and also in urban centers [107]. Nineteen of these indigenous areas are traditionally occupied areas and the other seven are Reserves [108], there are areas obtained and designated for indigenous [107].

Figura 16 - Map of the state of Santa Catarina with phytogeographic division and Indigenous Areas, whereas: 1,7, 15–25 are Guarani; 2-6, 9-14 are southern-Jê; 8, 12, 13 are Guarani and southern-Jê Indigenous Areas. 2, 14, 19-21, 23 and 24 are Reserves, while 1, 3-13, 15-18, 22 and 25 are traditionally occupied areas.



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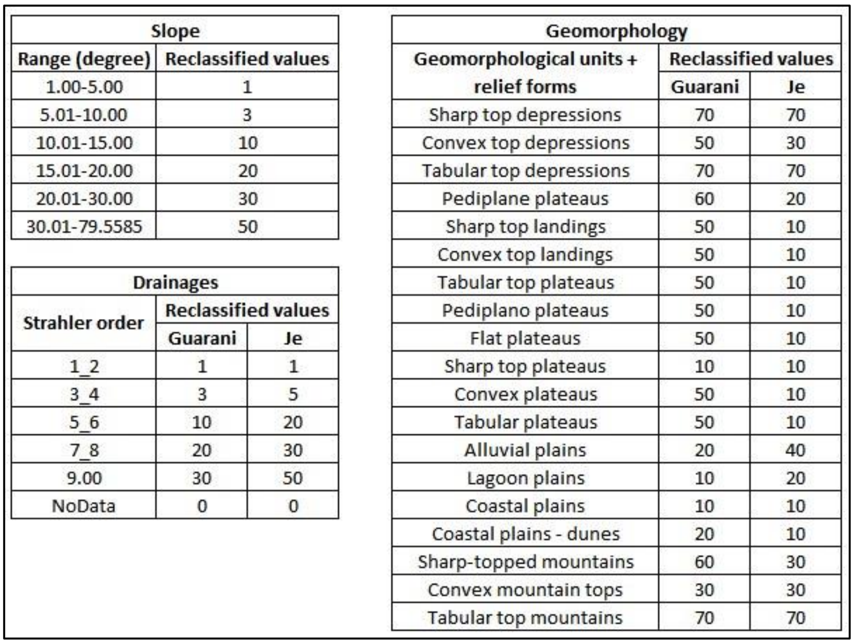
2.6. Data collection

For data collection, the first step was to use a Geographic Information System (QGIS) to superimpose data on the incidence and abundance of *Casearia sylvestris* (FlorestaSC, 2007 - 2011) with the Jê-meridional and Guarani occupation probability matrices. We will call these matrices "probability maps." and were created by niche modeling by Cruz and collaborators [24], based on the location of archaeological sites and with hydrological and topographic variables. We could obtain the cell value of the probability map on which the sampling unit (SU) containing the species is located. For this, the 'sample raster values' tool from QGis was used. Afterwards, the polygons of the Brazilian Indigenous Areas (IAs) were added [108], rasterized, and with the 'proximity' tool of the Saga package, a matrix file was generated with the proximity values of the IATIs. The variable distance from AIs was used because it represents long-term human presence. The state of Santa Catarina has eighteen indigenous areas of traditional occupation (representing a long-term presence) and seven. Reserves, which are areas designated for indigenous occupation, that is, that were not necessarily occupied in the past. However, we kept all areas in the analysis considering that the recent impact is more visible, as illustrated in figure 2. Next, the 'sample raster values' procedure was repeated to obtain the cell value. The process was repeated to obtain the values of environmental variables (minimum temperature in the coldest month and seasonality of temperature) provided by the WorldClim platform. Still in QGis, the image of the Guarani expansion model proposed by Bonomo and collaborators [25] was registered, which shows the expansion along rivers, and after that we added the hydrographic network [109]. The positioning of the SU with the presence of *C. sylvestris* on the model by Bonomo [25] was visually evaluated.

The cost of movement was calculated based on the distribution of Guarani and southern-Jê archaeological sites. Two cost surfaces were calculated, each with different values for the site categories. Cost surfaces are commonly used in least-cost analysis and involve classifying and assigning different costs to environmental and cultural variables [134, 135]. The higher the cost assigned, the more difficult it is to move through the cell in least-cost modeling. The cost surfaces were calculated using three variables: slope (generated from the MDT NASA/SRTMGL1v003), hydrography (ANA/BHO drainages), and geomorphological units subdivided by relief forms classified by the Brazilian Institute of Geography and Statistics (IBGE Geomorphology, 1:250,000). The procedures were performed in QGIS 3.28. A new field was created in the geomorphology vector, which combined the geomorphological units and the relief forms. Additionally, two new columns were created to assign different costs, one for Guarani and the other for southern-Jê. The hydrography and geomorphology vectors were then converted to a raster, selecting the Strahler order, and the two cost fields created for geomorphology units. The slope and hydrography were reclassified using the reclassify by table tool. The geomorphological raster did not require reclassification since the vector was already rasterized with the cost values. The cost values for each variable were estimated considering the bibliographic information [25,110-111,37], and the reclassified values are in the Figure 17. The cost of slope increases significantly for slopes that are 60° or greater [136]. Hydrography can either facilitate or hinder movement, with high or low values assigned respectively. The Guarani used rivers as facilitators of movement, so a lower cost was assigned for the watercourses [25]. In contrast, the southern-Jê considered the watercourses as borders and not easily navigable, so they were given a high cost [110-111]. The distribution of archaeological sample sites was used to determine the cost of geomorphological units. Finally, two cost surfaces were created by adding the reclassified rasters in the raster calculator: one for Guarani and the other for southern-Jê.

Figure 17 – Cost values based on bibliographic information.



Slope	
Range (degree)	Reclassified values
1.00-5.00	1
5.01-10.00	3
10.01-15.00	10
15.01-20.00	20
20.01-30.00	30
30.01-79.5585	50

Drainages		
Strahler order	Reclassified values	
	Guarani	Je
1_2	1	1
3_4	3	5
5_6	10	20
7_8	20	30
9.00	30	50
NoData	0	0

Geomorphology		
Geomorphological units + relief forms	Reclassified values	
	Guarani	Je
Sharp top depressions	70	70
Convex top depressions	50	30
Tabular top depressions	70	70
Pediplane plateaus	60	20
Sharp top landings	50	10
Convex top landings	50	10
Tabular top plateaus	50	10
Pediplano plateaus	50	10
Flat plateaus	50	10
Sharp top plateaus	10	10
Convex plateaus	50	10
Tabular plateaus	50	10
Alluvial plains	20	40
Lagoon plains	10	20
Coastal plains	10	10
Coastal plains - dunes	20	10
Sharp-topped mountains	60	30
Convex mountain tops	30	30
Tabular top mountains	70	70

Source: prepared by co-author Merencio.

2.6. Data analysis

We use generalized linear models. Previously, we removed collinear variables through the variance inflation factor (VIF), whenever VIF >3 [137]. The predictor variables used were: Probability on the Jê-meridional map, probability on the Guarani map, Jê-meridional cost surface, Guarani cost surface, distance from IAs, phytophysiognomy of each UA, temperature in the coldest month, and temperature seasonality. For the incidence data of the species, we used the binomial distribution. For abundance data, we used the negative binomial distribution. The models were validated through visual analyzes of the model residuals. The analyzes were performed in an R environment [112] using the car packages [113] to remove collinear variables, MASS [114] to generate generalized linear models, visreg to visualize the effects of the models, DHARMa for validating the models, and MuMIn to access the model goodness-of-fit.

3. Results

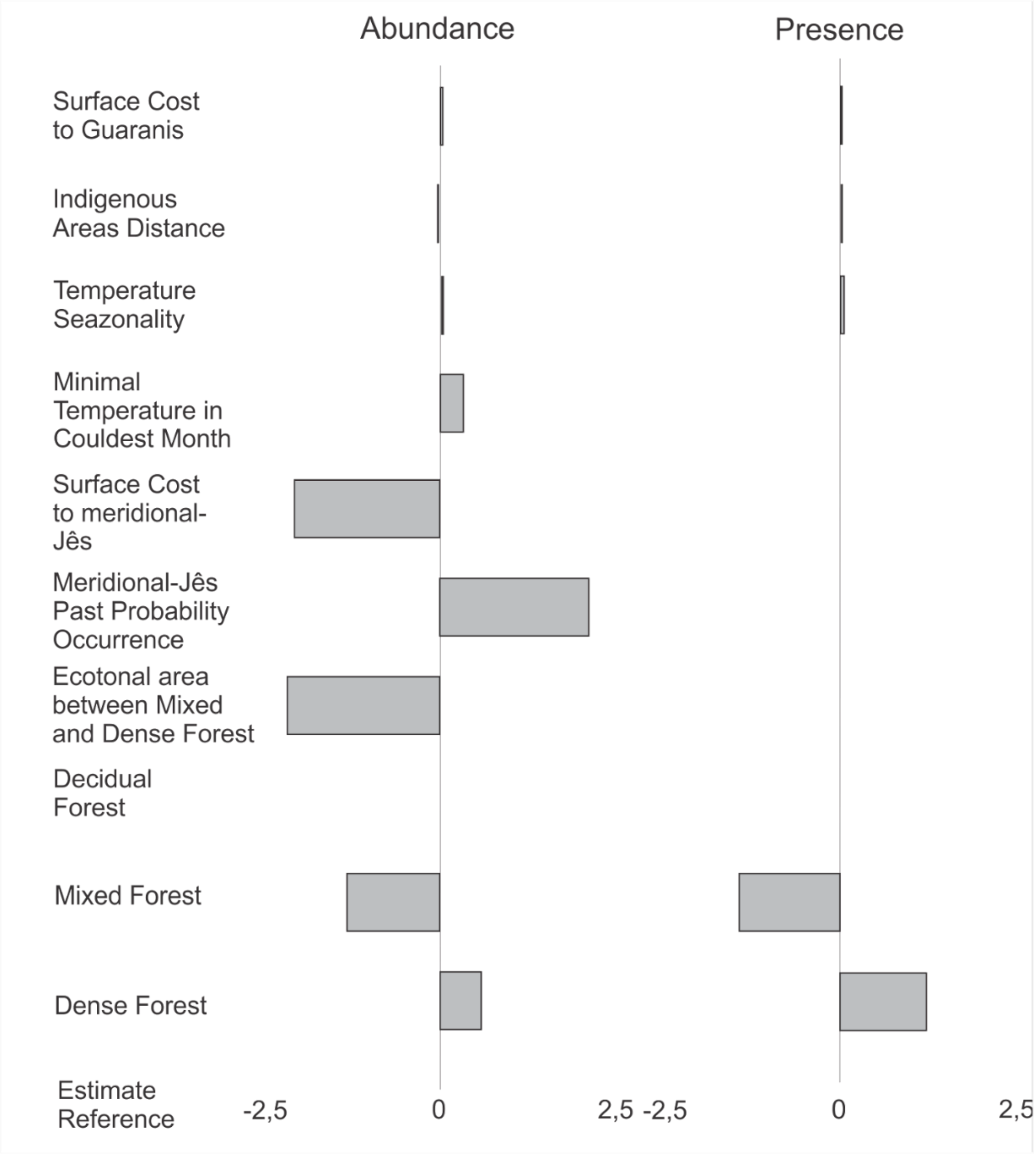
Our abundance and presence models explain, respectively: 67% and 37% of the total data variation. The results indicate that the abundance of the *Casearia sylvestris* species (Figure 4 and Figure 5, Table 2) is positively related to areas of likely Jê- meridional occupation in the past and negatively related to Jê-meridional paths, indicated by the cost surface variable. As for the Guaranis paths, the relationship with the surface cost was positive. Regarding the distance from Indigenous Lands, the smaller the distance, the greater the abundance of C. sylvestris. Temperature seasonality and minimum temperature in the coldest month showed a positive relationship with species abundance. As for the phytogeographic regions, there are negative relationships in the Mixed Ombrophylous Forest (MOF), and positive with the ODF. Considering the presence and absence of *C. sylvestris* (Figure 17 and Figure 18, Table 3), all the significant variables repeated the pattern found for abundance, namely: Surface cost for Guarani peoples; distance from Indigenous Lands; temperature seasonality; and for the ODF and MOF phytogeographic regions. The model coefficients for abundance and incidence are shown in Table 3.

Table 3 - Generalized mixed model coefficients for abundance and presence

	ABUNDANCE				PRESENCE			
Variables	**Estimate**	**Error**	**z**	**p**	**Estimate**	**Error**	**z**	**P**
Surface Cost to Guaranis	0.03	0.01	4.08	<0.01	0.02	0.001	2.933	<0.01
Indigenous Area Distance	-0.01	0.004	-2.06	<0.05	-0.01	0.01	2.32	<0.05
Temperature	0.02	0.001	3.147	<0.01	0.03	0.01	2.92	<0.01
Minimal Temperature in Coldest Month	0.32	0.08	3.75	<0.01				
Surface Cost to Jê-meridional	-2.02	0.01	-2.44	<0.01				
Jê-meridional past probability occurrence	2.07	0.71	2.91	<0.01				
Ecotonal area between Mixed and Dense Forest	-2.12	0.86	-2.46	<0.05				
Mixed Forest	-1.29	0.35	-3.67	<0.01	-1.43	0.45	-3.15	<0.01
Dense Forest	0.57	0.33	1.76	<0.1	1.20	0.43	2.80	<0.01

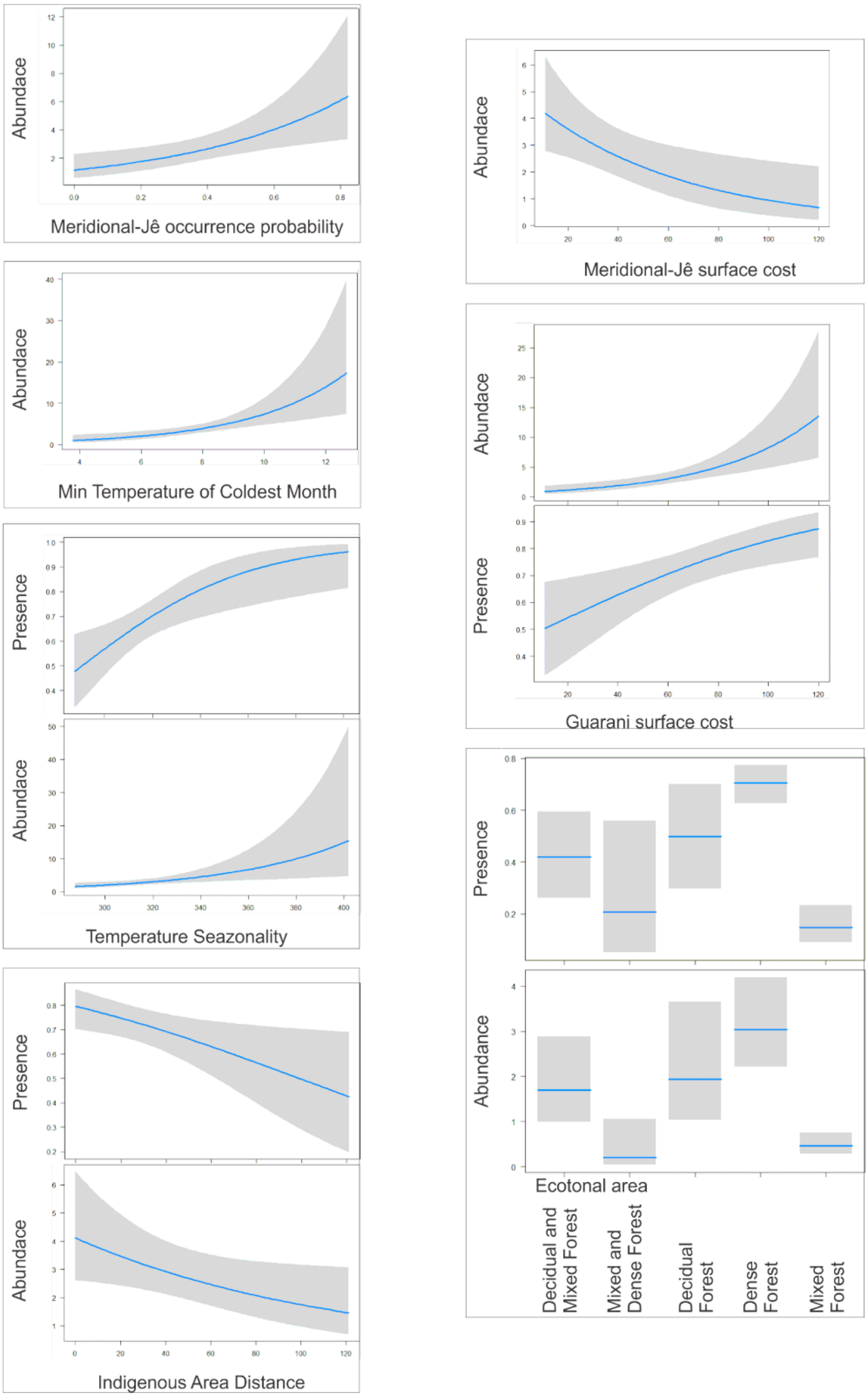
Source: author.

Figure 18 - Size and direction of the effect of variables on the abundance and presence of *C. sylvestris.*



Source: author.

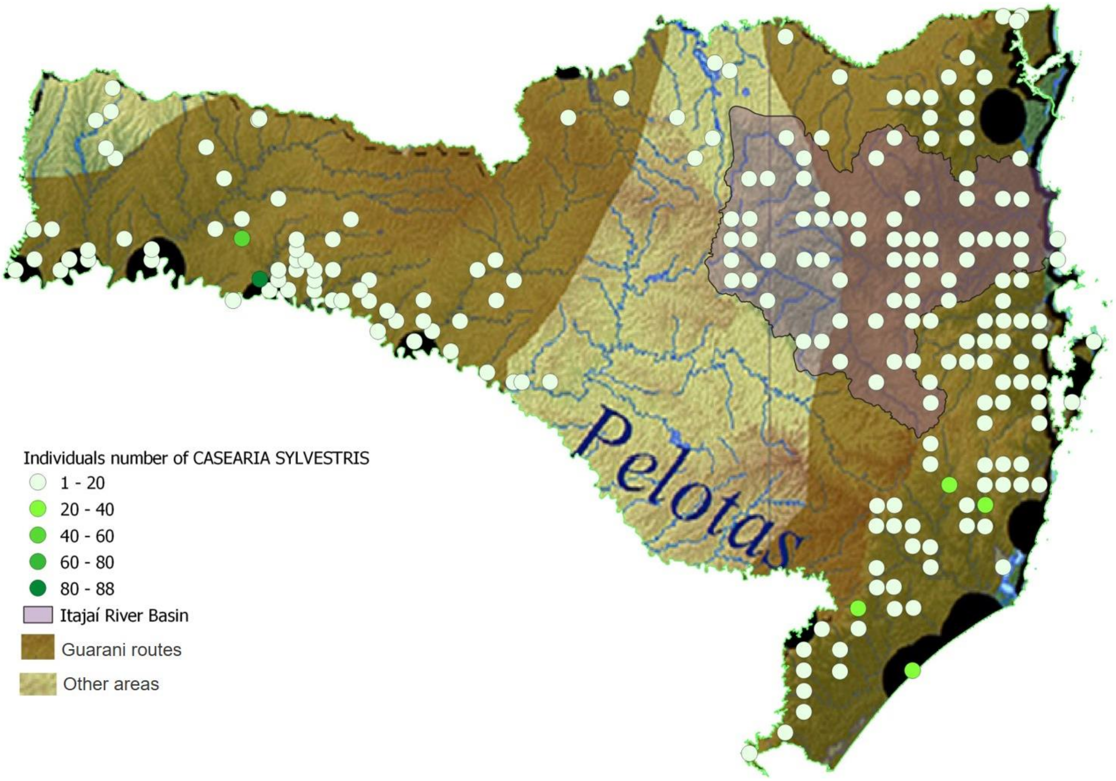
Figure 19 - Modeled effect of variables on the abundance and presence of *C. sylvestris*



Source: author.

Visual analysis of the model by Bonomo and coworkers [25] (Figure 20) shows that the occurrence of *C. sylvestris* is predominantly inserted in the brown belt, an indicative of Guarani routes, while most of the occurrences outside the brown belt are inserted in the Itajaí River Basin.

Figure 20 - Excerpt from the Guaranis route model by Bonomo et al. (2015) overlapped by the occurrence of *C. sylvestris* and by the boundary of the Itajaí River basin, Jê-Meridional occupation area.



Source: author.

4. Discussion

We identified patterns of increased abundance and presence of the *Casearia sylvestris* species in areas correlated with the occupation and movement of meridional Jê peoples. The processes that can explain such patterns, especially in relation to the occupation of a landscape by a cultural group, are those of selection, accumulation, and care, typical of agroforestry systems [115], which were the main food production systems from Jê populations [45-47, 28]. Regarding transit, the transplantation of useful species along routes is already well documented for another Jê group, the Kayapó people [22]. The maintenance of a medicinal species with an anti-ophidian potential, for example, such as *C. sylvestris*, could be very useful along the movement through paths and trails, justifying specimen transplants. Management would have favored the species over others, so that its presence in a culturally constructed niche in the landscapes occupied by the Jê peoples of the past can be considered as a legacy in current landscapes.

Regarding the Guarani peoples, both abundance and presence increase along with the surface cost, that is, there are more individuals of *C. sylvestris* in areas of difficult access for the Guarani peoples. However, visually, the species distribution coincides with the Guaranis route model proposed by Bonomo and coworkers [25], which leads us to propose that, despite being costly, they are areas close to those transited. Some possible explanations would be:

a) Compartmentalization of the landscape between Meridional-Jê and Guarani peoples. The Guarani peoples arrived in the southern region after the Meridional-Jê groups, and archaeological research indicates that there were territorial pressures between both groups in different areas, which resulted in the occupation of Jê territories by Guarani groups [116,117] when the Jê peoples began to occupy the plateaus more densely and build monuments delimiting their areas [116]. With the arrival of the Europeans, there is a Guarani emptying, which allows the Jê peoples to occupy and reoccupy Guarani paths [37]. Something that favors this hypothesis is the fact that the Itajaí River Basin, highlighted in Figure 6 on the model by Bonomo and coworkers [25], is the area that contains more occurrences of *C. sylvestris* that go beyond the referred model and, however, archaeological and ethnographic data indicates that this is an area of Meridional-Jê occupation [106,87].

b) The species would be selected for uses such as construction and combustion, for which the removal of individuals by cutting is necessary. However, we only found information on the use of *C. sylverstris* wood for the production of artifacts (gyraus and pestle sticks) in the literature on Meridional-Jê indigenous people [46].

c) They could be hunting areas, close to areas of transit and occupation where the species could be favored to attract, for example, the "teiú" lizard, of the Teiidade family, which is currently consumed [118] and present in the Guarani people archaeological records [119]. The Guarani peoples usually have "hunting gardens," located close to settlements, cultivation areas, and fallow land [120], which corresponds to our results (areas of costly access but close to paths). In addition, the use of attractive species for game animals is documented in several cultures. It could be a use of a pre-existing and attractive species to return at the time of fruiting, as is the "white araçá" (Myrtaceae) case, a tree with a significant place in the Laklãnõ-Xokleng culture, which in the fruiting period fed small animals, which, in turn, attracted larger and more attractive animals for hunting [28]. Or, it could be intentional planting, as in the case of the Kayapo people, who build patches of anthropogenic forests for different purposes, including hunting [22]. The presence of a species attractive to fauna expands the trophic networks, in order to increase the availability of animals beyond those that consume their resource directly [121]. This was confirmed in the subtropical Atlantic Forest, where evidence of the maintenance of vertebrate fauna was found due to the presence of *Acca sellowiana* [121]. This species is traditionally managed and presents characteristics of incipient domestication, which indicates a long time of human care and, therefore, its use since the original peoples. It is an example of niche construction to favor other species, as we supposed to have occurred with *C. sylvestris*. The literature points out that the studied species is of priority medicinal use. However, here it seems that the use is also indirectly for food if we consider the popular belief described by Carvalho [33]: "Teiús" (lizards of the Teeidade family) consume "guaçatonga" leaves (*C. sylvestris*) to protect themselves from the poison of jararacas. Thus, keeping the species in hunting areas would guarantee the presence of the largest lizard that occurs on Brazilian soil, a great source of protein. Reinforcing that, as already mentioned, both the vernacular "teiú" and "guaçatonga" have Guarani origin.

The results partially corroborate our first hypothesis. *C. sylvestris* is related to occupancy and the cost of moving Meridional-Jê. Just as it is related to the cost of Guarani movement, but in an inverse relationship, in the areas of greater shortness. Furthermore, our results do not indicate a relationship between the Guarani people occupation and the presence or abundance of *C. sylvestris.*

Our second hypothesis refers to the possibility that *C. sylvestris* is an indicator of Meridional-Jê and Guarani routes, and our results are indicating more clearly that the species is a good indicator of Meridional-Jê routes. However, they also indicate a relationship with Guarani people movement costs, but they are in higher cost areas, which is consistent with the model by Bonomo and coworkers [25].

Both the abundance and the presence of the species increase in the vicinity of Indigenous Areas, indicating a long duration in the relations between the original peoples and the species in question, which, in turn, suggests the legacy of maintaining a medicinal species in the landscapes. This corroborates our third hypothesis.

Analyzing the phytogeographic division, an abrupt reduction of the species in the Mixed Ombrophylous Forest (MOF) area is also observed in the ecotonal area between the Dense Ombrophylous Forest and the mixed forest. It is widely known that the MOF has well-defined environmental filters, such as severe winter and occurrence of frost. Here, we identified that lower minimum temperatures, as well as low seasonality, do not favor the occurrence of *C. sylvestris*. But the absence of Indigenous Lands throughout the South and Central portion of the MOF draws attention, since it is an area with a high probability of Meridional-Jê [24] occurrence and that presents archaeological monuments, an indicative of the complex social structure of these peoples [122,123,116]. In this phytogeographical region, indigenous people were added to the workforce of large farms or decimated/hunted by *bugreiros* [107].

There is a global pattern of biodiversity reduction accompanying the reduction of languages (cultures) [124]. Considering that humans change ecosystems in order to increase or build niches for themselves, and do that based on cultural decisions, the way of life continuity of indigenous peoples and traditional peoples and communities is fundamental for biological diversity conservation. Clement [125] documented the reduction of domesticated species in the Amazon after 1492, due to the reduction of indigenous populations. For southern Brazil, new publications have demonstrated the importance of traditional use for conservation, including in the face of climate change [87,126,127], which leads us to reinforce that to avoid the reduction of species it is necessary to guarantee the transmission and valorization of traditional knowledge. Even though it is a widely distributed species, our results indicate that where Amerindian peoples passed and occupied there are concentrations of *C. sylvestris*. And, The Indigenous Lands had a positive effect on both the abundance and presence of *C. sylvestris*, suggesting that this pattern likely results from millennia of stewardship by the original populations.

With this, we reinforce the importance of favoring the living conditions of social reproduction of indigenous peoples.

For the Amazon Forest, the Deforestation Alert System has been showing that deforestation in Indigenous Lands is much lower compared to private and possession areas, and between June 2022 and 2023, this comparison is 2% against 72%, respectively [128]. In the Atlantic Forest, what is documented is the difficulty in managing the overlap between Indigenous Lands and other protected areas [129,130]. An example of this challenge in Santa Catarina occurs within the Area of Relevant Ecological Interest (ARIE), which coincides with the Lãklaño territory [131]. Therefore, it is important to expand the dialogue on the long history of co-construction of the Atlantic Forest with human beings. Our results support that there is a relationship between the abundance and presence of a species with human actions, even if they do not show a direct association, and we worked with data from different temporalities. These results are consistent with what has already been demonstrated for other species of the subtropical Atlantic Forest [24,132,38]. Assuming that the Atlantic Forest (and any other biome) has been occupied for thousands of years, and that areas previously considered pristine are actually mature forests, it is fundamental for resolving conflicts on the human presence in conservation areas [133].This is because the "pristine" concept refers to untouched areas, inappropriate considering recent ecological discoveries and the postulates of Historical Ecology and disregarding the presence of original peoples. Our results point to the impact of past and recent Amerindian presence.

5. Conclusions

- *Casearia sylvestris* likely represents a legacy of precolonial Amerindian populations. In addition to the results of our models pointing out abundance and presence relationships with Guarani groups and abundance with Jê-meridional, we reinforce that the folk names attributed to the species refer to indigenous people, e.g. 'Chá de bugre' Tea of bugre ('bugre' is a pejorative way of referring to indigenous people from Southern Brazil); 'guaçatonga", word of Guarani origin; 'pau de lagarto' lizard wood, referring to a lizard that is a species significant in Guarani food culture. *C. sylvestris* is a probable marker of Meridional-Jê occupation and movement. Our results show a strong relationship between the increased abundance of species in areas correlated with the occupation and movement of meridional-Jê peoples.
- There are indications that *C. sylvestris* is a marker of the Guarani people movement. The presence is correlated with the Bonomo and collaborators model (2015), and our models indicate that there is a strong relation between Guarani routes (indicated as surface cost) above abundance and the presence of the *C. sylvestris*. However, the pattern observed may result from occupation by the Meridional-Jê before or after the arrival of Europeans, which significantly reduced

their population, thus opening up space for Meridional-Jê occupation and re-occupation.
- The pattern observed for Guarani peoples may still indicate hunting areas, as the species favors a lizard consumed by the Guarani peoples. However, this supposed favoritism is based on oral tradition and lacks scientific investigation.
- The Indigenous Lands had a positive effect on both the abundance and the presence of *C. sylvestris*, a pattern that probably reflects care actions built over millennia by the original populations.

Supplementary Materials:

Author Contributions: Conceptualization by Aline Cruz, Ariane Saldanha, Lucas Bueno, Nivaldo Peroni; Methodology by Aline Cruz, Fabiana Merencio, Rafael Sühs, Lucas Bueno, Nivaldo Peroni; Software by Aline Cruz, Fabiana Merencio, Rafael Sühs; Validation by Aline Cruz, Fabiana Merencio, Rafael Sühs; Formal analysis by Aline Cruz, Fabiana Merencio, Rafael Sühs; Investigation by Aline Cruz, Fabiana Merencio, Ariane Saldanha, Rafael Sühs, Lucas Bueno, Nivaldo Peroni; Resources by Laboratory of Human Ecology and Ethnobotany, Department of Biology, and Laboratory of Interdisciplinary Studies in Archeology, Department of History, both at the Federal University of Santa Catarina. Data curation: Aline Cruz; Fabiana Merencio. Writing—original draft preparation: Aline Cruz, Ariane Saldanha, Fabiana Merencio, Rafael Sühs, Lucas Bueno, Nivaldo Peroni. Writing—review and editing: Aline Cruz, Lucas Bueno, Nivaldo Peroni. Visualization: none. Supervision: Lucas Bueno and Nivaldo Peroni. Project administration: Aline Cruz, Lucas Bueno, Nivaldo Peroni. Funding acquisition: Lucas Bueno and Nivaldo Peroni. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement:

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4 CONSIDERAÇÕES FINAIS

Concluo que os processos de Construção Cultural de Nicho praticados por povos Ameríndios na Mata Atlântica Subtropical, desde pelo menos 10.000 anos atrás, têm legados visíveis na composição de espécies das formações florestais recentes. Esses legados são espécies florestais que tem sua presença e abundância relacionadas com a ocupação de Jê-meridional e Guarani desde antes da invasão européia. Há espécies assinatura de um grupo cultural, tais como *Araucaria angustifolia* e *Ilex paraguariensis* para os Jê-meridionais, e há espécies compartilhadas pelos dois grupos, como as palmeiras *Syagrus romanzoffiana* e *Euterpe edulis.* A *Casearia sylvestris*, que inicialmente foi associada com grupos Guaranis, em uma investigação mais profunda apresentou relações com ambos grupos culturais. As espécies descritas nesta tese são importantes atualmente, especialmente em usos alimentícios e medicinais. Pode se dizer que nossos antepassados deixaram verdadeiros tesouros para nós e para seus parentes mais próximos.

Ao incluir as Terras Indígenas atuais, foi possível notar que a manutenção de uma espécie mundialmente reconhecida pelo seu valor medicinal, *Casearia sylvestris*, está relacionada também com esses locais marcando possíveis caminhos de circulação de povos Ameríndios, como os Jê-meridional e os Guarani. É importante que ações de conservação considerem o protagonismo dos povos indígenas e de seus conhecimentos, e que seja considerada a referência temporal quanto à cobertura original da Mata Atlântica.

As práticas culturais de manejo da paisagem e de populações de arbóreas úteis por populações Ameríndias resultaram em modificações de nicho tão profundas que ainda podem ser identificadas nas paisagens recentes. Isso é surpreendente considerando que a pesquisa foi realizada com dados de diferentes camadas temporais e também devido às intensas modificações que a Mata Atlântica Subtropical vem sofrendo nas últimas décadas.

Na presente tese há parte da história de nossos antepassados e das paisagens em que estiveram entrelaçados, traduzidas de marcas da paisagem para a linguagem escrita. Este entrelaçamento, reforça a pertinência e relevância do exercício para desconstrução da problemática visão dicotômica entre cultura e natureza. Assim, reforço: as florestas da Mata Atlântica Subtropical, como outras, foram co-construídas com a força de transformação humana (com diferenças culturais), de outros organismos e de outras forças naturais.

Por fim, destaco grandes desafios para a inclusão da Ecologia Histórica nas políticas ambientais, que são: a desconstrução do discurso corrente para permitir a assimilação da importância da diversidade cultural para a diversidade biológica; e após, como prevenir que os conceitos da Ecologia Histórica sejam utilizados para justificar atividades de degradação.

O discurso corrente, citado no parágrafo acima, assume a ocorrência de áreas prístinas em locais que já foram ocupados desde milênios atrás. Está fortemente enraizado e foi criado a partir dos interesses coloniais, nos quais a história indígena não tinha relevância para o desenvolvimento que a coroa portuguesa almejava para o Brasil. Apesar de ser de amplo conhecimento que as terras da Mata Atlântica Subtropical já eram ocupadas por povos indígenas, não se associa essa informação de modo a questionar o conceito de áreas pristinas e o impacto antrópico. O forte enraizamento do conceito tradicional acaba por “sabotar” uma conclusão lógica: os povos indígenas já ocupavam e contribuíram para construir essas paisagens, que logo, não são pristinas. E não tão lógico, mas de compreensão necessária, que em áreas florestadas manejadas pelos povos indígenas a presença deles e de suas práticas fazem parte da continuidade dessas paisagens, bem como seus conhecimentos milenares transmitidos ao longo de gerações sobre o ambiente.

Dado o passo de compreender que a Mata Atlântica subtropical não é um ambiente prístino e que assim, humanos são parte de tal ecossistema, se assume um grande desafio. Que grupos humanos podem ser aliados da conservação biológica e da manutenção da diversidade cultural? A interpretação precisa ser cautelosa, para que o argumento de que humanos são parte das forças que moldaram as florestas não seja utilizado de modo a justificar novos impactos sobre a Mata Atlântica Subtropical.

Por fim, sugiro a continuidade de estudos envolvendo as 29 espécies aqui descritas para o avanço do conhecimento da Ecologia Histórica da Mata Atlântica Subtropical, especialmente da relação entre a *Casearia sylvestris* e lagartos da Família Teiidae.

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APÊNDICE A _ R SCRIPTS - PRE-COLONIAL AMERINDIAN LEGACIES IN FOREST COMPOSITION OF SOUTHERN BRAZIL

Aline Pereira Cruz, Eduardo Luis Hettwer Giehl, Carolina Levis, Juliana Salles Machado, Lucas Bueno, Nivaldo Peroni

February 26, 2020

4.1 S4 - REDUNDANCY ANALYSIS (RDA)

```
library(vegan)

## Loading required package: permute

## Loading required package: lattice

## This is vegan 2.5-3

library(RColorBrewer)
library(plyr)


sp <- read.table("S4_sps.csv", header=TRUE, sep=",", dec=".")
sp<-sp[,-1]
#sp<-as.data.frame(sp)
#row.names(sp)=as.character(sp[,1])
#sp<-as.matrix(sp)
co_occ<-read.table ("S4_cult.csv",header=TRUE, sep=",", dec=".")
co_occ<-co_occ[,-1]
#co_occ<-as.data.frame(co_occ)
#row.names(co_occ)=as.character(co_occ[,1])
#co_occ<-as.matrix(co_occ)
#removing rares
sp<-sp[,colSums(sp)>=30]
dim(sp[,colSums(decostand(sp, method="pa"))>=5])

## [1] 417 327

#Hellinger transformation of species matrix
sp_hel<-decostand(sp, method= 'hellinger')

ord_sp<-rda(sp_hel~jes+guaranis, data=co_occ)
summary(ord_sp)

##
## Call:
## rda(formula = sp_hel ~ jes + guaranis, data = co_occ)
##
## Partitioning of variance:
##               Inertia Proportion
## Total          0.80510    1.00000
```

```
## Constrained   0.05584    0.06936
## Unconstrained 0.74926    0.93064
##
## Eigenvalues, and their contribution to the variance
##
## Importance of components:
##                           RDA1    RDA2     PC1     PC2     PC3     
PC4
## Eigenvalue            0.04174 0.01410 0.08045 0.05704 0.03464 0.0
3175
## Proportion Explained  0.05185 0.01752 0.09993 0.07085 0.04303 0.0
3943
## Cumulative Proportion 0.05185 0.06936 0.16929 0.24014 0.28317 0.3
2260
##                            PC5     PC6     PC7     PC8     PC9     
PC10
## Eigenvalue            0.02542 0.01931 0.01887 0.01541 0.01511 0.0
1299
## Proportion Explained  0.03158 0.02399 0.02344 0.01914 0.01877 0.0
1614
## Cumulative Proportion 0.35418 0.37817 0.40161 0.42075 0.43952 0.4
5566
##                           PC11    PC12     PC13     PC14     PC15     
PC16
## Eigenvalue            0.01158 0.01032 0.009857 0.009119 0.008691 
0.008465
## Proportion Explained  0.01438 0.01282 0.012243 0.011326 0.010795 
0.010515
## Cumulative Proportion 0.47004 0.48286 0.495104 0.506430 0.517224 
0.527739
##                            PC17     PC18     PC19     PC20     PC2
1
## Eigenvalue            0.008223 0.007980 0.007828 0.007389 0.00711
0
## Proportion Explained  0.010214 0.009911 0.009723 0.009178 0.00883
1
## Cumulative Proportion 0.537953 0.547864 0.557587 0.566765 0.57559
6
##                            PC22     PC23     PC24     PC25     PC2
6
## Eigenvalue            0.007026 0.006706 0.006531 0.006251 0.00593
0
## Proportion Explained  0.008727 0.008329 0.008112 0.007764 0.00736
5
## Cumulative Proportion 0.584323 0.592652 0.600764 0.608528 0.61589
3
##                            PC27     PC28     PC29     PC30     PC3
1
## Eigenvalue            0.005644 0.005467 0.005359 0.005256 0.00512
```

```
0
## Proportion Explained  0.007010 0.006790 0.006656 0.006529 0.00635
9
## Cumulative Proportion 0.622903 0.629693 0.636349 0.642878 0.64923
7
##                           PC32     PC33     PC34     PC35     PC3
6
## Eigenvalue            0.004988 0.004775 0.004614 0.004490 0.00439
0
## Proportion Explained  0.006196 0.005931 0.005731 0.005576 0.00545
3
## Cumulative Proportion 0.655433 0.661364 0.667095 0.672672 0.67812
4
##                           PC37     PC38    PC39     PC40     PC41
PC42
## Eigenvalue            0.004350 0.004313 0.00417 0.003993 0.003966
0.003934
## Proportion Explained  0.005404 0.005357 0.00518 0.004960 0.004926
0.004887
## Cumulative Proportion 0.683528 0.688885 0.69407 0.699025 0.703951
0.708838
##                           PC43     PC44     PC45     PC46     PC4
7
## Eigenvalue            0.003781 0.003722 0.003642 0.003574 0.00353
1
## Proportion Explained  0.004697 0.004623 0.004524 0.004439 0.00438
6
## Cumulative Proportion 0.713535 0.718158 0.722682 0.727120 0.73150
7
##                           PC48     PC49     PC50     PC51     PC5
2
## Eigenvalue            0.003444 0.003375 0.003242 0.003191 0.00315
6
## Proportion Explained  0.004278 0.004193 0.004026 0.003963 0.00392
0
## Cumulative Proportion 0.735784 0.739977 0.744003 0.747966 0.75188
6
##                           PC53     PC54     PC55     PC56     PC5
7
## Eigenvalue            0.003109 0.003066 0.003009 0.002983 0.00288
3
## Proportion Explained  0.003862 0.003809 0.003737 0.003706 0.00358
1
## Cumulative Proportion 0.755748 0.759557 0.763294 0.766999 0.77058
1
##                           PC58     PC59     PC60     PC61     PC6
2
## Eigenvalue            0.002807 0.002789 0.002742 0.002711 0.00262
7
```

```
## Proportion Explained  0.003486 0.003464 0.003406 0.003368 0.00326
3
## Cumulative Proportion 0.774067 0.777532 0.780938 0.784306 0.78756
8
##                           PC63     PC64     PC65     PC66     PC6
7
## Eigenvalue            0.002555 0.002534 0.002526 0.002453 0.00240
5
## Proportion Explained  0.003173 0.003147 0.003137 0.003046 0.00298
8
## Cumulative Proportion 0.790741 0.793888 0.797025 0.800071 0.80305
9
##                           PC68     PC69     PC70     PC71     PC7
2
## Eigenvalue            0.002367 0.002351 0.002324 0.002274 0.00221
6
## Proportion Explained  0.002940 0.002920 0.002887 0.002824 0.00275
2
## Cumulative Proportion 0.806000 0.808920 0.811807 0.814631 0.81738
3
##                           PC73     PC74     PC75     PC76     PC7
7
## Eigenvalue            0.002208 0.002167 0.002135 0.002120 0.00207
4
## Proportion Explained  0.002743 0.002692 0.002652 0.002634 0.00257
6
## Cumulative Proportion 0.820126 0.822818 0.825470 0.828103 0.83068
0
##                           PC78     PC79     PC80     PC81     PC8
2
## Eigenvalue            0.002050 0.002018 0.001969 0.001958 0.00194
5
## Proportion Explained  0.002546 0.002507 0.002445 0.002432 0.00241
6
## Cumulative Proportion 0.833226 0.835732 0.838178 0.840609 0.84302
5
##                           PC83     PC84     PC85     PC86     PC8
7
## Eigenvalue            0.001926 0.001858 0.001826 0.001786 0.00175
9
## Proportion Explained  0.002392 0.002307 0.002268 0.002218 0.00218
5
## Cumulative Proportion 0.845417 0.847724 0.849992 0.852210 0.85439
5
##                           PC88     PC89     PC90     PC91     PC9
2
## Eigenvalue            0.001755 0.001722 0.001707 0.001676 0.00164
3
## Proportion Explained  0.002180 0.002139 0.002120 0.002082 0.00204
```

```
1
## Cumulative Proportion 0.856575 0.858714 0.860834 0.862917 0.86495
8
##                           PC93     PC94     PC95     PC96     PC9
7
## Eigenvalue            0.001595 0.001572 0.001560 0.001544 0.00152
2
## Proportion Explained  0.001981 0.001952 0.001938 0.001917 0.00189
1
## Cumulative Proportion 0.866939 0.868891 0.870829 0.872746 0.87463
7
##                           PC98     PC99    PC100    PC101    PC10
2
## Eigenvalue            0.001486 0.001465 0.001455 0.001425 0.00141
2
## Proportion Explained  0.001846 0.001820 0.001807 0.001770 0.00175
4
## Cumulative Proportion 0.876482 0.878302 0.880109 0.881880 0.88363
3
##                          PC103    PC104    PC105    PC106    PC10
7
## Eigenvalue            0.001379 0.001376 0.001360 0.001355 0.00131
8
## Proportion Explained  0.001713 0.001709 0.001689 0.001682 0.00163
7
## Cumulative Proportion 0.885346 0.887055 0.888744 0.890426 0.89206
3
##                          PC108    PC109    PC110    PC111    PC11
2
## Eigenvalue            0.001312 0.001281 0.001267 0.001254 0.00123
7
## Proportion Explained  0.001630 0.001591 0.001574 0.001557 0.00153
7
## Cumulative Proportion 0.893693 0.895284 0.896858 0.898415 0.89995
2
##                          PC113    PC114    PC115    PC116    PC11
7
## Eigenvalue            0.001221 0.001202 0.001186 0.001162 0.00114
6
## Proportion Explained  0.001516 0.001493 0.001473 0.001443 0.00142
3
## Cumulative Proportion 0.901468 0.902960 0.904433 0.905877 0.90730
0
##                          PC118    PC119    PC120    PC121   PC122
PC123
## Eigenvalue            0.001137 0.001113 0.001104 0.001085 0.00107
0.001065
## Proportion Explained  0.001412 0.001382 0.001371 0.001348 0.00133
0.001323
```

```
## Cumulative Proportion 0.908712 0.910094 0.911465 0.912813 0.91414
0.915465
##                          PC124    PC125    PC126     PC127    PC1
28
## Eigenvalue            0.001037 0.001031 0.001025 0.0009974 0.0009
93
## Proportion Explained  0.001288 0.001281 0.001273 0.0012388 0.0012
33
## Cumulative Proportion 0.916753 0.918034 0.919307 0.9205458 0.9217
79
##                           PC129    PC130     PC131     PC132     
PC133
## Eigenvalue            0.0009803 0.000969 0.0009588 0.0009412 0.00
09251
## Proportion Explained  0.0012177 0.001204 0.0011910 0.0011691 0.00
11490
## Cumulative Proportion 0.9229969 0.924200 0.9253914 0.9265604 0.92
77095
##                           PC134     PC135     PC136     PC137    
PC138
## Eigenvalue            0.0008992 0.0008943 0.0008856 0.0008797 0.0
008701
## Proportion Explained  0.0011168 0.0011107 0.0011000 0.0010927 0.0
010807
## Cumulative Proportion 0.9288263 0.9299370 0.9310371 0.9321298 0.9
332105
##                           PC139    PC140     PC141    PC142     P
C143
## Eigenvalue            0.0008577 0.000848 0.0008377 0.000822 0.000
8118
## Proportion Explained  0.0010653 0.001053 0.0010404 0.001021 0.001
0083
## Cumulative Proportion 0.9342758 0.935329 0.9363696 0.937391 0.938
3989
##                           PC144     PC145     PC146     PC147    
PC148
## Eigenvalue            0.0007980 0.0007793 0.0007711 0.0007652 0.0
007547
## Proportion Explained  0.0009912 0.0009679 0.0009577 0.0009504 0.0
009374
## Cumulative Proportion 0.9393901 0.9403581 0.9413158 0.9422662 0.9
432036
##                           PC149    PC150     PC151     PC152     
PC153
## Eigenvalue            0.0007475 0.000744 0.0007360 0.0007226 0.00
07172
## Proportion Explained  0.0009284 0.000924 0.0009142 0.0008975 0.00
08908
## Cumulative Proportion 0.9441320 0.945056 0.9459702 0.9468677 0.94
```

```
77585
##                              PC154     PC155     PC156     PC157     
PC158
## Eigenvalue            0.0006997 0.0006864 0.0006828 0.0006752 0.0
006626
## Proportion Explained  0.0008691 0.0008526 0.0008481 0.0008387 0.0
008230
## Cumulative Proportion 0.9486276 0.9494802 0.9503283 0.9511670 0.9
519900
##                              PC159     PC160     PC161     PC162     
PC163
## Eigenvalue            0.0006577 0.0006376 0.0006310 0.0006286 0.0
006201
## Proportion Explained  0.0008169 0.0007920 0.0007838 0.0007808 0.0
007702
## Cumulative Proportion 0.9528068 0.9535989 0.9543826 0.9551634 0.9
559336
##                              PC164     PC165     PC166     PC167     
PC168
## Eigenvalue            0.0006174 0.0006047 0.0006014 0.0005941 0.0
005870
## Proportion Explained  0.0007669 0.0007511 0.0007470 0.0007379 0.0
007291
## Cumulative Proportion 0.9567005 0.9574516 0.9581985 0.9589364 0.9
596655
##                              PC169     PC170     PC171     PC172     
PC173
## Eigenvalue            0.0005809 0.0005705 0.0005616 0.0005543 0.0
005428
## Proportion Explained  0.0007215 0.0007087 0.0006975 0.0006885 0.0
006742
## Cumulative Proportion 0.9603870 0.9610957 0.9617932 0.9624817 0.9
631559
##                              PC174     PC175     PC176     PC177     
PC178
## Eigenvalue            0.0005343 0.0005269 0.0005209 0.0005126 0.0
005111
## Proportion Explained  0.0006637 0.0006545 0.0006470 0.0006367 0.0
006348
## Cumulative Proportion 0.9638196 0.9644741 0.9651211 0.9657578 0.9
663926
##                              PC179     PC180     PC181     PC182     
PC183
## Eigenvalue            0.0005009 0.0004997 0.0004898 0.0004883 0.0
004775
## Proportion Explained  0.0006222 0.0006207 0.0006083 0.0006065 0.0
005931
## Cumulative Proportion 0.9670148 0.9676355 0.9682438 0.9688503 0.9
694434
```

```
##                              PC184     PC185     PC186     PC187
PC188
## Eigenvalue             0.0004638 0.0004586 0.0004546 0.0004469 0.0
004413
## Proportion Explained   0.0005761 0.0005696 0.0005646 0.0005550 0.0
005482
## Cumulative Proportion 0.9700195 0.9705890 0.9711536 0.9717087 0.9
722569
##                              PC189     PC190     PC191     PC192
PC193
## Eigenvalue             0.0004310 0.0004274 0.0004244 0.0004210 0.0
004116
## Proportion Explained   0.0005354 0.0005308 0.0005272 0.0005229 0.0
005112
## Cumulative Proportion 0.9727922 0.9733231 0.9738502 0.9743731 0.9
748843
##                              PC194     PC195     PC196     PC197
PC198
## Eigenvalue             0.0004027 0.0003981 0.0003917 0.0003901 0.0
003806
## Proportion Explained   0.0005002 0.0004945 0.0004865 0.0004845 0.0
004727
## Cumulative Proportion 0.9753844 0.9758789 0.9763654 0.9768499 0.9
773226
##                              PC199     PC200     PC201     PC202
PC203
## Eigenvalue             0.0003762 0.0003712 0.0003667 0.0003630 0.0
003552
## Proportion Explained   0.0004673 0.0004610 0.0004555 0.0004509 0.0
004412
## Cumulative Proportion 0.9777899 0.9782509 0.9787064 0.9791573 0.9
795984
##                              PC204     PC205     PC206     PC207
PC208
## Eigenvalue             0.0003499 0.0003484 0.0003452 0.0003424 0.0
003340
## Proportion Explained   0.0004346 0.0004328 0.0004287 0.0004253 0.0
004149
## Cumulative Proportion 0.9800330 0.9804658 0.9808946 0.9813198 0.9
817348
##                              PC209     PC210     PC211     PC212
PC213
## Eigenvalue             0.0003260 0.0003155 0.0003138 0.0003104 0.0
003058
## Proportion Explained   0.0004049 0.0003919 0.0003897 0.0003855 0.0
003798
## Cumulative Proportion 0.9821396 0.9825315 0.9829213 0.9833068 0.9
836866
##                              PC214     PC215     PC216     PC217
```

```
PC218
## Eigenvalue           0.0003029 0.0002985 0.0002918 0.0002876 0.0
002838
## Proportion Explained  0.0003762 0.0003708 0.0003624 0.0003572 0.0
003525
## Cumulative Proportion 0.9840629 0.9844336 0.9847961 0.9851533 0.9
855057
##                           PC219     PC220     PC221     PC222     
PC223
## Eigenvalue           0.0002813 0.0002700 0.0002676 0.0002633 0.0
002584
## Proportion Explained  0.0003494 0.0003354 0.0003324 0.0003271 0.0
003209
## Cumulative Proportion 0.9858551 0.9861905 0.9865229 0.9868499 0.9
871709
##                           PC224     PC225     PC226     PC227     
PC228
## Eigenvalue           0.0002522 0.0002450 0.0002435 0.0002366 0.0
002318
## Proportion Explained  0.0003132 0.0003043 0.0003024 0.0002939 0.0
002879
## Cumulative Proportion 0.9874841 0.9877884 0.9880908 0.9883847 0.9
886726
##                           PC229     PC230     PC231     PC232     
PC233
## Eigenvalue           0.0002278 0.0002235 0.0002225 0.0002183 0.0
002102
## Proportion Explained  0.0002830 0.0002776 0.0002764 0.0002712 0.0
002611
## Cumulative Proportion 0.9889556 0.9892332 0.9895096 0.9897807 0.9
900418
##                           PC234     PC235     PC236     PC237     
PC238
## Eigenvalue           0.0002062 0.0002031 0.0002006 0.0001982 0.0
001952
## Proportion Explained  0.0002561 0.0002523 0.0002492 0.0002461 0.0
002425
## Cumulative Proportion 0.9902979 0.9905502 0.9907994 0.9910455 0.9
912880
##                           PC239     PC240     PC241     PC242     
PC243
## Eigenvalue           0.0001892 0.0001881 0.0001813 0.0001792 0.0
001749
## Proportion Explained  0.0002350 0.0002336 0.0002252 0.0002225 0.0
002172
## Cumulative Proportion 0.9915230 0.9917566 0.9919817 0.9922043 0.9
924215
##                           PC244     PC245     PC246     PC247     
PC248
```

```
## Eigenvalue            0.0001740 0.0001669 0.0001633 0.0001624 0.0
001614
## Proportion Explained  0.0002162 0.0002073 0.0002029 0.0002017 0.0
002005
## Cumulative Proportion 0.9926377 0.9928450 0.9930479 0.9932496 0.9
934501
##                           PC249    PC250     PC251     PC252     
PC253
## Eigenvalue            0.0001566 0.000153 0.0001506 0.0001460 0.00
01438
## Proportion Explained  0.0001945 0.000190 0.0001871 0.0001814 0.00
01786
## Cumulative Proportion 0.9936446 0.993835 0.9940217 0.9942030 0.99
43816
##                           PC254     PC255     PC256     PC257    
PC258
## Eigenvalue            0.0001427 0.0001393 0.0001373 0.0001331 0.0
001279
## Proportion Explained  0.0001773 0.0001731 0.0001706 0.0001653 0.0
001589
## Cumulative Proportion 0.9945589 0.9947319 0.9949025 0.9950679 0.9
952267
##                           PC259     PC260     PC261     PC262    
PC263
## Eigenvalue            0.0001253 0.0001230 0.0001209 0.0001201 0.0
001158
## Proportion Explained  0.0001556 0.0001527 0.0001502 0.0001492 0.0
001439
## Cumulative Proportion 0.9953823 0.9955350 0.9956852 0.9958344 0.9
959783
##                           PC264     PC265     PC266     PC267    
PC268
## Eigenvalue            0.0001123 0.0001102 0.0001071 0.0001057 0.0
00103
## Proportion Explained  0.0001395 0.0001369 0.0001330 0.0001313 0.0
00128
## Cumulative Proportion 0.9961179 0.9962547 0.9963877 0.9965190 0.9
96647
##                           PC269     PC270     PC271     PC272    
PC273
## Eigenvalue            9.899e-05 9.768e-05 9.631e-05 9.263e-05 0.0
000918
## Proportion Explained  1.229e-04 1.213e-04 1.196e-04 1.151e-04 0.0
001140
## Cumulative Proportion 9.968e-01 9.969e-01 9.970e-01 9.971e-01 0.9
972400
##                           PC274     PC275     PC276     PC277    
PC278
## Eigenvalue            8.838e-05 8.641e-05 8.342e-05 8.040e-05 7.6
```

```
46e-05
## Proportion Explained  1.098e-04 1.073e-04 1.036e-04 9.986e-05 9.4
97e-05
## Cumulative Proportion 9.973e-01 9.975e-01 9.976e-01 9.977e-01 9.9
78e-01
##                           PC279     PC280     PC281     PC282     
PC283
## Eigenvalue            7.588e-05 7.362e-05 6.945e-05 6.901e-05 6.7
01e-05
## Proportion Explained  9.424e-05 9.145e-05 8.626e-05 8.572e-05 8.3
23e-05
## Cumulative Proportion 9.978e-01 9.979e-01 9.980e-01 9.981e-01 9.9
82e-01
##                           PC284     PC285     PC286     PC287     
PC288
## Eigenvalue            6.609e-05 6.493e-05 6.293e-05 6.098e-05 5.9
39e-05
## Proportion Explained  8.209e-05 8.065e-05 7.816e-05 7.574e-05 7.3
76e-05
## Cumulative Proportion 9.983e-01 9.984e-01 9.984e-01 9.985e-01 9.9
86e-01
##                           PC289     PC290     PC291     PC292     
PC293
## Eigenvalue            5.737e-05 5.505e-05 5.451e-05 5.083e-05 4.8
47e-05
## Proportion Explained  7.125e-05 6.838e-05 6.770e-05 6.314e-05 6.0
21e-05
## Cumulative Proportion 9.987e-01 9.987e-01 9.988e-01 9.989e-01 9.9
89e-01
##                           PC294     PC295     PC296     PC297     
PC298
## Eigenvalue            4.613e-05 4.590e-05 4.529e-05 4.179e-05 4.0
60e-05
## Proportion Explained  5.729e-05 5.701e-05 5.625e-05 5.190e-05 5.0
42e-05
## Cumulative Proportion 9.990e-01 9.990e-01 9.991e-01 9.991e-01 9.9
92e-01
##                           PC299     PC300     PC301     PC302     
PC303
## Eigenvalue            3.944e-05 3.758e-05 3.563e-05 3.545e-05 3.4
13e-05
## Proportion Explained  4.899e-05 4.667e-05 4.425e-05 4.404e-05 4.2
39e-05
## Cumulative Proportion 9.992e-01 9.993e-01 9.993e-01 9.994e-01 9.9
94e-01
##                           PC304     PC305     PC306     PC307     
PC308
## Eigenvalue            3.250e-05 3.059e-05 2.984e-05 2.831e-05 2.7
22e-05
```

```
## Proportion Explained  4.036e-05 3.800e-05 3.706e-05 3.516e-05 3.3
82e-05
## Cumulative Proportion 9.995e-01 9.995e-01 9.995e-01 9.996e-01 9.9
96e-01
##                           PC309     PC310     PC311     PC312     
PC313
## Eigenvalue            2.661e-05 2.596e-05 2.468e-05 2.289e-05 2.1
79e-05
## Proportion Explained  3.305e-05 3.225e-05 3.065e-05 2.843e-05 2.7
06e-05
## Cumulative Proportion 9.996e-01 9.997e-01 9.997e-01 9.997e-01 9.9
98e-01
##                           PC314     PC315     PC316     PC317     
PC318
## Eigenvalue            2.042e-05 2.023e-05 1.833e-05 1.707e-05 1.5
38e-05
## Proportion Explained  2.537e-05 2.513e-05 2.277e-05 2.120e-05 1.9
10e-05
## Cumulative Proportion 9.998e-01 9.998e-01 9.998e-01 9.998e-01 9.9
99e-01
##                           PC319     PC320     PC321     PC322     
PC323
## Eigenvalue            1.373e-05 1.319e-05 1.236e-05 1.151e-05 9.3
31e-06
## Proportion Explained  1.706e-05 1.638e-05 1.535e-05 1.429e-05 1.1
59e-05
## Cumulative Proportion 9.999e-01 9.999e-01 9.999e-01 9.999e-01 9.9
99e-01
##                           PC324     PC325     PC326     PC327     
PC328
## Eigenvalue            9.155e-06 8.565e-06 7.485e-06 6.718e-06 6.1
64e-06
## Proportion Explained  1.137e-05 1.064e-05 9.296e-06 8.345e-06 7.6
56e-06
## Cumulative Proportion 1.000e+00 1.000e+00 1.000e+00 1.000e+00 1.0
00e+00
##                           PC329     PC330
## Eigenvalue            5.084e-06 4.488e-06
## Proportion Explained  6.315e-06 5.574e-06
## Cumulative Proportion 1.000e+00 1.000e+00
## 
## Accumulated constrained eigenvalues
## Importance of components:
##                          RDA1   RDA2
## Eigenvalue            0.04174 0.0141
## Proportion Explained  0.74745 0.2526
## Cumulative Proportion 0.74745 1.0000
## 
## Scaling 2 for species and site scores
```

```
## * Species are scaled proportional to eigenvalues
## * Sites are unscaled: weighted dispersion equal on all dimensions
## * General scaling constant of scores:  4.277954
##
##
## Species scores
##
##              RDA1       RDA2        PC1        PC2        PC3
PC4
## sp1   -3.025e-02 -1.786e-02  0.0318724  0.0133461 -0.0117160  5.2
31e-03
## sp2    4.051e-02 -1.074e-02  0.0116996 -0.0097070 -0.0633444  6.5
75e-03
## sp4   -2.528e-02  1.730e-02 -0.0244339  0.0305999 -0.0033929 -2.5
38e-02
## sp7   -8.604e-03 -3.420e-03  0.0185763  0.0094973  0.0075971  4.5
23e-03
## sp11  -4.508e-02  1.038e-03  0.0269599  0.0171769 -0.0301715 -2.5
02e-02
## sp13   7.627e-03  3.742e-02 -0.0670165  0.0435151  0.0169792  9.5
83e-03
## sp15  -2.528e-02 -8.340e-04  0.0247689  0.0311814 -0.0305853 -2.9
02e-02
## sp16  -1.129e-02 -2.263e-03  0.0400256  0.0479771  0.0239607  9.7
95e-03
## sp17  -1.453e-01 -3.985e-02  0.2412503  0.1901762  0.0196478  1.4
74e-02
## sp19   5.967e-02  3.442e-02 -0.1512706  0.0385280  0.0335380 -3.3
71e-02
## sp20   1.821e-02 -2.779e-02 -0.0073556 -0.0253069  0.0073175 -1.7
90e-02
## sp22   1.851e-03  1.958e-02 -0.0290667  0.0007131 -0.0014881  8.0
85e-03
## sp23  -3.980e-02  5.543e-02 -0.0544779 -0.0040329  0.0127867 -1.1
64e-02
## sp24  -1.189e-02  1.552e-02  0.0249836  0.0189037  0.0091398  1.0
70e-03
## sp25  -5.780e-02 -1.116e-02  0.3629940  0.2976265  0.1942585  1.2
65e-01
## sp26  -5.737e-02 -1.678e-02  0.0311285  0.0009201 -0.0229910 -3.3
36e-03
## sp28  -4.412e-02 -2.366e-02  0.0146115 -0.0042701 -0.0152538 -2.3
53e-03
## sp29  -7.808e-02 -1.779e-02  0.0787695  0.0361570 -0.0322121 -6.5
66e-03
## sp31  -3.207e-02  5.328e-03  0.0248717  0.0185552 -0.0158212 -1.4
57e-02
## sp33   1.320e-02  1.359e-02 -0.0187736  0.0328763  0.0236978 -2.7
68e-02
```

```
## sp35   1.276e-02 -5.810e-03 -0.0170668  0.0113177 -0.0001176  9.2
53e-04
## sp36  -9.384e-02 -2.962e-02  0.0783674  0.0769085 -0.0794413 -7.7
34e-02
## sp37   1.091e-02  4.889e-02 -0.1114898  0.0540353  0.0141182  5.8
07e-03
## sp38  -3.901e-02 -1.719e-02  0.0217904  0.0056147 -0.0335332 -1.9
88e-02
## sp39  -1.561e-02  3.288e-02 -0.0612757  0.0210812  0.0153257 -1.6
37e-02
## sp41   2.669e-01 -1.375e-01 -0.0250046 -0.2916993 -0.2750219  8.1
49e-02
## sp43  -5.788e-02  1.955e-02  0.0405300  0.1197945  0.0006800  2.7
61e-02
## sp45   4.182e-04  1.596e-03  0.0158896  0.0135266  0.0017207  5.7
79e-03
## sp46   6.932e-04  1.308e-03  0.0028659  0.0153982 -0.0045318 -7.7
04e-03
## sp47  -8.450e-03  1.723e-02  0.0217930  0.0203840 -0.0023596  1.8
10e-03
## sp49   3.617e-03  1.374e-02 -0.0265128 -0.0028514  0.0066874  2.1
36e-03
## sp57   7.730e-03 -1.198e-03  0.0081118 -0.0116638  0.0061271  1.0
59e-02
## sp60  -1.523e-03  3.989e-02 -0.1164099  0.0569840  0.0187499 -1.4
48e-02
## sp62   2.635e-02  9.631e-03 -0.0593510  0.0043131 -0.0055058  1.1
92e-03
## sp63   3.363e-03 -3.012e-03 -0.0140806  0.0090981  0.0027698 -2.8
84e-03
## sp64  -8.225e-02 -5.059e-02  0.1426126  0.1602118 -0.0764251 -7.8
45e-02
## sp65  -1.495e-02  9.269e-03 -0.0481994  0.0325261 -0.0071227 -2.0
62e-02
## sp66   4.728e-02 -2.884e-02 -0.0049747 -0.0380433 -0.0574828  2.0
11e-02
## sp69  -2.729e-02 -5.686e-03  0.0172671  0.0095026 -0.0277506 -2.4
52e-02
## sp70  -4.609e-02 -8.460e-03  0.0293968  0.0225702 -0.0430999 -4.0
83e-02
## sp72  -1.038e-02  2.826e-03  0.0266287  0.0208168 -0.0158767 -9.4
90e-03
## sp76  -4.791e-02 -8.108e-03  0.1264702  0.0400893  0.0272424  8.6
17e-02
## sp77  -1.028e-01  5.260e-02  0.0553714  0.1798984  0.0521137 -6.5
65e-02
## sp82   2.721e-02 -3.106e-02 -0.0057693 -0.0488570 -0.0225347  9.6
62e-03
## sp83  -1.609e-02  1.450e-03  0.0413694  0.0455127  0.0064190 -4.5
```

```
67e-03
## sp85  -4.227e-02 -1.385e-02  0.0313702  0.0195240 -0.0320483 -2.6
42e-02
## sp89  -2.965e-02 -1.166e-02  0.0171872  0.0077389 -0.0202890 -1.5
28e-02
## sp90  -2.932e-03  9.978e-03 -0.0138726  0.0070024  0.0037843 -5.4
47e-03
## sp91  -1.977e-02 -3.000e-03  0.0088771  0.0047195 -0.0051569 -4.7
16e-03
## sp92   1.248e-03  6.685e-03 -0.0408678  0.0131092  0.0076911 -1.4
87e-03
## sp94   5.236e-02 -2.031e-04 -0.1112302 -0.0218747  0.0019195 -1.2
04e-02
## sp99   7.975e-02 -1.310e-02 -0.0452705 -0.0730167  0.0497297  5.0
67e-03
## sp101  4.191e-02  4.817e-03  0.0089492 -0.0093338  0.0449460 -7.8
96e-03
## sp102 -1.348e-01  8.702e-02 -0.0363772  0.1717310 -0.0039252 -6.8
49e-02
## sp104 -1.393e-01 -3.117e-02  0.0692347  0.0573388 -0.0994526 -9.6
11e-02
## sp105  9.551e-03  4.394e-02 -0.0966281  0.1268474  0.1157904 -1.5
88e-02
## sp107  6.039e-03  1.581e-02 -0.0501987  0.0155727  0.0067248 -2.3
47e-03
## sp113  7.036e-03 -7.450e-03 -0.0198669  0.0132858 -0.0013440 -1.5
28e-02
## sp115 -4.214e-03 -1.828e-03  0.0156947  0.0080517  0.0051949  7.2
68e-03
## sp120 -1.738e-02  6.605e-02 -0.0995187  0.0743455  0.0295624 -3.3
11e-02
## sp121 -1.378e-02  7.879e-03  0.0127186  0.0190530 -0.0096014 -1.5
12e-02
## sp122  3.050e-03  4.004e-02 -0.1054441  0.0677863  0.0259340 -1.9
38e-02
## sp123 -2.452e-02 -9.040e-03  0.0248230  0.0295989 -0.0059514 -1.1
09e-02
## sp124  6.957e-02 -6.107e-02 -0.0420502 -0.1302887 -0.1167005  5.3
21e-02
## sp125 -3.655e-03 -3.892e-03  0.0165059  0.0095291  0.0014111  1.0
36e-02
## sp126  7.643e-02 -6.247e-02 -0.0047061 -0.1466355 -0.0427996  1.0
57e-02
## sp127 -2.668e-04 -4.728e-03  0.0485549  0.0402553  0.0348878 -1.1
02e-02
## sp130 -2.332e-04  1.624e-02  0.0240602 -0.0225387  0.0163459  4.2
75e-02
## sp132 -7.787e-03  2.485e-03  0.0125005  0.0063589 -0.0058270 -4.6
62e-03
```

```
## sp135 -2.377e-02 -2.490e-03  0.0055580  0.0101066 -0.0160974 -1.5
57e-02
## sp138  2.824e-02 -1.107e-02 -0.0006887 -0.0077027 -0.0374071  8.0
90e-03
## sp139  1.427e-02  1.756e-02 -0.0144559  0.0136940  0.0231884 -2.1
19e-02
## sp143  8.425e-02 -7.417e-02  0.0943978 -0.2690425  0.0547812  1.3
03e-01
## sp144  1.241e-02  7.627e-03  0.0112758 -0.0155303  0.0038582 -1.9
67e-02
## sp145 -8.336e-02 -4.013e-02  0.0232400 -0.0264962 -0.0015838  3.2
04e-02
## sp149 -1.179e-02 -1.170e-03  0.0435566  0.0221866  0.0152972  2.7
96e-02
## sp152 -2.362e-02 -9.027e-03  0.0527197  0.0430844 -0.0120155 -3.4
17e-04
## sp154 -4.924e-03  3.554e-02 -0.0926772  0.0234283  0.0122194 -9.6
64e-03
## sp155 -1.330e-02  3.043e-02 -0.0240991  0.0168994  0.0097919 -8.4
51e-03
## sp157 -1.611e-02 -8.328e-03  0.0037769  0.0152821 -0.0113556 -1.3
96e-02
## sp158 -2.512e-02  4.077e-02 -0.0697893  0.0352337  0.0071524 -2.6
36e-02
## sp159 -4.098e-03 -6.621e-03  0.0243325  0.0045090  0.0239888 -3.1
55e-05
## sp160  9.823e-03  6.465e-03 -0.0340060  0.0034619  0.0095613  9.5
60e-03
## sp161 -3.777e-02 -4.906e-03  0.0180337  0.0112134 -0.0196061 -1.2
92e-02
## sp162 -1.260e-02 -4.497e-03  0.0590830  0.0133914  0.0828559  1.6
68e-02
## sp163  1.641e-03  4.720e-04 -0.0172189  0.0135983  0.0068106 -4.6
17e-04
## sp167 -8.147e-04  1.937e-03  0.0114451  0.0116773 -0.0049388 -4.5
58e-03
## sp170  3.349e-02  2.503e-02  0.0565526  0.0398424  0.0757502  4.2
17e-02
## sp171 -4.557e-02 -1.658e-02  0.1148618  0.0647487  0.0086321  2.8
45e-02
## sp172 -1.734e-02 -5.698e-03  0.0044496 -0.0006063 -0.0125009 -9.5
27e-03
## sp173  2.662e-02  1.200e-01 -0.2604359  0.1148390  0.0845442  7.2
34e-02
## sp175 -5.110e-03 -8.065e-04 -0.0038201  0.0041224  0.0027517 -6.1
12e-03
## sp177 -3.387e-02  9.061e-03  0.0454185  0.0061442 -0.0003440  2.0
20e-02
## sp178 -5.248e-02 -3.018e-02  0.0725007  0.0556894 -0.0276696 -1.7
```

```
21e-02
## sp181 -1.043e-01 -4.165e-02  0.2533468  0.1214876  0.1071242  1.1
73e-01
## sp190 -3.138e-03  2.128e-02  0.0427738 -0.0143858  0.0250350  4.2
94e-02
## sp191  2.309e-02 -1.549e-03 -0.0395263  0.0201505  0.0046241  3.4
35e-03
## sp197  1.913e-02  4.995e-03 -0.0079389 -0.0110264 -0.0059066 -2.9
16e-03
## sp198  3.127e-02  2.104e-03 -0.0141098 -0.0038609 -0.0080426  7.0
98e-03
## sp199  8.057e-03  9.778e-03 -0.0890363  0.0411820  0.0272429 -2.0
02e-02
## sp200  3.968e-01 -8.837e-02  0.1761923 -0.4772360  0.3785518 -4.9
39e-01
## sp203  5.616e-02  1.127e-02  0.0321722 -0.0459800 -0.0326290 -5.7
57e-02
## sp204  5.926e-02 -4.257e-02  0.0256982 -0.1061739 -0.0473790  5.7
91e-02
## sp205 -3.497e-02  1.288e-03  0.0499476  0.0250543 -0.0117370  1.9
24e-03
## sp207 -6.774e-03  5.156e-03  0.0083610  0.0064935  0.0016104 -6.1
00e-03
## sp211  1.022e-02  2.353e-02 -0.0290848  0.0316872  0.0136976 -1.0
32e-02
## sp215  9.968e-03  4.832e-03 -0.0114049 -0.0213684 -0.0073901  2.6
21e-02
## sp219 -7.071e-03  3.058e-03  0.0248603  0.0151305  0.0044547  1.2
19e-02
## sp225 -1.954e-02 -8.031e-03  0.0273453  0.0249013 -0.0095831 -7.4
61e-03
## sp227 -1.335e-02 -7.300e-03  0.0084736  0.0118843 -0.0049961 -1.0
54e-02
## sp231 -4.163e-03 -4.920e-03  0.0146535  0.0196706 -0.0026268 -3.4
42e-03
## sp236 -2.927e-03 -5.139e-03  0.0191949  0.0089851  0.0104735  9.4
11e-03
## sp237  1.586e-02 -1.738e-05  0.0093931 -0.0187445  0.0239445 -3.6
25e-02
## sp239 -1.611e-02 -8.873e-04  0.0260091 -0.0023126  0.0207705  3.9
38e-02
## sp244 -8.388e-03  2.448e-03  0.0089235  0.0163684 -0.0131271 -1.5
70e-02
## sp254  1.080e-02 -1.496e-03  0.0007279 -0.0300283 -0.0159786  1.6
34e-02
## sp257  2.356e-02 -1.019e-02 -0.0136654 -0.0112130 -0.0121773  7.5
51e-03
## sp259  4.047e-03  1.203e-03 -0.0210097  0.0252724  0.0020735 -1.1
14e-02
```

```
## sp267  2.329e-02  1.187e-03 -0.0472558  0.0115111 -0.0125549  2.9
86e-03
## sp269  2.363e-03  8.982e-03  0.0100729  0.0064966  0.0128138 -1.6
85e-02
## sp270 -1.917e-01 -6.959e-02  0.1345488  0.1713901 -0.1762633 -1.8
79e-01
## sp275 -5.698e-02 -1.998e-02  0.0033344  0.0248993 -0.0290711 -3.7
69e-02
## sp282 -2.062e-02  1.321e-02 -0.0179313  0.0423063  0.0073471 -6.2
38e-03
## sp284 -5.880e-02 -8.153e-03  0.0316648  0.0105475 -0.0433014 -3.2
13e-02
## sp286  4.216e-03  4.974e-03  0.0065479 -0.0226034 -0.0053364  2.2
03e-02
## sp290 -1.394e-01 -5.141e-02  0.1158637  0.0711050 -0.0365692 -1.5
06e-02
## sp291 -1.902e-02  2.134e-03  0.0077427  0.0084876 -0.0082827 -9.4
54e-03
## sp292 -6.736e-02 -5.398e-03  0.1756013  0.0711999  0.0521655  1.1
26e-01
## sp300 -8.379e-02 -3.976e-02  0.0479917  0.0323440 -0.0443209 -3.2
40e-02
## sp301  1.915e-02  2.284e-02 -0.0739373  0.0198076 -0.0168024  1.5
49e-02
## sp303  1.032e-02  4.225e-03 -0.0124977  0.0149959  0.0171795 -1.8
51e-02
## sp304 -1.893e-01 -9.467e-02  0.1307335  0.1409032 -0.1843802 -1.7
45e-01
## sp305 -9.192e-02 -2.370e-02  0.0670465  0.0390914 -0.0692509 -5.1
15e-02
## sp306 -4.146e-03  7.520e-03 -0.0467488  0.0232742  0.0115289 -1.4
84e-02
## sp307 -3.836e-02  9.548e-02 -0.1084397  0.0294632  0.0333436  6.7
47e-03
## sp311  2.612e-03 -3.107e-02 -0.0135566 -0.0510482 -0.0104330  3.2
69e-02
## sp312  1.466e-03 -2.307e-02  0.0382268 -0.0922435 -0.0091245  8.1
80e-02
## sp313  5.983e-03 -1.575e-02  0.0139103 -0.0412509  0.0056544  3.3
00e-02
## sp314  1.017e-01 -9.010e-02  0.0262254 -0.1669363  0.1170158  2.2
12e-02
## sp317 -4.949e-03 -3.245e-02  0.0997235 -0.1019180  0.0106878  1.2
18e-01
## sp319  3.424e-03  3.834e-03 -0.0010371  0.0083374 -0.0040252 -8.6
07e-03
## sp321  1.119e-02 -1.553e-02  0.0039708 -0.0373359  0.0026619 -1.4
87e-02
## sp322 -3.762e-02  3.057e-02 -0.0166560  0.0530376 -0.0017790 -4.7
```

```
16e-02
## sp324 -2.498e-02 -1.295e-02  0.0810174  0.0641784 -0.0004948  1.0
49e-02
## sp327  6.521e-03  2.780e-02 -0.0537233  0.0171247  0.0078771  5.8
56e-03
## sp328  1.533e-02 -1.096e-02 -0.0214344 -0.0010567  0.0211069 -2.7
71e-02
## sp329  1.178e-02  7.805e-03 -0.0211210  0.0015762  0.0058724  2.4
73e-03
## sp331  1.236e-02  1.019e-02  0.0179220 -0.0145217  0.0142717  1.5
24e-02
## sp332 -3.788e-03 -1.939e-02 -0.0016457 -0.0487492  0.0231274  2.1
66e-02
## sp336  3.716e-03  6.386e-03  0.0104944 -0.0015348  0.0045438  1.1
54e-02
## sp337  5.040e-02 -2.500e-02  0.0493168 -0.1050630  0.1194281  1.9
02e-02
## sp338 -9.489e-03 -1.423e-02  0.0418124 -0.0071158  0.0443827  4.5
89e-02
## sp339 -6.655e-03 -9.889e-03  0.0095929 -0.0020520  0.0067747  6.3
23e-03
## sp347  1.391e-01 -2.319e-02 -0.0559603 -0.1349995 -0.2493490  1.3
53e-01
## sp349 -1.073e-02  1.581e-02 -0.0125790  0.0317180 -0.0083136 -1.6
23e-02
## sp351  3.206e-02  1.420e-01 -0.3440935  0.0984005  0.0217686  6.9
85e-02
## sp354  5.295e-03  6.024e-03 -0.0012590 -0.0086481  0.0082248  8.5
84e-03
## sp357 -1.735e-02  5.683e-04  0.0057695  0.0024906 -0.0005725 -1.8
45e-03
## sp359  1.633e-02  3.125e-02 -0.1345692  0.0663376  0.0131934  9.3
42e-03
## sp360 -2.940e-02  8.627e-02 -0.2267066  0.1317473  0.0412271 -4.4
16e-02
## sp361 -2.584e-02  1.153e-02 -0.0096620  0.0098482 -0.0066306 -2.0
53e-02
## sp363 -4.211e-02 -2.532e-03  0.0391872  0.0408476 -0.0386852 -4.1
02e-02
## sp371 -1.463e-02  8.021e-04  0.0108631  0.0054233 -0.0178911 -1.5
49e-02
## sp374 -2.846e-02 -1.704e-02  0.0198846  0.0299378 -0.0278468 -3.2
23e-02
## sp377  1.536e-01 -5.373e-05 -0.2001607 -0.1383674  0.0254316  6.9
46e-02
## sp378 -1.360e-01 -3.001e-02  0.0861828  0.0243511 -0.0207616  1.9
43e-02
## sp384 -3.710e-02 -2.028e-02  0.0666670  0.0369641  0.0057056  2.1
75e-02
```

```
## sp388 -3.258e-02 -1.302e-02  0.0589970  0.0485591 -0.0101263 -3.9
75e-02
## sp390 -3.062e-02 -1.845e-02  0.0204270  0.0139658 -0.0224875 -1.5
35e-02
## sp391 -8.583e-02 -4.571e-02  0.0626203  0.0313281 -0.0447703 -2.1
19e-02
## sp395 -1.538e-01 -5.065e-02  0.0718567  0.0160243 -0.0859612 -5.3
07e-02
## sp400 -7.871e-03  2.810e-03  0.0059807 -0.0033019 -0.0011560  5.5
20e-03
## sp408  8.079e-02  5.046e-03  0.0102615 -0.1274910 -0.0326935 -9.7
95e-03
## sp421  8.497e-03  3.375e-02 -0.1674434  0.0550342  0.0178839 -1.1
33e-02
## sp424  8.862e-03 -7.811e-03  0.0036620 -0.0230116 -0.0100879  1.2
26e-02
## sp428  1.677e-02 -1.358e-04  0.0061150 -0.0213793 -0.0228843 -1.3
53e-03
## sp429  2.140e-02 -2.029e-02 -0.0012362 -0.0266216 -0.0044519 -5.9
72e-03
## sp433  1.743e-02 -1.362e-02  0.0057577 -0.0173611  0.0214730 -6.7
64e-03
## sp434  1.535e-02  4.633e-03  0.0351585 -0.0044423  0.0177473 -1.6
74e-02
## sp435 -5.608e-03 -5.295e-03  0.0171144 -0.0108234  0.0160581  1.9
04e-02
## sp439 -4.964e-03 -5.546e-03  0.0034209 -0.0065703  0.0051569  1.0
76e-02
## sp442 -2.172e-02 -3.850e-03  0.0139454  0.0055980 -0.0063164 -8.8
48e-03
## sp445 -6.167e-02 -2.029e-02  0.0458563 -0.0063618 -0.0020619  3.4
28e-02
## sp447 -1.987e-02 -1.977e-03  0.0079898 -0.0056407 -0.0030798  2.7
95e-03
## sp449 -1.323e-02 -7.116e-03  0.0156654  0.0087001 -0.0044450  2.3
62e-03
## sp450  3.807e-02 -5.605e-02  0.0219335 -0.1043530  0.0024984  2.1
53e-02
## sp451  1.285e-02  1.177e-02  0.0006300 -0.0105977  0.0100332 -1.1
58e-02
## sp452 -9.093e-03  3.505e-03  0.0491640 -0.0069324  0.0560793  5.6
15e-02
## sp457  2.182e-02  6.531e-03 -0.0133003 -0.0395658 -0.0323316  1.5
35e-02
## sp459  1.788e-02  1.584e-02  0.0003771 -0.0509087 -0.0381392  3.6
82e-02
## sp461 -9.489e-02 -2.887e-02  0.0727811  0.0400430 -0.0426231 -2.3
36e-02
## sp462 -1.920e-02  1.133e-02  0.0481196 -0.0240767  0.0242828  6.2
```

```
92e-02
## sp464  4.808e-03  4.652e-04  0.0207137 -0.0201656  0.0179882  2.1
05e-02
## sp468 -4.974e-02 -4.247e-04  0.0949100 -0.0201458  0.0554912  7.2
99e-02
## sp470 -3.119e-02 -4.286e-03  0.0350138  0.0285412 -0.0282074 -2.5
66e-02
## sp471  1.563e-02 -4.515e-03  0.0292665  0.0114901  0.0388909 -8.5
47e-03
## sp473  3.673e-02 -2.495e-02 -0.0183600 -0.0308220 -0.0594649  2.5
75e-02
## sp474  1.611e-02 -6.003e-03 -0.0416100  0.0118828  0.0015542 -4.4
61e-03
## sp476 -5.013e-03  6.736e-03  0.0124960  0.0013145  0.0054119 -8.1
64e-03
## sp479  3.186e-03  4.412e-02 -0.1222582  0.0868513  0.0143900 -1.9
32e-02
## sp481 -1.924e-02 -6.348e-03  0.0271852 -0.0071829  0.0262771  3.0
72e-02
## sp482  3.591e-02 -1.883e-02  0.0357469 -0.1233495 -0.0190863  4.6
94e-02
## sp483  1.611e-02  2.333e-02  0.0340088 -0.0601663  0.0252189  2.1
88e-02
## sp487 -1.051e-02 -2.346e-03  0.0196271 -0.0011775  0.0075586  2.6
14e-02
## sp491 -9.643e-03  4.658e-03  0.0229057  0.0048805  0.0107315  1.2
29e-02
## sp492 -2.444e-02  4.144e-02  0.0425153  0.0338960  0.0638029  6.4
16e-02
## sp494 -4.109e-03 -9.030e-03  0.0037367 -0.0011260  0.0009321 -4.5
20e-03
## sp496  1.988e-02 -9.892e-03 -0.0004535 -0.0198522  0.0262693  4.6
44e-03
## sp497  4.028e-02  1.184e-01 -0.2117258  0.0759246  0.0920845  7.0
00e-02
## sp498 -1.770e-02 -7.331e-03  0.0062294  0.0171883 -0.0192585 -2.3
58e-02
## sp499  7.311e-02  1.484e-01 -0.4236318  0.1838782  0.1122623 -4.6
81e-02
## sp500 -4.058e-02 -1.785e-02  0.0145231  0.0467115 -0.0454493 -5.7
74e-02
## sp501 -1.064e-01 -2.779e-02  0.1168973  0.0736217 -0.0407355 -1.6
86e-02
## sp502 -1.461e-02  6.532e-03  0.0124055  0.0064141  0.0076566  2.7
80e-03
## sp505 -4.580e-02  1.612e-02 -0.0117640  0.0475020  0.0261176  1.1
98e-02
## sp506 -7.129e-03 -7.046e-03  0.0131444 -0.0081485  0.0194638  2.0
45e-02
```

```
## sp507 -7.248e-02 -2.204e-02  0.0414120 -0.0013934 -0.0247832  2.8
54e-03
## sp508 -7.194e-03 -2.018e-03  0.0299555 -0.0109482  0.0204890  3.5
16e-02
## sp509 -4.730e-02 -1.915e-02  0.1226022  0.0892366  0.0127264  3.3
83e-02
## sp510 -5.395e-03 -1.128e-02  0.0723315  0.0002082  0.0478719  6.9
56e-02
## sp512  9.306e-03  1.615e-02 -0.0683512  0.0129067  0.0296730 -1.1
20e-03
## sp514 -4.173e-02 -1.153e-02  0.1192875  0.0641251  0.0312337  4.8
64e-02
## sp516 -1.441e-02 -2.113e-04  0.0392849  0.0123292  0.0203104  2.2
26e-02
## sp517  3.055e-03  7.958e-04  0.0136092 -0.0043692  0.0117399  2.1
02e-03
## sp522 -1.549e-02 -5.687e-03  0.0212370  0.0239061 -0.0202678 -2.0
55e-02
## sp524 -1.851e-02 -3.794e-03  0.0649385  0.0426548  0.0188739  2.0
12e-02
## sp526 -2.099e-02 -8.714e-04  0.0965473  0.0337138  0.0702361  5.1
58e-02
## sp527  5.966e-02 -1.054e-01  0.0017695 -0.1250618  0.0217958  5.1
35e-02
## sp528  1.157e-01  1.260e-01 -0.3332122  0.0788545  0.0621904  1.1
18e-01
## sp529  1.018e-01 -2.380e-02 -0.0384002 -0.1508507 -0.0801200  3.9
49e-02
## sp530 -5.062e-02 -3.037e-02  0.0326687 -0.0056852  0.0132326  2.6
71e-02
## sp531 -1.994e-02 -8.401e-03  0.0447884  0.0374715  0.0092673  7.2
22e-03
## sp533 -1.657e-02 -8.974e-03  0.0192117 -0.0048421  0.0184896  2.8
18e-02
## sp536 -2.586e-02 -4.121e-03  0.0499868  0.0178326  0.0093800  3.0
82e-02
## sp538 -1.098e-02 -3.341e-03  0.0102928 -0.0023507  0.0062365  1.4
26e-02
## sp539  1.202e-03  2.242e-03  0.0068623  0.0025080  0.0024156  6.9
33e-03
## sp540 -2.209e-02  1.710e-03  0.0331732 -0.0061819  0.0189767  5.0
14e-02
## sp541 -1.603e-02  3.608e-03  0.0026880  0.0040677 -0.0104433 -1.5
09e-02
## sp542  8.297e-03  4.572e-02 -0.1345839  0.0307636  0.0058982  8.2
24e-03
## sp546 -1.130e-01 -2.796e-02  0.0740234 -0.0022421 -0.0321804  1.5
13e-02
## sp547  6.605e-04  3.002e-03  0.0102934 -0.0118132  0.0069632 -2.7
```

```
96e-03
## sp548 -1.821e-03  1.594e-03  0.0202373 -0.0029186  0.0059714  2.2
42e-02
## sp552  7.913e-03  4.914e-03  0.0451527  0.0078443  0.0297762  2.6
47e-02
## sp553  5.704e-04  3.221e-02 -0.0768786  0.0687492  0.0068561 -1.9
09e-02
## sp558  9.819e-03  1.239e-02 -0.0604999  0.0396292  0.0182300 -7.1
27e-03
## sp559  2.459e-03  2.163e-02 -0.0949329  0.0542991  0.0195456 -2.0
10e-02
## sp560 -1.572e-02  1.107e-03  0.0289169 -0.0177824  0.0215833  4.1
16e-02
## sp568 -3.781e-02  1.355e-02  0.0016913  0.0123829 -0.0273171 -3.1
95e-02
## sp569 -7.580e-03 -3.809e-03 -0.0028869  0.0228153 -0.0082180 -1.6
12e-02
## sp570  3.500e-03  5.293e-03  0.0178337  0.0034387  0.0075102  1.4
46e-02
## sp571  7.812e-02 -4.952e-03  0.0697404 -0.0276681  0.0648190  5.3
44e-02
## sp572 -5.492e-02  8.358e-03  0.1381047  0.0307439  0.0408151  4.5
70e-02
## sp573 -9.703e-03 -4.250e-03  0.0095432 -0.0064165  0.0150824  1.7
56e-02
## sp574  7.671e-03  8.830e-03  0.0510478 -0.0225276  0.0352818  6.0
90e-02
## sp575 -2.272e-02  8.560e-03 -0.0256572  0.0433403 -0.0069356 -3.3
31e-02
## sp576 -2.763e-02 -1.616e-02  0.0133091  0.0188948 -0.0265801 -2.6
95e-02
## sp580  6.569e-04  3.137e-03  0.0226353  0.0036504  0.0180041  1.9
93e-02
## sp583  8.594e-02 -3.637e-02  0.0154677 -0.0370850 -0.1281982  4.9
12e-02
## sp584 -2.599e-02 -1.082e-02  0.0310429 -0.0072316  0.0160547  3.7
69e-02
## sp585 -5.581e-02 -1.216e-02  0.0744969  0.0319016  0.0164804  3.3
08e-02
## sp586 -2.391e-02 -9.100e-03  0.0067079 -0.0005227 -0.0136699 -1.0
55e-02
## sp590 -2.130e-02 -8.165e-04  0.0080767  0.0035210 -0.0092982 -9.7
53e-03
## sp592 -9.753e-02 -1.324e-02  0.0594322  0.0172604 -0.0633452 -4.0
67e-02
## sp593  1.165e-01 -4.580e-02 -0.1110821 -0.1022598  0.0647459  2.9
23e-02
## sp594 -3.015e-02 -5.452e-03  0.0254405  0.0314367 -0.0191479 -1.9
87e-02
```

```
## sp596 -1.744e-02 -2.400e-03  0.0090418 -0.0067415 -0.0057310  6.3
37e-03
## sp600 -3.657e-02 -1.192e-02  0.0095782 -0.0048377 -0.0199527 -1.4
55e-02
## sp604 -7.372e-02  1.123e-02  0.2588139  0.0998033  0.1051835  1.7
57e-01
## sp605 -2.425e-02 -1.349e-02  0.0098762  0.0093588 -0.0178037 -1.6
56e-02
## sp608  1.915e-02 -1.169e-02 -0.0060660 -0.0133524 -0.0346470  1.4
76e-02
## sp609  2.277e-03  1.715e-02 -0.0216785  0.0070423 -0.0011650  4.1
63e-03
## sp612 -1.222e-02  2.743e-02 -0.0252774  0.0053254  0.0071969 -4.6
08e-03
## sp617 -4.919e-04  1.144e-02  0.0189376 -0.0116350  0.0087702  4.7
85e-02
## sp622  3.534e-03  2.247e-02 -0.0408836  0.0123050  0.0071531 -8.0
27e-03
## sp626  8.295e-02  1.780e-02 -0.0436795 -0.0215458  0.0317852 -3.7
58e-02
## sp630 -3.112e-02 -1.140e-02  0.0507816  0.0251569  0.0103138  2.7
44e-02
## sp631 -2.535e-02  9.317e-03  0.0301573  0.0127369  0.0016182  1.1
07e-02
## sp632  1.765e-02 -1.507e-02 -0.0015959 -0.0078275 -0.0391819  1.5
79e-02
## sp634  2.667e-02  1.379e-04 -0.0233747 -0.0333707 -0.0428102  2.5
15e-02
## sp635 -2.919e-02 -2.926e-03  0.0109408  0.0051784 -0.0241260 -2.4
30e-02
## sp636  3.193e-02 -1.747e-02 -0.0052446 -0.0213706 -0.0398983  1.0
89e-02
## sp637  2.219e-02  1.238e-02 -0.0840454  0.0272892  0.0083489 -5.0
52e-03
## sp638  7.644e-02 -1.024e-02 -0.1475279 -0.0821192 -0.0679308  8.2
14e-02
## sp641 -6.238e-03 -4.222e-03  0.0157197  0.0282342 -0.0005590 -9.3
69e-03
## sp645 -3.879e-03  1.575e-02  0.0021588  0.0386154  0.0079904 -3.6
14e-03
## sp648  1.437e-03 -7.561e-03 -0.0023890 -0.0173164  0.0087725 -3.9
98e-03
## sp650 -1.223e-01 -5.171e-02  0.0718966  0.0320998 -0.0873432 -7.0
02e-02
## sp651  2.281e-02 -8.244e-03  0.0349708 -0.0207200  0.0633076  9.6
03e-03
## sp653 -7.257e-03  3.527e-03  0.0058662  0.0082799 -0.0036882 -6.5
14e-03
## sp654  9.071e-03  1.860e-02  0.0035146  0.0260046  0.0065306  3.9
```

```
57e-03
## sp658  5.507e-03  2.806e-02 -0.0524495  0.0062980  0.0337045 -2.1
60e-02
## sp660 -6.629e-03  1.337e-02  0.0243968  0.0133246  0.0062573 -8.8
00e-03
## sp662 -1.957e-04  1.039e-02  0.0166793  0.0089694  0.0008180  2.5
06e-03
## sp664  2.703e-02  1.959e-02 -0.0416173  0.0717099  0.0249947 -2.1
15e-02
## sp667 -3.172e-02  2.335e-02 -0.0024533  0.0599964  0.0102320 -3.8
98e-02
## sp668  5.301e-03  1.617e-02 -0.0483746  0.0107228  0.0025534 -7.3
68e-03
## sp670  5.432e-03  2.277e-03  0.0123985 -0.0007440  0.0056244  2.2
37e-03
## sp672  9.180e-02 -2.770e-02 -0.1010607 -0.0586421 -0.0124757  1.3
73e-02
## sp673 -1.019e-01  1.174e-01 -0.1681256  0.0246112  0.0807389 -2.1
80e-03
## sp681 -6.306e-03 -5.309e-03  0.0156907 -0.0068691  0.0202413  2.4
17e-02
## sp684 -7.070e-04  5.310e-04  0.0316359 -0.0268986  0.0374186  3.8
12e-02
## sp685  2.260e-02 -6.254e-03  0.0040393 -0.0162297  0.0039022 -3.9
01e-03
## sp687  3.290e-02 -1.965e-02 -0.0071184 -0.0311318 -0.0599763  2.3
38e-02
## sp689 -2.171e-02  2.549e-02  0.0046369  0.0084299 -0.0086955 -1.2
17e-02
## sp691 -1.316e-01 -4.174e-02  0.0441031 -0.0061914 -0.0808993 -5.4
27e-02
## sp695 -3.959e-02 -4.114e-03  0.0095302  0.0378982 -0.0139613 -3.1
82e-02
## sp699 -1.757e-02 -1.850e-02  0.0067290 -0.0011929  0.0006554  5.4
92e-03
## sp701 -2.647e-02 -1.267e-02  0.0140340 -0.0032749  0.0035193  5.2
66e-04
## sp702 -4.062e-04  4.196e-03  0.0178612 -0.0034634  0.0224323  1.5
62e-02
## sp705 -2.127e-02  2.216e-02 -0.0131339  0.0550652  0.0106261 -1.8
61e-02
## sp709 -2.421e-02  6.656e-02 -0.1267175  0.0596873  0.0337025 -3.8
36e-02
## sp711 -3.838e-02 -1.240e-02  0.0126627  0.0111937 -0.0214705 -2.6
52e-02
## sp714 -1.587e-02  3.768e-02 -0.0588925  0.0251158  0.0176396 -1.6
40e-02
## sp715 -3.953e-02 -1.107e-02  0.0257038  0.0040505 -0.0222759 -7.1
87e-03
```

```
## sp717  1.844e-03  1.382e-02 -0.0314130  0.0146962  0.0018249 -1.0
34e-03
## sp718 -6.183e-03  1.966e-03  0.0023997  0.0066404 -0.0005537 -2.8
11e-03
## sp720  1.062e-01 -2.003e-02  0.1205714 -0.1214363  0.1236290  4.1
67e-02
## sp721 -1.878e-05  2.305e-03  0.0223480  0.0131141  0.0010157  3.8
71e-03
## sp724 -3.879e-03 -1.295e-03  0.0352217  0.0093903  0.0216630 -2.7
82e-02
## sp725 -8.783e-02 -2.877e-02  0.0500131  0.0510435 -0.0920072 -9.2
14e-02
## sp726  1.318e-02  3.043e-02 -0.0272693 -0.0088374  0.0142886  3.2
00e-02
## sp728  3.214e-02  4.318e-03  0.0268470 -0.0410778  0.0312560 -5.8
51e-02
## sp729 -1.149e-03 -3.596e-02  0.0255198 -0.0353695  0.0437973  2.5
60e-02
## sp730 -6.369e-02 -2.795e-02  0.0368378  0.0135575 -0.0417545 -2.4
30e-02
## sp733  3.123e-02  2.269e-03 -0.0252242 -0.0219600 -0.0166660  2.7
82e-03
## sp735  5.718e-03  1.863e-02 -0.0341321  0.0021627 -0.0070889  6.1
75e-03
## sp736  1.563e-02 -7.998e-03 -0.0098863 -0.0255637 -0.0293462  1.8
40e-02
## sp737 -8.051e-04  1.544e-02 -0.0176864  0.0061971  0.0023038 -7.6
11e-03
## sp738  4.449e-02  3.382e-02 -0.0617951 -0.0416594 -0.0574692  5.0
29e-02
## sp739 -2.065e-02  4.141e-03  0.0217148  0.0170060 -0.0077021 -1.0
27e-02
##
##
## Site scores (weighted sums of species scores)
##
##             RDA1      RDA2        PC1        PC2        PC3
PC4
## row1   -0.087888  0.552914 -1.994e-01  0.2459549  0.0724544 -0.06
50095
## row2   -0.205832  0.311115 -3.274e-01  0.0605065  0.0643049 -0.18
37365
## row3   -0.428422 -0.272965  9.119e-02  0.1592684 -0.2725134 -0.32
53089
## row4   -0.188997  0.364438 -2.017e-01  0.0756182 -0.0447998 -0.22
68124
## row5   -0.289373 -0.003411  7.642e-02  0.0983490  0.0548153 -0.07
24957
## row6   -0.339221 -0.075242 -5.307e-02  0.0720461 -0.2339226 -0.38
```

```
47960
## row7   -0.473740 -0.349380  2.634e-01  0.2855188 -0.2113854 -0.14
78747
## row8   -0.498620 -0.433369  1.701e-01  0.1211944 -0.3390356 -0.34
26189
## row9   -0.344992 -0.056083  8.843e-02  0.2859688 -0.0545421 -0.24
69267
## row10  -0.376811 -0.100626  7.168e-02  0.0074241 -0.1674740 -0.18
68189
## row11  -0.456260 -0.269315  1.003e-01 -0.0028427 -0.2423244 -0.17
67280
## row12  -0.095137  0.061564 -5.082e-02 -0.2576152  0.0887715  0.23
84410
## row13  -0.189542  0.451514 -1.735e-01  0.1408304  0.0235338 -0.11
54163
## row14  -0.319898 -0.033892  1.132e-01  0.0985540 -0.0046735  0.01
30364
## row15  -0.208927  0.100407  1.297e-02 -0.0625584 -0.0327642  0.03
80976
## row16  -0.452689 -0.355251  1.411e-01  0.0757099 -0.3436267 -0.32
99325
## row17  -0.300695 -0.178972  1.490e-01 -0.0938493 -0.0894486  0.06
26617
## row18  -0.200736 -0.221699  2.291e-01 -0.1150121  0.0853169 -0.01
64590
## row19   0.294088 -0.408683  8.836e-02  0.0027313 -0.6993080  0.17
26124
## row20   0.307746 -0.471212  1.169e-01 -0.0002992 -0.7310116  0.19
05094
## row21  -0.304352 -0.112426  1.542e-01  0.1208635 -0.1071370 -0.08
01363
## row22  -0.109665  0.522015 -1.649e-01  0.0494310  0.0185084 -0.02
61440
## row23  -0.384123 -0.180387  5.313e-02 -0.3639258 -0.1389354 -0.12
66164
## row24   0.517517 -0.524138  5.544e-03 -0.3032055  0.1598692 -0.38
10124
## row25   0.336602 -0.475575 -7.177e-02 -0.1433286 -0.5661227  0.28
05755
## row26   0.304708 -0.539727  4.257e-03 -0.1964196 -0.3863852  0.22
14824
## row27  -0.126545  0.177555 -1.243e-02  0.0129411 -0.0088663  0.06
47849
## row28  -0.195365  0.309998  3.973e-02  0.0361072  0.0463888  0.02
09462
## row29  -0.400835 -0.027776  1.147e-01  0.2072205 -0.2180879 -0.30
96797
## row30   0.298471  0.268857 -2.875e-01  0.0806116 -0.2007819  0.26
15908
```

```
## row31   0.250674 -0.381831  6.439e-02  0.0329507 -0.5103130  0.06
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## row32   0.480707 -0.605575  1.934e-01 -0.1197812 -0.3614195 -0.29
32898
## row33  -0.346557 -0.239444  2.794e-01  0.1583847 -0.0823948  0.04
81413
## row34  -0.161356 -0.254205  3.695e-01  0.0957656  0.2607766  0.28
93102
## row35  -0.087153  0.147692  6.389e-02 -0.3148034  0.1034214  0.21
56664
## row36  -0.184523  0.425438 -1.581e-01 -0.0952531 -0.0806731 -0.17
92159
## row37  -0.274958 -0.079369  1.643e-01 -0.0311765 -0.0092977  0.03
46441
## row38   0.290063 -0.535902 -5.978e-02 -0.1463492 -0.5275183  0.25
93341
## row39   0.410311 -0.549496  7.248e-02 -0.1229301 -0.3966216 -0.08
70104
## row40   0.275348 -0.497751  1.751e-01  0.0767793 -0.6747238  0.05
76707
## row41   0.269161 -0.379895  5.191e-02 -0.1571947 -0.5228886  0.05
24482
## row42  -0.157884 -0.082727  1.081e-01  0.1275855  0.2623933  0.17
58715
## row43  -0.351991 -0.292322  2.414e-01  0.2553624 -0.1141328 -0.07
54330
## row44  -0.395161 -0.386192  3.053e-01  0.2497383 -0.1018768 -0.16
62097
## row45  -0.245999  0.316374 -6.371e-05  0.0548319 -0.0290353 -0.16
27630
## row46  -0.264015  0.326149  4.333e-02  0.0131810 -0.0749684 -0.01
86424
## row47  -0.339725 -0.363309  3.000e-01 -0.0478048 -0.0081376  0.25
32494
## row48   0.460406 -0.510651  2.853e-01 -0.2574740 -0.0040828 -0.46
43795
## row49   0.462701 -0.465446  2.910e-01 -0.2664020 -0.0594818 -0.51
14366
## row50   0.451930 -0.381883  9.798e-02 -0.4402519  0.2398949 -0.43
75590
## row51  -0.403473 -0.138627  2.850e-01  0.2238746 -0.1962521 -0.13
21546
## row52  -0.388061 -0.105661  1.777e-01  0.0386092 -0.1722640 -0.00
92999
## row53  -0.103308 -0.276470  2.496e-01 -0.0898869  0.3192269  0.28
56908
## row54  -0.368589 -0.286923  2.213e-01 -0.1296680 -0.1588238 -0.18
52478
## row55   0.263216 -0.422956 -9.295e-02 -0.1227870 -0.4731731  0.24
```

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96078
## row56   0.458313 -0.452132  2.984e-01 -0.2475628  0.0823021 -0.56
81046
## row57   0.507927 -0.434156  2.446e-01 -0.2805515  0.1459925 -0.48
27923
## row58   0.426098 -0.352732  2.662e-01 -0.1889800  0.0820810 -0.66
03390
## row59   0.344388 -0.297748  1.097e-01 -0.4188706  0.0002829 -0.42
07097
## row60  -0.389965 -0.380890  3.661e-01  0.2368215 -0.1411109 -0.07
61540
## row61  -0.196842 -0.325975  2.639e-01  0.0211679  0.1535612  0.33
06185
## row62  -0.452548 -0.362994  2.896e-01  0.0782281 -0.1797895  0.03
54592
## row63  -0.479994 -0.399784  2.682e-01  0.2400309  0.0018544  0.04
57271
## row64  -0.488443 -0.360938  2.757e-01 -0.0645583 -0.2157796 -0.10
65061
## row65   0.427337 -0.494563 -6.490e-02 -0.2550007 -0.4350815  0.13
28753
## row66   0.299271 -0.429519 -5.293e-02 -0.1918574 -0.5071834  0.28
50913
## row67   0.370427 -0.355371  8.709e-02 -0.0699437 -0.5741294  0.15
20383
## row68   0.439468 -0.389399  2.992e-01 -0.2400188  0.1537244 -0.66
77396
## row69   0.439395 -0.442540  2.762e-01 -0.2758654  0.2069380 -0.44
64346
## row70   0.317662  0.138477  7.864e-02  0.1551699  0.2216037 -0.24
39770
## row71  -0.084337 -0.072029  3.052e-01  0.0422674  0.2431409  0.30
31854
## row72   0.160568 -0.441605 -7.683e-02 -0.3757153  0.0695379  0.29
33237
## row73   0.287271 -0.161189  1.358e-01 -0.0784098 -0.0296264  0.03
73616
## row74   0.418003 -0.092164  9.122e-02 -0.0628574  0.3101850 -0.26
85636
## row75   0.154739  0.234595  1.177e-02  0.2171241 -0.0102360 -0.26
22801
## row76   0.121759  0.228763 -4.174e-02 -0.0393228  0.3311589  0.06
56610
## row77  -0.424098 -0.220033  1.685e-01  0.3238089 -0.1114694 -0.08
68964
## row78  -0.335208 -0.250506  1.873e-01  0.0636596  0.0398395  0.26
52030
## row79  -0.165829 -0.289056  6.296e-02 -0.3366152  0.2528081  0.40
03081
```

```
## row80   0.362266 -0.169825 -1.236e-02 -0.3215840 -0.1376463  0.15
66219
## row81   0.190251 -0.001144 -6.283e-02 -0.1721758 -0.3308382  0.16
15099
## row82   0.272757  0.012687  6.920e-02 -0.2300912  0.0114792  0.19
50768
## row83  -0.017171  0.166011  1.884e-01  0.1006717  0.2637695  0.17
35667
## row84  -0.380427 -0.058361  8.493e-02  0.2954548  0.0348875 -0.03
80200
## row85  -0.379243 -0.479967  1.230e-01  0.0095748 -0.1516805 -0.01
54332
## row86  -0.218900 -0.287299  1.084e-01 -0.2154676  0.0491990  0.27
77874
## row87  -0.391189 -0.407972  1.293e-01 -0.1942573 -0.0951527  0.15
10672
## row88   0.383724 -0.259127  2.019e-02 -0.2893902 -0.1736247  0.21
72046
## row89   0.385130 -0.369046  3.993e-02 -0.3834043 -0.1242485 -0.11
64078
## row90   0.300321 -0.263189  2.184e-02 -0.3642813 -0.2208707  0.16
60391
## row91   0.196219  0.021074  1.383e-01 -0.1443087  0.2055776  0.06
91493
## row92  -0.057156 -0.007903  2.852e-01 -0.1731822  0.0661943  0.41
71313
## row93   0.022277 -0.210910  2.529e-01 -0.3979543 -0.0789296  0.39
83251
## row94   0.199856 -0.114210  1.589e-01 -0.4446637  0.1364447  0.20
19583
## row95   0.264473  0.199238 -6.599e-02 -0.1034910  0.2308431 -0.21
50748
## row96  -0.021851 -0.225141  1.937e-01 -0.1658896 -0.0815346  0.28
81529
## row97   0.044819 -0.181915  1.897e-01 -0.0581855  0.4693016  0.28
91481
## row98  -0.441830 -0.479584  1.510e-01  0.0910504 -0.1213577 -0.02
29867
## row99  -0.310737 -0.350058  3.196e-02  0.0494065 -0.0723954 -0.11
46818
## row100 -0.313421 -0.114543  1.546e-03 -0.0114063  0.0325578  0.09
70700
## row101  0.347056  0.156355 -1.871e-01 -0.2427486 -0.1938506  0.08
67869
## row102  0.290711  0.143813 -1.287e-01 -0.2464242 -0.1154259  0.20
58150
## row103  0.409967 -0.475803  5.796e-02 -0.5133568 -0.3947230  0.12
87492
## row104  0.329673 -0.003625 -8.144e-02 -0.2255582 -0.0364061  0.06
```

```
09931
## row105  0.104601 -0.191703  2.664e-01 -0.0642278  0.1678152  0.10
07850
## row106 -0.017425  0.553012 -7.734e-02  0.2795930  0.1008711  0.16
82890
## row107 -0.004583  0.235283  1.494e-01  0.1391938  0.1585812  0.27
63267
## row108 -0.045733  0.054636  1.992e-01  0.0619746  0.1353856  0.29
56827
## row109 -0.155161  0.090745  1.975e-01  0.1308851  0.0889723  0.30
76270
## row110 -0.022909  0.176063  5.826e-02 -0.0749900  0.2160744  0.37
59550
## row111 -0.105434 -0.139576  2.018e-01  0.1060811  0.5115118  0.18
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## row112 -0.286214 -0.273908  7.656e-02  0.0723294  0.3329659  0.30
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## row113 -0.233232 -0.509177  4.483e-02 -0.0736938 -0.0264496  0.03
29822
## row114 -0.512038 -0.228842  2.118e-02  0.1221380 -0.2471083 -0.30
54223
## row115  0.467914 -0.232160 -6.135e-03 -0.2685611 -0.1127829 -0.02
46794
## row116  0.350595  0.071782 -1.011e-01 -0.3393897 -0.1266022  0.27
93465
## row117  0.370961 -0.202899  7.692e-04 -0.2955510 -0.4013961  0.08
02537
## row118 -0.106676  0.584918 -6.188e-02  0.3192560  0.0071071 -0.04
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## row119 -0.142803  0.192797  1.661e-01  0.2074493  0.0479742  0.14
20492
## row120 -0.070287 -0.059961  2.606e-01  0.0793364  0.3079435  0.39
65692
## row121 -0.016679 -0.074543  2.882e-01  0.0878590  0.3415024  0.33
71633
## row122 -0.006272 -0.262611  1.896e-01 -0.0886232  0.3211023  0.30
77577
## row123 -0.285876 -0.313202  2.206e-01  0.2145449  0.2819618  0.16
18158
## row124 -0.373779 -0.590069  6.828e-02 -0.0639759 -0.0062442  0.09
65411
## row125 -0.277344 -0.377353  1.173e-01  0.0488738  0.4053325  0.28
48126
## row126 -0.316018 -0.265986  3.280e-02 -0.2960714  0.0425320  0.18
23376
## row127  0.214531  0.448937 -2.109e-01  0.0387296  0.0797806  0.11
42340
## row128  0.148585  0.768291 -3.890e-01  0.1852815  0.0308002  0.06
52364
```

```
## row129  0.462407 -0.325125 -4.620e-02 -0.2597042 -0.2238748  0.02
66291
## row130  0.324633  0.054996  3.991e-02  0.0376867  0.1658841 -0.37
88983
## row131  0.226165 -0.147519  1.528e-01 -0.2362169  0.3766136 -0.06
73063
## row132  0.215777 -0.052879  2.890e-02 -0.2304744 -0.1066203  0.24
40576
## row133 -0.190632 -0.014113  2.836e-01  0.3278893  0.1076721  0.13
66064
## row134 -0.052324 -0.063934  2.517e-01  0.0725933  0.2549865  0.25
39337
## row135 -0.207240  0.235273 -1.994e-03  0.3422338  0.0946410  0.00
45908
## row136 -0.268323 -0.108223  1.768e-01  0.2508836  0.0247417  0.03
36037
## row137 -0.503737 -0.552431  2.119e-01  0.1161068 -0.1201550  0.01
66581
## row138 -0.315000 -0.484774  1.363e-01 -0.0782269 -0.0401237  0.08
23503
## row139 -0.500580 -0.407530  1.889e-01  0.2447668 -0.0897872 -0.08
59453
## row140 -0.349836  0.097154 -1.650e-01  0.1799253 -0.0428844 -0.16
75118
## row141 -0.534460 -0.506129  1.626e-01  0.0476115 -0.0680801 -0.04
68448
## row142 -0.003507  0.937139 -2.968e-01  0.2009103  0.0672407  0.01
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## row143  0.090143  0.850384 -3.498e-01  0.3080192  0.0744872 -0.01
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## row144  0.230513  0.590580 -3.469e-01  0.2503879 -0.0434273  0.10
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## row145  0.310962 -0.041155 -1.952e-01 -0.0783739 -0.2290886  0.07
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## row146  0.424688 -0.503808 -4.163e-02 -0.2787833 -0.4813830  0.20
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## row147  0.487042 -0.460513  1.830e-01 -0.4708423  0.2386021 -0.43
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## row148  0.441662 -0.415022  2.027e-01 -0.3230993  0.3508648 -0.54
59519
## row149  0.051581  0.611677 -1.931e-01  0.0152889  0.0675947 -0.04
02478
## row150 -0.291253 -0.190914  3.967e-01  0.3149206  0.0571322  0.09
46976
## row151 -0.448975 -0.356029  3.509e-01  0.3835602 -0.1926320 -0.12
31675
## row152 -0.420440 -0.285746  3.107e-01  0.3632518 -0.0655772 -0.05
40524
## row153 -0.409404 -0.335187  1.961e-01  0.1237080  0.0196804  0.14
```

```
01002
## row154 -0.381349 -0.422046  1.842e-01  0.0290298  0.0437505  0.24
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## row155 -0.212031 -0.280007  1.757e-01 -0.0040751  0.2686190  0.34
77797
## row156 -0.541202 -0.413003  1.069e-01  0.1326844 -0.0835722 -0.06
35822
## row157  0.400148 -0.008532 -1.789e-01 -0.0838715 -0.0564316  0.06
12187
## row158 -0.006858  0.544657 -1.989e-01  0.2450727 -0.0295420 -0.14
09518
## row159  0.158884  0.871024 -3.402e-01  0.3313243  0.0501595  0.11
36501
## row160  0.179987  0.691502 -3.747e-01  0.2532785  0.0782537  0.06
31155
## row161 -0.230240 -0.117699  2.510e-01  0.0924118  0.0031924  0.24
04947
## row162 -0.272150 -0.151543  2.734e-01  0.3364537  0.0297155 -0.02
47413
## row163 -0.344361 -0.164120  3.556e-01  0.2737691  0.0421197  0.09
97056
## row164 -0.283351 -0.215635  3.526e-01  0.1525799  0.1164599  0.35
65282
## row165 -0.415351 -0.399318  3.818e-01  0.3059217 -0.0229037  0.16
46256
## row166 -0.411029 -0.429875  2.193e-01  0.2118367  0.0463563  0.03
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## row167 -0.505567 -0.273966  5.394e-02  0.1652846 -0.2118961 -0.25
19551
## row168 -0.385613 -0.426103  1.897e-01  0.0024086 -0.1710276  0.05
05808
## row169 -0.476492 -0.508321  9.096e-02  0.0836281 -0.2906982 -0.28
43692
## row170 -0.535244 -0.276582  8.482e-03 -0.0552587 -0.1592211 -0.25
24128
## row171  0.322269  0.062057 -1.941e-01 -0.0155194 -0.3841555  0.26
86261
## row172  0.111189  0.655824 -3.573e-01  0.0723228  0.0499608 -0.05
41217
## row173  0.127697  0.614658 -2.837e-01  0.3387271  0.0378603  0.01
00351
## row174  0.213268  0.299363 -1.815e-01  0.1094090  0.0453654  0.14
99412
## row175  0.385400 -0.378083 -1.339e-01 -0.2144204 -0.4421179  0.28
40937
## row176  0.535679 -0.449752  1.018e-03 -0.3094155 -0.2124636 -0.04
77564
## row177  0.340580 -0.211685  1.537e-01 -0.1561876  0.2322781 -0.52
14112
```

```
## row178 -0.041174  0.114951  1.456e-01  0.0833258  0.2219230  0.18
27649
## row179 -0.121205  0.143978  2.321e-01  0.0937375  0.1520730  0.21
97969
## row180 -0.164486  0.187646  1.566e-01  0.2082967  0.1775396  0.13
43728
## row181 -0.454015 -0.203524  2.927e-01  0.3528895 -0.1137267 -0.10
88691
## row182 -0.089263 -0.270668  3.050e-01 -0.0954796  0.3203395 -0.03
60201
## row183 -0.367953 -0.107112  1.948e-01  0.2070932 -0.0537075 -0.07
23519
## row184 -0.403513 -0.238042  1.827e-01  0.2869072 -0.1713809 -0.20
75530
## row185 -0.415432 -0.314537  2.827e-01  0.2476965  0.0802542  0.14
91010
## row186 -0.281202 -0.365935  2.026e-01  0.0388977  0.1252628  0.28
99372
## row187 -0.568657 -0.549659  8.991e-02  0.1376177 -0.3414578 -0.32
50236
## row188 -0.416101 -0.412078 -3.102e-03 -0.2629571 -0.1126484 -0.09
33296
## row189  0.065356  0.691432 -3.081e-01  0.1942889 -0.0173165 -0.02
75054
## row190  0.211486  0.175726  4.443e-02  0.1346167  0.3043911 -0.02
87904
## row191  0.300912 -0.114823 -1.044e-01 -0.0863590 -0.0517742  0.17
63494
## row192  0.326875  0.138068 -2.609e-01  0.0114876  0.1671763 -0.05
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## row193  0.481501 -0.483632  3.686e-02 -0.3285947 -0.1499981  0.00
06761
## row194  0.461302 -0.432121  1.960e-01 -0.3508711  0.3142638 -0.55
80728
## row195 -0.229408 -0.198972  4.047e-01  0.2120545  0.1999857  0.29
32807
## row196 -0.245706  0.111732  2.954e-01  0.3627929  0.1549010  0.14
64276
## row197 -0.417625 -0.295236  2.225e-01  0.2774189 -0.1471488 -0.20
85390
## row198 -0.572179 -0.548605  3.017e-01  0.2289939 -0.2714664 -0.19
31488
## row199 -0.500983 -0.426687  2.193e-01  0.1392795 -0.2487295 -0.10
69861
## row200 -0.576891 -0.458124  2.000e-01  0.2370083 -0.2746196 -0.19
97471
## row201 -0.447921 -0.435285  1.173e-01  0.0753300 -0.1375309 -0.03
45269
## row202 -0.489490 -0.483277  1.837e-01  0.0973551 -0.1390133 -0.02
```

```
24541
## row203 -0.392554 -0.370533 -9.958e-03 -0.0623121 -0.0583791  0.04
00030
## row204 -0.267883 -0.257588 -3.221e-02 -0.1924770  0.0483007  0.20
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## row205 -0.417166 -0.301867  4.034e-02 -0.1677094  0.0301824  0.02
46950
## row206  0.087821  0.768316 -3.255e-01  0.3357847  0.1527557 -0.07
98133
## row207  0.111077  0.487758 -2.872e-01  0.3065937  0.0085620  0.04
01336
## row208  0.119536  0.579013 -3.055e-01  0.2528690 -0.0117014  0.12
34741
## row209  0.266584  0.347557 -3.235e-01  0.0317167  0.0073626  0.17
50597
## row210  0.395466 -0.274586 -1.864e-01 -0.1587695 -0.0873024  0.11
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## row211  0.439670  0.194024 -1.890e-01 -0.0966456  0.1501080 -0.08
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## row212 -0.262947 -0.216837  4.159e-01  0.2807754  0.0176540  0.25
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## row213 -0.212013  0.167387  1.816e-01  0.3064016  0.0493375 -0.04
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## row214 -0.072849 -0.001103  3.135e-01  0.1671255  0.2693863  0.13
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## row226  0.343983 -0.016126 -9.923e-02 -0.0484564  0.0222574  0.01
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```

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## row229  0.391075 -0.513438  2.202e-01 -0.3211589  0.1110717 -0.36
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## row230  0.022838 -0.283917  2.321e-01 -0.0107140 -0.0564160  0.25
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## row231  0.312647 -0.030329 -4.133e-02 -0.2351202  0.0172983  0.29
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## row233 -0.054548  0.516660 -1.606e-01  0.2306901  0.0034929 -0.11
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## row249 -0.234663 -0.201207  3.458e-01  0.1772564 -0.0281205  0.19
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## row251 -0.277355 -0.081846  1.270e-01  0.2878169 -0.2537308 -0.23
```

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## row255  0.380717 -0.559011 -9.614e-02 -0.2928243 -0.1833784  0.14
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## row256  0.477518 -0.671578  1.268e-02 -0.5048929  0.0721435 -0.02
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## row257  0.431970 -0.480859  5.586e-02 -0.3765949  0.3638965 -0.27
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## row275  0.312868 -0.355681  9.534e-02 -0.0961660  0.0599228 -0.00
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## row299  0.309684 -0.602251 -2.041e-02 -0.2102351 -0.1873295  0.18
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## row300  0.002221 -0.257359  2.904e-01 -0.0254133  0.3097264  0.03
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## row304 -0.432025 -0.412790  1.186e-01  0.1837403 -0.3623480 -0.40
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## row324  0.262805 -0.257919 -1.277e-01 -0.0954488  0.0184955  0.03
03453
```

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## row329 -0.402509 -0.330492  7.875e-02 -0.2063914 -0.2566489 -0.16
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## row330 -0.444965 -0.509698  1.420e-01  0.0775184 -0.3372923 -0.27
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## row331 -0.390309 -0.331256  1.031e-01 -0.1642943 -0.1917616 -0.08
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## row349  0.185397  0.523614 -2.668e-01  0.0696335 -0.1037720  0.16
```

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## row355 -0.089497  0.695271 -1.925e-01 -0.0010086  0.0744513 -0.15
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```

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## row397  0.298818 -0.281275 -1.014e-01 -0.2410308  0.0487115  0.17
17279
## row398  0.285319 -0.483768 -1.287e-01 -0.2663653 -0.2805819  0.22
```

```
89558
## row399 -0.030474  0.770380 -2.902e-01  0.2278822  0.0439496 -0.11
70225
## row400 -0.015638  0.720951 -3.577e-01  0.2457587  0.0841843 -0.11
07608
## row401  0.042098  0.513404 -2.499e-01  0.1774877  0.0113380  0.04
06807
## row402 -0.029791  0.649282 -2.920e-01  0.2759179  0.0778414 -0.14
44217
## row403  0.035928  0.742812 -3.644e-01  0.2202518  0.1093809 -0.08
77470
## row404 -0.016595  0.698103 -2.907e-01  0.2313020  0.0812285 -0.05
66156
## row405 -0.028801  0.738869 -3.750e-01  0.2737005  0.1355194 -0.09
88141
## row406  0.144160  0.651906 -4.005e-01  0.1403306  0.0873335  0.03
68998
## row407  0.536817 -0.442951 -2.058e-03 -0.3594957  0.2427913 -0.43
85907
## row408  0.454020 -0.397737  1.084e-01 -0.4816169 -0.1007727 -0.01
71326
## row409  0.429477 -0.305773  1.551e-01 -0.2084262  0.3474323 -0.38
39959
## row410  0.148809  0.656535 -2.825e-01  0.2645575  0.1083676 -0.02
11197
## row411  0.168319 -0.374791  7.313e-02 -0.1083193 -0.0573447  0.14
77163
## row412 -0.045215  0.115751  1.264e-01  0.2743248  0.2093527  0.13
18480
## row413 -0.010723  0.602663 -3.058e-01  0.1354262  0.0461216 -0.10
66651
## row414  0.430633 -0.005407 -2.278e-01 -0.1986050  0.2428654 -0.33
13752
## row415  0.319463  0.084021 -1.812e-01 -0.0578948  0.2827060 -0.22
30556
## row416 -0.388495 -0.383613  7.615e-02 -0.2690893 -0.0401608  0.10
61439
## row417 -0.411998 -0.379206  9.710e-02 -0.2074297 -0.1943617 -0.12
15599
##
##
## Site constraints (linear combinations of constraining variables)
##
##                RDA1       RDA2        PC1        PC2        PC3
PC4
## row1   -0.0127920  1.224e-02 -1.994e-01  0.2459549  0.0724544 -0.
0650095
## row2   -0.4068613 -3.100e-01 -3.274e-01  0.0605065  0.0643049 -0.
1837365
```

```
## row3   -0.1229280 -1.457e-01  9.119e-02  0.1592684 -0.2725134 -0.
3253089
## row4   -0.2602638  2.633e-02 -2.017e-01  0.0756182 -0.0447998 -0.
2268124
## row5   -0.1999637 -8.675e-02  7.642e-02  0.0983490  0.0548153 -0.
0724957
## row6   -0.3006499 -3.491e-02 -5.307e-02  0.0720461 -0.2339226 -0.
3847960
## row7   -0.0113889 -1.316e-01  2.634e-01  0.2855188 -0.2113854 -0.
1478747
## row8   -0.2229594 -3.326e-02  1.701e-01  0.1211944 -0.3390356 -0.
3426189
## row9   -0.1337754 -5.022e-02  8.843e-02  0.2859688 -0.0545421 -0.
2469267
## row10  -0.2241371 -4.102e-02  7.168e-02  0.0074241 -0.1674740 -0.
1868189
## row11  -0.2258868 -1.617e-02  1.003e-01 -0.0028427 -0.2423244 -0.
1767280
## row12  -0.2547203  3.564e-02 -5.082e-02 -0.2576152  0.0887715  0.
2384410
## row13  -0.1721291  3.410e-02 -1.735e-01  0.1408304  0.0235338 -0.
1154163
## row14  -0.1841137  4.187e-02  1.132e-01  0.0985540 -0.0046735  0.
0130364
## row15  -0.1866709  2.969e-02  1.297e-02 -0.0625584 -0.0327642  0.
0380976
## row16  -0.1866709  2.969e-02  1.411e-01  0.0757099 -0.3436267 -0.
3299325
## row17  -0.1271842  1.519e-01  1.490e-01 -0.0938493 -0.0894486  0.
0626617
## row18  -0.1271842  1.519e-01  2.291e-01 -0.1150121  0.0853169 -0.
0164590
## row19   0.4530559 -7.523e-02  8.836e-02  0.0027313 -0.6993080  0.
1726124
## row20   0.4635987 -2.324e-02  1.169e-01 -0.0002992 -0.7310116  0.
1905094
## row21  -0.1271842  1.519e-01  1.542e-01  0.1208635 -0.1071370 -0.
0801363
## row22  -0.1788811  1.249e-01 -1.649e-01  0.0494310  0.0185084 -0.
0261440
## row23  -0.6199877  3.274e-01  5.313e-02 -0.3639258 -0.1389354 -0.
1266164
## row24   0.2358012 -2.532e-01  5.544e-03 -0.3032055  0.1598692 -0.
3810124
## row25   0.2063117 -2.710e-01 -7.177e-02 -0.1433286 -0.5661227  0.
2805755
## row26   0.2272634 -2.915e-01  4.257e-03 -0.1964196 -0.3863852  0.
2214824
## row27  -0.0062150  9.593e-02 -1.243e-02  0.0129411 -0.0088663  0.
```

```
0647849
## row28  -0.1547090  1.714e-01  3.973e-02  0.0361072  0.0463888  0.
0209462
## row29  -0.1547090  1.714e-01  1.147e-01  0.2072205 -0.2180879 -0.
3096797
## row30   0.2388211 -2.159e-01 -2.875e-01  0.0806116 -0.2007819  0.
2615908
## row31   0.3635458 -2.111e-01  6.439e-02  0.0329507 -0.5103130  0.
0661320
## row32   0.5339711 -3.606e-02  1.934e-01 -0.1197812 -0.3614195 -0.
2932898
## row33  -0.0098871  9.608e-02  2.794e-01  0.1583847 -0.0823948  0.
0481413
## row34  -0.0098871  9.608e-02  3.695e-01  0.0957656  0.2607766  0.
2893102
## row35  -0.2927464  4.092e-01  6.389e-02 -0.3148034  0.1034214  0.
2156664
## row36  -0.3576918  3.458e-01 -1.581e-01 -0.0952531 -0.0806731 -0.
1792159
## row37  -0.2541708  2.716e-01  1.643e-01 -0.0311765 -0.0092977  0.
0346441
## row38   0.1491303 -3.431e-01 -5.978e-02 -0.1463492 -0.5275183  0.
2593341
## row39   0.3571774 -1.925e-01  7.248e-02 -0.1229301 -0.3966216 -0.
0870104
## row40   0.5558333  5.227e-02  1.751e-01  0.0767793 -0.6747238  0.
0576707
## row41   0.1650987 -3.190e-02  5.191e-02 -0.1571947 -0.5228886  0.
0524482
## row42  -0.1356726 -1.405e-01  1.081e-01  0.1275855  0.2623933  0.
1758715
## row43  -0.0645243  3.326e-06  2.414e-01  0.2553624 -0.1141328 -0.
0754330
## row44  -0.0645243  3.326e-06  3.053e-01  0.2497383 -0.1018768 -0.
1662097
## row45  -0.1791008  3.388e-01 -6.371e-05  0.0548319 -0.0290353 -0.
1627630
## row46  -0.0950763  2.504e-01  4.333e-02  0.0131810 -0.0749684 -0.
0186424
## row47  -0.1694459  1.984e-01  3.000e-01 -0.0478048 -0.0081376  0.
2532494
## row48   0.4848239  1.501e-01  2.853e-01 -0.2574740 -0.0040828 -0.
4643795
## row49   0.4557960  2.574e-01  2.910e-01 -0.2664020 -0.0594818 -0.
5114366
## row50   0.0580200  2.090e-02  9.798e-02 -0.4402519  0.2398949 -0.
4375590
## row51   0.0341750  1.941e-01  2.850e-01  0.2238746 -0.1962521 -0.
1321546
```

```
## row52  -0.0275299  1.525e-01  1.777e-01  0.0386092 -0.1722640 -0.
0092999
## row53  -0.1128926  5.861e-02  2.496e-01 -0.0898869  0.3192269  0.
2856908
## row54  -0.3146722  3.851e-01  2.213e-01 -0.1296680 -0.1588238 -0.
1852478
## row55   0.1370138 -3.177e-01 -9.295e-02 -0.1227870 -0.4731731  0.
2496078
## row56   0.4841320  2.267e-01  2.984e-01 -0.2475628  0.0823021 -0.
5681046
## row57   0.4557960  2.574e-01  2.446e-01 -0.2805515  0.1459925 -0.
4827923
## row58   0.4502186  1.379e-01  2.662e-01 -0.1889800  0.0820810 -0.
6603390
## row59  -0.0526229  1.730e-01  1.097e-01 -0.4188706  0.0002829 -0.
4207097
## row60  -0.0526229  1.730e-01  3.661e-01  0.2368215 -0.1411109 -0.
0761540
## row61  -0.0139430 -1.060e-02  2.639e-01  0.0211679  0.1535612  0.
3306185
## row62  -0.0332967  1.389e-01  2.896e-01  0.0782281 -0.1797895  0.
0354592
## row63  -0.2278770 -1.705e-01  2.682e-01  0.2400309  0.0018544  0.
0457271
## row64  -0.3339032  3.024e-01  2.757e-01 -0.0645583 -0.2157796 -0.
1065061
## row65   0.2018551 -2.035e-01 -6.490e-02 -0.2550007 -0.4350815  0.
1328753
## row66   0.1482151 -1.868e-01 -5.293e-02 -0.1918574 -0.5071834  0.
2850913
## row67   0.4431394 -7.395e-03  8.709e-02 -0.0699437 -0.5741294  0.
1520383
## row68   0.4597668  2.272e-01  2.992e-01 -0.2400188  0.1537244 -0.
6677396
## row69   0.4363207  1.093e-01  2.762e-01 -0.2758654  0.2069380 -0.
4464346
## row70   0.4574207  9.925e-02  7.864e-02  0.1551699  0.2216037 -0.
2439770
## row71   0.0389812  1.533e-01  3.052e-01  0.0422674  0.2431409  0.
3031854
## row72  -0.2187624 -3.273e-01 -7.683e-02 -0.3757153  0.0695379  0.
2933237
## row73   0.3078756  1.540e-01  1.358e-01 -0.0784098 -0.0296264  0.
0373616
## row74   0.4072004  4.297e-02  9.122e-02 -0.0628574  0.3101850 -0.
2685636
## row75   0.3719384  1.891e-01  1.177e-02  0.2171241 -0.0102360 -0.
2622801
## row76  -0.1389153 -3.534e-02 -4.174e-02 -0.0393228  0.3311589  0.
```

```
0656610
## row77  -0.0683222 -1.680e-01  1.685e-01  0.3238089 -0.1114694 -0.
0868964
## row78  -0.1004149 -1.245e-01  1.873e-01  0.0636596  0.0398395  0.
2652030
## row79  -0.5489052 -4.801e-02  6.296e-02 -0.3366152  0.2528081  0.
4003081
## row80   0.0932675  2.481e-01 -1.236e-02 -0.3215840 -0.1376463  0.
1566219
## row81   0.0178595  2.302e-01 -6.283e-02 -0.1721758 -0.3308382  0.
1615099
## row82   0.1204927  2.397e-01  6.920e-02 -0.2300912  0.0114792  0.
1950768
## row83   0.0169655  1.992e-01  1.884e-01  0.1006717  0.2637695  0.
1735667
## row84  -0.0920350 -2.202e-01  8.493e-02  0.2954548  0.0348875 -0.
0380200
## row85  -0.0920350 -2.202e-01  1.230e-01  0.0095748 -0.1516805 -0.
0154332
## row86  -0.2938791  3.046e-02  1.084e-01 -0.2154676  0.0491990  0.
2777874
## row87  -0.2938791  3.046e-02  1.293e-01 -0.1942573 -0.0951527  0.
1510672
## row88   0.2100184  1.667e-01  2.019e-02 -0.2893902 -0.1736247  0.
2172046
## row89   0.0393806  1.528e-01  3.993e-02 -0.3834043 -0.1242485 -0.
1164078
## row90   0.0337239  2.087e-01  2.184e-02 -0.3642813 -0.2208707  0.
1660391
## row91   0.1643925  1.636e-01  1.383e-01 -0.1443087  0.2055776  0.
0691493
## row92  -0.0645885  4.383e-01  2.852e-01 -0.1731822  0.0661943  0.
4171313
## row93  -0.1216132  5.155e-01  2.529e-01 -0.3979543 -0.0789296  0.
3983251
## row94  -0.1216132  5.155e-01  1.589e-01 -0.4446637  0.1364447  0.
2019583
## row95   0.0615777  2.025e-01 -6.599e-02 -0.1034910  0.2308431 -0.
2150748
## row96   0.0088667  1.620e-01  1.937e-01 -0.1658896 -0.0815346  0.
2881529
## row97  -0.0803081 -1.328e-01  1.897e-01 -0.0581855  0.4693016  0.
2891481
## row98  -0.1666377 -2.902e-01  1.510e-01  0.0910504 -0.1213577 -0.
0229867
## row99  -0.1666377 -2.902e-01  3.196e-02  0.0494065 -0.0723954 -0.
1146818
## row100 -0.2395524 -1.943e-01  1.546e-03 -0.0114063  0.0325578  0.
0970700
```

```
## row101  0.0193690  2.665e-01 -1.871e-01 -0.2427486 -0.1938506  0.
0867869
## row102  0.0174988  2.835e-01 -1.287e-01 -0.2464242 -0.1154259  0.
2058150
## row103 -0.0053870  1.851e-01  5.796e-02 -0.5133568 -0.3947230  0.
1287492
## row104  0.0845538  3.926e-02 -8.144e-02 -0.2255582 -0.0364061  0.
0609931
## row105  0.1794889  1.346e-01  2.664e-01 -0.0642278  0.1678152  0.
1007850
## row106  0.1109025  5.944e-02 -7.734e-02  0.2795930  0.1008711  0.
1682890
## row107  0.0903979  1.504e-01  1.494e-01  0.1391938  0.1585812  0.
2763267
## row108  0.1068130  8.855e-02  1.992e-01  0.0619746  0.1353856  0.
2956827
## row109  0.1036542  9.955e-02  1.975e-01  0.1308851  0.0889723  0.
3076270
## row110 -0.0128492 -8.807e-03  5.826e-02 -0.0749900  0.2160744  0.
3759550
## row111 -0.1596901 -2.335e-01  2.018e-01  0.1060811  0.5115118  0.
1889270
## row112 -0.3314460 -4.581e-01  7.656e-02  0.0723294  0.3329659  0.
3018640
## row113 -0.2040536 -3.347e-01  4.483e-02 -0.0736938 -0.0264496  0.
0329822
## row114 -0.3083257 -1.707e-01  2.118e-02  0.1221380 -0.2471083 -0.
3054223
## row115  0.1898732  8.980e-02 -6.135e-03 -0.2685611 -0.1127829 -0.
0246794
## row116 -0.0001058  2.754e-01 -1.011e-01 -0.3393897 -0.1266022  0.
2793465
## row117  0.1427707  2.338e-01  7.692e-04 -0.2955510 -0.4013961  0.
0802537
## row118  0.1421268  8.189e-02 -6.188e-02  0.3192560  0.0071071 -0.
0411419
## row119  0.1398326  1.118e-01  1.661e-01  0.2074493  0.0479742  0.
1420492
## row120  0.0446450 -1.133e-02  2.606e-01  0.0793364  0.3079435  0.
3965692
## row121  0.0703757 -2.110e-02  2.882e-01  0.0878590  0.3415024  0.
3371633
## row122 -0.0364203 -1.450e-01  1.896e-01 -0.0886232  0.3211023  0.
3077577
## row123 -0.1842640 -2.973e-01  2.206e-01  0.2145449  0.2819618  0.
1618158
## row124 -0.2985289 -4.354e-01  6.828e-02 -0.0639759 -0.0062442  0.
0965411
## row125 -0.3832938 -5.122e-01  1.173e-01  0.0488738  0.4053325  0.
```

```
2848126
## row126 -0.4766281 -5.737e-02  3.280e-02 -0.2960714  0.0425320  0.
1823376
## row127  0.1216303  1.119e-01 -2.109e-01  0.0387296  0.0797806  0.
1142340
## row128  0.0876036  4.060e-02 -3.890e-01  0.1852815  0.0308002  0.
0652364
## row129  0.2456054  1.236e-02 -4.620e-02 -0.2597042 -0.2238748  0.
0266291
## row130  0.3269933  6.947e-02  3.991e-02  0.0376867  0.1658841 -0.
3788983
## row131  0.0354844  1.245e-01  1.528e-01 -0.2362169  0.3766136 -0.
0673063
## row132  0.0515734  1.825e-01  2.890e-02 -0.2304744 -0.1066203  0.
2440576
## row133  0.0961475  6.739e-02  2.836e-01  0.3278893  0.1076721  0.
1366064
## row134  0.1074446  4.362e-02  2.517e-01  0.0725933  0.2549865  0.
2539337
## row135 -0.0430603 -1.600e-01 -1.994e-03  0.3422338  0.0946410  0.
0045908
## row136 -0.0690178 -1.319e-01  1.768e-01  0.2508836  0.0247417  0.
0336037
## row137 -0.1964843 -2.475e-01  2.119e-01  0.1161068 -0.1201550  0.
0166581
## row138 -0.1911398 -2.587e-01  1.363e-01 -0.0782269 -0.0401237  0.
0823503
## row139 -0.1994406 -2.957e-01  1.889e-01  0.2447668 -0.0897872 -0.
0859453
## row140 -0.2694781 -3.906e-01 -1.650e-01  0.1799253 -0.0428844 -0.
1675118
## row141 -0.4240070 -1.588e-01  1.626e-01  0.0476115 -0.0680801 -0.
0468448
## row142  0.0603974  2.351e-01 -2.968e-01  0.2009103  0.0672407  0.
0190022
## row143  0.1735871 -1.790e-02 -3.498e-01  0.3080192  0.0744872 -0.
0101566
## row144  0.2708833 -1.340e-01 -3.469e-01  0.2503879 -0.0434273  0.
1084810
## row145  0.1534961 -2.328e-02 -1.952e-01 -0.0783739 -0.2290886  0.
0785619
## row146  0.1892882 -1.099e-01 -4.163e-02 -0.2787833 -0.4813830  0.
2087492
## row147  0.1333295  2.299e-01  1.830e-01 -0.4708423  0.2386021 -0.
4358164
## row148  0.2260897  7.337e-02  2.027e-01 -0.3230993  0.3508648 -0.
5459519
## row149 -0.0270408  1.919e-01 -1.931e-01  0.0152889  0.0675947 -0.
0402478
```

```
## row150  0.0050176  1.902e-01  3.967e-01  0.3149206  0.0571322  0.
0946976
## row151  0.0578401  1.069e-02  3.509e-01  0.3835602 -0.1926320 -0.
1231675
## row152 -0.0329802 -5.223e-02  3.107e-01  0.3632518 -0.0655772 -0.
0540524
## row153 -0.1710344 -1.558e-01  1.961e-01  0.1237080  0.0196804  0.
1401002
## row154 -0.2150844 -2.248e-01  1.842e-01  0.0290298  0.0437505  0.
2472907
## row155 -0.2150844 -2.248e-01  1.757e-01 -0.0040751  0.2686190  0.
3477797
## row156 -0.2861410 -3.787e-01  1.069e-01  0.1326844 -0.0835722 -0.
0635822
## row157  0.2255863 -1.686e-01 -1.789e-01 -0.0838715 -0.0564316  0.
0612187
## row158  0.1251539  1.002e-01 -1.989e-01  0.2450727 -0.0295420 -0.
1409518
## row159  0.2929960 -4.260e-02 -3.402e-01  0.3313243  0.0501595  0.
1136501
## row160  0.2321150 -9.819e-02 -3.747e-01  0.2532785  0.0782537  0.
0631155
## row161  0.0684145  6.702e-02  2.510e-01  0.0924118  0.0031924  0.
2404947
## row162  0.0084382  5.201e-02  2.734e-01  0.3364537  0.0297155 -0.
0247413
## row163 -0.0376139  6.572e-02  3.556e-01  0.2737691  0.0421197  0.
0997056
## row164  0.0077485  8.787e-02  3.526e-01  0.1525799  0.1164599  0.
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## row165  0.0439417 -4.382e-02  3.818e-01  0.3059217 -0.0229037  0.
1646256
## row166 -0.2362726 -3.028e-01  2.193e-01  0.2118367  0.0463563  0.
0386532
## row167 -0.2325257 -2.392e-01  5.394e-02  0.1652846 -0.2118961 -0.
2519551
## row168 -0.0905585 -9.440e-02  1.897e-01  0.0024086 -0.1710276  0.
0505808
## row169 -0.2627517 -2.041e-01  9.096e-02  0.0836281 -0.2906982 -0.
2843692
## row170 -0.5564589 -9.380e-02  8.482e-03 -0.0552587 -0.1592211 -0.
2524128
## row171  0.2553241 -1.410e-01 -1.941e-01 -0.0155194 -0.3841555  0.
2686261
## row172 -0.0245035  1.533e-01 -3.573e-01  0.0723228  0.0499608 -0.
0541217
## row173  0.2811262 -5.629e-02 -2.837e-01  0.3387271  0.0378603  0.
0100351
## row174  0.2058251 -1.195e-01 -1.815e-01  0.1094090  0.0453654  0.
```

```
1499412
## row175  0.1659934 -1.812e-01 -1.339e-01 -0.2144204 -0.4421179  0.
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## row176  0.2809977 -3.167e-02  1.018e-03 -0.3094155 -0.2124636 -0.
0477564
## row177  0.2841331  1.592e-01  1.537e-01 -0.1561876  0.2322781 -0.
5214112
## row178  0.0304306 -2.731e-02  1.456e-01  0.0833258  0.2219230  0.
1827649
## row179  0.0062296  1.858e-01  2.321e-01  0.0937375  0.1520730  0.
2197969
## row180 -0.0511259  6.505e-02  1.566e-01  0.2082967  0.1775396  0.
1343728
## row181 -0.0449794  1.645e-02  2.927e-01  0.3528895 -0.1137267 -0.
1088691
## row182 -0.1331172  1.569e-01  3.050e-01 -0.0954796  0.3203395 -0.
0360201
## row183 -0.0796051  5.918e-02  1.948e-01  0.2070932 -0.0537075 -0.
0723519
## row184 -0.0257224 -8.540e-02  1.827e-01  0.2869072 -0.1713809 -0.
2075530
## row185 -0.0848816 -2.250e-01  2.827e-01  0.2476965  0.0802542  0.
1491010
## row186 -0.1183389 -1.584e-01  2.026e-01  0.0388977  0.1252628  0.
2899372
## row187 -0.2801599 -2.929e-01  8.991e-02  0.1376177 -0.3414578 -0.
3250236
## row188 -0.5694009 -7.464e-02 -3.102e-03 -0.2629571 -0.1126484 -0.
0933296
## row189  0.0662274 -3.481e-03 -3.081e-01  0.1942889 -0.0173165 -0.
0275054
## row190  0.2602532  3.432e-02  4.443e-02  0.1346167  0.3043911 -0.
0287904
## row191  0.2400239 -4.402e-02 -1.044e-01 -0.0863590 -0.0517742  0.
1763494
## row192  0.1493935 -2.456e-01 -2.609e-01  0.0114876  0.1671763 -0.
0565297
## row193  0.2824003 -1.513e-01  3.686e-02 -0.3285947 -0.1499981  0.
0006761
## row194  0.2442489  6.456e-02  1.960e-01 -0.3508711  0.3142638 -0.
5580728
## row195  0.0619920  6.073e-02  4.047e-01  0.2120545  0.1999857  0.
2932807
## row196  0.0891841  1.166e-01  2.954e-01  0.3627929  0.1549010  0.
1464276
## row197 -0.1254374 -7.041e-03  2.225e-01  0.2774189 -0.1471488 -0.
2085390
## row198 -0.1119708 -4.100e-02  3.017e-01  0.2289939 -0.2714664 -0.
1931488
```

```
## row199 -0.1000223 -8.482e-02  2.193e-01  0.1392795 -0.2487295 -0.
1069861
## row200 -0.1075602 -2.138e-01  2.000e-01  0.2370083 -0.2746196 -0.
1997471
## row201 -0.2243733 -2.345e-01  1.173e-01  0.0753300 -0.1375309 -0.
0345269
## row202 -0.2243733 -2.345e-01  1.837e-01  0.0973551 -0.1390133 -0.
0224541
## row203 -0.3047971 -3.888e-01 -9.958e-03 -0.0623121 -0.0583791  0.
0400030
## row204 -0.3573369 -3.253e-01 -3.221e-02 -0.1924770  0.0483007  0.
2012441
## row205 -0.5588096 -8.523e-02  4.034e-02 -0.1677094  0.0301824  0.
0246950
## row206  0.1706309 -1.171e-01 -3.255e-01  0.3357847  0.1527557 -0.
0798133
## row207  0.2489711 -1.976e-01 -2.872e-01  0.3065937  0.0085620  0.
0401336
## row208  0.2280392 -2.052e-01 -3.055e-01  0.2528690 -0.0117014  0.
1234741
## row209  0.1308463 -1.661e-01 -3.235e-01  0.0317167  0.0073626  0.
1750597
## row210  0.1692430 -2.523e-01 -1.864e-01 -0.1587695 -0.0873024  0.
1139289
## row211  0.2235659 -1.802e-01 -1.890e-01 -0.0966456  0.1501080 -0.
0865409
## row212  0.1182898  1.805e-01  4.159e-01  0.2807754  0.0176540  0.
2523696
## row213  0.0101324  1.921e-01  1.816e-01  0.3064016  0.0493375 -0.
0491855
## row214  0.0483743  2.076e-01  3.135e-01  0.1671255  0.2693863  0.
1373813
## row215 -0.0893044  2.880e-01  4.042e-02  0.0656518  0.2973356  0.
0933976
## row216 -0.0773508  7.841e-02  3.007e-01  0.2078541  0.2097290  0.
1118215
## row217 -0.0990042 -1.560e-01  2.287e-01  0.3057795  0.2614404  0.
0889148
## row218  0.0046054 -3.374e-02  2.993e-01  0.1329058  0.1908263  0.
3793889
## row219  0.0046054 -3.374e-02  2.298e-01  0.2846758 -0.0733827 -0.
1214833
## row220  0.0350841 -1.533e-01 -3.513e-01  0.0821753  0.1058997  0.
1741406
## row221  0.1033782 -2.061e-01 -1.391e-01 -0.2826699  0.0593396 -0.
1225193
## row222  0.1317893 -1.562e-01  5.690e-02 -0.3791809  0.2964554 -0.
3135358
## row223  0.1317893 -1.562e-01  6.623e-02 -0.3555447  0.1984113 -0.
```

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2862006
## row224  0.0893556 -2.924e-01 -3.193e-02 -0.3027663 -0.0184460  0.
1153361
## row225  0.1316877 -2.482e-01 -7.646e-02 -0.3220520  0.2276743 -0.
2416541
## row226  0.2784631 -9.754e-02 -9.923e-02 -0.0484564  0.0222574  0.
0133875
## row227  0.0961011 -2.318e-01 -7.878e-02 -0.3409779 -0.0980300  0.
0471017
## row228  0.1692163 -3.087e-01 -1.983e-02 -0.3161562 -0.0966533  0.
0342521
## row229  0.3016550  1.518e-01  2.202e-01 -0.3211589  0.1110717 -0.
3615223
## row230  0.3016550  1.518e-01  2.321e-01 -0.0107140 -0.0564160  0.
2589023
## row231  0.1160846  8.510e-02 -4.133e-02 -0.2351202  0.0172983  0.
2930790
## row232 -0.0292902  1.451e-01  3.602e-01  0.2961631 -0.0170242  0.
0406659
## row233  0.0646583  1.015e-01 -1.606e-01  0.2306901  0.0034929 -0.
1179410
## row234  0.0423517  1.403e-01  5.257e-02  0.2378998 -0.2134254 -0.
2454670
## row235 -0.0517226  1.335e-01  8.180e-02  0.2404392 -0.3734401 -0.
4509179
## row236 -0.1251055 -4.077e-02  6.946e-02  0.1837105 -0.2947638 -0.
3728647
## row237 -0.0918536 -1.011e-01  1.987e-01  0.2363586 -0.3784944 -0.
3154842
## row238 -0.2326216 -2.067e-01  1.364e-01  0.1992052 -0.2554170 -0.
2954722
## row239 -0.5417262 -4.208e-02  2.322e-02 -0.2005968 -0.2350914 -0.
2122650
## row240  0.0618410 -2.824e-01 -5.195e-02 -0.3472341  0.3649009 -0.
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## row241  0.2149272 -2.742e-01  3.775e-04 -0.1869604 -0.3764637  0.
2343314
## row242  0.1149337 -2.724e-02  1.105e-01 -0.2542070 -0.0806626  0.
3353486
## row243  0.1552593  1.755e-01  6.661e-02 -0.1135934  0.3354718 -0.
2697680
## row244 -0.0121202  1.746e-01  1.562e-01  0.0789870  0.0609880 -0.
0722148
## row245  0.1687487  1.511e-03 -7.030e-02  0.2508112  0.0067282 -0.
0834440
## row246  0.0254753  1.087e-01  9.955e-02 -0.2917922  0.2782775 -0.
1150581
## row247  0.0462778  1.269e-01  8.229e-02  0.2172121 -0.0032390  0.
0268655
```

```
## row248  0.2721769  2.409e-01  4.016e-01  0.3711050  0.0346109  0.
0195254
## row249  0.1397284  1.822e-01  3.458e-01  0.1772564 -0.0281205  0.
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## row250  0.0442032  9.306e-02  3.710e-01  0.0371362  0.2279452  0.
2566310
## row251  0.0442032  9.306e-02  1.270e-01  0.2878169 -0.2537308 -0.
2364299
## row252 -0.1885269 -1.909e-01 -6.416e-03  0.1476099 -0.3028266 -0.
4040685
## row253 -0.5629034 -1.043e-02  4.827e-03 -0.2837189 -0.1040994 -0.
0173185
## row254  0.2433578  3.851e-02 -3.394e-01  0.1910489 -0.1022432  0.
1690614
## row255  0.0927618 -2.464e-01 -9.614e-02 -0.2928243 -0.1833784  0.
1457162
## row256  0.0026881 -3.102e-01  1.268e-02 -0.5048929  0.0721435 -0.
0284919
## row257  0.0546040 -3.065e-01  5.586e-02 -0.3765949  0.3638965 -0.
2787072
## row258  0.2149272 -2.742e-01  9.577e-02 -0.3108348  0.4000790 -0.
5856795
## row259  0.1571774 -3.217e-01 -5.545e-02 -0.2399073  0.0232505  0.
2792371
## row260  0.1516497 -2.236e-01  2.325e-01  0.1885837  0.4461095  0.
0689050
## row261  0.0181559  1.738e-01  2.661e-02 -0.2357878  0.1370599  0.
1083196
## row262  0.0532692  1.742e-01  9.619e-02 -0.2421764  0.1657991  0.
1523235
## row263  0.4045109  1.896e-01  3.366e-01  0.4968690  0.0414879  0.
1278403
## row264  0.2562481  2.104e-01  2.897e-01 -0.0588295  0.0441730  0.
2906172
## row265  0.2137431  9.940e-02  4.230e-01  0.3108215  0.2043793  0.
2222606
## row266  0.2137431  9.940e-02  4.064e-01  0.1657424  0.2118734  0.
3995667
## row267 -0.0964343  1.015e-01 -1.269e-02  0.0755240 -0.2131303 -0.
1542831
## row268 -0.2670943 -3.154e-01  3.864e-02  0.0635652 -0.2059852 -0.
1778452
## row269  0.0166782 -3.218e-01 -2.363e-01 -0.0793891  0.3372462 -0.
0823526
## row270  0.2433578  3.851e-02 -2.092e-01  0.0371457 -0.2306531  0.
2021167
## row271  0.0280291 -3.996e-01 -2.213e-02 -0.4210582  0.1915996 -0.
2974301
## row272  0.1230311 -2.688e-01 -6.579e-02 -0.1197772  0.3920739 -0.
```

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1473295
## row273  0.1230311 -2.688e-01 -2.056e-01 -0.0145286  0.3231762  0.
0085640
## row274  0.1718645  1.888e-01  3.634e-01  0.1894490  0.1571291  0.
3858705
## row275  0.3655623  1.962e-02  9.534e-02 -0.0961660  0.0599228 -0.
0050746
## row276  0.2952661 -7.717e-02  6.754e-02 -0.1891631  0.2127665 -0.
0706267
## row277 -0.0006716  1.355e-03  2.148e-01  0.2656532  0.1499227  0.
2708906
## row278 -0.0178170  9.188e-02  2.214e-01 -0.1629222  0.1740621  0.
2665968
## row279 -0.1242669  5.909e-02  3.668e-02  0.1260044 -0.3412572 -0.
3397830
## row280 -0.1814727 -1.242e-01  2.405e-01  0.2421297 -0.0348974 -0.
0646901
## row281 -0.5435987 -2.881e-02  9.500e-04 -0.2483441 -0.0908877 -0.
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## row282  0.0994641 -3.559e-02 -2.609e-01  0.1413117 -0.0276394  0.
0746032
## row283 -0.0186165 -3.164e-01 -1.939e-01 -0.1399987  0.3227035  0.
0407426
## row284  0.1597582 -2.973e-01 -3.232e-02 -0.3014480  0.2968907 -0.
1339014
## row285  0.1597582 -2.973e-01  3.102e-02 -0.1994188  0.4728240 -0.
4189173
## row286  0.0715496 -3.479e-01  7.118e-02  0.0428418  0.4161379 -0.
1568185
## row287  0.2092914  1.135e-01 -1.359e-01  0.0614933 -0.3183160  0.
1436790
## row288  0.2019198 -2.866e-02 -1.421e-01  0.1005785 -0.0212307  0.
1779792
## row289  0.2535424 -1.401e-01  4.012e-02 -0.2004878 -0.1862329  0.
2333113
## row290  0.2847452 -1.317e-01 -7.040e-03 -0.2487479  0.1289742 -0.
1970800
## row291  0.0550738  1.027e-01  3.144e-01  0.1149012  0.1106649  0.
3176376
## row292  0.0197155  1.552e-01  2.603e-01  0.2451711 -0.4773575 -0.
3618973
## row293 -0.0932453 -2.770e-02  3.050e-02  0.2059198 -0.2308911 -0.
2726689
## row294 -0.0052129 -2.855e-01 -5.235e-02 -0.0831323  0.3953253 -0.
2399519
## row295  0.0420275 -2.954e-01 -2.329e-01 -0.0494894  0.2812827  0.
1088391
## row296  0.1090460 -3.317e-01  3.358e-02 -0.2116214  0.4508355 -0.
4478111
```

```
## row297  0.0555939 -3.538e-01 -1.064e-01 -0.3061212 -0.1356819  0.
2961795
## row298  0.1213878 -1.687e-01 -4.731e-02 -0.0060133  0.1225089  0.
0474685
## row299  0.1627547 -2.034e-01 -2.041e-02 -0.2102351 -0.1873295  0.
1878689
## row300  0.0728104 -3.450e-02  2.904e-01 -0.0254133  0.3097264  0.
0306645
## row301 -0.3050552 -2.690e-01 -2.079e-01  0.1661707  0.0561373 -0.
1483181
## row302 -0.2350637 -2.636e-01 -4.730e-02  0.1858056 -0.1573401 -0.
3069170
## row303 -0.2394658 -1.634e-01  6.571e-02  0.0855608 -0.3772195 -0.
4079961
## row304 -0.1487677 -5.768e-02  1.186e-01  0.1837403 -0.3623480 -0.
4054053
## row305  0.2092914  1.135e-01 -2.634e-01  0.0983013 -0.1391350  0.
1500190
## row306 -0.0954783 -1.185e-01 -4.075e-01 -0.0986699 -0.0740658  0.
1359118
## row307  0.0763165 -6.665e-02 -5.830e-02 -0.1591823  0.0740195  0.
1929199
## row308  0.0041495 -3.633e-01 -1.299e-01 -0.2025632 -0.0310174  0.
1598026
## row309  0.0836929 -2.994e-01 -5.384e-02 -0.2049044 -0.0328953  0.
0780836
## row310  0.1371155 -2.958e-01 -7.358e-02 -0.3101236 -0.0482173  0.
1089654
## row311  0.1868383 -2.232e-01 -1.608e-01  0.1024394  0.0421049  0.
0792457
## row312  0.1663168  1.467e-02  1.561e-01 -0.1646128  0.1172527  0.
1310563
## row313 -0.0696305 -1.503e-01  1.774e-01  0.2625826 -0.0940482 -0.
1190991
## row314 -0.2907607 -2.720e-01  9.787e-02 -0.0036324  0.4498647  0.
0873229
## row315 -0.2907607 -2.720e-01  2.297e-02  0.0214539 -0.2146492 -0.
2048816
## row316 -0.4811928 -1.402e-01  2.147e-02 -0.1903028 -0.1094555 -0.
0428210
## row317 -0.0257537 -3.372e-01 -1.377e-01 -0.0431031  0.1916476  0.
1300537
## row318  0.1497847 -2.300e-01 -1.886e-02 -0.3354939 -0.1984641  0.
1987510
## row319  0.1615986  2.966e-02  2.674e-02 -0.1794617  0.3296267 -0.
2574161
## row320 -0.1298226 -2.960e-01 -1.954e-02  0.2268814 -0.1130847 -0.
1667477
## row321 -0.2061893  3.551e-02  6.351e-02  0.0255926 -0.2244267 -0.
```

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1969638
## row322 -0.0493579 -3.051e-01 -1.952e-01 -0.2129033 -0.1456806  0.
2486883
## row323  0.0397069 -2.592e-01 -4.782e-02 -0.1255414  0.0637406  0.
2784200
## row324  0.0690591 -2.648e-01 -1.277e-01 -0.0954488  0.0184955  0.
0303453
## row325  0.1247549  8.756e-02 -2.381e-02 -0.2467764 -0.4918892  0.
2709115
## row326  0.1957106 -1.230e-02 -1.116e-01 -0.1217310 -0.3051237  0.
2069965
## row327 -0.3778478 -3.936e-01 -1.026e-01 -0.3147719  0.3224880  0.
1474171
## row328 -0.4725637 -3.193e-01 -7.799e-02 -0.2607538  0.1563539  0.
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## row329 -0.4041890  1.756e-01  7.875e-02 -0.2063914 -0.2566489 -0.
1683570
## row330 -0.1837819 -6.318e-02  1.420e-01  0.0775184 -0.3372923 -0.
2757186
## row331 -0.3601083  1.217e-01  1.031e-01 -0.1642943 -0.1917616 -0.
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## row332  0.0122027  3.063e-01 -2.912e-01  0.0004458 -0.0480493  0.
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## row333 -0.0361510  4.022e-01 -2.198e-01 -0.1740281 -0.1625558  0.
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## row335  0.1195621  3.228e-01 -5.883e-02 -0.2866334 -0.2186847  0.
2482353
## row336 -0.0817127  5.428e-01 -2.682e-01 -0.0927415 -0.1107771  0.
1048170
## row337 -0.0424174  2.916e-01 -1.763e-02 -0.3677030 -0.1401633  0.
1365972
## row338 -0.0721192  4.062e-01 -2.742e-01  0.0155985 -0.0502391  0.
0885922
## row339  0.0036732  3.179e-01 -3.257e-01  0.0098588  0.0130005  0.
1010411
## row340 -0.0670300  3.706e-01 -2.619e-01 -0.0818981 -0.1344905  0.
0697959
## row341 -0.0357419  2.653e-01 -1.913e-01  0.0122900  0.0222664 -0.
0507951
## row342 -0.2335173  3.557e-01 -2.295e-01 -0.0330094  0.1417705  0.
0027476
## row343 -0.0272044  2.830e-01 -3.312e-01  0.0575309  0.0350474  0.
0959181
## row344 -0.0136254  2.630e-01 -3.626e-01  0.1577793  0.0659636 -0.
0062816
## row345  0.1216303  1.119e-01 -2.379e-01  0.1769067  0.0682505  0.
1362739
```

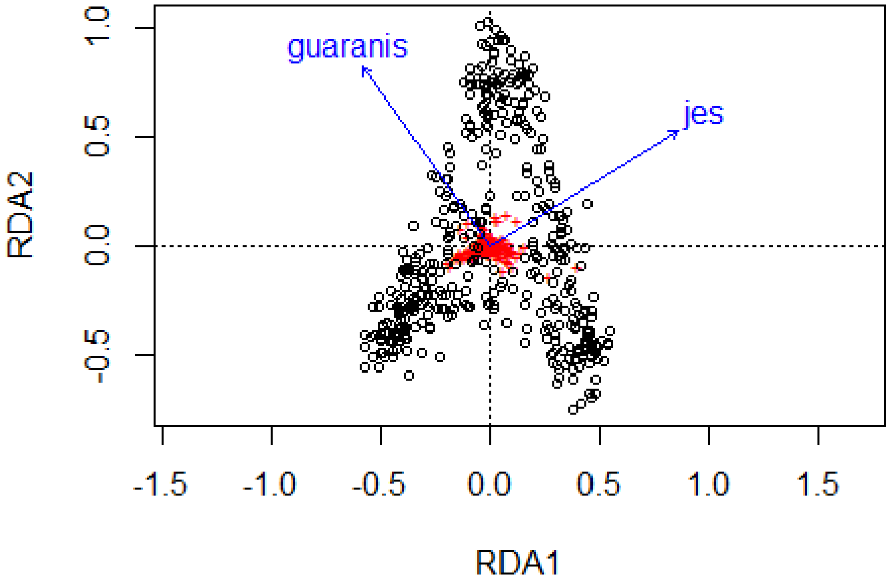
```
## row346  0.0565421  7.673e-02 -3.721e-01  0.2168524  0.0663800  0.
0242383
## row347 -0.1457687  3.748e-01 -2.130e-01 -0.1442756  0.0152198  0.
1785453
## row348 -0.0136254  2.630e-01 -3.037e-01  0.1040434  0.0844215  0.
0732537
## row349  0.0876036  4.060e-02 -2.668e-01  0.0696335 -0.1037720  0.
1661616
## row350 -0.1879606  4.506e-01 -1.478e-01 -0.0748502  0.0443362 -0.
0109303
## row351 -0.3168261  4.981e-01 -3.040e-01 -0.1279295  0.0967059  0.
0188710
## row352 -0.1098702  3.346e-01 -3.294e-01  0.1096577  0.1067464 -0.
0186936
## row353  0.1415020 -4.063e-02 -3.235e-01  0.2887699  0.0590078 -0.
0492649
## row354 -0.2413650  3.501e-01 -3.178e-01 -0.0105986  0.0853915 -0.
0841154
## row355 -0.2160471  3.885e-01 -1.925e-01 -0.0010086  0.0744513 -0.
1554344
## row356 -0.1875179  4.015e-01 -2.217e-01  0.0081904  0.0710458 -0.
1372061
## row357  0.0036831  2.793e-01 -3.041e-01  0.2005010  0.1067114 -0.
0105744
## row358  0.0252013  2.578e-01 -1.148e-01  0.1119280 -0.0554695 -0.
0476007
## row359 -0.0561467  2.477e-01 -1.013e-01  0.0771389  0.0491685 -0.
0848041
## row360 -0.0296910  1.310e-01 -2.506e-01  0.1309965  0.0870747 -0.
0424291
## row361  0.0462332  9.642e-02 -3.395e-01  0.1276867  0.0870617  0.
1128584
## row362  0.2089906 -9.082e-02 -2.738e-01  0.1264981  0.0100287  0.
0837725
## row363  0.0767910 -3.066e-01 -8.672e-02 -0.2722089 -0.1556110 -0.
0117563
## row364  0.0767910 -3.066e-01 -1.203e-01 -0.3281453 -0.1533518  0.
0597444
## row365 -0.4292477  4.983e-01 -1.983e-01 -0.1466902  0.0919047 -0.
1482148
## row366 -0.3067247  3.654e-01 -2.712e-01 -0.1427093  0.0313154 -0.
0660755
## row367 -0.0125557  2.799e-01 -2.739e-01  0.1628264  0.0158522 -0.
0548594
## row368 -0.0125557  2.799e-01 -2.394e-01  0.0593560  0.0195063 -0.
0148273
## row369 -0.0296910  1.310e-01 -3.519e-01  0.1731819  0.1189899  0.
0471182
## row370 -0.0887360  8.540e-02 -3.456e-01  0.1212960  0.0835381 -0.
```

```
0546197
## row371  0.1251539  1.002e-01 -3.458e-01  0.1646618  0.0512198  0.
1289918
## row372  0.1861697 -7.360e-02 -3.246e-01  0.3019158  0.0665971  0.
0402653
## row373  0.1668867 -7.668e-02 -2.979e-01  0.3054687 -0.0165957  0.
0132088
## row374  0.2929960 -4.260e-02 -2.904e-01  0.2745163  0.0590707  0.
0873284
## row375 -0.2974021  3.496e-01 -3.249e-01 -0.0939291  0.0298112 -0.
0249595
## row376 -0.1256340  3.426e-01 -2.477e-01  0.0537940  0.0719116 -0.
1498246
## row377 -0.2750421  3.720e-01 -1.691e-01 -0.2045047  0.0722768  0.
0022554
## row378 -0.2622270  3.651e-01 -2.245e-01  0.0075852  0.0869008 -0.
1148197
## row379  0.1340190  8.635e-02 -3.244e-01  0.2862012  0.0372968 -0.
0817570
## row380  0.1340190  8.635e-02 -2.559e-01  0.2547517  0.0676635  0.
0538997
## row381  0.1528812 -1.541e-01 -3.478e-01  0.1307106  0.2069684  0.
0657545
## row382 -0.2974021  3.496e-01 -3.315e-01 -0.1501093  0.0410792  0.
0046638
## row383 -0.2750421  3.720e-01 -2.754e-01 -0.0838538  0.0906406  0.
0583582
## row384 -0.2622270  3.651e-01 -3.568e-01 -0.0178815  0.1195547 -0.
0466450
## row385  0.1340190  8.635e-02 -2.077e-01  0.2537831  0.1138727 -0.
0754871
## row386 -0.0837327  1.565e-01 -2.873e-01  0.1474601  0.1125082 -0.
1172322
## row387 -0.1690155  9.522e-02 -3.322e-01  0.0549107  0.0981670 -0.
1029660
## row388  0.1954943  4.824e-02 -3.229e-01  0.3613070  0.0543069 -0.
0953373
## row389 -0.1538960  1.209e-01 -2.950e-01  0.0835657  0.1127128 -0.
1087355
## row390 -0.0500354  1.499e-01 -2.834e-01  0.0029947 -0.0609547  0.
0634503
## row391 -0.1668734  1.958e-01 -2.801e-01 -0.0021596  0.0761178 -0.
1371291
## row392  0.0026480  4.587e-02 -1.916e-01  0.1337777 -0.0224931 -0.
1249927
## row393  0.0662274 -3.481e-03 -2.099e-01  0.1843101 -0.0007311 -0.
1348903
## row394 -0.1189219  8.364e-03 -3.710e-01  0.1061733  0.1262350 -0.
0865008
```

```
## row395  0.0185785 -4.854e-02 -3.636e-01  0.2011268  0.0783115  0.
0229193
## row396  0.0350841 -1.533e-01 -4.341e-01  0.2209991  0.1803378  0.
0527031
## row397  0.0767910 -3.066e-01 -1.014e-01 -0.2410308  0.0487115  0.
1717279
## row398  0.0767910 -3.066e-01 -1.287e-01 -0.2663653 -0.2805819  0.
2289558
## row399  0.0738839  2.843e-02 -2.902e-01  0.2278822  0.0439496 -0.
1170225
## row400  0.0352179 -8.667e-02 -3.577e-01  0.2457587  0.0841843 -0.
1107608
## row401  0.0577775 -7.882e-02 -2.499e-01  0.1774877  0.0113380  0.
0406807
## row402  0.1055856 -6.472e-02 -2.920e-01  0.2759179  0.0778414 -0.
1444217
## row403  0.0360584 -1.034e-02 -3.644e-01  0.2202518  0.1093809 -0.
0877470
## row404  0.1055856 -6.472e-02 -2.907e-01  0.2313020  0.0812285 -0.
0566156
## row405 -0.0007242 -2.361e-01 -3.750e-01  0.2737005  0.1355194 -0.
0988141
## row406 -0.0054329 -1.016e-02 -4.005e-01  0.1403306  0.0873335  0.
0368998
## row407  0.1387167 -1.917e-01 -2.058e-03 -0.3594957  0.2427913 -0.
4385907
## row408  0.1195621  3.228e-01  1.084e-01 -0.4816169 -0.1007727 -0.
0171326
## row409  0.2044175  3.741e-02  1.551e-01 -0.2084262  0.3474323 -0.
3839959
## row410  0.2044175  3.741e-02 -2.825e-01  0.2645575  0.1083676 -0.
0211197
## row411  0.0994641 -3.559e-02  7.313e-02 -0.1083193 -0.0573447  0.
1477163
## row412  0.0994641 -3.559e-02  1.264e-01  0.2743248  0.2093527  0.
1318480
## row413 -0.0054329 -1.016e-02 -3.058e-01  0.1354262  0.0461216 -0.
1066651
## row414  0.0555528 -2.033e-01 -2.278e-01 -0.1986050  0.2428654 -0.
3313752
## row415  0.0555528 -2.033e-01 -1.812e-01 -0.0578948  0.2827060 -0.
2230556
## row416 -0.4766281 -5.737e-02  7.615e-02 -0.2690893 -0.0401608  0.
1061439
## row417 -0.4041890  1.756e-01  9.710e-02 -0.2074297 -0.1943617 -0.
1215599
## 
## 
## Biplot scores for constraining variables
```

```
##
##              RDA1   RDA2 PC1 PC2 PC3 PC4
## jes        0.8503 0.5263   0   0   0   0
## guaranis -0.5788 0.8155   0   0   0   0
```

```
plot(ord_sp)
```



```
vif.cca(ord_sp)
```

```
##      jes guaranis
## 1.003977 1.003977
```

```
sp_scores<-scores(ord_sp, choices=c(1,2), display="species")
write.csv(sp_scores, file = "sp_rda_scores.csv", sep=",", dec=".")
```

```
## Warning in write.csv(sp_scores, file = "sp_rda_scores.csv", sep =
",", dec
## = "."): attempt to set 'sep' ignored

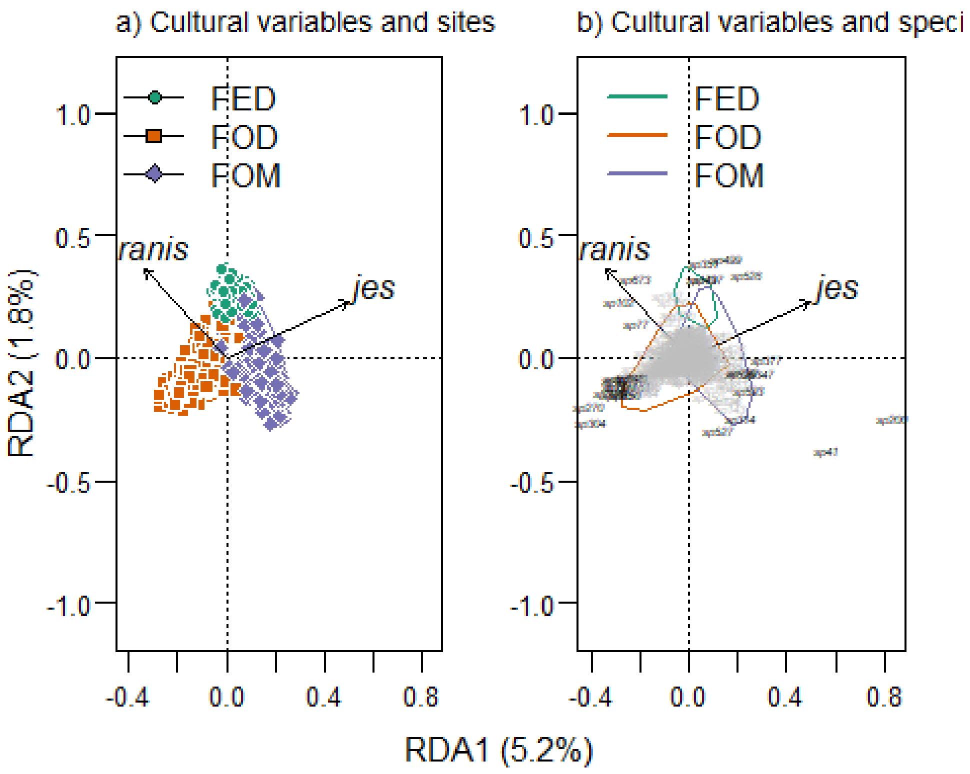
## Warning in write.csv(sp_scores, file = "sp_rda_scores.csv", sep =
",", dec
## = "."): attempt to set 'dec' ignored
```

```
#abbreviates species names

spnames<-make.cepnames(colnames(sp))
ptcols <- brewer.pal(3, "Dark2")

fisio <- co_occ$fitofisionomia
rda.tab <- summary(ord_sp)$cont$importance
```

```
spe.cols <- ifelse(abs(scores(ord_sp, display="species", choice=1))
> 0.1 |
  abs(scores(ord_sp, display="species", choice=2)) > 0.1, "black", "
grey")
```



S3 -
Environmental Niche

```
library(raster)

## Loading required package: sp

library(sp)
library(rgeos)

## rgeos version: 0.3-28, (SVN revision 572)
##  GEOS runtime version: 3.6.1-CAPI-1.10.1 r0
##  Linking to sp version: 1.3-1
##  Polygon checking: TRUE

library(rgdal)

## rgdal: version: 1.3-4, (SVN revision 766)
##  Geospatial Data Abstraction Library extensions to R successfully
loaded
##  Loaded GDAL runtime: GDAL 2.2.3, released 2017/11/20
##  Path to GDAL shared files: C:/Users/aline/Documents/R/win-librar
y/3.5/rgdal/gdal
##  GDAL binary built with GEOS: TRUE
##  Loaded PROJ.4 runtime: Rel. 4.9.3, 15 August 2016, [PJ_VERSION:
493]
```

```
##  Path to PROJ.4 shared files: C:/Users/aline/Documents/R/win-libr
ary/3.5/rgdal/proj
##  Linking to sp version: 1.3-1

library(fields)

## Loading required package: spam

## Loading required package: dotCall64

## Loading required package: grid

## Spam version 2.2-0 (2018-06-19) is loaded.
## Type 'help( Spam)' or 'demo( spam)' for a short introduction
## and overview of this package.
## Help for individual functions is also obtained by adding the
## suffix '.spam' to the function name, e.g. 'help( chol.spam)'.

##
## Attaching package: 'spam'

## The following objects are masked from 'package:base':
##
##     backsolve, forwardsolve

## Loading required package: maps

##
## Attaching package: 'maps'

## The following object is masked from 'package:plyr':
##
##     ozone

## See www.image.ucar.edu/~nychka/Fields for
##  a vignette and other supplements.

library(shapefiles)

## Loading required package: foreign

##
## Attaching package: 'shapefiles'

## The following objects are masked from 'package:foreign':
##
##     read.dbf, write.dbf

library(maptools)

## Checking rgeos availability: TRUE

library(maps)
```

```
occup<-shapefile("S3_BOTH_OCC.shp")#high probability of Souther-Je o
r Garani occurrence area, create in Qgis using the ENM results raste
rs by "Poligonize Raster" function.
occup<-spTransform(occup, CRS('+init=EPSG:31982'))
occup2<-spTransform(occup, CRS("+proj=longlat +datum=WGS84"))
ext_occup<-extent(occup)
ext_occup2<-extent(occup2)

#Import and standardize the most importat vabiables in ecological ni
che models: elevation, sea distance, main rivers distance, third ord
er (intermediate) rivers distance

elevation<-raster("h1k_dem.asc")#download file in Ambdata
projection(elevation)<-"+proj=longlat +datum=WGS84"
elevation<-crop(elevation,ext_occup2)
limit_occup2.r<-rasterize(occup2, elevation)
elevation<-elevation * limit_occup2.r
range(elevation)#min 0 max 1681

## Warning in range(new("RasterLayer", file = new(".RasterFile", nam
e = "", :
## Nothing to summarize if you provide a single RasterLayer; see cel
lStats

## class       : RasterLayer
## dimensions  : 1550, 1210, 1875500  (nrow, ncol, ncell)
## resolution  : 0.009, 0.009  (x, y)
## extent      : -58.59033, -47.70033, -34.29333, -20.34333  (xmin,
xmax, ymin, ymax)
## coord. ref. : +proj=longlat +datum=WGS84 +ellps=WGS84 +towgs84=0,
0,0
## data source : in memory
## names       : layer
## values      : 0, 1681  (min, max)

sea<-raster("S3_SEA.tif")
crs(sea) <- CRS('+init=EPSG:31982')
sea<-crop(sea,ext_occup)
limit_occup.r<-rasterize(occup,sea)
sea<-sea *limit_occup.r
sea<-sea*10#correct metric
range(sea)#min 0 max 470

## Warning in range(new("RasterLayer", file = new(".RasterFile", nam
e = "", :
## Nothing to summarize if you provide a single RasterLayer; see cel
lStats

## class       : RasterLayer
## dimensions  : 1567, 1060, 1661020  (nrow, ncol, ncell)
## resolution  : 1000, 1000  (x, y)
```

```
## extent       : -226589.5, 833410.5, 6183484, 7750484  (xmin, xmax,
ymin, ymax)
## coord. ref. : +init=EPSG:31982 +proj=utm +zone=22 +south +ellps=G
RS80 +towgs84=0,0,0,0,0,0,0 +units=m +no_defs
## data source : in memory
## names       : layer
## values      : 0, 470  (min, max)
```

```
main<-raster("S3_MAIN.tif")
crs(main) <- CRS('+init=EPSG:31982')
main<-crop(main,ext_occup)
main<-resample(main,sea, method="bilinear")
main<-main *limit_occup.r
main<-main*10
range(main)#0-29
```

```
## Warning in range(new("RasterLayer", file = new(".RasterFile", nam
e = "", :
## Nothing to summarize if you provide a single RasterLayer; see cel
lStats
```

```
## class       : RasterLayer
## dimensions  : 1567, 1060, 1661020  (nrow, ncol, ncell)
## resolution  : 1000, 1000  (x, y)
## extent      : -226589.5, 833410.5, 6183484, 7750484  (xmin, xmax,
ymin, ymax)
## coord. ref. : +init=EPSG:31982 +proj=utm +zone=22 +south +ellps=G
RS80 +towgs84=0,0,0,0,0,0,0 +units=m +no_defs
## data source : in memory
## names       : layer
## values      : 0, 290  (min, max)
```

```
third<-raster("S3_THIRD.tif")
crs(third) <- CRS('+init=EPSG:31982')
third<-crop(third,ext_occup)
third<-resample(third,sea, method="bilinear")
third<-third * limit_occup.r
third<-third*10
range(third)# 0 - 19
```

```
## Warning in range(new("RasterLayer", file = new(".RasterFile", nam
e = "", :
## Nothing to summarize if you provide a single RasterLayer; see cel
lStats
```

```
## class       : RasterLayer
## dimensions  : 1567, 1060, 1661020  (nrow, ncol, ncell)
## resolution  : 1000, 1000  (x, y)
## extent      : -226589.5, 833410.5, 6183484, 7750484  (xmin, xmax,
ymin, ymax)
## coord. ref. : +init=EPSG:31982 +proj=utm +zone=22 +south +ellps=G
```

```
RS80 +towgs84=0,0,0,0,0,0,0 +units=m +no_defs
## data source : in memory
## names       : layer
## values      : 0, 190  (min, max)

#Create 1000 random points into each cultural group area of highest
probability of occupation;

#to elevation
je_occ2<-shapefile("S3_JE.shp")
je_occ2<-spTransform(je_occ2, CRS('+init=EPSG:31982'))
ptsJe2 <- spsample(je_occ2, 1000, type = 'random')

gua_occ2<-shapefile("S3_GUA.shp")
gua_occ2<-spTransform(gua_occ2, CRS('+init=EPSG:31982'))
ptsGua2 <- spsample(gua_occ2, 1000, type = 'random')

#to other variables
je_occ<-shapefile("S3_JE.shp")
projection(je_occ)<-"+proj=longlat +datum=WGS84"
ptsJe <- spsample(je_occ, 1000, type = 'random')

gua_occ<-shapefile("S3_GUA.shp")
projection(gua_occ)<-"+proj=longlat +datum=WGS84"
ptsGua <- spsample(gua_occ, 1000, type = 'random')

#Extract topographic and hydrographic values to each cultural group
points
ele_je<-as.data.frame(extract(elevation,ptsJe2))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster

ele_gua<-as.data.frame(extract(elevation,ptsGua2))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster

# remove NA's
ele_je <- na.omit(ele_je)
ele_gua<-na.omit(ele_gua)
elevationJe<-write.csv(ele_je, file="elevation_je.csv", row.names=T)
elevationGua<-write.csv(ele_gua, file="elevation_guaranis.csv", row.
names=T)

main_je<-as.data.frame(extract(main,ptsJe))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster
```

```
main_gua<-as.data.frame(extract(main,ptsGua))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster

main_je <- na.omit(main_je)
main_gua<-na.omit(main_gua)
main_river_je<-write.csv(main_je, file="main_riversJe.csv", row.name
s=T)
main_river_gua<-write.csv(main_gua, file="main_rivers_guaranis.csv",
row.names=T)

third_je<-as.data.frame(extract(third,ptsJe))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster

third_gua<-as.data.frame(extract(third,ptsGua))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster

third_je <- na.omit(third_je)
third_gua<-na.omit(third_gua)
third_rivers_je<-write.csv(third_je, file="third_rivers_Je.csv", row
.names=T)
third_rivers_gua<-write.csv(third_gua, file="third_rivers_Guarani.cs
v", row.names=T)

sea_je<-as.data.frame(extract(sea,ptsJe))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster

sea_gua<-as.data.frame(extract(sea,ptsGua))

## Warning in .local(x, y, ...): Transforming SpatialPoints to the C
RS of the
## Raster

sea_je <- na.omit(sea_je)
sea_gua<-na.omit(sea_gua)
sea_dist_je<-write.csv(sea_je, file="seaJe.csv", row.names=T)
sea_dist_guagua<-write.csv(sea_gua, file="seaGuarani.csv", row.names
=T)

#Tables with the values of each variable for the two cultural groups
were set up in an electronic spreadsheet, with one table for each va
```

```
riable.

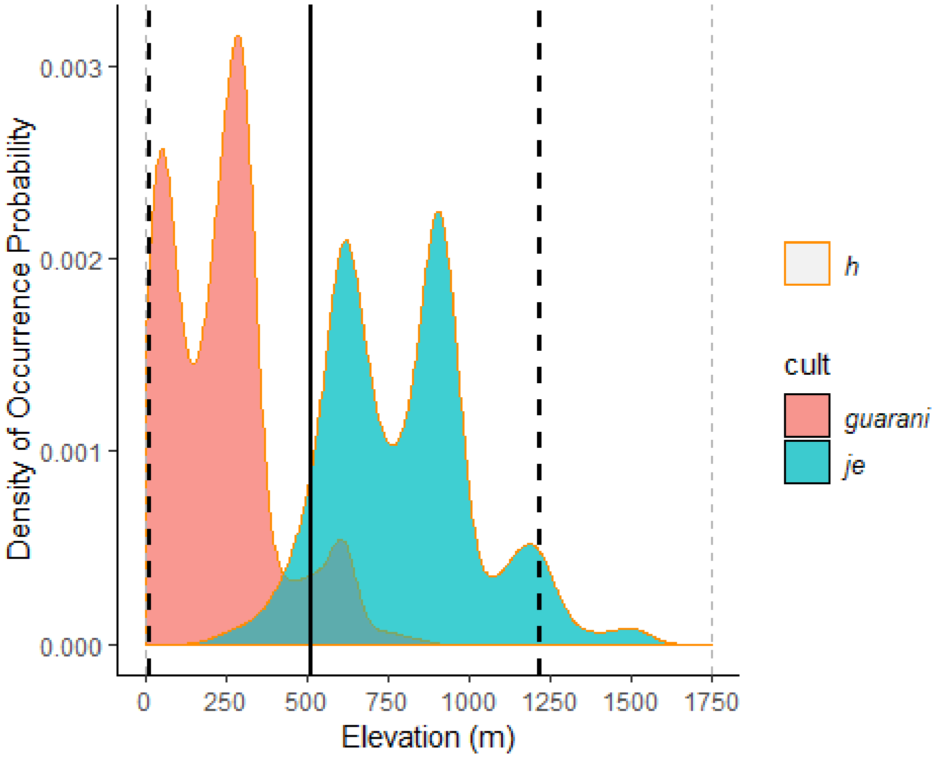

#Create Graphs
library(ggplot2)
values<-read.csv("S3_values.csv", header=T, sep=",", dec=".")


#create elevation graph
H<-values[,-c(3:5)]
names(H)<-c("cult","h")
head(H)

##      cult   h
## 1 guarani 512
## 2 guarani 196
## 3 guarani 155
## 4 guarani 197
## 5 guarani 288
## 6 guarani 757

breaks = c(0,250,500,750,1000,1250,1500, 1750)
  labels = as.character(breaks)
  plot.h = ggplot(H, aes(x=h, y=..density..)) +
    geom_density(aes(fill=cult,color= 'h'), alpha=.5)+
    geom_vline(aes(xintercept=mean(h)),color="darkorange",linetype="
solid",size=1)+
geom_vline(aes(xintercept=quantile(h,0.975)),color="darkorange",line
type="dashed",size=1)+
 geom_vline(aes(xintercept=quantile(h,0.025)),color="darkorange",lin
etype="dashed",size=1)+
    geom_density(aes(h, fill=cult,color='h'),alpha=.5) +
    geom_vline(aes(xintercept=mean(h)),color="black",linetype="solid
",size=1)+
    geom_vline(aes(xintercept=quantile(h,0.975)),color="black",linet
ype="dashed",size=1) +
    geom_vline(aes(xintercept=quantile(h,0.025)),color="black",linet
ype="dashed",size=1)+
    geom_vline(xintercept = c(0, 1750), colour="gray70", linetype="d
ashed") +
    scale_x_continuous(limits = c(0, 1750), breaks = breaks, labels
= labels)+
    scale_color_manual(values = c('h' = 'darkorange', 'h '= 'black')
)
        plot.h =  plot.h + theme(panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
                             legend.text = element_text(face=
"italic", size=10),
                             panel.background = element_blank(
), axis.line = element_line(colour = "black"))  +
```

```
      labs(x="Elevation (m)", y = "Density of Occurrence Probability
",size=10) +
      labs(col = "") +
      theme(axis.title.x = element_text(size = rel(1))) +
      theme(axis.title.y = element_text(size = rel(1))) +
      theme(axis.text.x = element_text(size = rel(1))) +
      theme(axis.text.y = element_text(size = rel(1)))
  ggsave("elevation.pdf",plot=plot.h,width=20,height=10)
print(plot.h)
```



```
#create coastline distance graph
sea<-values[,-c(2:4)]
names(sea)<-c("cult","dist")
head(sea)

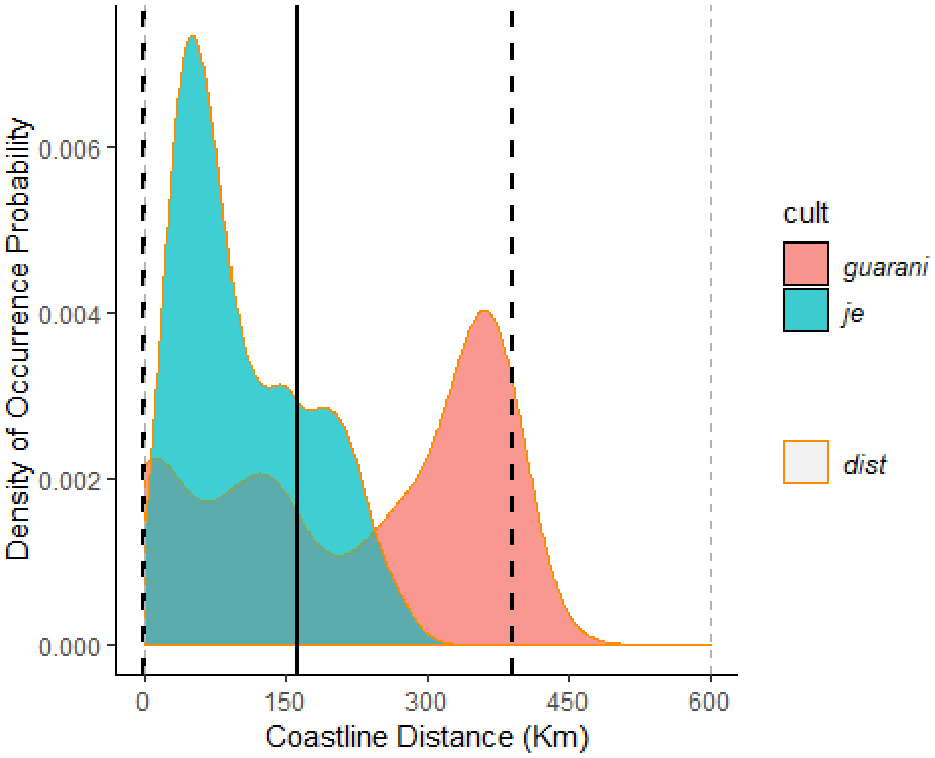
##       cult dist
## 1 guarani    0
## 2 guarani    0
## 3 guarani   90
## 4 guarani  410
## 5 guarani  180
## 6 guarani  380

head(sea)

##       cult dist
## 1 guarani    0
## 2 guarani    0
## 3 guarani   90
```

```
## 4 guarani  410
## 5 guarani  180
## 6 guarani  380

  breaks = c(0,150,300,450, 600)
  labels = as.character(breaks)
  plot.sea = ggplot(sea, aes(x=dist, y=..density..)) +
    geom_density(aes(fill=cult,color= 'dist'), alpha=.5)+
    geom_vline(aes(xintercept=mean(dist)),color="darkorange",linetype="solid",size=1)+
    geom_vline(aes(xintercept=quantile(dist,0.975)),color="darkorange",linetype="dashed",size=1)+
    geom_vline(aes(xintercept=quantile(dist,0.025)),color="darkorange",linetype="dashed",size=1)+
    geom_density(aes(dist, fill=cult,color='dist'),alpha=.5) +
    geom_vline(aes(xintercept=mean(dist)),color="black",linetype="solid",size=1)+
    geom_vline(aes(xintercept=quantile(dist,0.975)),color="black",linetype="dashed",size=1) +
    geom_vline(aes(xintercept=quantile(dist,0.025)),color="black",linetype="dashed",size=1)+
    geom_vline(xintercept = c(0, 600), colour="gray70", linetype="dashed") +
    scale_x_continuous(limits = c(0, 600), breaks = breaks, labels = labels)+
    scale_color_manual(values = c('dist' = 'darkorange', 'h '= 'black'))
  plot.sea =  plot.sea + theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
                               legend.text = element_text(face= "italic", size=10),
                               panel.background = element_blank(), axis.line = element_line(colour = "black"))  +
    labs(x="Coastline Distance (Km)", y = "Density of Occurrence Probability",size=10) +
    labs(col = "") +
    theme(axis.title.x = element_text(size = rel(1))) +
    theme(axis.title.y = element_text(size = rel(1))) +
    theme(axis.text.x = element_text(size = rel(1))) +
    theme(axis.text.y = element_text(size = rel(1)))
 # ggsave("sea.pdf",plot=plot.sea,width=20,height=10)
print(plot.sea)
```

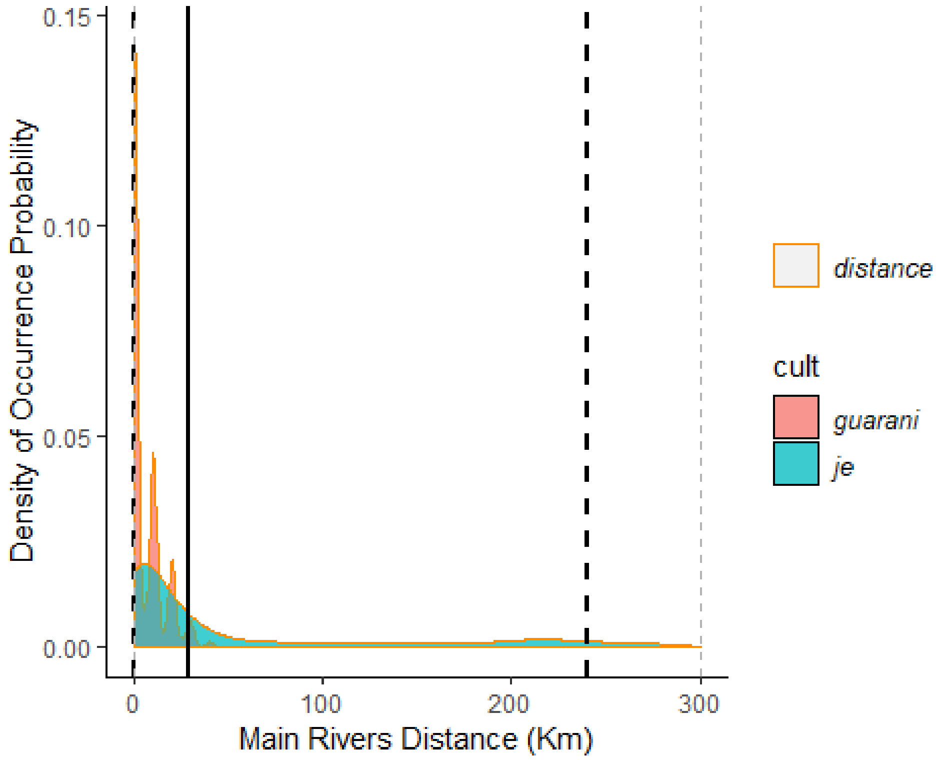


```
#create main rivers distance graph
main<-values[,-c(2,4,5)]
names(main)<-c("cult","distance")
head(main)

##      cult distance
## 1 guarani        0
## 2 guarani        0
## 3 guarani        0
## 4 guarani       10
## 5 guarani        0
## 6 guarani       10

breaks = c(0,100,200,300)
  labels = as.character(breaks)
  plot.main = ggplot(main, aes(x=distance, y=..density..)) +
    geom_density(aes(fill=cult,color= 'distance'), alpha=.5)+
    geom_vline(aes(xintercept=mean(distance)),color="darkorange",lin
etype="solid",size=1)+
geom_vline(aes(xintercept=quantile(distance,0.975)),color="darkorang
e",linetype="dashed",size=1)+
 geom_vline(aes(xintercept=quantile(distance,0.025)),color="darkoran
ge",linetype="dashed",size=1)+
    geom_density(aes(distance, fill=cult,color='distance'),alpha=.5)
+
    geom_vline(aes(xintercept=mean(distance)),color="black",linetype
="solid",size=1)+
    geom_vline(aes(xintercept=quantile(distance,0.975)),color="black
",linetype="dashed",size=1) +
```

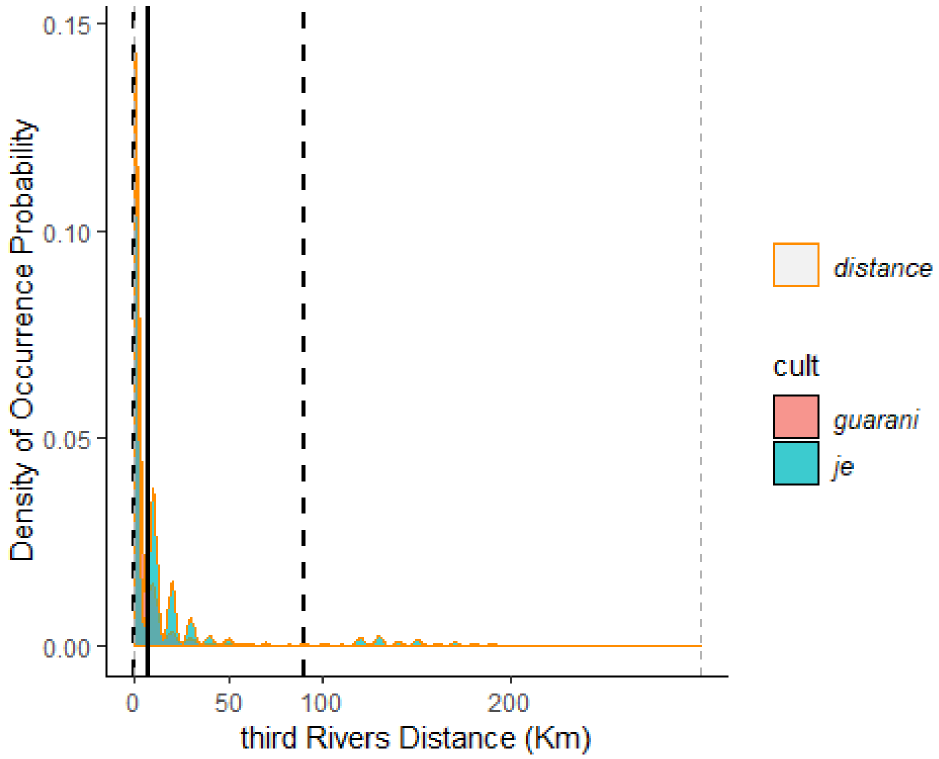
```
    geom_vline(aes(xintercept=quantile(distance,0.025)),color="black",linetype="dashed",size=1)+
    geom_vline(xintercept = c(0, 300), colour="gray70", linetype="dashed") +
    scale_x_continuous(limits = c(0, 300), breaks = breaks, labels = labels)+
    scale_color_manual(values = c('distance' = 'darkorange', 'h '= 'black'))
        plot.main =  plot.main + theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
                                   legend.text = element_text(face="italic", size=10),
                                   panel.background = element_blank(), axis.line = element_line(colour = "black"))  +
      labs(x="Main Rivers Distance (Km)", y = "Density of Occurrence Probability",size=10) +
      labs(col = "") +
      theme(axis.title.x = element_text(size = rel(1))) +
      theme(axis.title.y = element_text(size = rel(1))) +
      theme(axis.text.x = element_text(size = rel(1))) +
      theme(axis.text.y = element_text(size = rel(1)))
ggsave("mainrivers.pdf",plot=plot.main,width=20,height=10)
        print(plot.main)
```



```
        #create third rivers distance graph
third<-values[,-c(2,3,5)]
names(third)<-c("cult","distance")
head(third)
```

```
##      cult  distance
## 1 guarani  0.000000
## 2 guarani 30.000000
## 3 guarani  0.000000
## 4 guarani 10.000000
## 5 guarani  0.000000
## 6 guarani  7.920211
```

```
breaks = c(0,50,100,200)
  labels = as.character(breaks)
  plot.third = ggplot(third, aes(x=distance, y=..density..)) +
    geom_density(aes(fill=cult,color= 'distance'), alpha=.5)+
    geom_vline(aes(xintercept=mean(distance)),color="darkorange",lin
etype="solid",size=1)+
geom_vline(aes(xintercept=quantile(distance,0.975)),color="darkorang
e",linetype="dashed",size=1)+
 geom_vline(aes(xintercept=quantile(distance,0.025)),color="darkoran
ge",linetype="dashed",size=1)+
    geom_density(aes(distance, fill=cult,color='distance'),alpha=.5)
+
    geom_vline(aes(xintercept=mean(distance)),color="black",linetype
="solid",size=1)+
    geom_vline(aes(xintercept=quantile(distance,0.975)),color="black
",linetype="dashed",size=1) +
    geom_vline(aes(xintercept=quantile(distance,0.025)),color="black
",linetype="dashed",size=1)+
    geom_vline(xintercept = c(0, 300), colour="gray70", linetype="da
shed") +
    scale_x_continuous(limits = c(0, 300), breaks = breaks, labels =
labels)+
    scale_color_manual(values = c('distance' = 'darkorange', 'h '= '
black'))
        plot.third =  plot.third + theme(panel.grid.major = element_
blank(), panel.grid.minor = element_blank(),
                                   legend.text = element_text(face=
"italic", size=10),
                                   panel.background = element_blank(
), axis.line = element_line(colour = "black"))  +
      labs(x="third Rivers Distance (Km)", y = "Density of Occurrenc
e Probability",size=10) +
      labs(col = "") +
      theme(axis.title.x = element_text(size = rel(1))) +
      theme(axis.title.y = element_text(size = rel(1))) +
      theme(axis.text.x = element_text(size = rel(1))) +
      theme(axis.text.y = element_text(size = rel(1)))
ggsave("thirdrivers.pdf",plot=plot.third,width=20,height=10)
        print(plot.third)
```



S2 - Niche Overlap

```
library(ENMeval)

## Loading required package: dismo

library(raster)
library(sp)
library(rgeos)
library(rgdal)
library(fields)
library(shapefiles)
library(maptools)
library(maps)
#import ENM results, named "S1A_result.tif" and "S2A_result.tif"

#import Souther-Je occurrence limit shapefile and use to crop raster
s in the same size

je_occ<-shapefile("S1B.shp")
je_occ<-spTransform(je_occ, CRS("+proj=longlat +datum=WGS84"))

#import ENM results, named "S1A_result.tif" and "S2A_result.tif"

S1A<-raster("S1A_result.tif")#Guarani
projection(S1A)<-"+proj=longlat +datum=WGS84"
S1A<-crop(S1A,extent(je_occ))

S1B<-raster("S1B_result.tif")#Southern-Je
projection(S1B)<-"+proj=longlat +datum=WGS84"
```

```
S1B<-crop(S1B,extent(je_occ))

#remove NAs
S1A[is.na(S1A)] <- 999
S1B[is.na(S1B)] <- 999

#stack
cult<-stack(S1A,S1B)
names(cult)<-c('Guarani','Je')
projection(cult)<-"+proj=longlat +datum=WGS84"

#calc overlap niche
overlap<-calc.niche.overlap(cult, stat = "I", maxent.args(RMvalues =
seq(0.5, 4, 0.5),
fc = c("L", "LQ", "H", "LQH", "LQHP", "LQHPT"),
labels = TRUE))

##
  |
  |
|   0%
  |
  |==================================================================
| 100%

summary(overlap)

##     Guarani               Je
##   Min.   :0.6924   Min.   : NA
##   1st Qu.:0.6924   1st Qu.: NA
##   Median :0.6924   Median : NA
##   Mean   :0.6924   Mean   :NaN
##   3rd Qu.:0.6924   3rd Qu.: NA
##   Max.   :0.6924   Max.   : NA
##   NA's   :1        NA's   :2
```

4.2 S1 - NICHE ECOLOGICAL MODELS (ENM)

**Final Results in raster format are available for download. See “S1A_result.tif” and “S2A_result.tif”

```
library(raster)
library(sp)
library(rgeos)
library(rgdal)
library(fields)
library(shapefiles)
library(maptools)
library(maps)
library(rJava)
```

```
#### S1A - Guarani

# Import The Occurrence Limit#
#Download the file named **"S1A.shp"**, available in supplementary material. This shapefile corresponds to The "Area of Guarani Occurrence", and was preliminarily delimited in the Qgis Software.


gua_occ<-shapefile("S1A.shp")#Guarani Occurrence Limit
gua_occ<-spTransform(gua_occ, CRS("+proj=longlat +datum=WGS84"))#Enter the coordinate system

#Import and standardize topographic and hydrographic variables
#Download Elevation and Slope variables in Ambdata (http://www.dpi.inpe.br/Ambdata/)

#HAND variable is available in Ambdata, but was processed in the QGis Software to increase pixel size, using GRASS command "r.resamp.interp". This 10 km pixel raster is available for download in the supplementary material, with the name **"SA_HAND.tif"**.

#Coastline Distance and Water Courses distance are available in the supplementary material, with the names: **"SA_SEA.tif"**; **"SA_1_2.tif"**; **"SA_3.tif"**; **"SA_4.tif"**; **"SA_5_8.tif"**. Distance rasters was generated using Qgis.

#Height Above the Nearest Drainage (HAND)
hand<-raster("S1_HAND.tif")
projection(hand)<-"+proj=longlat +datum=WGS84"
ext.gua_occ<-extent(gua_occ)
hand<-crop(hand,extent(gua_occ))
limit_gua.r<-rasterize(gua_occ, hand)
hand.gua<-hand * limit_gua.r
ext.limit_gua<-extent(gua_occ)
hand.gua<-crop(hand.gua, ext.limit_gua)
hand.mask<- hand.gua
hand.mask[hand.gua >= minValue(hand.gua)] <- 1
#Elevation
elevation<-raster("h1k_dem.asc")#download file in Ambdata
projection(elevation)<-"+proj=longlat +datum=WGS84"
elevation<-crop(elevation,ext.limit_gua)
elevation<-resample(elevation,hand, method="bilinear")
elevation<-elevation * limit_gua.r
elevation.mask<-elevation
elevation.mask[elevation >= minValue(elevation)] <- 1
#Slope
slope<-raster("h1k_slope.asc")
projection(slope)<-"+proj=longlat +datum=WGS84"
slope<-crop(slope,ext.limit_gua)
slope<-resample(slope,hand.gua, method="bilinear")
```

```
slope<-slope * limit_gua.r
slope.mask<-slope
slope.mask[slope >= minValue(slope)] <- 1
#Coastline Distance
sea<-raster("S1_SEA.tif")
projection(sea)<-"+proj=longlat +datum=WGS84"
sea<-crop(sea,ext.limit_gua)
sea<-resample(sea,hand.gua,method="bilinear")
sea<-sea * limit_gua.r
sea.mask<-sea
sea.mask[sea >= minValue(sea)] <- 1

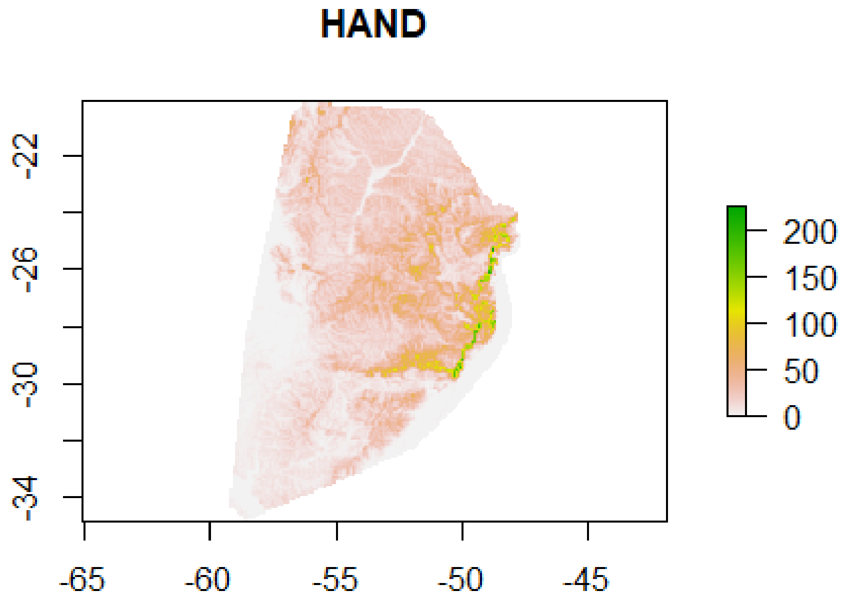
#Water Courses
#1st and 2nd River Classes Distance (Main Rivers)
main<-raster("S1_1ST2ND.tif")
projection(main)<-"+proj=longlat +datum=WGS84"
main<-crop(main,ext.limit_gua)
main<-resample(main,hand.gua, method="bilinear")
main<-main * limit_gua.r
main.mask<-main
main.mask[main >= minValue(main)] <- 1
#3rd River Class Distance
third<-raster("S1_3RD.tif")
projection(third)<-"+proj=longlat +datum=WGS84"
third<-crop(third,ext.limit_gua)
third<-resample(third,hand.gua, method="bilinear")
third<-third * limit_gua.r
third.mask<-third
third.mask[third>= minValue(third)] <- 1
#4th River Class Distance
fourth<-raster("S1_4TH.tif")
projection(fourth)<-"+proj=longlat +datum=WGS84"
fourth<-crop(fourth,ext.limit_gua)
fourth<-resample(fourth,hand.gua, method="bilinear")
fourth<-fourth * limit_gua.r
fourth.mask<-fourth
fourth.mask[fourth>= minValue(fourth)] <- 1
#Minor Rivers
minor<-raster("S1_5_8TH.tif")
projection(minor)<-"+proj=longlat +datum=WGS84"
minor<-crop(minor,ext.limit_gua)
minor<-resample(minor,hand.gua, method="bilinear")
minor<-minor * limit_gua.r
minor.mask<-minor
minor.mask[minor>= minValue(minor)] <- 1

#Creat a variables collection

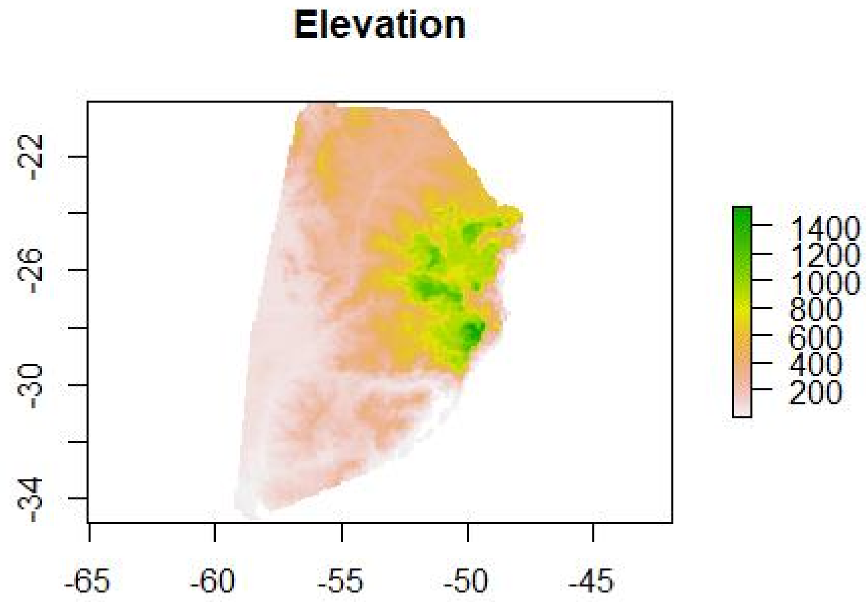
env<-stack(hand,elevation,slope,sea,main,third,fourth,minor)
env.mask<-hand.mask*elevation.mask*slope.mask*sea.mask*main.mask*thi
```

```
rd.mask*fourth.mask*minor.mask
env<-env*env.mask
names(env)<-c('hand','elevation','slope','sea','main', 'third','four
th','minor')
projection(env)<-"+proj=longlat +datum=WGS84"

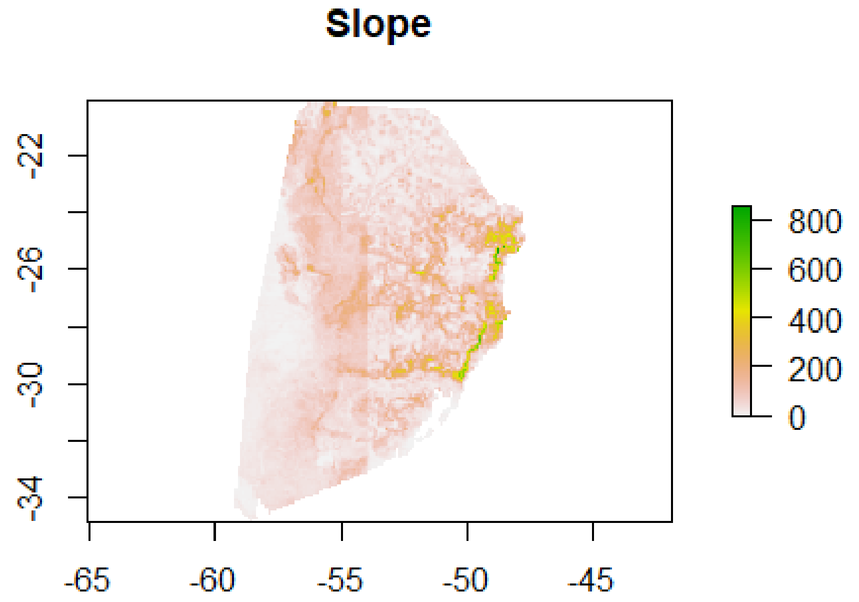

plot(hand.gua, main="HAND")
```



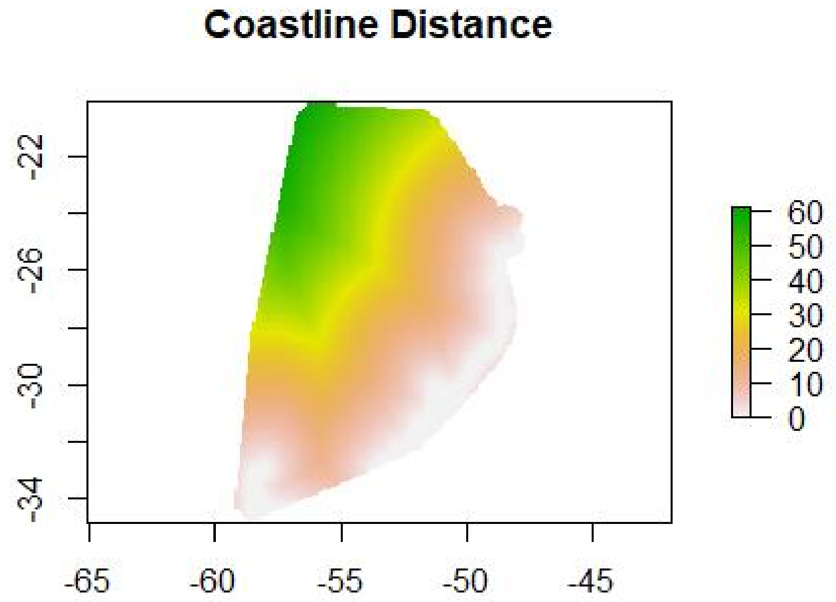
```
plot(elevation, main="Elevation")
```



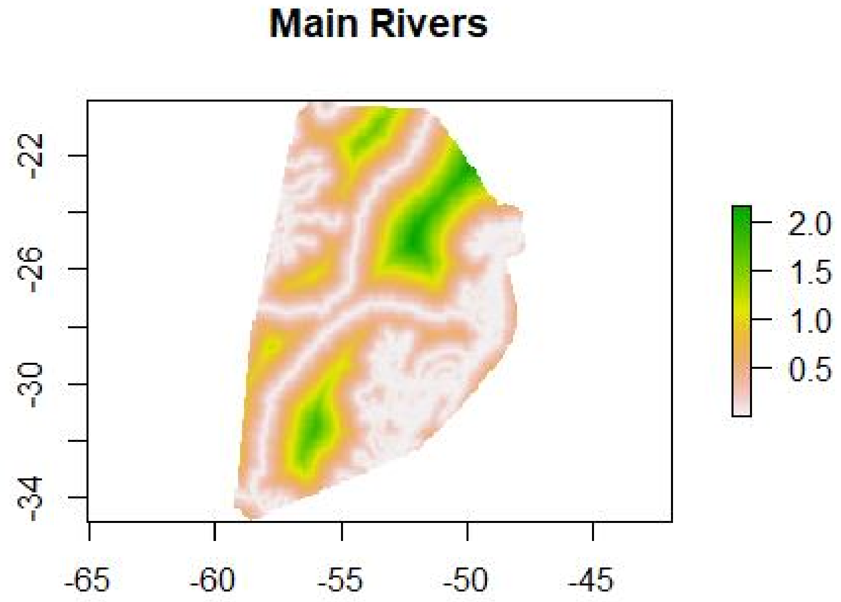
```r
plot(slope, main="Slope")
```



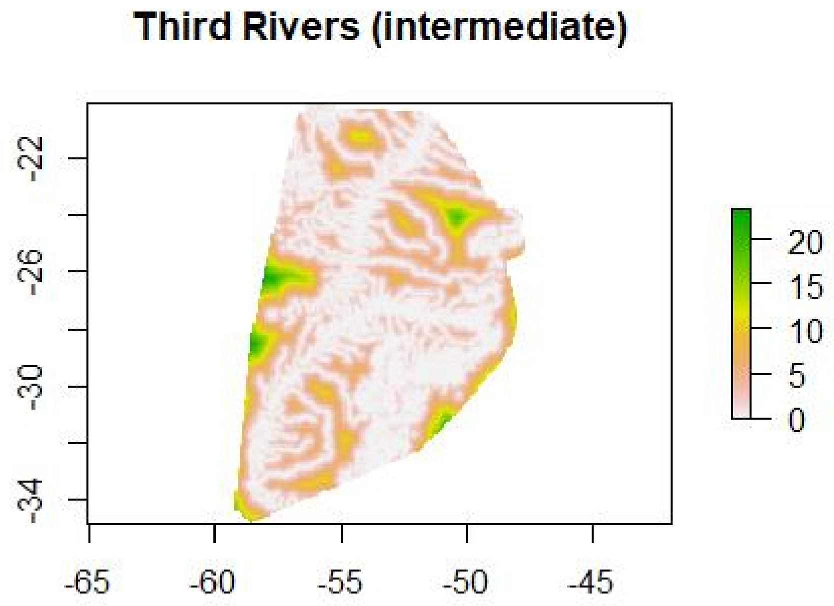
```r
plot(sea, main="Coastline Distance")
```



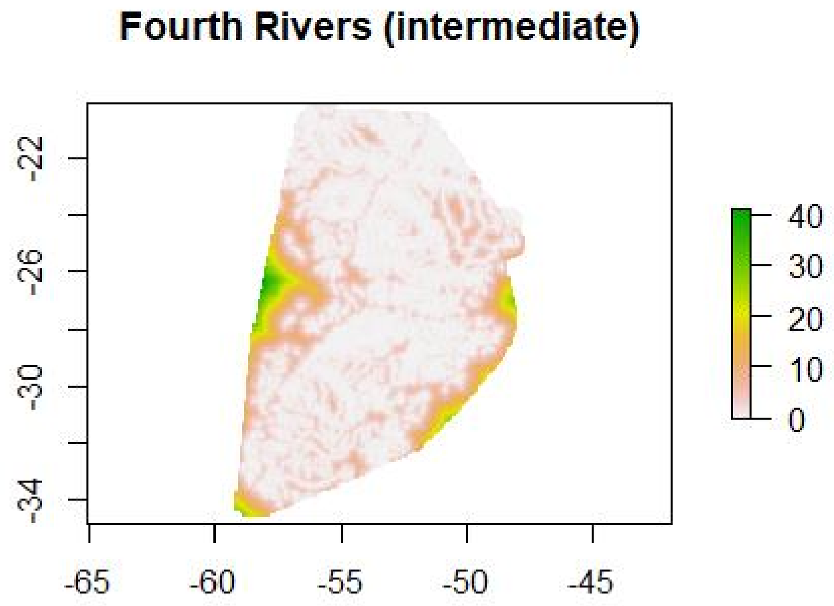
```
plot(main, main="Main Rivers")
```



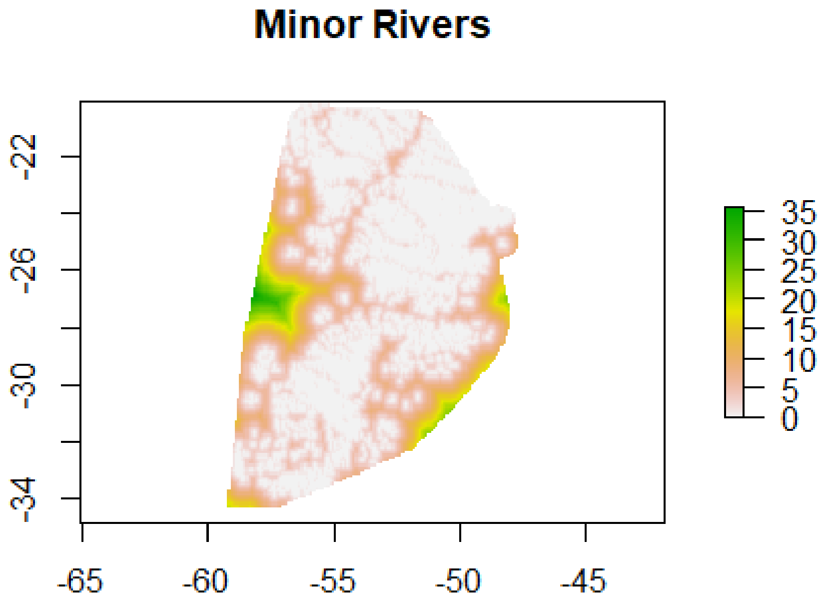
```
plot(third, main="Third Rivers (intermediate)")
```



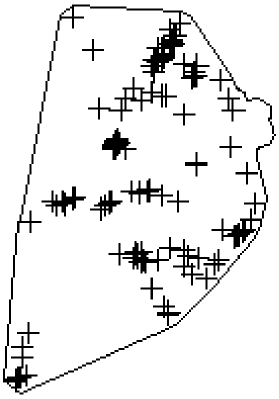
```r
plot(fourth, main="Fourth Rivers (intermediate)")
```



```r
plot(minor, main = "Minor Rivers")
```



```
#Import the occurrence points of Guarani Archaeological Sites Guarani Arqueological Occurrence Points are available as *.kmz file, in Bonomo et al(2015) Supplementar Material (doi:0.1016/j.quaint.2014.10.050). We use a Qgis Software to save occurrence points in *.csv format: "S1A_POINTS.csv"

gua_pt<-read.csv("S1A_POINTS.csv", sep=",",dec=".", header=T, row.names=NULL)
gua_pt.spdf<-SpatialPointsDataFrame(gua_pt[,c(1,2)],gua_pt, proj4string=CRS("+init=epsg:4326"))
gua_pt.spdf<-spTransform(gua_pt.spdf, CRS("+proj=longlat +datum=WGS84"))
plot(gua_occ)
plot(gua_pt.spdf, add=T, main="Guarani Occurrence Points")
```

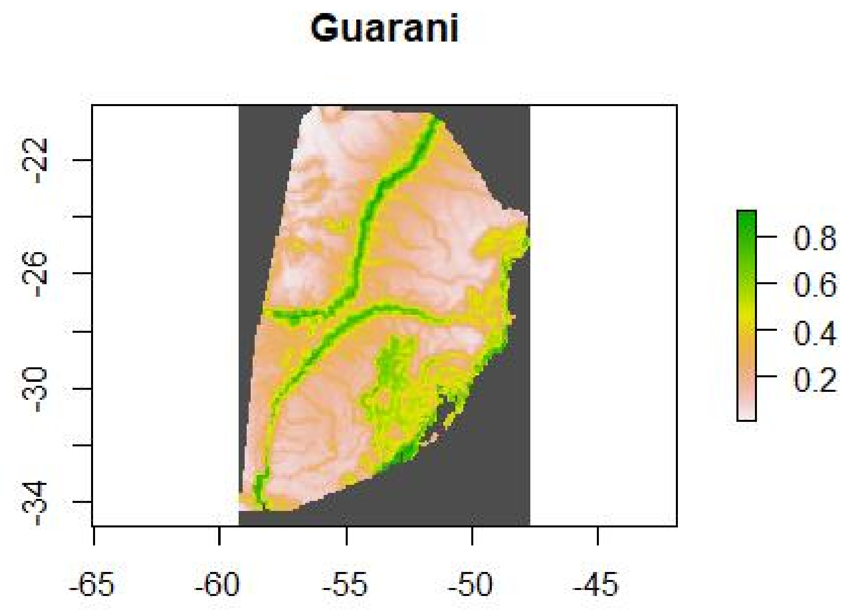


```
#ENM

library(ENMeval)
bck.na<-env[[1]]
bck.na[]<-NA
r.gua<-rasterize(coordinates(gua_pt.spdf),bck.na,fun='count')
gua.pa<-rasterToPoints(r.gua,fun=function(x){x>0}, spatial=T)
set.seed(1234)
bg<-randomPoints(env[[1]],5000)

#ENMevaluate: In this step, several models are generated, which are
ordered to select the models with the highest AUC and the lowest ove
rfitting. It is computationally expensive, so the commands are isola
ted by "#". Select model is below.
#m1gua<-ENMevaluate(env=env, occ=coordinates(gua.pa), bg.coords=bg,
RMvalues=seq(0.5,4,0.5),                     fc=c("L","LQ","LQP","H","
LQH"),                    method="randomkfold",kfolds=4, parallel = T
)

#m1gua@results
#plot(m1gua@results)
#m1gua@predictions
#plot(m1gua@predictions)
#m1gua@models  #: list of model objects

#m1gua@occ.pts     #: data.frame of occurrence coordinates
#m1gua@occ.grp     #: vector of bins for occurrence points
#m1gua@bg.pts      #: data.frame of background coordinates
```

```
#m1gua@bg.grp

#ord<-order(m1gua@results$avg.diff.AUC, decreasing=T)
#lista<-m1gua@results[ord,c(2,3,13,16,5,7)]
#lista



#Below is the selected model, which presented the best balance betwe
en auc and overfitting. # feature = H rm = 2.0 aic = 1910.935 parame
ters = 20 auc = 0.8037023 diff = 0.03442758

h2<-maxent(env, p=gua.pa, a=bg,
            removeDuplicates=TRUE,
            args=c("-P", 'outputformat=raw', 'noautofeature',
                   'nothreshold', 'noproduct','nolinear','noquadrati
c','noaddsamplestobackground',
                   'betamultiplier=2'))
```

```
## Warning in .local(x, p, ...): 3 (2.56%) of the presence points ha
ve NA
## predictor values
```

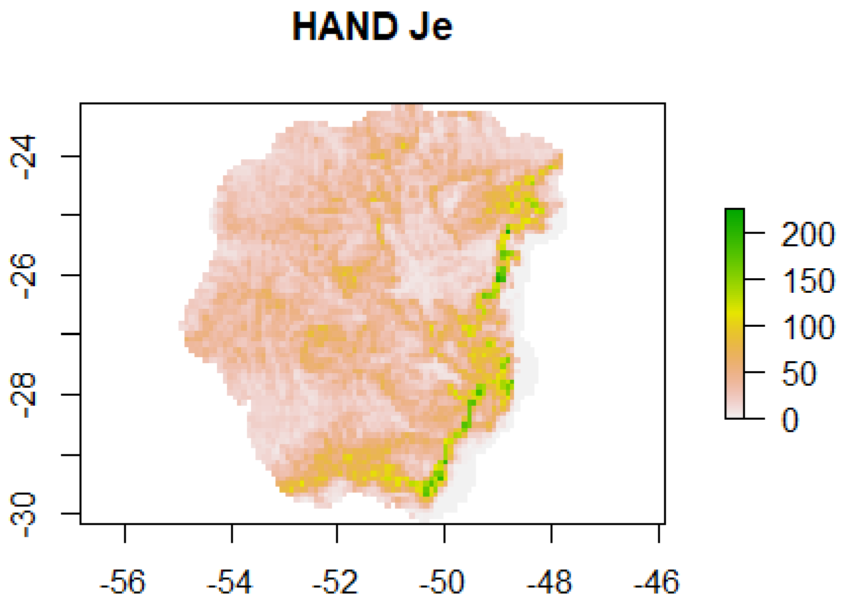
```
plog.h2<- predict(h2, env,args=c('outputformat=logistic'))
plog.h2.def<-calc(plog.h2, fun=mean)
plot(plog.h2 ,main="Guarani" ,colNA="gray30")
```



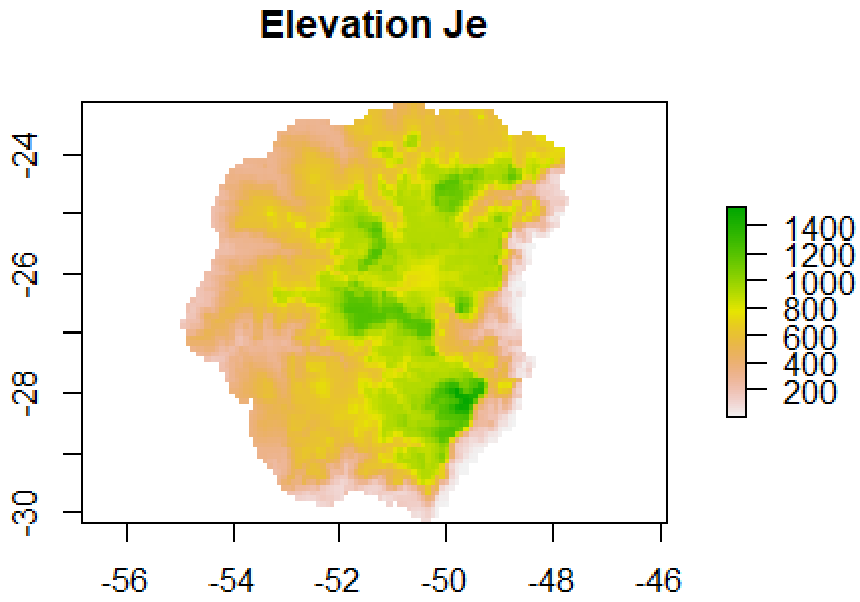
```
#### S1B Southern-Jê
```

```
je_occ<-shapefile("S1B.shp") #Southern-Je occurrence area
je_occ<-spTransform(je_occ, CRS("+proj=longlat +datum=WGS84"))

#Environmental variables
 hand_je<-raster("S1_HAND.tif")##download file in Ambdata
  projection(hand_je)<-"+proj=longlat +datum=WGS84"
  ext.je_occ<-extent(je_occ)
  hand_je<-crop(hand_je,extent(je_occ))
  limit_je.r<-rasterize(je_occ, hand_je)
  hand.je<-hand_je * limit_je.r
  hand.je.mask<- hand.je
  hand.je.mask[hand.je >= minValue(hand.je)] <- 1
#Elevation
elevation_je<-raster("h1k_dem.asc")#download file in Ambdata
  projection(elevation_je)<-"+proj=longlat +datum=WGS84"
  elevation_je<-crop(elevation_je,ext.je_occ)
  elevation_je<-resample(elevation_je,hand_je, method="bilinear")
  elevation_je<-elevation_je * limit_je.r
  elevation.je.mask<-elevation_je
  elevation.je.mask[elevation_je >= minValue(elevation)] <- 1
#Slope
slope_je<-raster("h1k_slope.asc")
projection(slope_je)<-"+proj=longlat +datum=WGS84"
slope_je<-crop(slope_je,ext.je_occ)
slope_je<-resample(slope_je,hand.je, method="bilinear")
slope_je<-slope_je * limit_je.r
slope.je.mask<-slope_je
slope.je.mask[slope_je >= minValue(slope_je)] <- 1
#Coastline Distance
sea_je<-raster("S1_SEA.tif")
projection(sea_je)<-"+proj=longlat +datum=WGS84"
sea_je<-crop(sea_je,ext.je_occ)
sea_je<-resample(sea_je,hand.je,method="bilinear")
sea_je<-sea_je * limit_je.r
sea.je.mask<-sea_je
sea.je.mask[sea_je >= minValue(sea_je)] <- 1
#Water Courses
#1st and 2nd River Classes Distance (Main Rivers)
main_je<-raster("S1_1ST2ND.tif")
projection(main_je)<-"+proj=longlat +datum=WGS84"
main_je<-crop(main_je,ext.je_occ)
main_je<-resample(main_je,hand.je, method="bilinear")
main_je<-main_je * limit_je.r
main.je.mask<-main_je
main.je.mask[main_je >= minValue(main_je)] <- 1
#3rd River Class Distance
third_je<-raster("S1_3RD.tif")
projection(third_je)<-"+proj=longlat +datum=WGS84"
third_je<-crop(third_je,ext.je_occ)
```

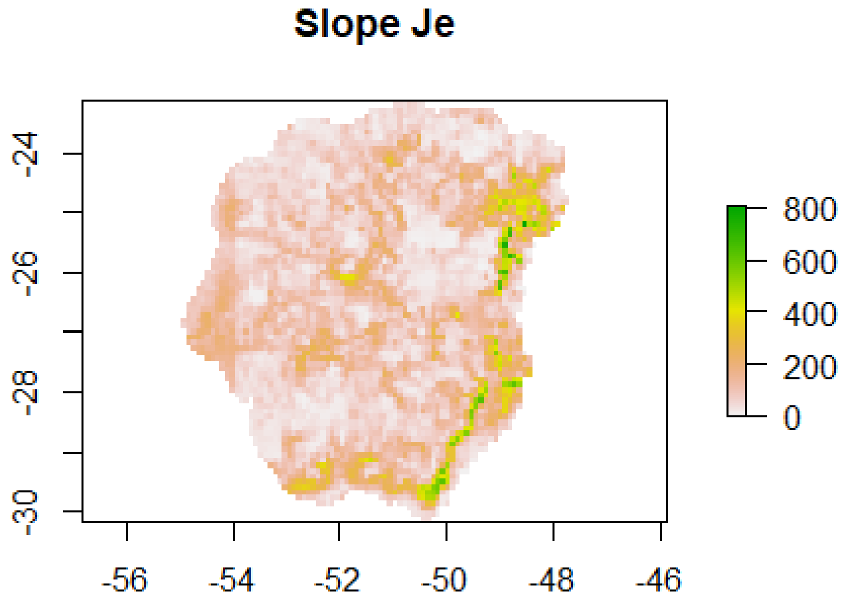
```
third_je<-resample(third_je,hand.je, method="bilinear")
third_je<-third_je * limit_je.r
third.je.mask<-third_je
third.je.mask[third_je>= minValue(third_je)] <- 1
#4th River Class Distance
fourth_je<-raster("S1_4TH.tif")
projection(fourth_je)<-"+proj=longlat +datum=WGS84"
fourth_je<-crop(fourth_je,ext.je_occ)
fourth_je<-resample(fourth_je,hand.je, method="bilinear")
fourth_je<-fourth_je * limit_je.r
fourth.je.mask<-fourth_je
fourth.je.mask[fourth_je>= minValue(fourth_je)] <- 1
#Minor Rivers
minor_je<-raster("S1_5_8TH.tif")
projection(minor_je)<-"+proj=longlat +datum=WGS84"
minor_je<-crop(minor_je,ext.je_occ)
minor_je<-resample(minor_je,hand.je, method="bilinear")
minor_je<-minor_je * limit_je.r
minor.je.mask<-minor_je
minor.je.mask[minor_je>= minValue(minor_je)] <- 1

plot(hand.je, main="HAND Je")
```



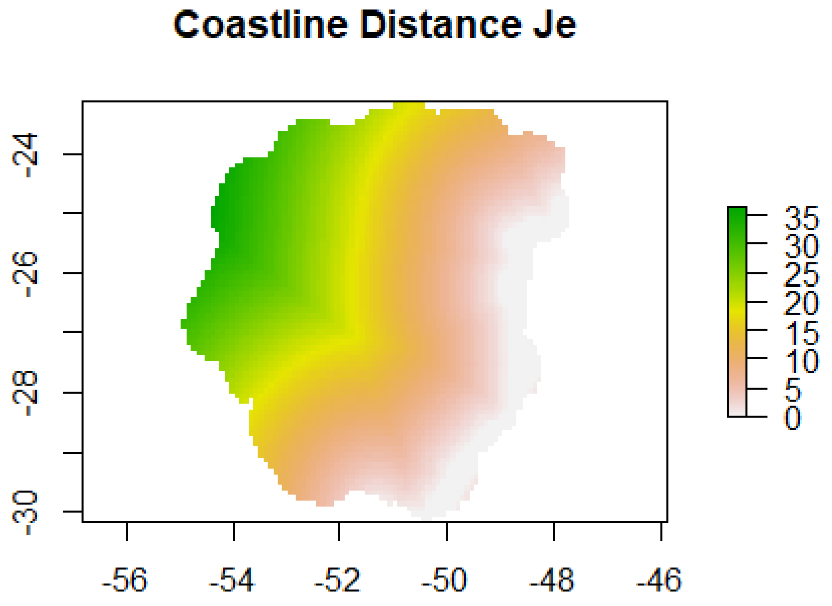
```
plot(elevation_je, main="Elevation Je")
```



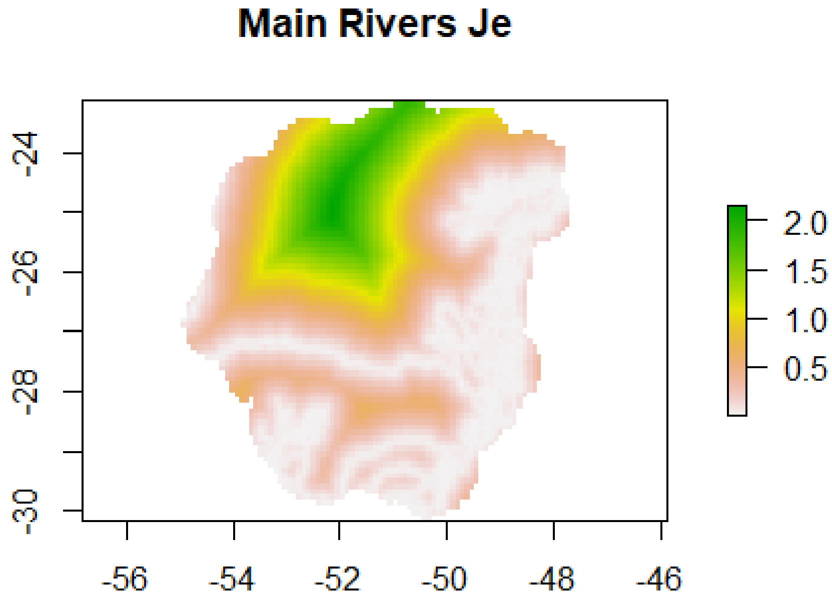
```
plot(slope_je, main="Slope Je")
```



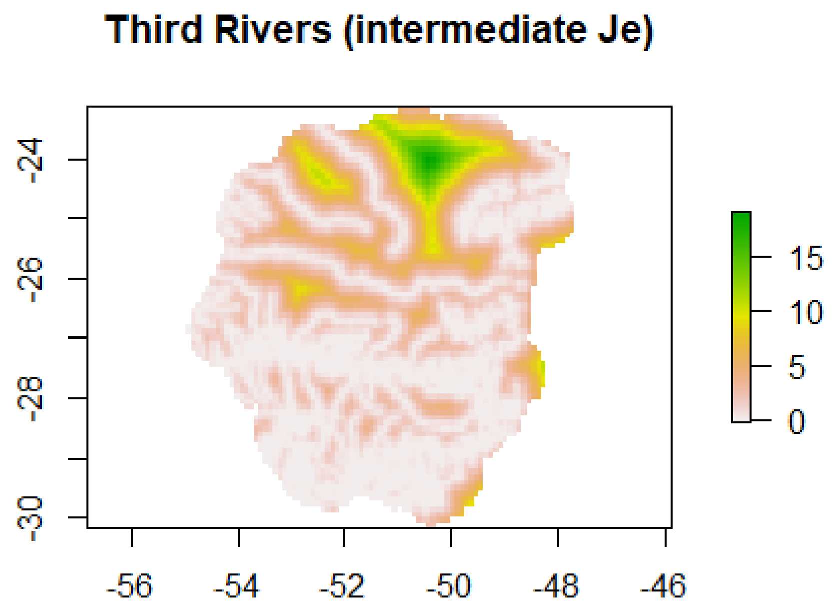
```
plot(sea_je, main="Coastline Distance Je")
```



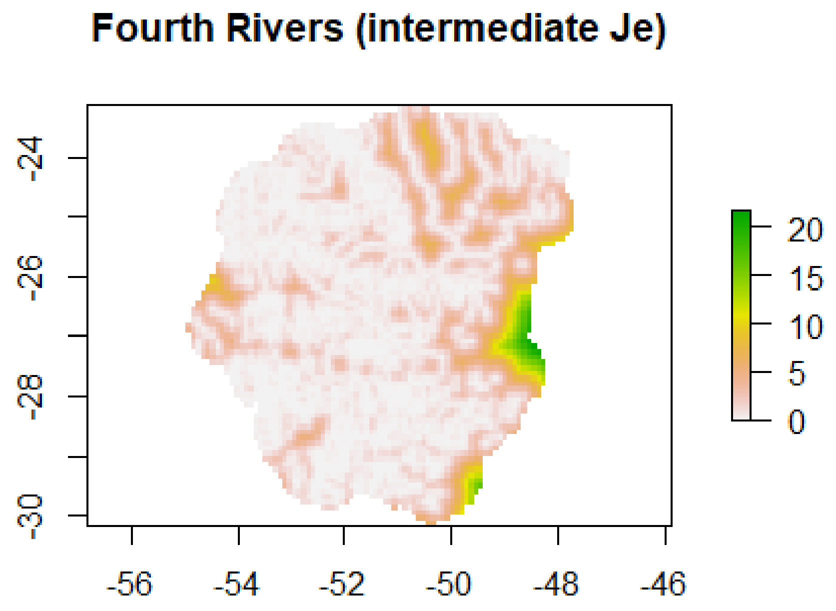
```r
plot(main_je, main="Main Rivers Je")
```



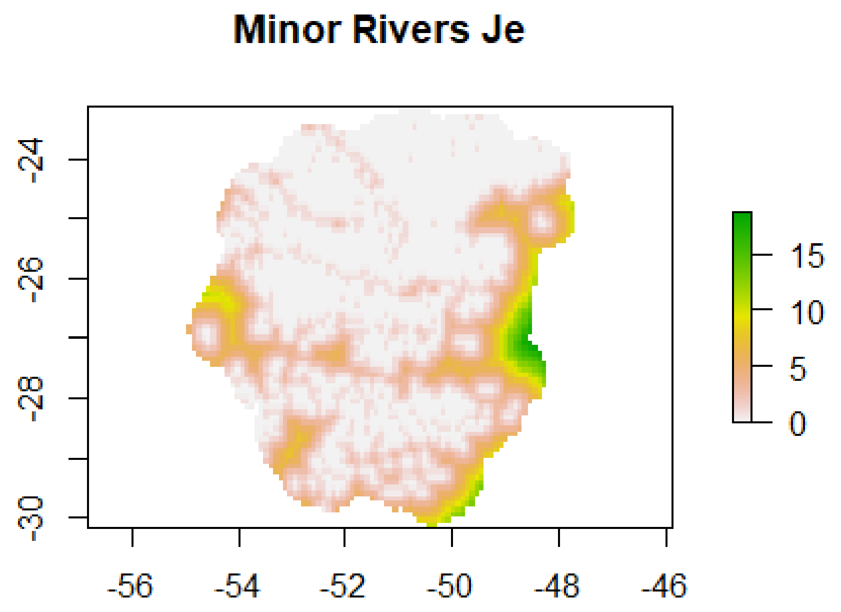
```r
plot(third_je, main="Third Rivers (intermediate Je)")
```



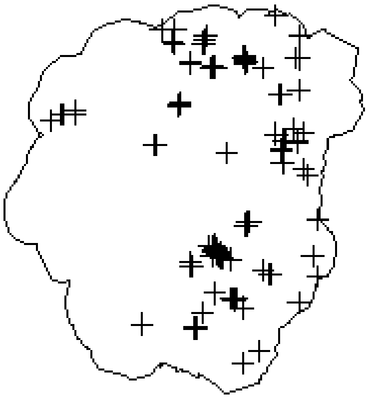
```
plot(fourth_je, main="Fourth Rivers (intermediate Je)")
```



```
plot(minor_je, main = "Minor Rivers Je")
```



```
#Creat a variables collection

  env_je<-stack(hand.je,elevation_je,slope_je,sea_je,main_je,third_je,fourth_je,minor_je)
  env.je.mask<-hand.je.mask*elevation.je.mask*slope.je.mask*sea.je.mask*main.je.mask*third.je.mask*fourth.je.mask*minor.je.mask
  env_je<-env_je*env.je.mask
names(env_je)<-c('hand','elevation','slope','sea','main', 'third','fourth','minor')
projection(env_je)<-"+proj=longlat +datum=WGS84"


#Import the occurrence points of Southern-Je Archaeological Sites.We make available a part of the points that we use (those that are already published and that were not given by third parties) in the named file "S1B_POINTS.csv"


je_pt<-read.csv("S1B_POINTS.csv", sep=",",dec=".", header=T, row.names=NULL)
je_pt.spdf<-SpatialPointsDataFrame(je_pt[,c(1,2)],je_pt, proj4string=CRS("+init=epsg:4326"))
je_pt.spdf<-spTransform(je_pt.spdf, CRS("+proj=longlat +datum=WGS84"))
plot(je_occ)
plot(je_pt.spdf, add=T, main="Souther-Je Occurrence Points")
```



```
#ENM

library(ENMeval)
bck.na_je<-env_je[[1]]
bck.na_je[]<-NA
r.je<-rasterize(coordinates(je_pt.spdf),bck.na_je,fun='count')
je.pa<-rasterToPoints(r.je,fun=function(x){x>0}, spatial=T)
set.seed(1234)
bg_je<-randomPoints(env_je[[1]],5000)

## Warning in randomPoints(env_je[[1]], 5000): generated random poin
ts =
## 0.8836 times requested number

 #ENMevaluate: In this step, several models are generated, which are
ordered to select the models with the highest AUC and the lowest ove
rfitting. It is computationally expensive, so the commands are isola
ted by "#". Select model is below.
# mje<- ENMevaluate(env=env_je, occ=coordinates(je.pa), bg.coords=bg
_je,                 RMvalues=seq(0.5,4,0.5),                 fc=c("L","
LQ","LQP", "H", "LQH"),              method="randomkfold",kfolds=4,
parallel = T)

#mje@results
#plot(mje@results)
#mje@predictions
#plot(mje@predictions)
#mje@models  #: list of model objects
```

```
#mje@occ.pts     #: data.frame of occurrence coordinates
#mje@occ.grp     #: vector of bins for occurrence points
#mje@bg.pts      #: data.frame of background coordinates
#mje@bg.grp

#ord<-order(mje@results$avg.diff.AUC, decreasing=T)


#Below is the selected model, which presented the best balance betwe
en auc and overfitting. # feature = LQP rm = 4 auc = 0.7
lqp.4<-maxent(env_je, p=je.pa, a=bg_je,
            removeDuplicates=TRUE,
            args=c("-P", 'outputformat=raw', 'noautofeature',
                   'nothreshold', 'nohinge','noaddsamplestobackgroun
d',
                   'betamultiplier=4'))

## Warning in .local(x, p, ...): 2 (2.86%) of the presence points ha
ve NA
## predictor values

plog.lqp4<- predict(lqp.4, env,args=c('outputformat=logistic'))
plog.lqp4.def<-calc(plog.lqp4, fun=mean)
```