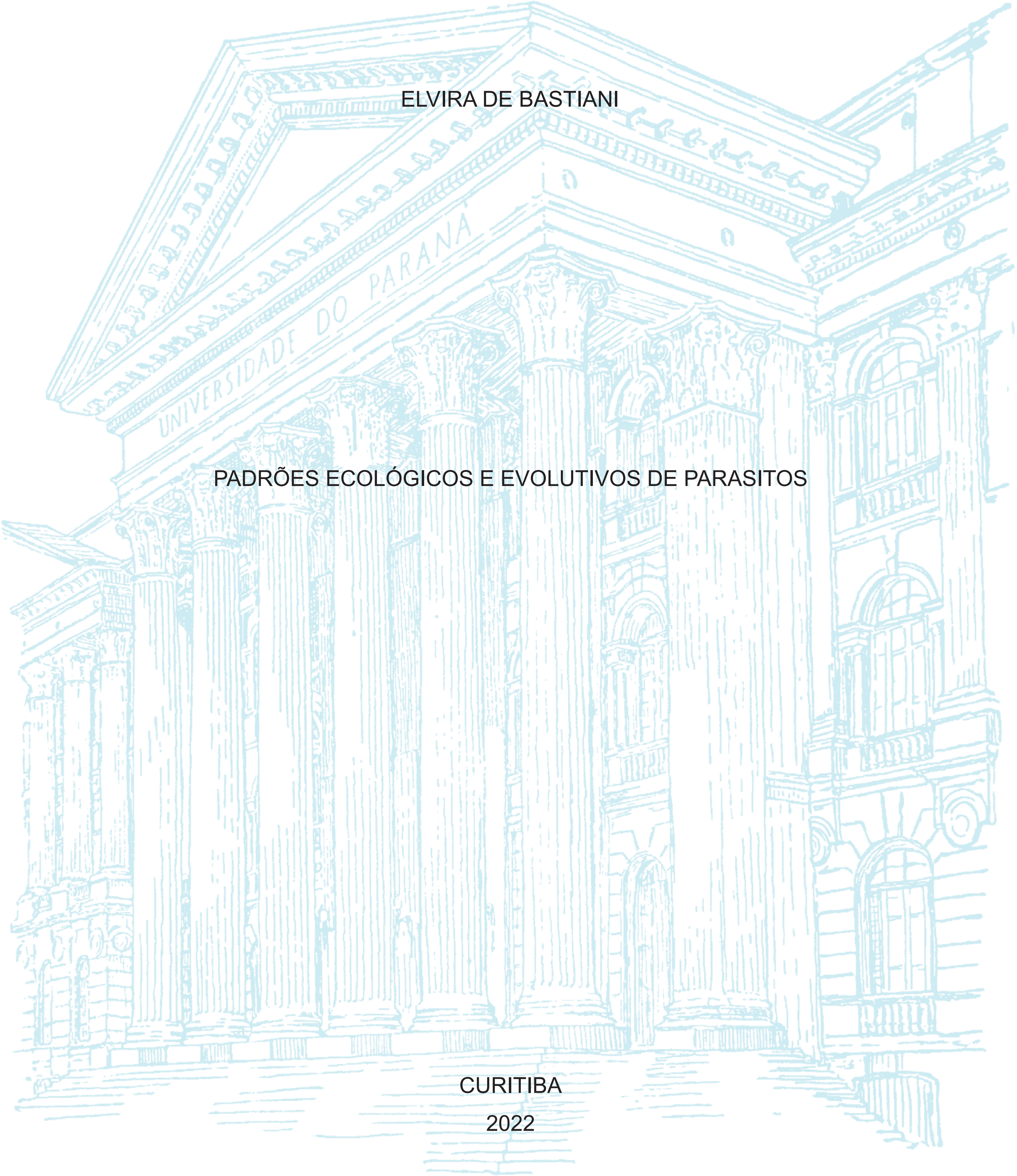
UNIVERSIDADE FEDERAL DO PARANÁ



ELVIRA DE BASTIANI

# PADRÕES ECOLÓGICOS E EVOLUTIVOS DE PARASITOS

CURITIBA
2022

ELVIRA DE BASTIANI

# PADRÕES ECOLÓGICOS E EVOLUTIVOS DE PARASITOS

Tese apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutora em Ecologia e Conservação.

Orientadora: Prof(a). Dr(a). Sabrina Borges Lino Araujo
Coorientadora: Prof(a). Dr(a). Karla Magalhães Campião

CURITIBA

2022

DADOS INTERNACIONAIS DE CATALOGAÇÃO NA PUBLICAÇÃO (CIP)
UNIVERSIDADE FEDERAL DO PARANÁ
SISTEMA DE BIBLIOTECAS – BIBLIOTECA DE CIÊNCIAS BIOLÓGICAS

De Bastiani, Elvira
Padrões ecológicos e evolutivos de parasitos / Elvira De Bastiani. – Curitiba, 2022.
1 recurso on-line : PDF.

Tese (Doutorado) – Universidade Federal do Paraná, Setor de Ciências Biológicas, Programa de Pós-Graduação em Ecologia e Conservação.
Orientadora: Prof(a). Dr(a). Sabrina Borges Lino Araujo.
Coorientador: Prof(a). Dr(a). Karla Magalhães Campião.

1. Parasitismo. 2. Relação hospedeiro-parasito. 3. Ecologia animal. I. Araújo, Sabrina Borges Lino, 1982- . II. Campião, Karla Magalhães, 1985-. III. Universidade Federal do Paraná. Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação. IV. Título.

Bibliotecária: Giana Mara Seniski Silva CRB-9/1406

MINISTÉRIO DA EDUCAÇÃO
SETOR DE CIÊNCIAS BIOLÓGICAS
UNIVERSIDADE FEDERAL DO PARANÁ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO ECOLOGIA E CONSERVAÇÃO - 40001016048P6

# TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **ELVIRA DE BASTIANI** intitulada: **PADRÕES ECOLÓGICOS E EVOLUTIVOS DE PARASITOS**, sob orientação da Profa. Dra. SABRINA BORGES LINO ARAÚJO, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutora está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

CURITIBA, 06 de Maio de 2022.

Assinatura Eletrônica
09/05/2022 13:52:28.0
SABRINA BORGES LINO ARAÚJO
Presidente da Banca Examinadora

Assinatura Eletrônica
09/05/2022 14:48:38.0
MARCUS ALOIZIO MARTINEZ DE AGUIAR
Avaliador Externo (UNIVERSIDADE ESTADUAL DE CAMPINAS)

Assinatura Eletrônica
09/05/2022 11:30:56.0
PAULO ROBERTO GUIMARAES JUNIOR
Avaliador Externo (UNIVERSIDADE DE SÃO PAULO)

Assinatura Eletrônica
09/05/2022 16:33:00.0
MARIANA PIRES BRAGA
Avaliador Externo (DEPARTMENT OF ECOLOGY, SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES)

MINISTÉRIO DA EDUCAÇÃO
SETOR DE CIÊNCIAS BIOLÓGICAS
UNIVERSIDADE FEDERAL DO PARANÁ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO ECOLOGIA E CONSERVAÇÃO - 40001016048P6

**ATA Nº231**

# ATA DE SESSÃO PÚBLICA DE DEFESA DE DOUTORADO PARA A OBTENÇÃO DO GRAU DE DOUTORA EM ECOLOGIA E CONSERVAÇÃO

No dia seis de maio de dois mil e vinte e dois às 14 horas, na sala https://teams.microsoft.com/l/meetup-join/19%3AVO_n9aQTn4d1spcaMLoR6H45-O86gjod3E78clhqMJY1%40thread.tacv2/1649275160828?context=%7B%22Tid%22%3A%22c37b37a3-e9e2-42f9-bc67-4b9b738e1df0%22%2C%22Oi, Modalidade Videoconferência, foram instaladas as atividades pertinentes ao rito de defesa de tese da doutoranda **ELVIRA DE BASTIANI**, intitulada**: PADRÕES ECOLÓGICOS E EVOLUTIVOS DE PARASITOS**, sob orientação da Profa. Dra. SABRINA BORGES LINO ARAÚJO. A Banca Examinadora, designada pelo Colegiado do Programa de Pós-Graduação ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná, foi constituída pelos seguintes Membros: SABRINA BORGES LINO ARAÚJO (UNIVERSIDADE FEDERAL DO PARANÁ), MARCUS ALOIZIO MARTINEZ DE AGUIAR (UNIVERSIDADE ESTADUAL DE CAMPINAS), PAULO ROBERTO GUIMARAES JUNIOR (UNIVERSIDADE DE SÃO PAULO), MARIANA PIRES BRAGA (DEPARTMENT OF ECOLOGY, SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES). A presidência iniciou os ritos definidos pelo Colegiado do Programa e, após exarados os pareceres dos membros do comitê examinador e da respectiva contra argumentação, ocorreu a leitura do parecer final da banca examinadora, que decidiu pela APROVAÇÃO. Este resultado deverá ser homologado pelo Colegiado do programa, mediante o atendimento de todas as indicações e correções solicitadas pela banca dentro dos prazos regimentais definidos pelo programa. A outorga de título de doutora está condicionada ao atendimento de todos os requisitos e prazos determinados no regimento do Programa de Pós-Graduação. Nada mais havendo a tratar a presidência deu por encerrada a sessão, da qual eu, SABRINA BORGES LINO ARAÚJO, lavrei a presente ata, que vai assinada por mim e pelos demais membros da Comissão Examinadora.

CURITIBA, 06 de Maio de 2022.

Assinatura Eletrônica
09/05/2022 13:52:28.0
SABRINA BORGES LINO ARAÚJO
Presidente da Banca Examinadora

Assinatura Eletrônica
09/05/2022 14:48:38.0
MARCUS ALOIZIO MARTINEZ DE AGUIAR
Avaliador Externo (UNIVERSIDADE ESTADUAL DE CAMPINAS)

Assinatura Eletrônica
09/05/2022 11:30:56.0
PAULO ROBERTO GUIMARAES JUNIOR
Avaliador Externo (UNIVERSIDADE DE SÃO PAULO)

Assinatura Eletrônica
09/05/2022 16:33:00.0
MARIANA PIRES BRAGA
Avaliador Externo (DEPARTMENT OF ECOLOGY, SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES)

*Dedico minha tese à:*
*todos os pesquisadores e cientistas*
*que fazem ciência de qualidade e lutam por uma educação de qualidade*
*e gratuita no nosso país;*

*às minhas orientadoras por toda dedicação, ensinamentos e carinho durante*
*os seis anos e meio de orientação. Sem vocês meus dias do mestrado e doutorado não*
*teriam sido os mesmos! Vocês são ótimas!;*

*e à minha mãe Marta, meu pai Alvir, meu irmão Marlos, minha irmã Carla,*
*meu namorado Andrey, a minha cunhada Patrícia e aos meus amados sobrinhos Maria*
*Clara e Pedro, por sempre me apoiarem e por serem o*
*meu porto seguro. Amo muito vocês.*

# AGRADECIMENTOS

Primeiramente gostaria de agradecer a minha família por me apoiarem. Dedico o meu doutorado a vocês. Pai (Alvir) e mãe (Marta), vocês foram os primeiros exemplos que eu segui, vocês me ensinaram que se eu quiser alguma "coisa", eu preciso "correr" atrás e que meus sonhos são possíveis. Marlos (meu irmão) obrigada por todo apoio, sua ajuda foi essencial para eu chegar até aqui. Carla (minha irmã), obrigada por todas as conversas e apoio durante o meu mestrado e doutorado, ter sua companhia durante esse período, foi sem dúvidas essencial para me manter feliz morando em Curitiba longe da nossa família. Pati (minha cunhada) obrigada por sempre me lembrar que sem o meu bem-estar, não existia doutorado, obrigada pelas conversas e por ter me dado dois sobrinhos maravilhosos, que me fazem uma pessoa ainda mais feliz. Maria Clara e Pedro (meus sobrinhos), espero que vocês leiam estes agradecimentos algum dia. Morar longe de vocês não é fácil, sinto muita falta de vocês, de presenciar cada coisa nova que vocês fazem e apreendem! Mas, cada momento que passamos juntos, é uma delícia! Eu amo ensinar vocês a pegar sapos e insetos na casa do Nonno Vico e da Nonna Marta! Me faltam palavras pra agradecer, mas enfim - amo muito vocês e muito obrigada por tudo! Andrey, eu agradeço muito pelo seu carinho, compreensão, parceria, conversas sobre a vida, e o apoio incondicional durante os últimos dois anos! Obrigada por ser o meu companheiro! Espero ter você na minha vida pra sempre! Amo você!

Foram muitas as pessoas que contribuíram para o meu desenvolvimento profissional e é difícil demonstrar em poucas palavras o quanto sou grata a todos vocês. Me perdoem caso eu esqueça de alguém! Mas deixo aqui os meus sinceros agradecimentos a todos que conviveram comigo durante os últimos e contribuiram de alguma forma durante a execução deste projeto! Todos vocês contribuíram para o meu desenvolvimento pessoal e profissional.

Agradeço a Sabrina (Sá), minha orientadora, por toda a dedicação, carinho e tempo que dedicou durante estes seis anos à mim. Você é uma das minhas inspirações! E não tenho dúvidas de que sua orientação foi fundamental para a minha formação profissional! Aprendi muito com você e tenho muito orgulho de ter sido sua aluna, muito mesmo! Muito obrigada por me aceitar como sua orientada, por me ensinar a desconfiar das minhas análises e resultados, por ter acreditado/apostado em mim e por ter me ensinado sobre o que é modelagem teórica! Obrigada por todos os conselhos e sugestões durante estes últimos seis anos. Te admiro muito Sá! Por toda sua história e por ser quem você é!

Agradeço muito a Karla, minha coorientadora, por toda a dedicação, carinho e tempo que também dedicou durante estes seis anos à mim. Você também é uma das minhas inspirações! E também não tenho dúvidas de que sua orientação foi fundamental para a minha formação profissional. Aprendi muito com você e tenho muito orgulho de ter sido sua aluna! Muito obrigada por me aceitar como sua aluna, por me ensinar sobre ecologia e principalmente por me ensinar sobre ecologia de parasitos! Sua paixão por parasitos e pela ciência me inspira muito! Obrigada por todos os conselhos, sugestões durante estes últimos seis anos Karla, te admiro muito!

Aos meus amigos e colegas do Laboratório de Interações Biológicas, prof. Walter A. Boeger, Rafael Baggio (oooh Baggioo..me ajuda aqui), Sofia Galvão Feronato (Calma Elvira!!), Allan Alvarenga, Pedro Bolanho, Marcelo Borges, Angie Souza, Simone Czarnobai, Osmar Freitas, Juliana Ciccheto, Rafael Euclydes, Lucimara Silveira, Sandro P. Faria, Cauê Pinheiro Teixeira , Gabriel de La Torre e "demais integrantes" muito obrigada por todas as conversas, discussões, colaborações, revisões e outras ajudas durante estes últimos quatro/seis anos! Dividir um espaço no mesmo laboratório com vocês foi uma experiência incrível! Sinto falta das nossas conversas durante o cafezinho!

Agradeço ao Programa de Pós-Graduação em Ecologia e Conservação, aos professores e colegas com quem convivi nestes últimos anos, foi muito enriquecedor conviver e conversar sobre ecologia com vocês! Agradeço o comprometimento das pessoas envolvidas no nosso programa de pós-graduação, obrigada por contribuírem com o desenvolvimento das nossas pesquisas. Agradeço em especial, aos coordenadores e professores que atuaram no colegiado durante os últimos anos, André Padial e Karla Campião, Rosana Moreira da Rocha, Lucelia Donatti por todo o suporte prestado a mim e aos outros alunos. Agradeço também a nossa secretária Juliana Aparecida da Silva Leao por toda atenção e suporte.

Agradeço a Débora Principe, nossa colaboradora, por toda dedicação, suporte e sugestões durante o desenvolvimento do nosso modelo teórico. Muito obrigada Dé, adoro suas sugestões, sempre construtivas e bem estruturadas, isso me inspira muito! Agradeço também ao professor Marcus Aguiar, a Flávia M.

Marquitti e ao laboratório do professor Marcus (UNICAMP), por todas as conversas e sugestões sobre o modelo teórico do capítulo um.

Agradeço ao professor Niklas Janz por todas as conversas e suporte durante as seleções de doutorado-sanduíche. Sempre muito receptivo às minhas ideias, espero que possamos tirar os nossos projetos do papel em breve!

Agradeço ao professor Boris R. Krasnov, também sempre muito receptivo às minhas ideias e respondendo super rápido as minhas dúvidas e perguntas. Foi lendo os seus trabalhos e principalmente o seu livro "*Functional and Evolutionary Ecology of Fleas: a model for ecological parasitology.*" que me encantei pela associação pulga-roedor! São organismos fantásticos! Espero no futuro continuar estudando estes organismos!

Durante o doutorado participei de escolas que tiveram muita importância para o meu crescimento enquanto pesquisadora e cientista. Gostaria de agradecer aos organizadores, professores e alunos da *IX Southern-Summer School on Mathematical Biology* e da *School on Community Ecology: from patterns to principles* por todo conhecimento que ensinado durante estas escolas.

Gostaria de agradecer também ao Guimarães Lab (USP), coordenado pelo professor Paulo R. Guimarães Jr. (Miúdo). Quase no final do meu doutorado participei/estou participando do "*Virtual Traineeship*" do Guimarães Lab. Gente, muito obrigada!! Especialmente a Kate Maia, Leandro G. Cosmo, Pâmela Friedemann e Lucas Nascimento (Taio)! Em plena pandemia, trabalhando em casa durante os últimos dois anos do meu doutorado, apresentar meu modelo, explicar e conversar com vocês foi muito importante nessa reta final do doutorado. Foram conversas que direcionaram os meus pensamentos para outros horizontes da Ecologia de interações. Obrigada!

Agradeço ao professor André de Camargo Guaraldo por todas as conversas e suporte durante as análises estatísticas referente ao capítulo dois, muito obrigada André. Gostaria de agradecer ao Teacher Daves Reyes por toda paciência durante as minhas aulas de inglês e também pelas correções dos meus manuscritos. Gostaria de agradecer também a Val, por todo carinho e atenção durante estes últimos anos. Você me ajudou muito. Obrigada por todo apoio e suporte.

Agradeço ao Douglas Viana, Lais Grossel, e a Carla de Bastiani, por compartilharem o apartamento comigo em Curitiba. Meus dias foram tranquilos com vocês do meu lado! Agradeço também às meninas e mulheres que participam das atividades do nosso projeto “Mulheres na Ecologia”! Vocês são demais! E também me inspiram muito! Adoro receber e ler a biografia de vocês!

E por fim gostaria de agradecer à Coordenação Brasileira de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de doutorado durante estes quatro anos e a Universidade Federal do Paraná por todo suporte.

*Se der medo, vai com medo mesmo!*
(Autor desconhecido)

*A gente cresce com uma sociedade ditando que temos que ser "perfeitos", mas a realidade não é bem assim. Errar também é aprendizado e está tudo bem!*
(D'Bastiani, e. 2022)

# RESUMO

O parasitismo é um estilo de vida fascinante e extremamente bem sucedido entre os animais. Uma ideia tradicional sobre a associação parasito-hospedeiro é que parasitos são altamente especializados em seus hospedeiros e, portanto, a coespeciação poderia ser esperada. No entanto, existem muitas evidências de que parasitos são amplamente capazes de incorporar novos hospedeiros com histórias evolutivas independentes e isso não resultaria em coespeciação. Espera-se que a incorporação e o compartilhamento de novas espécies de hospedeiros sejam mediados principalmente pela compatibilidade e oportunidade de interação no tempo e espaço, mas pouco se sabe sobre como estes fatores afetam a dinâmica ecológica e evolutiva das espécies de parasitos. Durante meu doutorado busquei entender como os eventos de troca de hospedeiro influenciam a ecologia e a evolução de espécies de parasitos. A minha tese é formada por três capítulos. No primeiro capítulo investigamos como a intensidade da troca de hospedeiros, mediada pela distância filogenética dos hospedeiros, afeta os padrões ecológicos e evolutivos das espécies de parasitos. Desenvolvemos um modelo baseado em indivíduos que permite a diversificação dos parasitos ao longo da história evolutiva dos hospedeiros. Observamos que existe uma faixa ótima de intensidade de troca de hospedeiro que pode reproduzir padrões eco-evolutivos observados em estudos empíricos. Além disso, observamos que estudos empíricos de escala espacial local têm uma maior intensidade de troca de hospedeiros quando comparados a estudos regionais. Isso indica que a escala espacial é provavelmente uma limitação crucial dos eventos de troca de hospedeiro. No segundo capítulo utilizamos nosso modelo para avaliar como os atributos funcionais e a variabilidade filogenética dos hospedeiros podem estar associadas aos eventos de troca de hospedeiro. Analisando dez estudos empíricos de interação pulga-roedor, observamos que a intensidade de troca de hospedeiro prevista variou entre os estudos empíricos analisados. Tal variação não foi associada à diversidade funcional e nem com a variabilidade filogenética dos hospedeiros de cada estudo empírico, mas pode estar associada à média de cada atributo funcional das espécies de hospedeiros (massa corporal, amplitude da dieta, área de vida, densidade populacional e tamanho da ninhada). No terceiro capítulo nós analisamos a variação na composição de comunidades de parasitos entre espécies de hospedeiros por meio de uma abordagem clássica de ecologia de comunidades. O objetivo deste estudo foi investigar: (i) Qual é o componente da diversidade beta (aninhamento ou *turnover*) que mais contribui para a composição de parasitos entre as espécies de anuros; (ii) Se diversidade beta de parasitos difere de um padrão aleatório? e se (iii) A dissimilaridade na composição das comunidades de parasitos está relacionada à dissimilaridade filogenética ou funcional dos anuros. Utilizamos seis estudos empíricos de interações entre endoparasitos e anuros. Observamos que o *turnover* de espécies de parasitos entre as espécies de anuros foi o principal componente da diversidade beta, mas a variação observada na diversidade beta total e em seus componentes não diferiram dos respectivos modelos nulos. Nossos resultados de dissimilaridade de parasitos entre as comunidades não foram relacionados à variabilidade filogenética das espécies de hospedeiros e nem com dissimilaridade funcional das espécies de anuros para a maioria das localidades analisadas. Nossos resultados indicam um processo de rastreamento de recursos pelas espécies de parasitos.

**Palavras-chave**: composição de comunidades, dinâmica ecológica e evolutiva dos parasitos, interações, modelo baseado em indivíduos, parasitismo e troca de hospedeiro.

# ABSTRACT

Parasitism is a fascinating and extremely successful lifestyle among animals. A traditional idea about the parasite-host association is that parasites are highly specialized in their hosts and therefore cospeciation could be expected. However, there is much evidence that parasites are largely capable of incorporating new hosts with independent evolutionary histories and this would not result in cospeciation. The incorporation and sharing of new host species are expected to be mediated mainly by compatibility and opportunity for interaction in time and space, but little is known about how these factors affect the ecological and evolutionary dynamics of parasite species. During my PhD, I tried to understand how host-switching events influence the ecology and evolution of parasite species. My thesis consists of three chapters. In the first chapter, we investigated how the intensity of host-switching, mediated by the phylogenetic distance of the hosts, affects the ecological and evolutionary patterns of parasite species. We developed a model based on individuals that allow the diversification of parasites throughout the evolutionary history of the hosts. We observed that there is an optimal range of host-switching intensity that can reproduce eco-evolutionary patterns observed in empirical studies. Furthermore, we observed that empirical studies of local spatial scale have a higher intensity of host-switching when compared to regional studies. This indicates that spatial scale is likely to be a crucial limitation of host switching events. In the second chapter, we use our model to assess how the functional attributes and phylogenetic variability of hosts may be associated with host-switching events. Analyzing ten empirical studies of flea-rodent interaction, we observed that the predicted host-switching intensity varied among the analyzed empirical studies. Such variation was not associated with functional diversity nor with the phylogenetic variability of the hosts of each empirical study, but it may be associated with the average of each functional attribute of the host species (body mass, diet amplitude, home range, population density and litter size). In the third chapter, we analyze the variation in the composition of parasite communities between host species using a classical community ecology approach. This study aimed to investigate: (i) What is the component of beta diversity (nestedness or turnover) that most contributes to the composition of parasites among anuran species; (ii) Whether beta diversity of parasites differ from a random pattern? and if (iii) The dissimilarity in the composition of the parasite communities is related to the phylogenetic or functional dissimilarity of the anurans. We used six empirical studies of interactions between endoparasites and anurans. We observed that the turnover of parasite species among frog species was the main component of beta diversity, but the variation observed in total beta diversity and its components did not differ from the respective null models. Our results of parasite dissimilarity between communities were not related to the phylogenetic variability of the host species nor the functional dissimilarity of the anuran species for most of the analyzed localities. Our results indicate a resource tracking process by the parasite species.

**Keywords**: community composition, ecological and evolutionary dynamics of parasites, interactions, individual-based model, parasitism and host-switching.

# LISTA DE FIGURAS

Capítulo 1

Capítulo 2

Capítulo 3

# LISTA DE TABELAS

**Capítulo 1**

**Capítulo 2**

**Capítulo 3**

# LISTA DE ABREVIATURAS OU SIGLAS

$\tau_{a}$ - Minimal time for parasites to speciate due to isolation by host use
$P_{hs}(n)$ - Host-switching probability
*ID* - Empirical study
$HSI_{C}$ - Host-switching intensity of the community
$HSI_{S}$ - Host-switching intensity by host species
$I_{n}$ - Normalised Sackin index
$\beta_{SIM}$ - Turnover
*SES.PD* - Functional diversity

*PSVs* - Phylogenetic species variability

*BM* - Adult body mass

*DB* - diet breadth

*PD* - population density

*HR* - home range

*LS* - litter size

*C* - Rodent communities

*S* - Host species

*LMM* - Generalised mixed-effects model

*FD* - Functional diversity

$\beta_{SOR}$ - Total beta diversity
$\beta_{NES}$ - Nestedness
*ANC* - Anchieta
*CAS* - Caseara
*DIN* - Diamante do Norte
*PAN* - Pantanal
*PER* - Pernambuco
*PAR* - Paraitinga

# SUMÁRIO

## Introdução geral

O parasitismo é um estilo de vida fascinante e extremamente bem sucedido entre os animais. Acredita-se que todo organismo de vida livre abriga pelo menos uma espécie de parasito. O sistema parasito-hospedeiro é um bom modelo biológico para estudar a ecologia e a evolução, porque a diversificação das espécies de parasitos está relacionada à ecologia e evolução de seus hospedeiros. A maior parte dos parasitos sobrevivem e se reproduzem com necessidade de uma outra espécie, seja de forma direta ou indireta. Em particular, as associações atuais entre as espécies de parasitos e seus hospedeiros foram moldadas por eventos históricos e provavelmente as espécies de parasitos enfrentaram muitas barreiras para se reproduzirem, sobreviverem e permanecerem interagindo com seus hospedeiros.

Uma das características mais intrigantes dos parasitos é a relação íntima com seus hospedeiros em escalas temporais ecológicas e evolutivas. Historicamente, pensava-se que os parasitos eram altamente específicos com os seus hospedeiros (veja Brooks & McLennan 2002;  Ehrlich & Raven 1964). Isso é especialmente verdadeiro para a suposição de que hospedeiros e parasitos “deveriam” ter filogenias congruentes. Porém este cenário seria um *beco evolutivo sem saída* (do inglês - *inherent evolutionary ‘dead end’* - Moran 1988; Wiegmann et al. 1993; Agosta et al. 2010) pois quando os hospedeiros coevoluídos fossem extintos, os parasitos também seriam por falta de alternativa. Essa visão da coevolução parasito-hospedeiro como um processo determinado principalmente por eventos de coespeciação mudou completamente nos últimos anos, principalmente devido às frequentes trocas de espécies de hospedeiros observadas empiricamente (Veja Meinilä et al. 2004; Woolhouse et al. 2005; Agosta et al. 2010; Habermannová et al. 2013; Nylin et al. 2014; Dominguez et al. 2015; Müller et al. 2018; Boyd et al. 2022).

Essa mudança levou ao reconhecimento de que as espécies de parasitos não são apenas "*companheiras*" passivos de suas espécies hospedeiras, mas sim organismos com sua própria biologia e características independentes do seu hospedeiro (Mácová 2018).

Uma vez que o padrão de cofilogenia de co-especiação foi rejeitado como um fator predominante da especiação e distribuição das espécies de parasitos entre as espécies de hospedeiros, hipóteses alternativas foram desenvolvidas. O ajuste ecológico (do inglês *Ecological fitting* - Agosta & Klemens 2008), por exemplo, é uma hipótese bem estabelecida, que tem sido adotada como um mecanismo para a colonização de novos hospedeiros por uma espécie de parasito (Agosta et al. 2010; Araujo et al. 2015). Esta hipótese prevê que, em alguns casos, as adaptações evoluíram em um hospedeiro particular e podem permitir que o organismo sobreviva sob diferentes condições e colonize com sucesso o novo hospedeiro. Quando os organismos parasitos encontram novas condições (oportunidade ecológica), estes organismos sobrevivem e persistem, e se coacomodam usando as características que já possuem (pré-existentes) no momento do contato (Janzen 1980; 1985; Brooks & McLennan 2002; Agosta & Klemens 2008). Essa coacomodação não é um ponto final, mas um passo fundamental no processo de expansão e evolução biológica em resposta às mudanças ambientais (Hoberg & Brooks 2008; 2013; Brooks & Agosta 2012; Mácová 2018).

Existem alguns mecanismos que podem contribuir para a ocorrência de eventos de troca de hospedeiro por ajuste ecológico. Primeiro, a plasticidade fenotípica pode permitir que os genótipos expressem o potencial latente de colonizar e possivelmente se adaptar a novas condições (Agosta & Klemens 2008). Em segundo lugar, os traços não evoluem independentemente. A evolução da característica correlacionada, no qual a seleção direta na característica A pode causar seleção indireta na característica B e vice-versa (Lande & Arnold 1983; Agosta & Klemens 2008), pode produzir fenótipos emergentes que são pré-adaptados a alguma condição nova futura. E por último, parte da informação genética é conservada dentro de linhagens filogenéticas. O conservadorismo filogenético de características relacionadas ao uso de recursos pode fornecer o potencial latente para os parasitos terem sucesso sob novas condições. Nesse cenário, um parasito que contata uma nova espécie de hospedeiro teria sucesso porque o novo hospedeiro é suficientemente semelhante a algumas espécies hospedeiras ancestrais (Brooks & McLennan 2002; Agosta & Klemens 2008). Assim, em resumo, o fato de que os genótipos são fenotipicamente plásticos, que as características não evoluem independentemente e que a informação genética é conservada dentro de linhagens filogenéticas dá origem ao chamado espaço de aptidão relaxado (do inglês *sloppy fitness space* - Agosta & Klemens 2008).

O espaço de aptidão relaxado refere-se à diferença entre o que um parasito está fazendo (realizado) e o que o parasito poderia fazer (fundamental). Portanto, quanto maior for essa diferença (tempo e espaço) para uma espécie de parasito, maior será a possibilidade de o parasito persistir quando o ambiente em que vive mudar (Brooks & Agosta 2012). Para esses organismos, este espaço de aptidão relaxado oferece uma ampla capacidade de rastrear recursos de hospedeiros filogeneticamente conservados ou convergentes. E com isso, o uso de novas espécies de hospedeiros depende do nível de equivalência ecológica e fisiológica entre a espécie de hospedeiro e a espécie de parasito (Harvey et al. 2012). Portanto, mudar para uma espécie de hospedeiro filogeneticamente semelhante ao hospedeiro original deve ser mais fácil do que mudar para espécies de hospedeiros muito diferentes do hospedeiro original (Charleston & Robertson 2002). Assim, quanto maior a distância filogenética entre o novo e o hospedeiro original menor a probabilidade da espécie de parasito persistir (Brooks & Agosta 2012).

Afim de se reunir novos arcabouços teóricos que explicam a associação parasito-hospedeiro, recentemente foi proposto o "*Paradigma de Estocolmo*". Além da hipótese do ajuste ecológico mencionado acima, outros três conceitos são combinados (Brooks et al. 2019). A (i) Teoria da coevolução do mosaico geográfico; (ii) Hipótese de Pulso de táxons; e a (iii) Hipótese de Oscilação. A *Teoria do Mosaico Geográfico da Coevolução* analisa como a biologia das espécies fornece a matéria-prima para a coevolução de longo prazo. Considera como a coadaptação local forma o módulo básico da mudança coevolutiva, e explora como o processo coevolutivo remodela as interações nas paisagens em constante mudança. Essa teoria incorpora os efeitos da distribuição geográfica heterogênea de espécies de parasitos e hospedeiros sobre as dinâmicas evolutivas (Thompson 2005). Essa teoria permite, mas não exige, a evolução recíproca das características de defesa e contra defesa, e destaca que é o isolamento geográfico que leva à diversificação. A hipótese de *Pulso de táxons* refere-se tanto a dispersão quanto a especiação isoladamente, incluindo a diversificação ecológica em aspectos filogenéticos que ocorrem em períodos relativamente longos. Estes períodos são caracterizados pela expansão e contração do uso de ambientes ao longo do tempo evolutivo (Erwin 1985; Hoberg & Brooks 2010). Essa expansão e retração acontece devido a existência de barreiras que mudam ao longo do tempo e alteram as relações do ambiente de origem. E por fim, a *Hipótese de Oscilação* postula que as linhagens de patógenos passam por fases alternadas de expansão e restrição do uso de recursos, prevendo uma relação positiva entre a ocorrência e a amplitude dessas oscilações e a taxa de diversificação, pois são os ancestrais generalistas que dão origem a novas espécies especialistas (Janz & Nylin 2008; Nylin et al. 2014). Em escalas de tempo relativamente curto e  escalas espaciais pequenas, as oscilações aparecem como mudanças localizadas no repertório de hospedeiros associadas a flutuações nas condições ambientais (Janz & Nylin 2008; Nylin et al. 2014). De forma geral, o Paradigma de Estocolmo busca compreender  questões da teoria evolutiva relacionadas às associações parasitos-hospedeiros e sua implicação no contexto de doenças emergentes (Brooks et al. 2019).

A colonização de uma nova espécie de hospedeiro levou a algumas das epidemias de doenças mais devastadoras registradas até hoje, incluindo a pandemia de HIV/AIDS em comunidades humanas em todo o mundo (Hahn et al. 2000), a dizimação da população de coelhos europeus por mixomatose em meados do século XX, e o impacto catastrófico da peste bovina em ruminantes africanos durante o final do século XIX (Fenner & Fantini 1999; Hahn et al. 2000; Hudson et al. 2002). Foi até argumentado que muitas das principais doenças mortais de humanos (por exemplo, sarampo, tuberculose, gripe e varíola) surgiram através de patógenos que saltaram de animais domésticos para humanos no passado (Diamond 2002). Os saltos de espécies também deram origem a epidemias devastadoras de patógenos de plantas em espécies cultivadas (como por exemplo de batata) e em espécies de plantas selvagens (por exemplo, a quase extinção de castanheiros americanos pela praga da castanheira) (Milgroom et al. 1996; Anderson et al. 2004). E mais recentemente a pandemia de COVID-19 é uma demonstração do impacto devastador de uma doença zoonótica, pela qual provavelmente o vírus SARS-CoV-2 saltou de animais para infectar humanos (Holmes 2022).

A emergência de doenças zoonóticas parecem estar aumentando como consequência das mudanças no uso da terra, urbanização e crescente conectividade global (Jones et al. 2008; Olival  et al. 2017; Agosta & Brooks 2020; Wille et al. 2021). Os parasitos, por exemplo, durante as expansões bióticas são capazes de infectar hospedeiros aos quais nunca foram expostos, podendo ampliar seu repertório de hospedeiros (Agosta & Brooks 2020). Provavelmente é assim que a evolução produz associações persistentes (Brooks et al. 2019; Agosta & Brooks 2020). No contexto atual, as mudanças climáticas globais alteram os padrões de movimento e a distribuição geográfica das espécies juntamente com seus parasitos, e aumentam a conectividade entre espécies, facilitando que organismos explorem novas oportunidades e ambientes (Brooks et al. 2019; Agosta & Brooks 2020). Com isso novas doenças infecciosas podem surgir ou ressurgir (Brooks & Hoberg 2006; Agosta & Brooks 2020). A variação espacial também altera o conjunto de hospedeiros de uma comunidade à qual um parasito está exposto, e a capacidade pré-existente permite a troca de hospedeiros em novas oportunidades emergentes (Brooks et al. 2019; Agosta & Brooks 2020). Logo, sob uma determinada condição, as espécies de parasitos em um ambiente podem ser isoladas e especializadas e exploram essas condições “estáveis”, porém, quando esta condição muda, algumas espécies de parasitos podem ser extintas, mas esse ambiente em mudança também cria oportunidades para novas espécies colonizarem e evoluírem (Brooks et al. 2019; Agosta & Brooks 2020). Então, em vez de esperar a próxima pandemia chegar, precisamos compreender os mecanismos envolvidos na dinâmica ecológica e evolutiva dos parasitos (Brooks et al. 2019; Agosta & Brooks 2020) e utilizar este conhecimento na elaboração de políticas de saúde pública.

## MINHA TESE

A complexidade dos fenômenos ecológicos e evolutivos envolvidos durante a diversificação das espécies de parasitos me fascina [descobri durante o doutorado que sou muito feliz por estudar e tentar entender essas interações :) ]. Durante meu doutorado busquei entender como os eventos de troca de hospedeiro influenciam a ecologia e a evolução de espécies de parasitos. A minha tese é formada por três capítulos. Seguindo o arcabouço teórico apresentado na introdução, a partir da perspectiva do parasito, no primeiro capítulo exploramos como a intensidade da troca de hospedeiros, mediada pela distância filogenética dos hospedeiros, afeta os padrões ecológicos e evolutivos das espécies de parasitos por meio de um modelo teórico baseado em indivíduos que permite a diversificação dos parasitos ao longo da história evolutiva dos hospedeiros (obs: manuscrito referente a este capítulo está sob revisão). No capítulo dois utilizando o modelo teórico proposto no capítulo um, investigamos como os atributos funcionais e a variabilidade filogenética das espécies de hospedeiros podem estar associadas aos eventos de troca de hospedeiro (obs: manuscrito referente a este capítulo está sendo escrito, estamos na fase de discussão dos resultados). E por fim, no terceiro capítulo nós analisamos a variação na composição de comunidades de parasitos entre espécies de hospedeiros por meio de uma abordagem clássica de ecologia de comunidades. O manuscrito referente a este capítulo está publicado na revista *Parasitology*.

## Referências

Agosta, S. J., & Brooks, D. R. (2020). The Major Metaphors of Evolution. Series in Evolutionary Biology: New Perspectives in Its Development. Cham: Springer

Nature Switzerland.

Agosta, S. J., & Klemens, J. A. (2008). Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. Ecology Letters, 11(11), 1123-1134.

Agosta, S. J., Janz, N., & Brooks, D. R. (2010). How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. Zoologia (Curitiba), 27(2), 151-162.

Anderson, P. K., Cunningham, A. A., Patel, N. G., Morales, F. J., Epstein, P. R., & Daszak, P. (2004). Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. Trends in ecology & evolution, 19(10), 535-544.

Boyd, B. M., Nguyen, N. P., Allen, J. M., Waterhouse, R. M., Vo, K. B., Sweet, A. D., ... & Johnson, K. P. (2022). Long-distance dispersal of pigeons and doves generated new ecological opportunities for host-switching and adaptive radiation by their parasites. Proceedings of the Royal Society B, 289(1970), 20220042.

Brooks, D. R., & Agosta, S. J. (2012). Children of time: The extended synthesis and major metaphors of evolution. Zoologia (Curitiba), 29, 497-514.

Brooks, D. R., & Hoberg, E. P. (2006). Systematics and emerging infectious diseases: from management to solution. Journal of Parasitology, 92(2), 426-429.

McLennan, D. A., & Brooks, D. R. (2002). Complex histories of speciation and dispersal in communities: a re-analysis of some Australian bird data using BPA. Journal of Biogeography, 29(8), 1055-1066.

Brooks, D. R., Hoberg, E. P., & Boeger, W. A. (2019). The Stockholm paradigm: climate change and emerging disease. University of Chicago Press.

Charleston, M. A., & Robertson, D. L. (2002). Preferential host switching by primate lentiviruses can account for phylogenetic similarity with the primate phylogeny. Systematic biology, 51(3), 528-535.

Diamond, J. (2002). Evolution, consequences and future of plant and animal domestication. Nature, 418(6898), 700-707.

Dominguez, M., de la Colina, M. A., Di Giacomo, A. G., Reboreda, J. C., & Mahler, B. (2015). Host switching in cowbird brood parasites: how often does it occur?. Journal of evolutionary biology, 28(6), 1290-1297.

Ehrlich, P. R., & Raven, P. H. (1964). Butterflies and plants: a study in coevolution. Evolution, 586-608.

Erwin, T. L. (1985). The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. Taxonomy, phylogeny, and zoogeography of beetles and ants, 437-472.

Fenner, F., & Fantini, B. (1999). Biological control of vertebrate pests. CABI publishing.

Habermannová, J., Bogusch, P., & Straka, J. (2013). Flexible host choice and common host switches in the evolution of generalist and specialist cuckoo bees (Anthophila: Sphecodes). PLoS One, 8(5), e64537.

Hahn, B. H., Shaw, G. M., De, K. M., Cock, & Sharp, P. M. (2000). AIDS as a zoonosis: scientific and public health implications. Science, 287(5453), 607-614.

Harvey, J. A., Ximénez de Embún, M. G., Bukovinszky, T., & Gols, R. (2012). The roles of ecological fitting, phylogeny and physiological equivalence in understanding realized and fundamental host ranges in endoparasitoid wasps. Journal of Evolutionary Biology, 25(10), 2139-2148.

Hoberg, E. P., & Brooks, D. R. (2010). Beyond vicariance: integrating taxon pulses, ecological fitting, and oscillation in evolution and historical biogeography. The biogeography of host-parasite interactions, 7, 20.

Hoberg, E. P., & Brooks, D. R. (2008). A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. Journal of Biogeography, 35(9), 1533-1550.

Hoberg, E. P., & Brooks, D. R. (2013). 14 Episodic processes, invasion and faunal mosaics in evolutionary and ecological time. The balance of nature and human impact, 199.

Holmes, E. C. (2022). COVID-19—lessons for zoonotic disease. Science. Vol 375(6585) 1114-1115.

Hudson, P. J., Rizzoli, A., Grenfell, B. T., Heesterbeek, H., & Dobson, A. P. (Eds.). (2002). The ecology of wildlife diseases (pp. 1-5). Oxford: Oxford University Press.

Janz, N., & Nylin, S. (2008). The oscillation hypothesis of host-plant range and speciation. Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects, 2008, 203-215.

JANZEN, Daniel H. When is it coevolution? 1980.

Janzen, D. H. (1985). On ecological fitting.

Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. Nature, 451(7181), 990-993.

Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. Evolution, 1210-1226.

Mácová, A., Hoblíková, A., Hypša, V., Stanko, M., Martinů, J., & Kvičerová, J. (2018). Mysteries of host switching: Diversification and host specificity in rodent-coccidia associations. Molecular phylogenetics and evolution, 127, 179-189.

Meinilä, M., Kuusela, J., Ziętara, M. S., & Lumme, J. (2004). Initial steps of speciation by geographic isolation and host switch in salmonid pathogen Gyrodactylus salaris (Monogenea: Gyrodactylidae). International Journal for Parasitology, 34(4), 515-526.

Milgroom, M. G., Wang, K., Zhou, Y., Lipari, S. E., & Kaneko, S. (1996). Intercontinental population structure of the chestnut blight fungus, Cryphonectria parasitica. Mycologia, 88(2), 179-190.

Moran, N. A. (1988). The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. The American Naturalist, 132(5), 681-706.

Müller, M.I., Morais, D.H., Costa‐Silva, G.J., Aguiar, A., Avila, R.W. & da Silva, R.J. (2018). Diversity in the genus Rhabdias (Nematoda, Rhabdiasidae): Evidence for cryptic speciation. Zoologica Scripta, 47, 595-607.

Nylin, S., Slove, J., & Janz, N. (2014). Host plant utilization, host range oscillations and diversification in nymphalid butterflies: a phylogenetic investigation. Evolution, 68(1), 105-124.

Olival, K. J., Hosseini, P. R., Zambrana-Torrelio, C., Ross, N., Bogich, T. L., & Daszak, P. (2017). Host and viral traits predict zoonotic spillover from mammals. Nature, 546(7660), 646-650.

Thompson, J. N. (2005). The geographic mosaic of coevolution. University of Chicago Press.

Wiegmann, B. M., Mitter, C., & Farrell, B. (1993). Diversification of carnivorous parasitic insects: extraordinary radiation or specialized dead end?. The American Naturalist, 142(5), 737-754.

Wille, M., Geoghegan, J. L., & Holmes, E. C. (2021). How accurately can we assess zoonotic risk?. PLoS biology, 19(4), e3001135.

Woolhouse, M. E., Haydon, D. T., & Antia, R. (2005). Emerging pathogens: the epidemiology and evolution of species jumps. Trends in ecology & evolution, 20(5), 238-244.

# CAPÍTULO 1

## In review - Systematic Biology

# Effect of host-switching on the eco-evolutionary patterns of parasites

[1*]Elvira D'Bastiani, [2]Débora Princepe, [2,3]Flavia MD Marquitti, [1,4]Walter A Boeger, [1,4]Karla M Campião, [1,5]Sabrina LB Araujo

[1]Laboratório de Interações Biológicas, Universidade Federal do Paraná, UFPR

[2]Instituto de Física "Gleb Wataghin", Universidade Estadual de Campinas, UNICAMP

[3]Insituto de Biologia, Universidade Estadual de Campinas, UNICAMP

[4]Departamento de Zoologia, Universidade Federal do Paraná, UFPR

[5]Departamento de Física, Universidade Federal do Paraná, UFPR

***Corresponding author**: Elvira D'Bastiani e-mail: elviradbastiani@gmail.com

**Authorship statement**:

Conceived and designed the experiments: EDB, SBLA and DP

Performed the experiments and analysed the data: EDB, SBLA and DP

Wrote the paper: EDB, SLB, KMC, DP, WB, FMDM

Other contributions: EDB, DP, FMDM, WB, KMC and SLBA

**Emails**:

Elvira D'Bastiani <elviradbastiani@gmail.com>

Débora Princepe <princepe@ifi.unicamp.br>

Flavia MD Marquitti <flamarquitti@gmail.com>

Walter A Boeger <wboeger@gmail.com>

Karla M. Campião <kcampiao@gmail.com>

Sabrina LB Araujo <araujosbl@gmail.com>

**Short running title**: Host-switching influences parasite patterns

**Abstract:** Increasing empirical evidence has revealed that host-switchings are common in the history of parasites. Still, few have explored how the evolutionary histories of hosts might influence such switches and then the evolution of parasites. Here, we investigated how the intensity of host-switching, assumed to depend on the phylogenetic distance between hosts, affects the ecological and evolutionary patterns of parasite species. We developed an individual-based model where parasites can explore and colonise hosts under variable host-switching intensity and have evolution driven by mutation, genetic drift, and mating restriction. We hypothesised that our model can reproduce ecological and evolutionary patterns of empirical studies, characterised by turnover among host species and tree imbalance, respectively. We found an optimum range of host-switching intensity that can predict similar patterns as those observed in the empirical studies, validating our hypothesis. Our results showed that the turnover decreased as the host-switching intensity increased with low variation among the model replications. On the other hand, the tree imbalance had not a monotonic tendency but a wide variation. These results revealed that while the tree imbalance is a sensitive metric to stochastic events, the turnover may be a proxy for host-switching. Furthermore, local empirical studies corresponded to higher host-switching intensity when compared to regional studies, highlighting that spatial scale is probably the crucial limitation of host-switching.

**Key-words**: dispersal of parasites, opportunity and compatibility of interaction, phylogenetic conservatism, and structure of the community of parasites.

## INTRODUCTION

The dispersal of parasite individuals followed by colonisation of a new host lineage, known as host-switching, is a common event observed during the evolutionary trajectory of many parasite lineages (De Vienne et al. 2013). Initially, host-switching results in the increase of the host repertoire of a parasite (Braga et al. 2021). The colonisation of the new hosts can result in reproductive isolation, and consequently in speciation of parasite lineages, characterising the dynamics of the Oscillation Hypothesis (Nylin & Soren 2018). Empirical examples showing high levels of host-switching include symbiotic interactions ranging from host-parasite (Meinilä et al. 2004; Agosta et al. 2010; Müller et al. 2018, Fecchio et al. 2019; Boyd et al. 2022) and plant-insect systems to microbial pathogens (Woolhouse et al. 2005), brood parasitism (Habermannová et al. 2013; Dominguez et al. 2015), plant-feeding insects, and parasitic plants (Nylin et al. 2014). Consequently, understanding the factors influencing the success of host-switching and subsequent speciation events is critical for understanding parasites diversification.

A general framework that has been used to understand infectious disease, the Stockholm Paradigm, explores the evolutionary dynamics of host-parasite associations  (Brooks et al. 2014; Brooks et al. 2019). This framework suggests that parasites perform host-switching by ecological fitting hypothesis (Agosta & Klemmens 2008; Agosta & Brooks 2020). Ecological fitting explains how the process whereby organisms colonise and persist in novel environments, use novel resources, or form novel associations with other species through a set of traits/capabilities they already possess (see Agosta & Klemmens 2008; Brooks et al. 2014; Brooks et al. 2019; Agosta & Brooks 2020). The expression of these unexplored capabilities is mediated by the opportunity of interaction (temporal and spatial) and determines the possibility of encounters between hosts and unfamiliar parasites. After the encounter, and if the interaction is compatible, it is followed by the resolution of subsequent conflicts that emerge from the basic dynamics of “living together”, which should result in co-accommodation (Brooks & McLennan 2002; Araujo et al. 2015).

Ecological and life-history traits also influence the chances of parasites dispersing from one host species to another. Characteristics of all organisms within the interaction system, such as niche similarity among host species, modes of transmission of parasites, dietary preferences of the vector (if there is one), and also ecosystemic characteristics as the host community composition and shared phylogenetic history are relevant factors that define the chances of host-switching (Bush et al. 2006; Jaramillo & Rivera-Parra 2018). Niche similarity among host species is one fundamental element constraining the incorporation of new host species by ecological fitting. This is because the capacity of a parasite species to use new resources is related to the phylogenetic conservatism of the resource provided by the host species. Phylogenetic distance between the original and new host species can represent an adequate proxy for the nature of the resource, which is tracked by the parasite lineage (Charleston & Robertson 2002; Agosta & Klemmens 2008; Engelstädter & Fortuna 2019). Consequently, the host phylogenetic conservatism can define the arena of possibilities for host-switching.

Several studies have indicated the ubiquity of host-switching in nature (see Cuthill & Charleston 2013; De Vienne et al. 2013; Engelstädter & Fortuna 2019; Fecchio et al. 2019; Hayward et al. 2021), but (or yet) few studies have explored to which extent the switches are constrained by inherited possibilities and limitations across hosts evolutionary histories. Among many potential factors determining host-switching, it seems that host phylogeny and geographic distributions are two major players (Sanaei et al. 2021). Moreover, the relation between host-switching and the opportunity for parasite dispersal, as well as their capacity to explore new hosts, is mostly unexplored (Brooks et al. 2019). Here, we aim to fill these unexplored gaps by proposing a novel approach to investigate how the intensity of host-switching affects the ecology and phylogenetic history of the parasites. For this, we assume that compatibility and the opportunity for interaction (spatial and temporal) may be expressed through the evolutionary histories of the hosts, and this can influence the host-switching events.

In this study, we propose a theoretical model based on parasite individuals that can switch among host species and speciate over time. Host-switching is mediated by phylogenetic conservatism; that is, the probability of parasites switching hosts decreases with increasing divergence in the evolutionary time of the hosts. The overall intensity of host-switching is a controlled parameter of the model. Under the absence of host-switching, the model is adjusted to parasites speciate due to limitation of host use, resulting in a pattern of cophylogeny and in paired specialised interaction (each parasite species interacting with one exclusive host species). We then investigate the eco-evolutionary patterns under different host-switching intensities, hypothesising that there is an optimum range of host-switching intensity that can result in the same eco-evolutionary patterns observed in the empirical studies. These patterns were characterised by species interaction turnover and tree imbalance, respectively. The model predictions were compared to nine empirical studies, validating our hypothesis.

## MATERIAL AND METHODS

### The Model

We performed simulations of eco-evolutionary trajectories of parasites influenced by their host evolutionary history and host-switching events using an individual-based model (IBM). We assumed that the evolutionary history of the host can represent a proxy for the resources for parasite species (Agosta et al. 2010; Imrie et al. 2021), and also assumed that the probability of host-switching decreases as the phylogenetic distance between the species of host involved in the event (original and new host species) increases (Araujo et al. 2015; Engelstädter & Fortuna 2019). The model assumes that parasite evolution occurs at the same evolutionary time scale as the host, which increases possibilities for host-switching as host speciation occurs (Figure 1).

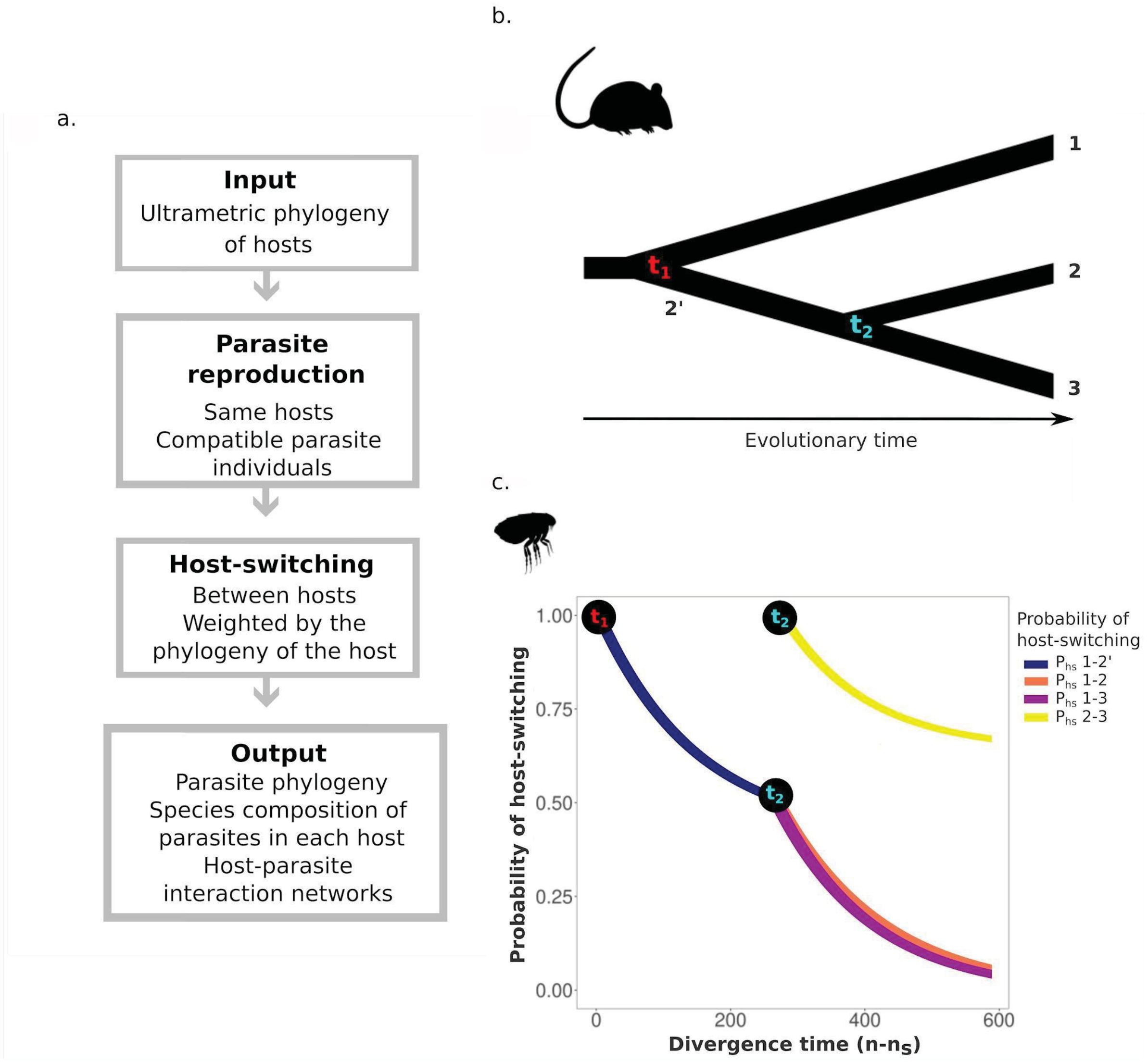


**Figure 1.** Schematic representation of the model. **a**. The general sequence of the model dynamics. **b**. Hypothetical host phylogeny. **c**. Probability of host-switching ($P_{hs}$) over time. Each parasite individual can host-switch after the first speciation event ($t_1$). One host is drawn for each parasite individual, and the probability of a successful host-switching depends on the divergent time between the two involved hosts. At $t_1$ the first speciation event occurs and the probability of host-switching is maximum. As time goes on, this probability decreases. At $t_2$ another speciation event occurs, increasing the number of migration possibilities. At this time the two younger host species (2 and 3) have the maximum probability of switching hosts ($P_{hs}$ 2-3), but the probability of host-switching between 1 and 2 or between 1 and 3 keeps decreasing. The colours highlight the 2', 1, 2, and 3 host lineage presented in **b**.

Parasite individuals are explicitly described by biallelic sequences of infinite sites, a simplified form to represent their genomes and heritable trait. Individuals are monoic and engage in sexual reproduction, with non-overlapping generations, following the model proposed by Higgs & Derrida (1991) and Manzo & Peliti (1994). Population evolution is driven by mutation, genetic drift, and restriction to mating in the absence of natural selection. With a certain set of parameters, parasite speciation occurs. Each parasite individual is also characterised by the host species that it interacts. The host species are modelled as resources that impose a carrying capacity of $K$ parasite individuals, analogous to islands in the Manzo-Pelit model (Manzo & Peliti 1994), but, in our model, the islands (hosts species in our case) emerge (as a new host species that speciate) according to a predetermined host diversification time (i.e. based on ultrametric empirical phylogenies - an ultrametric tree is a kind of additive tree in which the tips of the trees are all equidistant from the root of the tree). Thus, the overall carrying capacity increases by $K$ individuals at each new host speciation. The model does not consider the selection pressure imposed by parasites on the evolution of the resource (host). Therefore, we are not modelling a process of reciprocal evolution, or co-evolution.

*Reproduction of parasites*

Reproduction is sexual and occurs between parasite individuals that are in the same host and that have a minimum genetic similarity, $q_{min}$, measured based on the Hamming distance between genomes. In each host species, at each generation, $K$ offspring individuals replace the parental population, with no generation overlapping. We establish a maximum of $K$ random trials with reposition to find one compatible partner. The offspring is generated by *locus* recombination of the parents and each *locus* has a probability of mutation (μ). We set $q_{min} = 0.5q_0$, where $q_0$ is the expected mean similarity within one population in equilibrium: $q_0 = \frac{1}{1+4\mu K}$. For a detailed demonstration of the above equation see SI1. The restriction $q_{min} = 0.5q_0$ is arbitrary and only assures that no parasite speciation occurs when using a unique host (i.e., avoids sympatric speciation in the context of Higgs & Derrida (1991)). Consequently, parasite speciation only happens when more than one host species is used.

*Temporal scaling*

The empirical studies have evolutionary times in the order of millions of years, and to maintain this time scale in the model would demand a high computational cost. As proposed by Costa et al. (2019), in our approach we adopted a high value of mutation rate (μ=0.025) in order to decrease the number of iterations (time steps or generations) necessary for speciation to occur. Furthermore, we assumed that, due to the shorter life cycle of parasites, they have a faster speciation rate when compared to their hosts (Dowton & Austin 1995; Light & Hafner 2007). To satisfy these conditions, we rescaled the whole host phylogeny assuming that the smaller branch length consists of the minimal time for parasites to speciate due to isolation by host use (see the demonstration in SM1):

$$\tau_a = \frac{1}{4\mu} log(\frac{1}{q_{min}}). \qquad (2)$$

The minimal time for speciation decreases with $q_{min}$. Therefore, making the reproduction more restricted (i.e., increasing $q_{min}$) facilitates the formation of parasite species in a shorter time. The simulation starts with a clonal parasite population using a unique host species. Also, the first host speciation occurred only after $\tau_a$ generations for the parasite populations to accumulate genetic diversity before the first splitting event.

*Host-switching events*

After the first host speciation, parasite individuals in a host species may switch to another host. For each parasite individual, we randomly selected a host species, including the one in use. If the selected host species is not the original host (donor), we follow a probability function for the host-switching event. This probability of host-switching events ($P_{hs}$) decreases over time, representing the product of opportunity for contact and compatibility of the interaction of parasites associated with the evolutionary history of hosts (Figure 1c). Then, we are assuming that compatibility, the opportunity of interaction are expressed through the evolutionary history of hosts. The probability of a parasite individual successfully migrates (host-switching) from one host to another host species, in a given generation $n$, is defined as:

$$P_{hs}(n)=exp[- r * (n - n_s)] . \qquad (3)$$

where $r$ is a positive parameter that controls the decay of the host-switching probability, and $n_s$ is the generation that the common host ancestor had speciated (then, $n$-$n_s$ is how long the two host species had diverged). If $r = 0,$ these probabilities are equal to 1 regardless of the host divergence time, meaning that there is no restriction to host-switching. As a consequence, parasite gene flow is continuous and speciation does not occur. At the other extreme, for sufficiently large $r$ values ($P_{hs}$~0), host-switching is absent and cospeciation between hosts and parasites is expected. For intermediary *r* value, some parasite individuals can eventually switch hosts (Figure 2 and Figure S1). This will increase the host repertoire of the parasitic species, and also enable speciation by isolation (by host use), similar to the speciation by founder's effect (Mayr 1999; Gavrilets & Hastings 1996). The effect of the overall host-switching in a community does not depend only on *r*, but also on the particularities of each host phylogeny that is used as input for the calculation of the host-switching probability. Therefore, to better interpret the effect of parameter *r* on the trajectories and compare the results between the communities, we do not present our results in terms of *r,* but how much it changes the overall host-switching events. To obtain this overall metric, we calculated the mean percentage of parasite individuals that switch hosts over the entire simulation and we call it ***host-switching intensity*** (Figure 2).

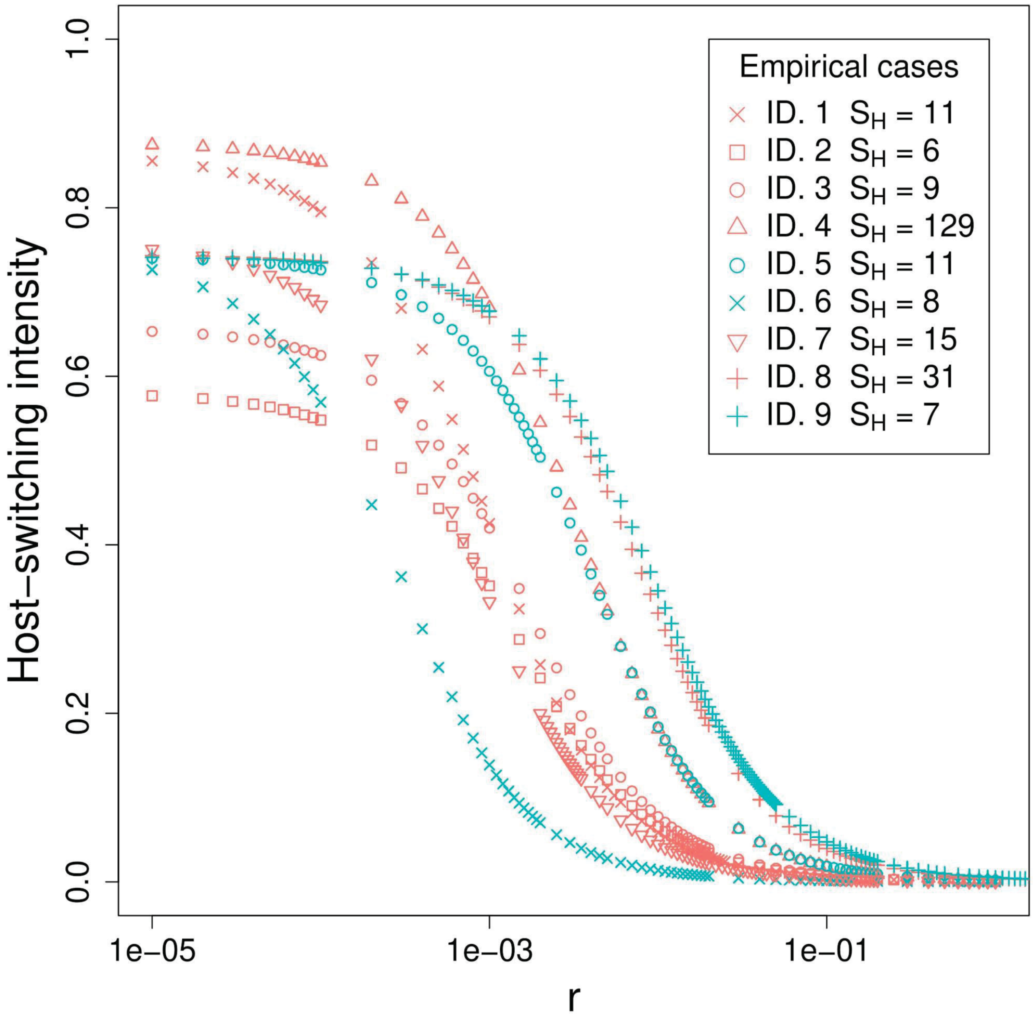


**Figure 2**. Relation between *r* (a parameter that defines the host-switching decay, Eq. 3) and the intensity of host-switching for each simulated community. Each ID represents empirical studies and $S_H$ represents the host richness. ID. 1 - Birds and feather mites. ID. 2 - Mammals and lice. ID. 3 - Wildlife and ectoparasites. ID. 4 and 5 - Rodents and fleas. ID. 6 - Fish and Monogeneans (Gyrodactylidae). ID. 7 - Frogs and monogeneans (Polystomatidae). ID. 8 - Frogs and lungworms (*Rhabdias* spp. ). ID. 9 - Frogs and gut worms (*Oswaldocruzia* spp.). Regional spatial scale studies are represented by salmon colour and local spatial scale studies by blue.

### *Parameters of the model*

For the results presented here we fixed the population size per host ($K$ = 250) and mutation probability per locus ($\mu$ = 0.025). With these parameters, we can observe species formation with reasonable computational time. Since the empirical studies varied in the number of host species and branch size, the total number of iterations also varied (Table S1). The parameter *r* varied ($0<r<1$) for each empirical study**.** A total of 50 replicates were performed for each parameter combination. We have also analysed the model predictions under other values of population size ($K = \{50, 500,1000\}$) and mutation rate ($\mu = 0.001$) (Table S1). Our qualitative conclusions did not change under these parameter variations (Figure S2-S4).

### Validation with empirical data

The development of a new method to assess the host-switching intensity allowed us to compare the results of our simulations with empirical data from different groups of parasites and their respective hosts. This method uses information on the evolutionary history of the host species as a proxy for resource similarity. We used nine studies from empirical studies of parasite-host associations (Table 1) for comparative purposes. The selection criteria was that, in addition to information on species interaction, these empirical studies essentially needed to have phylogenies for hosts and parasites (see the details in Figure S5-S13). We separated these empirical studies according to the spatial scale (Table 1). Spatial scale refers to the spatial extent of ecological processes and the spatial interpretation of the data. In this study, we assumed that studies in the local spatial scale are essentially in a geographic radius less than or equal to 35km, while on a regional scale they were collected essentially in a geographic radius greater than 35km, in the original article respectively.

**Table 1**. Description of the host sample size and parasite richness for each empirical study, of which host phylogenies were used as model parameters and host-parasite association to validate the simulations of the model. Legend: ID = Empirical study.

| ID | Host group | Host richness | Parasites group | Parasite richness | Spatial scale | Reference |
|---|---|---|---|---|---|---|
| 1 | Bird | 11 | Feather mites (*Trouessartia* spp.) | 11 | regional | Donã et al. 2017 |
| 2 | Mammals | 6 | Lice (*Pediculus* spp. and *Pthirus* spp.) | 7 | regional | Reed et al. 2007 |
| 3 | Wildlife | 9 | Arthropods* | 8 | regional | Becker et al. 2018 |
| 4 | Rodents | 129 | Fleas* | 202 | regional | Krasnov et al. 2016 |
| 5 | Rodents | 11 | Fleas* | 19 | local | Krasnov et al. 2016 |
| 6 | Fish | 7 | Monogeneans (Gyrodactylidae) | 16 | local | Patella et al. 2017 |
| 7 | Frogs | 15 | Monogeneans | 13 | regional | Badets et al. 2011 |
| 8 | Frogs | 31 | Lungworms (*Rhabdias* spp. ) | 18 | regional | Müller et al. 2018 |
| 9 | Frogs | 7 | Gut worms *(Oswaldocruzia* spp.) | 5 | local | Willkens et al. 2021 |

*include different parasite groups

## Characterization of the ecological and evolutionary patterns of parasites

We compared both the structure of turnover of parasite species (ecological pattern) and the imbalance of parasite phylogenies (evolutionary pattern) in the empirical studies with those resulting from the simulations. To characterise the composition of parasite species we used the metric that gives information about the beta diversity of multiple-site dissimilarities ($\beta_{SOR}$ - Baselga 2010; 2013a, b). The beta diversity may reflect two different phenomena: turnover ($\beta_{SIM}$) and nestedness ($\beta_{NES}$) (Baselga et al. 2007; Baselga 2010; 2013a, b). Here, we choose only to work with the Simpson-based multiple-site dissimilarity, that is turnover ($\beta_{SIM}$), since it is non-dependent on species richness (Baselga et al. 2007; Baselga 2010). This refers to the replacement of some species by others as a consequence of environmental sorting or spatial and historical constraints. In our case, we compared the variation in parasite species composition between host species. The Simpson-based multiple-site dissimilarity is then:

$$\beta_{SIM} = \frac{\left[\sum_{i<j} min(b_{ij}, b_{ji})\right]}{2\left[\sum_{i} S_i - S_T\right] + \left[\sum_{i<j} min(b_{ij}, b_{ji})\right]}, \qquad (4)$$

where $S_i$ is the total number of species in site *i*, $S_T$ is the total number of species in all sites (hosts in our case) and $min(b_{ij}, b_{ji})$ is the minimal number of species exclusive to sites i and j in pairwise comparison (Baselga 2010).

To characterise the structure of the phylogenetic trees we used the metric that gives information about the tree imbalance. Tree imbalance is one of the most common phylogenetic structural patterns and measures asymmetries between the numbers of species on each side of the tree’s branches (Marquitti et al. 2020). Tree imbalance is widely measured using the Sackin index (*I*) (Sackin 1972; Blum & François 2005; Frost & Volz 2013; Dearlove & Frost 2015). The I has a dependence on the number of leaves, making it unsuitable for comparing trees with different numbers of species. To make this comparison possible, we use the normalised Sackin index ($I_n$) given by:

$$I_n(R) = \frac{I(R) - E[I(R)]}{\sqrt{\sigma_R^2}}, \qquad (5)$$

where tree imbalance is the I(R), and $E(I_n)$ and $\sigma_R^2$ the expected and variance of trees generated by the Yule model which have the same number of leaves (species) as the observed tree (Cardona et al. 2013; Marquitti et al. 2020). Although $I_n(R)$ would be close to zero for trees generated with the Yule model, independent of the species richness R, different modes of speciation may introduce important deviations from the behaviour of the Yule model (Marquitti et al. 2020).

As each empirical study represents particular ecological and evolutionary processes, we analysed whether there was an optimal range of host-switching intensity in our simulated cases that retrieves information about turnover ($\beta_{SIM}$) and normalised Sackin index ($I_n$) of each study. We considered that simulations that reproduced both the $\beta_{SIM}$ and the $I_n$ metrics simultaneously (within a $\pm5\%$ confidence interval) were the best fit to the empirical examples. Then we compared the best fitting of host-switching intensity among the empirical studies to understand how it varied for different evolutionary histories. Although species extinctions occur in the model, this aspect was not included in the analyses since we do not have information about extinctions in the empirical studies. These analyses were performed using ‘ape’ (Paradis & Schliep 2019), ‘betapart’ (Baselga et al. 2018) ‘picante’ (Kembel et al. 2010), ‘phytools’ (Revell 2012), and ‘vegan’ (Oksanen et al. 2013) R packages.  See the details in SI3.

## Statistical analysis

To test whether the spatial scale modulates the best fitting host-switching intensities, a linear mixed-effects model (LMM) was performed using the *lmer* function from the ‘lme4’ package (Bates et al. 2011). We assumed the host-switching intensity as the response variable, the spatial scale as a fixed variable, and empirical studies were treated as random variables (intensity~ scale+(1|study)). After performing the LMM analysis, an analysis of variance (ANOVA) was used to determine significant differences (p-value ≤ 0.01) using the Anova function in the ‘car’ package (Fox & Weisberg 2019). All statistical analyses were performed in R v.4.0.0 (R Core Team 2020) and Rstudio v.1.3.959 (RStudio Team 2020).

## RESULTS

The turnover and normalised Sackin index of parasites varied according to the mean percentage of parasite individuals that switch hosts during the entire history of the host community (the host-switching intensity). To illustrate the turnover and normalised Sackin index according to the host-switching intensity, we present an example of a model application with fleas associated with rodents (ID. 5, Figure 3). As expected, turnover decreases as host-switching intensity increases (Figure 3a and Figure S14). This occurs because the increase of host-switching promotes the interaction of different host species with the same parasite species. Additionally, for each value of host-switching intensity, there is a small variation in the turnover (Figure 3a and Figure S14). The only exception was ID. 4, which resulted in a wide variation in turnover under high host-switching intensity (Figure S14).

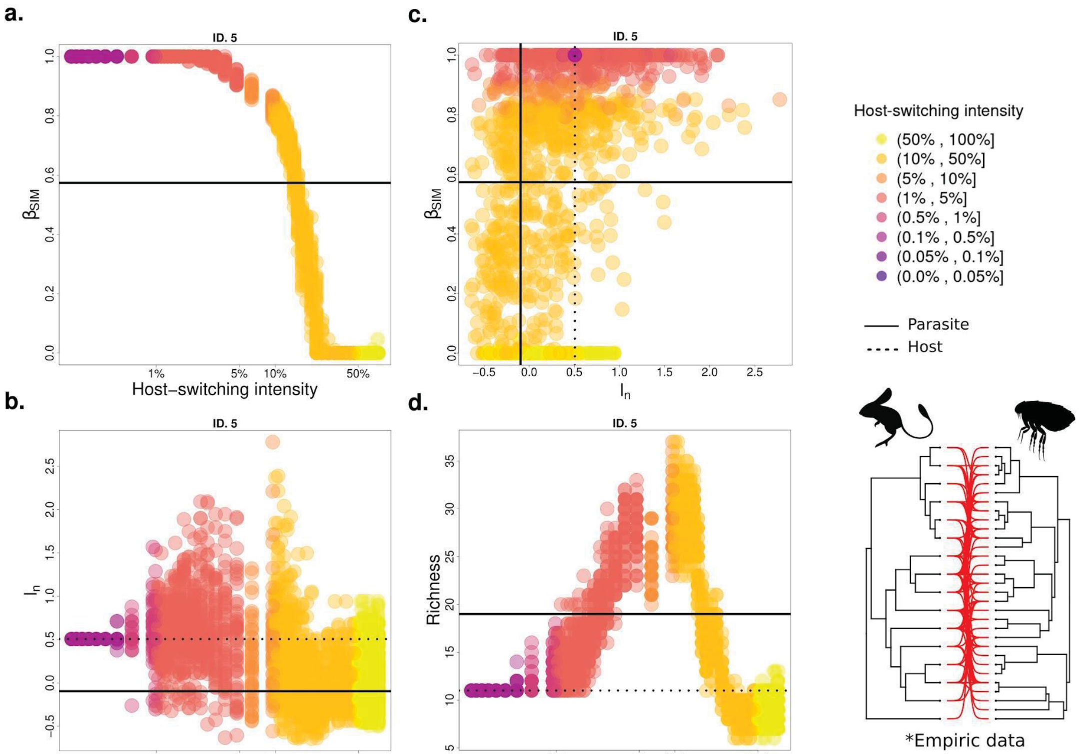


**Figure 3.** Influence of host-switching events on the eco-evolutionary patterns of simulated parasites for fleas associated with rodents (see Table 1 for details). Here we demonstrated the relationship between: **a**. Host-switching intensity and turnover of parasite species ($\beta_{SIM}$) between host species; **b**. Host-switching intensity and parasite normalised Sackin index ($I_n$); **c**. Relationship between $\beta_{SIM}$, $I_n$, and the host-switching intensity. **d**. Host-switching intensity and parasite richness. The lines refer to empirical information on the parasite (continuous) and host (dotted). The coloured dots are redundant with the x-axis scale of graphs (a) and (b) but intend to guide the interpretation of (c). A total of 50 replicates were performed with 250 individuals for each configuration of the parameters of host-switching intensity.

As imposed by the model, the parasite richness ends the same as hosts in the absence of host-switching (Figure S16). But, for intermediary values of host-switching, parasites can colonise the new host and then speciate, resulting in an overwhelming increase in parasite speciation (see the dynamics in the movie available in S17, Figure S18, and Figure 3d).

When host-switching intensity is low (below 1%), the normalised Sackin index ($I_n$) for the simulated parasite phylogenies results in the exactly same value as the one obtained from the empirical phylogeny of the host (note the dashed line in Figure 3b and also Figure S15). This is because the low host-switching intensity does not allow the establishment of the parasite in a new host and, as a consequence, the simulated parasite phylogenies have the same normalised Sackin index of the empirical host phylogeny. Colonisation followed by speciation is more likely to occur under a higher host-switching intensity, in which the normalised Sackin index varies over simulations even when they are under the same host-switching intensity (Figure 3b and Figure S15). The wide variation in the normalised Sackin index for a given host-switching intensity reveals that stochastic host-switching events, even if host-switching is more likely to occur between closely related species, can change the structure of the resulting phylogenetic tree. Despite not having a monotonic tendency, the normalised Sackin index tends towards zero (balanced tree) as host-switching intensity goes to one, regardless of the community (Figure S15), resembling a neutral speciation scenario Yule model (Yule 1924; Aldous 2001).

For all empirical studies analysed, there is a range of host-switching intensity that simultaneously reproduces the observed turnover and the parasite normalised Sackin index (Figure 4). As mentioned, both metrics are sensitive to host-switching intensity but each one varies independently of the other (see in Figure 4). Generally, the turnover and the parasite normalised Sackin index obtained under high host-switching intensity (greater than 50%) are far from the empirical pattern (see Figure 4, the yellow dots rarely approach the intersection of the solid lines).

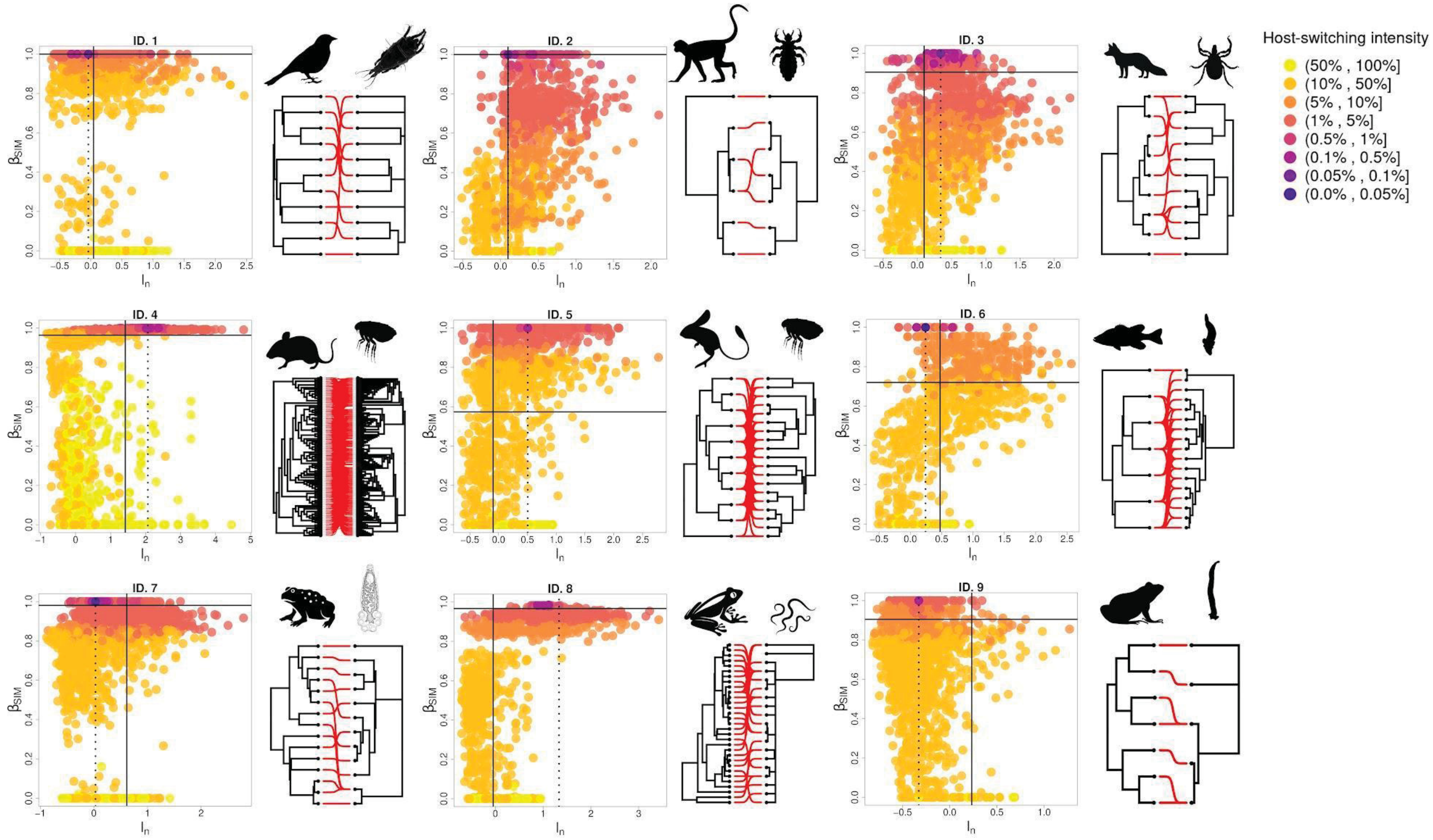


**Figure 4.** The relationship between variation in the turnover of parasite species, normalised Sackin index of parasite species, and host-switching intensity for nine empirical studies: the parasites' turnover, measured by the metric turnover($\beta_{SIM}$) on the y-axis and the normalised Sackin index ($I_n$)

on the x-axis. Each ID represents an empirical studies. The lines refer to empirical information of parasite (continuous) and host (dotted). Colour scales represent each percentage interval of host-switching intensity. A total of 50 runs were performed with 250 individuals of carrying capacity, for each configuration of the parameters of host-switching intensity.

The simulated host-switching intensity that simultaneously fit parasite turnover and normalised Sackin index recovered a range of 0.06% to 22.07% of host-switching intensity through the analysed empirical studies. Within this range, the associations between mammals and lice presented the lowest host-switching intensity (case ID. 2 with 0.07% - 1.13%), followed by that involving wildlife and arthropod parasites (case ID. 3 with 0.43% - 2.69%), frogs and monogeneans (case ID. 7 with 0.22% - 3.71%), frogs and lungworms (case ID. 8 with 1.99% - 4.94%), frogs and gut worms (case ID. 9 with 5.29% - 9.35%), birds and feather mites (case ID. 1 with 0.06% - 8.17%), fish and monogeneans (case ID. 6 with 8.26% - 11.64%), - the highest intensities of host-switching were observed between rodents and fleas (case ID. 5 with 14.45% - 16.87% and case ID. 4 with 0.43% - 22.07%). We also observed that the host-switching events are more frequent in studies conducted in a local scale (blue colour in Figure 5) than in regional scales (salmon colour in Figure 3) (LMM: relationship of host-switching intensity on spatial scale: beta= 0.08, SE= 0.01, df = 6.92, t= 5.25, p = 0.001, ANOVA: F = 27.56, p = 0.001, Figure 5).

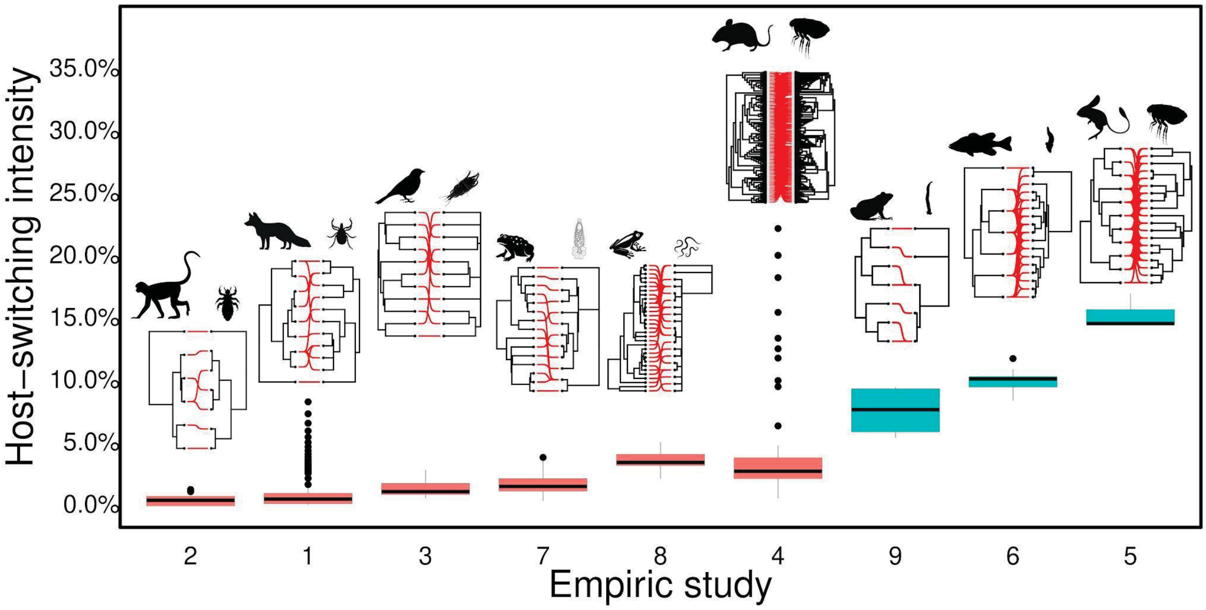


**Figure 5**. Calculated host-switching intensity among empirical studies. The boxplots show the distributions of simulated host-switching intensities for each empirical study. Regional spatial scale

studies are represented by salmon, and local scale studies are in blue. The number in axis x represents the empirical studies: ID. 1 - Birds and feather mites. ID. 2 - Mammals and lice. ID. 3 - Wildlife and ectoparasites. ID. 4 and 5 - Rodents and fleas. ID. 6 - Fish and Monogeneans (Gyrodactylidae). ID. 7 - Frogs and monogeneans (Polystomatidae). ID. 8 - Frogs and lungworms (*Rhabdias* spp. ). ID. 9 - Frogs and gut worms (*Oswaldocruzia* spp.).

## DISCUSSION

In this study, we developed a novel methodological framework to understand how the intensity of host-switching shapes some aspects of ecological and evolutionary patterns of parasites, here characterised by species interaction turnover and tree imbalance, respectively. Our three main results are 1) We found an optimum range of host-switching intensity that can predict similar patterns as those observed in the empirical studies, which validates our model; 2) The model showed that the increase of host-switching intensity promoted an increase in turnover, but the tree imbalance did not follow any monotonic tendency. Moreover, for a specific host-switching intensity, we observed a small variation in the turnover and a wide variation in the tree imbalance; 3) The predicted values of host-switching intensity varied among the empirical studies and those at a local spatial scale resulted in values higher than the ones at the regional scale.

The fact that our model rebuilt the eco-evolutionary patterns of all empirical studies supports the idea that host-switching mediated by host evolutionary proximity is a good predictor of parasite associations. According to the framework of the Stockholm Paradigm (Brooks et al. 2019), parasites can colonise new host species due to preexisting compatibility, which is expressed when there is an opportunity for contact. Compatibility emerges greatly from the ancestral capacity in which both hosts and parasites must be physiologically compatible to establish a long-term association (Brooks & McLennan 2002; Kolbe et al. 2004; Brooks et al. 2019). Hence, for a given lineage of the parasite, the closer (phylogenetically) the original and the new host species, the greater the possibility that the adequate resource is conserved or is at least similar. In fact, phylogenetic proximity has been widely recognized as a potential criterion to anticipate new associations (Streicker et al. 2010; Damas et al. 2020; Filion et al. 2022).

Another element of the Stockholm Paradigm (Brooks et al. 2019) that we observed over the temporal dynamics of our model is the Oscillation Hypothesis (Janz & Nylin 2008): parasites first increase their host repertoire (generalise) and then speciate (specialise). In our model, at each time step, a parasite individual can switch hosts, promoting the increase of host repertoire for the parasite species. However, as we assume that the probability of host-switching decreases as hosts diverge, given time, the probability of individuals from the same parasite species maintaining the gene flow between those host species decreases, and parasite speciation is likely to occur (see the dynamics in the movie available in S17 and S18). Consequently, in our model, host-switches promote host repertoire oscillation, as hypothesised by Janz & Nylin (2008), and favour parasites to speciate at a greater rate than their host, which is empirically evidenced (Poulin & Morand 2000). Although the mean argument behind the difference in speciation rate between host and parasite is the parasite's shorter life cycle, we support the idea that frequent host exploitation is another important mechanism to parasite diversification (Hay et al. 2020, Boeger et al. 2022).

The tree imbalance did not have a monotonic tendency and showed a wide variation for a given host-switching intensity. This reveals that stochastic events can change the evolutionary trajectory of parasites. Although our model assumed that host-switching most likely occurs between closely related species, eventually, a parasite can switch to a phylogenetically distant host, changing the diversification history completely. This distant host-switching was observed in most of the empirical studies presented here, where the parasites were able to colonise hosts from different genera (ID 2 and 6), families (IDs 1, 4, 5, 7, 8, and 9), and even order (ID 3). For example, in study ID8 the *Rhabdias* lung-worm anuran parasites occurred mostly in Bufonidae hosts and only one species in the Hylidae host (Müller et al. 2018). Species extinction is another class of stochastic event present in our model that could contribute to the varied outputs on parasite evolution. As we use data only of extant species, when a species goes extinct all its history is lost, also impacting the imbalance of the tree (Costa et al. 2019, Marquitti 2020)

Unlike the tree imbalance, our results showed that the turnover has a monotonic tendency: it decreased as the host-switching intensity increased. This pattern was expected since the model imposes that as host-switching intensity increases, the limitation to use a new host decreases (Figure 2). Moreover, we did not observe a wide variation in the turnover for a given host-switching intensity over the model replications. This reveals that those stochastics events mentioned before can not produce significant changes in the turnover. It probably occurs because when host-switching occurs, it produces a decrease in the turnover no matter what parasite species switched to what host species. In other words, the identities of the species are not relevant since turnover emerges not from a given species characteristic, but from the similarities between species, or even spatial and temporal amplitudes (Fallon et al. 2004, Baselga et al. 2007, Baselga, et al. 2022). This reinforces the idea that species turnover is a robust metric to compare species assemblages (Baselga, et al. 2022) and may also be a good proxy for host-switching intensity.

The host-switching intensity varied across empirical studies and we observed that it is higher in empirical studies of local spatial scale than regional spatial scale. This evidence shows that the amplitude of the spatial scale is a fundamental factor in determining the extent of host-switching. The opportunity for interaction is larger in host empirical studies at a local scale, as this reduces the likelihood that barriers exist, hampering the encounter of potential actors. This is evident when comparing rodent and flea associations at regional (ID. 4) and local spatial scales (ID. 5). Similarly, since the association of *Rhabdias* spp. and frogs (ID. 8) are defined geographically (and not by host taxa) it was assumed that host-switching by ecological fitting was evolutionarily more important than association with particular host taxa (Kuzmin et al. 2014; Müller et al. 2018). Different intensities of host-switching observed in our results may also be influenced by biological variations of the species that make up the empirical studies analysed. For instance, these studies include a great diversity of organisms (fleas, lice, feather mites, helminths, platyhelminthes), with profound differences in their biological characteristics. Expanding analyses to a broader sample of empirical studies, including variations in the type of parasitism (e.g., mono *vs.* heteroxenic, ecto *vs.* endoparasite) and host attributes can provide important insights into key features related to the process of incorporation of new hosts.

In nature, host-parasite systems are more complex than those modelled here. Although the model can reconstruct eco-evolutionary patterns of empirical studies, our model has some limitations. For example, the carrying capacity of all host species is the same and the host's body size, their abundances, and spatial distribution were not explicitly considered. The selective pressure is not explicitly modelled, contrary to what we observe in nature (Krasnov et al. 2005, Krasnov et al. 2021). Furthermore, all parasite individuals and species are equivalent, and may compete for the same resources. Except for resource competition, our model didn't consider intra and interspecific interactions among parasites. Finally, the phylogenies are still scarce, especially for parasite species, which limited the number of tests with the model. Phylogenetic data on parasites is extremely important to clarify the role of host-switching in the ecological and evolutionary patterns of parasite lineages. Still, we recovered compatible eco-evolutionary patterns for modelled parasites and their respective hosts. Our model has important implications for predicting host switching, especially in scenarios of anthropogenic change. With anthropogenic changes constantly modifying natural environments and altering the geographic distribution of parasites, many species that were once restricted to specific areas are now expanding their range into new geographic locations and changing the composition of communities (see Brooks et al. 2014). As we showed, parasites can follow different evolutionary paths, and eventually can switch to non-related hosts, ultimately, determining the migration of a parasite to other species (and clades), in some cases, including humans. To conclude, we show that a model in which host-switching mediated by evolutionary proximity between hosts is a predictor for parasitic associations over evolutionary time, as well as for the origins of parasite diversity. We see this as an important step in our understanding of parasite diversification processes.

## ACKNOWLEDGEMENTS

We thank the researchers who collected and reported the field data, our institutions, and the many colleagues who helped us in different ways during this project for their comments and suggestions, especially to Professor Dr. Marcus Aguiar. The authors acknowledge the computational support from Professor Carlos M. de Carvalho at LFTC-DFis-UFPR.

## FINANCIAL SUPPORT

EDB was supported by Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES). DP was supported by the São Paulo Research Foundation (FAPESP), grants #2018/11187-8, #2019/24449-3, and #2016/01343-7 (ICTP-SAIFR). SBLA was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq: #11284/2021-3).

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA ACCESSIBILITY STATEMENT

The model, phylogenies, and interactions of all analysed studies are available at https://github.com/elviradbastiani/host_switching_model.

## REFERENCES

Agosta S. J., Janz N., Brooks D. R. 2010. How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. Zoologia (Curitiba), 27(2), 151-162.

Agosta S. J., Klemens J. A. 2008. Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. Ecology Letters, 11, 1123-1134.

Agosta S. J., Brooks D. R. 2020. The major metaphors of evolution: Darwinism then and now (Vol. 2). Springer Nature, Switzerland AG. pp. XVII - 273.

Aldous D. J. 2001. Stochastic models and descriptive statistics for phylogenetic trees, from Yule to today. Statistical Science, 16, 23-34.3

Araujo S. B., Braga M. P., Brooks D. R., Agosta S. J., Hoberg E. P., von Hartenthal F. W., Boeger W. A. 2015. Understanding host-switching by ecological fitting. PLoS One, 10(10), e0139225.

Baselga A., Jiménez-Valverde A., Niccolini G. 2007. A multiple-site similarity measure independent of richness. Biology Letters, 6, 642-645.

Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global ecology and biogeography, 19, 134-143.

Baselga A. 2013a. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. Methods in Ecology and Evolution, 4, 552-557.

Baselga A. 2013b. Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. Ecography, 36, 124-128.

Baselga A., Orme D., Villéger S., De Bortoli J., Leprieur F., Logez M., Henriques-Silva R. 2018. Partitioning beta diversity into turnover and nestedness components. Package ‘betapart’. Version, 1(1).

Baselga A., Gómez-Rodríguez C., Araújo M. B., Castro-Insua A., Arenas M., Posada D., Vogler A. P. 2022. Joint analysis of species and genetic variation to quantify the role of dispersal and environmental constraints in community turnover. Ecography, e05808.

Bates D., Maechler M., Bolker B., Walker S., Christensen R. H. B., Singmann H. Grothendieck G. 2011. Package ‘lme4’. Linear mixed-effects models using S4 classes. R package version, 1(6).

Blum M. G. François O. 2005. On statistical tests of phylogenetic tree imbalance: the Sackin and other indices revisited. Mathematical biosciences, 195, 141-153.

Boeger W. A., Brooks D. R., Trivellone V., Agosta S., Hoberg E. 2022. Ecological Super-Spreaders Drive Host-Range Oscillations: Omicron and Risk-Space for Emerging infectious Disease. In press.

Boyd B. M., Nguyen N. P., Allen J. M., Waterhouse R. M., Vo K. B., Sweet A. D., Johnson K. P. 2022. Long-distance dispersal of pigeons and doves generated new ecological opportunities for host-switching and adaptive radiation by their parasites. Proceedings of the Royal Society B, 289(1970), 20220042.

Braga M. P. Janz N. 2021. Host repertoires and changing insect–plant interactions. Ecological Entomology, 46, 1241–1253.

Brooks D. R., McLennan D. A. 2002. The nature of diversity. University of Chicago Press.

Brooks D. R., Hoberg E. P.  Boeger W. A. 2019. The Stockholm paradigm: climate change and emerging disease. University of Chicago Press, pp. 400.

Brooks D. R., Hoberg E. P., Boeger W. A., Gardner S. L., Galbreath K. E., Herczeg D. Dursahinhan A. T. 2014. Finding them before they find us: informatics, parasites, and environments in accelerating climate change. Comparative Parasitology, 81, 155-164.

Bush S. E., Sohn E. Clayton D. H. 2006. Ecomorphology of parasite attachment: experiments with feather lice. Journal of Parasitology, 92, 25-31.

Cardona G., Mir A., Rosselló F. 2013. Exact formulas for the variance of several balance indices under the Yule model. Journal of Mathematical Biology, 67(6), 1833-1846.

Charleston M. A.  Robertson D. L. 2002. Preferential host switching by primate lentiviruses can account for phylogenetic similarity with the primate phylogeny. Systematic biology, 51, 528-535.

Costa C. L., Lemos-Costa P., Marquitti F. M., Fernandes L. D., Ramos, M. F., Schneider D. M. de Aguiar M. A. 2019. Signatures of microevolutionary processes in phylogenetic patterns. Systematic biology, 68, 131-144.

Cuthill J. H.  Charleston M. A. 2013. A simple model explains the dynamics of preferential host switching among mammal RNA viruses. Evolution: International Journal of Organic Evolution, 67, 980-990.

Damas J., Hughes G. M., Keough K. C., Painter C. A., Persky N. S., Corbo M. Lewin H. A. 2020. Broad host range of SARS-CoV-2 predicted by comparative and structural analysis of ACE2 in vertebrates. Proceedings of the National Academy of Sciences, 117, 22311-22322.

De Vienne D. M., Refrégier G., López-Villavicencio M., Tellier A., Hood M. E. Giraud T. 2013. Cospeciation *vs* host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytologist, 198, 347-385.

Dearlove B. L., Frost S. D. 2015. Measuring asymmetry in time-stamped phylogenies. PLoS computational biology, 11(7), e1004312.

Dominguez M., de la Colina M. A., Di Giacomo A. G., Reboreda J. C., Mahler B. 2015. Host switching in cowbird brood parasites: how often does it occur? Journal of evolutionary biology, 28(6), 1290-1297.

Dowton M. Austin A. D. 1995. Increased genetic diversity in mitochondrial genes is correlated with the evolution of parasitism in the Hymenoptera. Journal of Molecular Evolution, 41, 958-965.

Engelstädter J. Fortuna N. Z. 2019. The dynamics of preferential host switching: Host phylogeny as a key predictor of parasite distribution. Evolution, 73, 1330-1340.

Fallon S. M., Ricklefs R. E., Latta S. C., Bermingham E. 2004. Temporal stability of insular avian malarial parasite communities. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271(1538), 493-500.

Fecchio A., Wells K., Bell, J.A., Tkach V. V., Lutz H. L., Weckstein J. D. Clark N. J. 2019. Climate variation influences host specificity in avian malaria parasites. Ecology Letters, 22, 547-557.

Filion A., Doherty J. F., Poulin R., Godfrey S. S. 2022. Building a comprehensive phylogenetic framework in disease ecology. Trends in Parasitology.

Fox J. Weisberg S. 2019. Nonlinear Regression, Nonlinear Least Squares, and Nonlinear Mixed Models in R. population, 150, 200.

Frost S. D., Volz E. M. 2013. Modelling tree shape and structure in viral phylodynamics. Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1614), 20120208.

Gavrilets S. Hastings A. 1996. Founder effect speciation: a theoretical reassessment. The American Naturalist, 147, 466-491.

Habermannová J., Bogusch P., Straka J. 2013. Flexible host choice and common host switches in the evolution of generalist and specialist cuckoo bees (Anthophila: Sphecodes). PLoS One, 8(5), e64537.

Hay E. M., Poulin R., Jorge F. 2020. Macroevolutionary dynamics of parasite diversification: A reality check. Journal of Evolutionary Biology, 33(12), 1758-1769.

Hayward A., Poulin R. Nakagawa S. 2021. A broadscale analysis of host-symbiont cophylogeny reveals the drivers of phylogenetic congruence. Ecology Letters, 24, 1681–1696.

Higgs P. G., Derrida B. 1991. Stochastic models for species formation in evolving populations. Journal of Physics A: Mathematical and General, 24(17), L985.

Imrie R. M., Roberts K. E. Longdon B. 2021. Between virus correlations in the outcome of infection across host species: Evidence of virus by host species interactions. Evolution letters, 5, 472-483.

Janz N., Nylin S. 2008. The oscillation hypothesis of host-plant range and speciation. Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects, 2008, 203-215.

Jaramillo M.  Rivera-Parra J. L. 2018. Host-Switching: How It Starts. In Disease Ecology. Springer, Cham, pp. 139-156.

Kembel S.W., Cowan P.D., Helmus M. R., Cornwell W. K., Morlon H., Ackerly D. D. Webb C. O. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics, 26, 1463-1464.

Kolbe J. J., Glor R. E., Rodríguez Schettino L., Lara A. C., Larson A., Losos J. B. 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature, 431(7005), 177-181.

Krasnov B. R., Burdelova N. V., Khokhlova I. S., Shenbrot G. I., Degen A. 2005. Larval interspecific competition in two flea species parasitic on the same rodent host. Ecological Entomology, 30(2), 146-155.

Krasnov B. R., Spickett A., Junker K., Van der Mescht L., Matthee S. 2021. Functional and phylogenetic uniqueness of helminth and flea assemblages of two South African rodents. International journal for parasitology, 51(10), 865-876.

Kuzmin Y., de Vasconcelos Melo F. T.  Dos Santos J. N. 2014. A new species of *Serpentirhabdias* Tkach, Kuzmin Snyder, 2014 (Nematoda: Rhabdiasidae) parasitic in the brown ground snake *Atractus major* Boulenger (Reptilia: Serpentes: Dipsadidae) in Brazil. Systematic Parasitology, 89, 101-106.

Light J. E.  Hafner M. S. 2007. Cophylogeny and disparate rates of evolution in sympatric lineages of chewing lice on pocket gophers. Molecular phylogenetics and evolution, 45, 997-1013.

Manzo F., Peliti L. 1994. Geographic speciation in the Derrida-Higgs model of species formation. Journal of Physics A: Mathematical and General, 27(21), 7079.

Marquitti F. M. D., Fernandes L. D., de Aguiar M. A. M. 2020. Allopatry increases the balance of phylogenetic trees during radiation under neutral speciation. Ecography, 43(10), 1487-1498.

Mayr E. 1999. Systematics and the origin of species, from the viewpoint of a zoologist. Harvard University Press, pp. 372.

Meinilä M., Kuusela J., Ziętara M. S., Lumme J. 2004. Initial steps of speciation by geographic isolation and host switch in salmonid pathogen *Gyrodactylus salaris* (Monogenea: Gyrodactylidae). International Journal for Parasitology, 34(4), 515-526.

Nylin S., Slove J.  Janz N. 2014. Host plant utilization, host range oscillations and diversification in nymphalid butterflies: a phylogenetic investigation. Evolution, 68, 105-124.

Nylin S., Agosta S., Bensch S., Boeger W. A., Braga M. P., Brooks D. R. Janz, N. 2018. Embracing colonizations: a new paradigm for species association dynamics. Trends in ecology evolution, 33, 4-14.

Oksanen J., Blanchet F. G., Kindt R., Legendre P., Minchin P. R., O'hara R. B. Oksanen M. J. 2013. Package 'vegan'. Community ecology package, version, 2, 1-295.

Poulin R., Morand S. 2000. The diversity of parasites. The quarterly review of biology, 75(3), 277-293.

Revell L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in ecology and evolution, 3, 217-223.

Sackin M. J. 1972. "Good" and "bad" phenograms. Systematic Biology, 21(2), 225-226.

Sanaei E., Charlat S., Engelstädter J. 2021. *Wolbachia* host shifts: routes, mechanisms, constraints and evolutionary consequences. Biological Reviews, 96(2), 433-453.

Streicker D. G., Turmelle A. S., Vonhof M. J., Kuzmin I. V., McCracken G. F. Rupprecht C. E. 2010. Host phylogeny constrains cross-species emergence and establishment of rabies virus in bats. Science, 329, 676-679.

Team R. 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. Available at: https://www.rstudio.com/. Last accessed 05 april 2022.

Team R. C. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria: Available at: https://www. R-project. org/. Last accessed 05 april 2022.

Woolhouse M. E., Haydon D. T., Antia R. 2005. Emerging pathogens: the epidemiology and evolution of species jumps. Trends in ecology & evolution, 20(5), 238-244.

Yule U. G. 1925. A mathematical theory of evolution, based on the conclusions of Dr. JC Willis, FRS. Philosophical Transactions of the Royal Society of London Series B, 213, 21-87.

[Dataset] Badets M., Whittington I., Lalubin F., Allienne J. F., Maspimby J. L., Bentz S. Verneau O. 2011. Correlating early evolution of parasitic platyhelminths to Gondwana breakup. Systematic Biology, 60, 762-781. Accession number: EDB_10.1093/sysbio/syr078

[Dataset] Becker D. J., Streicker D. G. Altizer S. 2018. Using host species traits to understand the consequences of resource provisioning for host–parasite interactions. Journal of Animal Ecology, 87, 511-525. Accession number: EDB_10.1111/1365-2656.12765

[Dataset] Doña J., Sweet A. D., Johnson K. P., Serrano D., Mironov S. Jovani R. 2017. Cophylogenetic analyses reveal extensive host-shift speciation in a highly specialized and host-specific symbiont system. Molecular phylogenetics and evolution, 115, 190-196. Accession number: EDB_10.1016/j.ympev.2017.08.005

[Dataset] Krasnov B. R., Shenbrot G. I., Khokhlova I. S. Degen A. A. 2016. Trait-based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. Oikos, 125, 29-38. Accession number: EDB_10.1111/oik.02178

[Dataset] Müller M. I., Morais D. H., Costa-Silva G. J., Aguiar A., Avila R.W. da Silva R. J. 2018. Diversity in the genus *Rhabdias* (Nematoda, Rhabdiasidae): Evidence for cryptic speciation. Zoologica Scripta, 47, 595-607. Accession number: EDB_10.1111/zsc.12304

[Dataset] Patella L., Brooks D. R.  Boeger W. A. 2017. Phylogeny and ecology illuminate the evolution of associations under the Stockholm paradigm: *Aglaiogyrodactylus* spp. (Platyhelminthes, Monogenoidea, Gyrodactylidae) and species of Loricariidae (Actinopterygii, Siluriformes). Vie Et Milieu, 67, 91-102. Accession number: EDB_20183235432

[Dataset] Reed D. L., Light J. E., Allen J. M. Kirchman J. J. 2007. Pair of lice lost or parasites regained: the evolutionary history of anthropoid primate lice. Bmc Biology, 5, 1-11. Accession number: EDB_10.1186/1741-7007-5-7

[Dataset] Willkens Y., Furtado A. P., Dos Santos J. N.  de Vasconcelos Melo F. T. 2021. Do host habitat use and cospeciation matter in the evolution of *Oswaldocruzia* (Nematoda, Molineidae) from neotropical amphibians? Journal of Helminthology, 95, e33. Accession number: EDB_10.1017/S0022149X21000250

# SUPPLEMENTARY MATERIAL

## MATERIAL AND METHODS

### Additional information for the model

*Derrida-Higgs model*

The model introduced by Derrida and Higgs (1991) considers a sympatric population of *K* haploid individuals (population carrying capacity) whose genomes are represented by binary strings of size *B*, $\{S_1^{\alpha}, S_2^{\alpha} ... S_B^{\alpha}\}$ where $S_i^{\alpha}$, can assume the values ±1. Each locus of the genome is dumbed as a gene and the values +1 and -1 the corresponding alleles. The number of individuals at each generation is kept constant and the population is characterised by a $K \times K$ matrix *q* measuring the degree of genetic similarity between pairs of individuals:

$$q_{\alpha\beta} = \frac{1}{B}\sum_{i=1}^{B} S_i^{\alpha} S_i^{\beta}. \qquad (1)$$

If the genomes of *α* and *β* are identical $q_{\alpha\beta}= 1$ whereas two genomes with random entries will have $q_{\alpha\beta}$ close to zero. Each generation is constructed from the previous one as follows: a first parent $P_1$ is chosen at random. The second parent $P_2$ has to be genetically compatible with the first, i.e., their degree of similarity has to satisfy $q_{P_1P_2} \geq q_{min}$. Individuals $P_2$ are then randomly selected until this condition is met with *K* trials. If no such individual is found, $P_1$ is discarded and a new first parent is selected. The offspring inherits, gene by gene, the allele of either parent with equal probability (sexual reproduction). The process is repeated until *K* offspring have been generated. Individuals are also subjected to a mutation rate $\mu$ per gene, which is typically small.

*Dynamics*

To understand how the similarity matrix changes through generations, consider first an asexual population where each individual α has a single parent *P₁* in the previous generation. The allele $S_i^{\alpha}$ will be equal to $S_i^{P(\alpha)}$ with probability $\frac{1}{2}(1 + e^{-2\mu}) \approx 1 - \mu$ and -$S_i^{P(\alpha)}$ with probability $\frac{1}{2}(1 - e^{-2\mu}) \approx \mu$, so that the expected value is $E(S_i^{\alpha}) = e^{-2\mu} S_i^{P(\alpha)}$. For independent genes, the expected value of the similarity between *α* and *β* is, therefore, $E(q_{\alpha,\beta}) = e^{-4\mu} q_{P(\alpha),P(\beta)}$. In sexual populations *α* and *β* have two parents each, $P_1^{\alpha}$, $P_2^{\alpha}$ and $P_1^{\beta}$, $P_2^{\beta}$, and since each inherits (on average) half the alleles from each parent, we obtain

$$E(S_i^{\alpha}) = \frac{1}{2}\left(S_i^{P_1(\alpha)}\frac{1+e^{-2\mu}}{2} - S_i^{P_1(\alpha)}\frac{1+e^{-2\mu}}{2}\right) + \frac{1}{2}\left(S_i^{P_2(\alpha)}\frac{1+e^{-2\mu}}{2} - S_i^{P_2(\alpha)}\frac{1+e^{-2\mu}}{2}\right)$$

$$= \frac{e^{-2\mu}}{2}\left(S_i^{P_1(\alpha)} + S_i^{P_2(\alpha)}\right). \qquad (2)$$

It follows that, on average, the similarity between *α* and *β* is

$$q_{\alpha\beta} = \frac{e^{-4\mu}}{4}\left(q_{P_1(\alpha),P_1(\beta)} + q_{P_2(\alpha),P_1(\beta)} + q_{P_1(\alpha),P_2(\beta)} + q_{P_2(\alpha),P_2(\beta)}\right), \quad (3)$$

with $q_{\alpha\alpha} \equiv 1$. In the limit of infinitely many genes, $B \to \infty$ , this expression becomes exact and the entire dynamics can be obtained by simply updating the similarity matrix.

If there is no restriction on mating, $q_{min} = 0$, we can demonstrate that the overlaps $q_{\alpha\beta}$ converge to a stationary distribution (Derrida & Higgs, 1991), as follows. At generation *t*, the probability that *α* and *β* have one parent in common, $P_1^{\alpha} = P_1^{\beta}$, $P_1^{\alpha} = P_2^{\beta}$,$P_2^{\alpha} = P_1^{\beta}$ or $P_2^{\alpha} = P_2^{\beta}$, is *4/K*. In this case, the average similarity $< q_{\alpha\beta} >$ between *α* and *β* is given by $< q_{\alpha\beta} > = \frac{e^{-4\mu}}{4}(1 + 3\bar{q})$, where $\bar{q}$ is the average similarity in the previous generation. If *α* and *β* do not share a parent, which happens with probability *1-4/K*, then $< q_{\alpha\beta} >= e^{-4\mu}\bar{q}$. Therefore, at generation *t+1* we get

$$\bar{q}_{t+1} = \frac{4}{K}\frac{e^{-4\mu}}{4}(1 + 3\bar{q}_t) + (1 - \frac{4}{K})e^{-4\mu}\bar{q}_t = e^{-4\mu}[(1 - \frac{1}{K})\bar{q}_t + \frac{1}{K}] \,.(4)$$

Setting $\bar{q}_{t+1} = \bar{q}_t = q_0$ , we find the equilibrium at

$$q_0 = \frac{1}{1+4\mu K}. \qquad (5)$$

The approximation holds for $\mu$ and *1/K* much smaller than one, which is always the case for real populations. For example, with *K* = 250 and $\mu$ = 0.025, population similarity will reach an equilibrium with $q_0$= 0.038. If $q_{min} \leq q_0$, the genetic distribution reaches this equilibrium and no species will arise. On the other hand, if the minimal similarity $q_{min}$ satisfies $q_{min} > q_0$, sympatric speciation will occur and we can estimate the time for it to occur. Subtracting $\bar{q}_t$ from both sides of Equation (4) and approximating $\bar{q}_{t+1} - \bar{q}_t = \frac{dq}{dt}$, we get the differential equation

$$\frac{dq}{dt} = \frac{1}{K}(1 - \frac{q_t}{q_0}) \qquad (6)$$

with solution given by

$$q(t) = q_0 + (1 - q_0)\, e^{-t/Mq_0}. \qquad (7)$$

The time $\tau$ to speciation can be estimated as the time $q(t)$ takes to reach $q_{min}$. Setting $q(\tau) = q_{min}$ we find

$$\tau = Mq_0 log(\frac{1-q_0}{q_{min}-q_0}). \qquad (8)$$

*Manzo-Pelliti model of allopatric speciation and definition of* $\tau_a$

Manzo and Peliti (1994) extended the Derrida-Higgs model to describe populations geographically isolated in islands to investigate the possibility of allopatric speciation in the presence of gene flow. They considered two islands with $K$ individuals each following the Derrida-Higgs model with sexual reproduction. The interaction between individuals of different islands occurs only via migration: after reproduction with partners of the same island, individuals can migrate to the other island with probability $\varepsilon$. The genetic variation of the populations is measured by the quantity $q_{\alpha\beta}$, which is the similarity between individuals $\alpha$ and $\beta$ on the same island, and a new quantity $p_{\alpha\beta}$ is introduced to measure the similarity of individuals belonging to different islands. Similarly to the Derrida-Higgs model, the description of dynamical properties of the system, such as the values of the similarities in the equilibrium, $q_0$ and $p_0$, can be obtained in the approximation of infinitely large genomes and in the regime of small mutation rate and large population (Manzo and Pelliti, 1994).

In special, Manzo and Pelliti (1994) were interested in exploring the feasibility of the regime where $p_0 < q_{min} < q_0$: there is no speciation in the islands and each one beares a single species, but the islands differentiate from each other, i.e., the species are endemic. Therefore, the differentiation occurs only due to the exchange of individuals between the islands. In our model (Fig. 1 in the main text), we are similarly interested in studying the speciation of the parasite purely induced by host-switching (equivalent to migration events in the two islands model). Then, we also adopt $q_{min} < q_0$ to inhibit the speciation of parasites that would occur within hosts in the absence of host-switching (we use $q_{min} = 0.5q_0$). However, our model can not be further described by the expressions of Manzo-Pelliti because the host-switching probability depends on time and multiple hosts (islands) emerge over the simulation. Nevertheless, we still can use this description for the scenario where there is no migration/host-switching, i.e., the allopatric speciation. As follows, we demonstrate how to calculate the time for allopatric speciation, $\tau_a$, which is a parameter to rescale the input phylogenies in our simulations.

*Dynamics in the two-islands model*

In the case of two islands, we need to distinguish the similarities between individuals inhabiting the same island, *q*, or different islands, *p*, as stated previously. For individuals *α* and *β* that belong to the same island, the average similarity $\bar{q}_{t+1}$ follows equation (4), $\bar{q}_{t+1} = e^{-4\mu}[(1 - \frac{1}{K})\bar{q}_t + \frac{1}{K}] = e^{-4\mu} Q(\bar{q}_t, K)$. Otherwise, if they were born in different islands, their similarity evolves as $\bar{p}_{t+1} = e^{-4\mu}\bar{p}_t$since they do not have any parents in common. After reproduction, pair of individuals of the same island keep their original geographic relation if they do not migrate or both migrate, with probability $(1 - \epsilon)^2 + \epsilon^2 \equiv a(\epsilon)$. The probability of a pair of individuals changing their geographic relative position is given by $2\epsilon(1 - \epsilon) \equiv b(\epsilon)$, that accounts for one individual staying at the island and the other migrating (note that $a(\epsilon) + b(\epsilon) = 1$). Therefore, the dynamics of *q* and *p* is given by

$$q_{t+1} = a(\epsilon)\, e^{-4\mu}\, Q(q_t, K) + b(\epsilon)\, e^{-4\mu}\, p_t \qquad (9)$$

$$p_{t+1} = b(\epsilon)\, e^{-4\mu}\, Q(q_t, K) + a(\epsilon)\, e^{-4\mu}\, p_t \qquad (10)$$

where we omitted the bars for simplicity. For $\epsilon$, $\mu$ and 1/K all much smaller than 1, the equations can be approximated by

$$q_{t+1} = (1 - 2\epsilon - 4\mu - 1/K)q_t + 2\epsilon p_t \qquad (11)$$

$$p_{t+1} = 2\epsilon q_t + (1 - 2\epsilon - 4\mu)\ p_t. \qquad (12)$$

We obtain the coupled dynamical equations for *q(t)* and *p(t)* from equations 11 and 12 using the approximations $q_{t+1} - q_t = dq/dt$ and $p_{t+1} - p_t = dp/dt$, as done previously:

$$\frac{dq}{dt} =- (2\epsilon + 4\mu + 1/K)q(t) + 2\epsilon p(t) \qquad (13)$$

$$\frac{dp}{dt} = 2\epsilon q(t) - (2\epsilon + 4\mu)p(t). \qquad (14)$$

When in strict allopatry, $\epsilon = 0$, the similarity between islands is simply given by $p(t) = e^{-4\mu t}$, i.e., it depends only on the mutation rate. The time for the diversification due to geographical isolation $\tau_a$ can be calculated by $p(\tau_a) = e^{-4\mu\tau_a} = q_{min}$. The time for allopatry is then

$$\tau_a = \frac{1}{4\mu} log(\frac{1}{q_{min}}). \qquad (15)$$

The time for allopatry decreases with $q_{min}$: making the reproduction more restricted (increasing $q_{min}$) facilitates the differentiation between islands, which occurs in a smaller time.

In our simulations, we find the relation between the length of the branches in the host phylogeny and the time in generations by assuming that the smaller branch corresponds to the minimal time to parasites speciate due to geographical isolation.$\tau_a$ is calculated by equation (15) with the input parameters and $q_{min} = 0.5\, q_0$, with $q_0$ given by equation (5). Also, we consider that the first host species (the root of the phylogeny) must evolve for $\tau_a$ generations for the parasite populations to accumulate genetic diversity before the first splitting event.

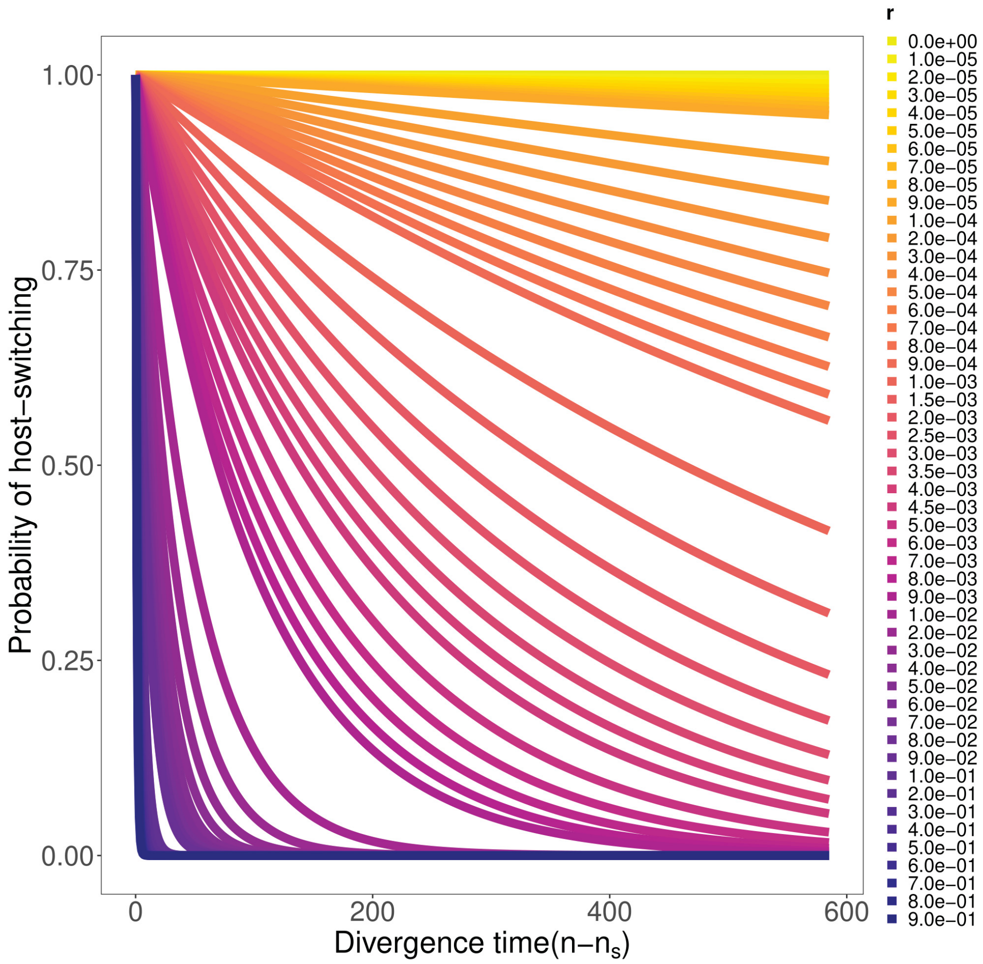


**Figure S1**. Probability of a parasite individual successfully host-switching from a host to another host species as a function of the divergence time (how long the two host species had diverged). If *r*=0 the probability is equal to 1 regardless of the divergence time, however this probability decreases if higher values of *r* are considered.

### *Parameters used*

The parameters involved in the model are described in Table S1. We considered four different carrying capacities *K* = {50,250,500,1000}. When we vary the population size (Figure S2 and S3) we do not observe differences in the patterns of beta diversity (β) and tree imbalance (normalised Sackin index - $I_n$) between the host-switching intensity, therefore we do not include the variation in the parasite species richness in our main results. Due to computational cost limitations, we selected the least rich host case (ID. 2) to show the influence of all population sizes and we had no qualitative difference between them (see species richness in Figure S4). The model is not too sensitive in response to changes in parasites' population size, which allows us to fix the values. Then, for the parasite population, we selected $K = 250$. Similarly, we also choose the $\mu = 0.025$, to carry out the simulations with different scenarios of host-switching intensity. We replicated each combination of the parameters for each empirical study 50 times. We included an initial transition time using the value of allopatric time in the model to eliminate the effect of the initial condition on evolutionary patterns. $t$ represent the evolutionary time of the parasites was parameterized according to the evolutionary time of the hosts and the time of allopatric speciation for each empirical study. Simulations were performed separately for each host phylogenies (Table S1).

**Table S1**. Model parameters with a short description and the investigated values.

| Parameters | Short definition | Investigated values |
|---|---|---|
| $K$ | Carrying capacity of parasite species per host species. | 50, **250**, 500, 1000 |
| $\mu$ | Mutation rate. | 0.001, **0.025** |
| $q_{min}$ | Minimal genetic similarity. | **0.5***$q_0$ |
| $r$ | Intensity of decline in host-switching probabilities as the phylogenetic distance increases between hosts. | **0-1** |

| | |
|---|---|
| Number of simulation repetitions for a given set of parameters. | **50** |
| Total number of iterations | ID 1. 1812*<br>ID 2. 1491*<br>ID 3. 1343*<br>ID 4. 702*<br>ID 5. 624*<br>ID 6. 541*<br>ID 7. 2614*<br>ID 8. 339*<br>ID 9. 248* |

Note: The bold values are the fixed values used in the presented results, while the other parameters used for the sensibility test.*total time for each empirical studies.

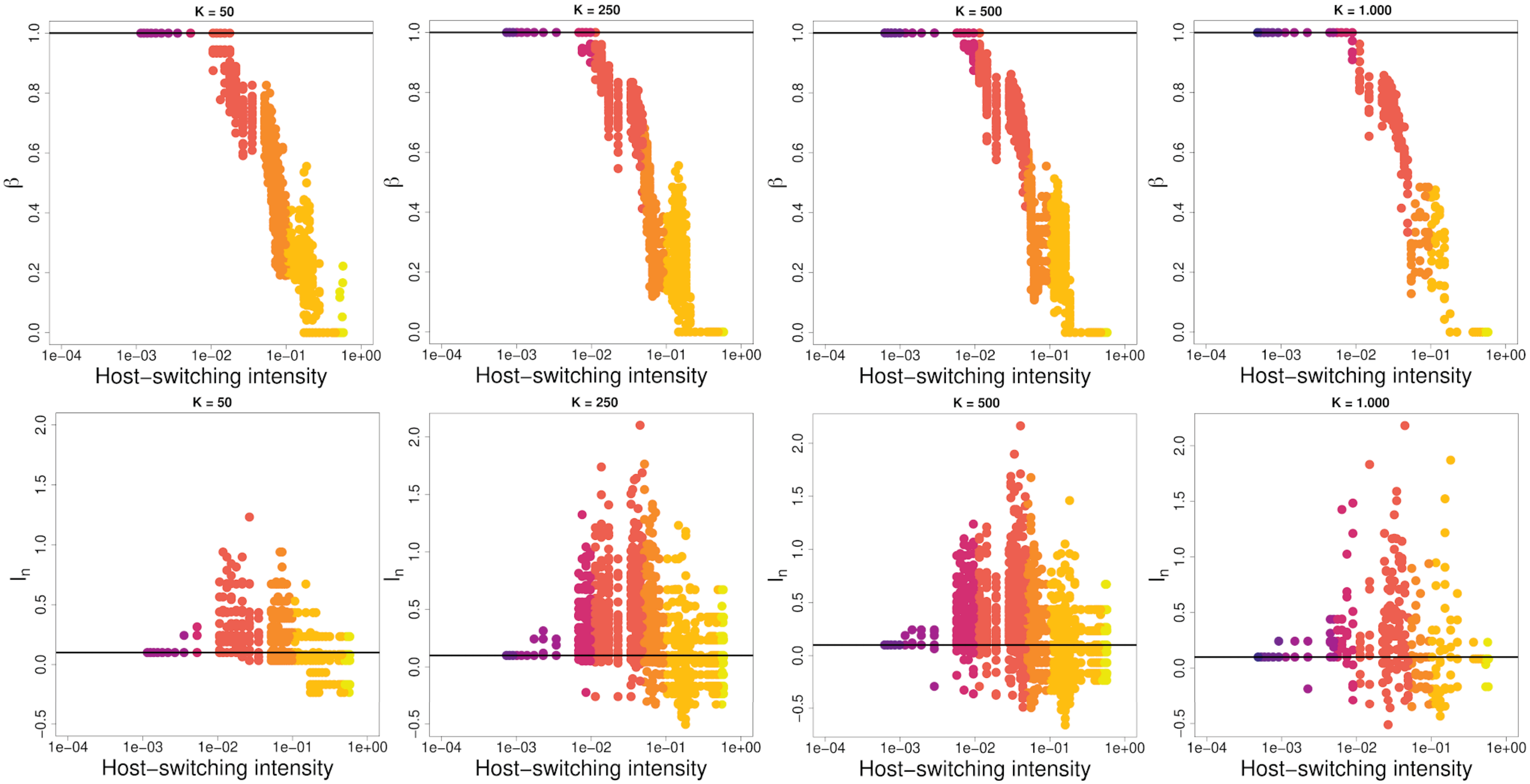


**Figure S2**. Population size test. Relationship between variation in the composition and host-switching intensity (a-d) and the tree imbalance (normalised Sackin index - $I_n$) and host-switching intensity (e-h) for different population sizes for empirical study ID. 2. Each *K* represents the population size tested. The lines refer to empirical information of parasite (continuous) and host (dotted). For this case, these lines overlap. The colored dots are redundant with the x-axis scale of graphs, but are intended to guide the interpretation. For each configuration of the parameters of host-switching intensity a total of 50 runs were performed for each carrying capacity, with the exception of $K = 1000$, which demanded more time for running. For this case, a total of 10 runs were performed.

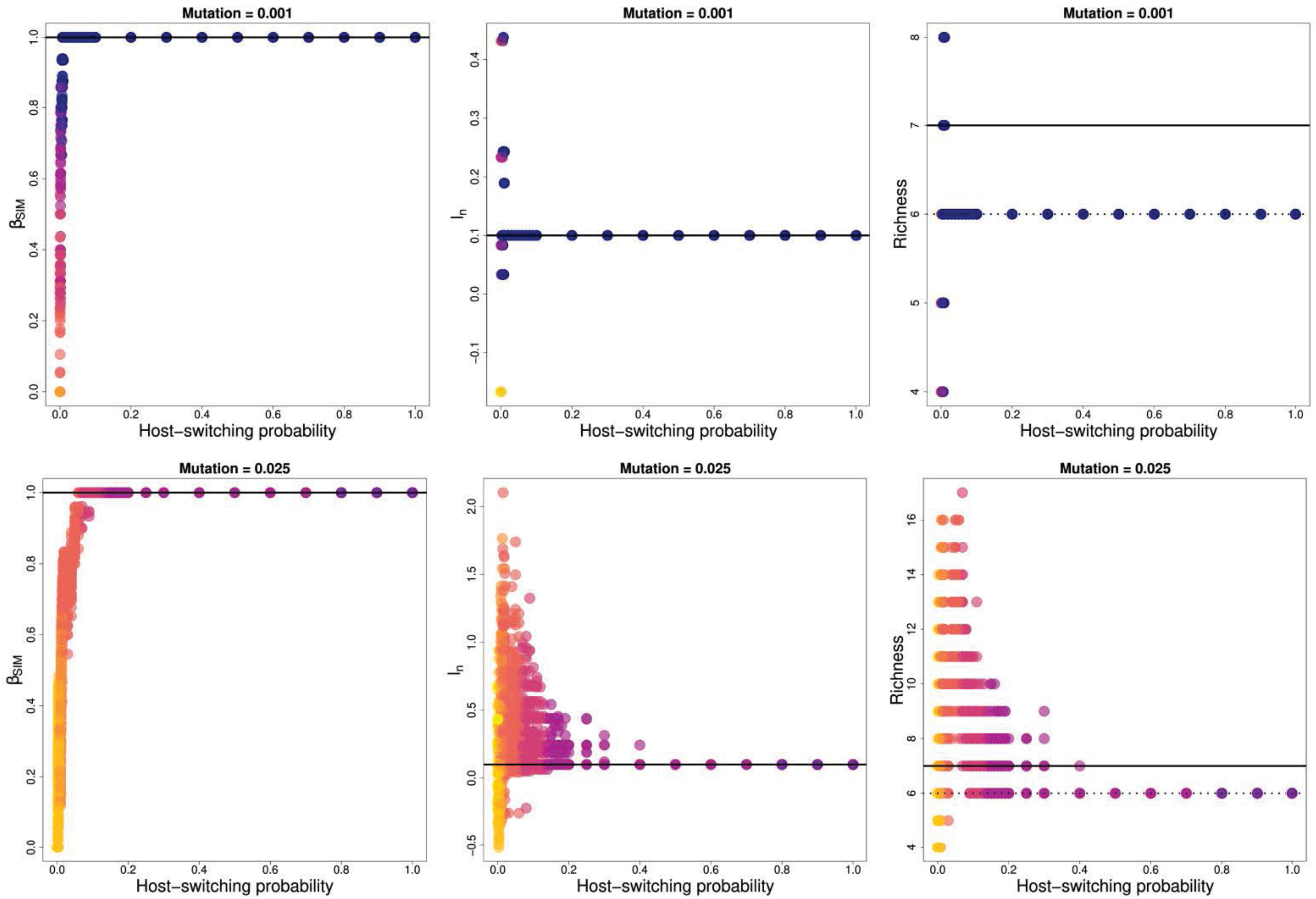

Mutation = 0.001
$\beta_{SIM}$
1.0
0.8
0.6
0.4
0.2
0.0
Host−switching probability
0.0
0.2
0.4
0.6
0.8
1.0
Mutation = 0.001
$I_n$
0.4
0.3
0.2
0.1
0.0
−0.1
Host−switching probability
Mutation = 0.001
Richness
8
7
6
5
4
Host−switching probability
Mutation = 0.025
$\beta_{SIM}$
Host−switching probability
Mutation = 0.025
$I_n$
2.0
1.5
1.0
0.5
0.0
−0.5
Host−switching probability
Mutation = 0.025
Richness
16
14
12
10
8
6
4
Host−switching probability

**Figure S3**. Mutation test. Relationship between variation in the composition and host-switching intensity (a-d) and the tree imbalance (normalised Sackin index - $I_n$) and host-switching intensity (e-h) for two mutation rates for empirical study ID. 2. Each $\mu$ represents the mutation rate tested. The lines refer to empirical information of the parasite (continuous) and host (dotted). For this case, these lines overlap. The coloured dots are redundant with the x-axis scale of graphs but are intended to guide the interpretation. For each configuration of the parameters of host-switching intensity, a total of 50 runs were performed for each carrying capacity, with K = 250.

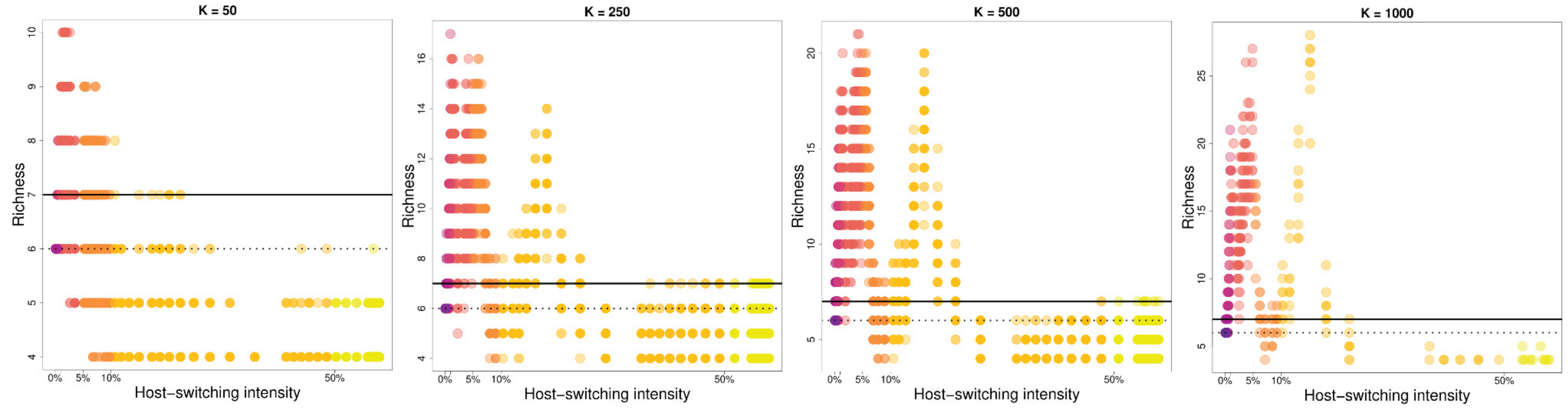


**Figure S4**. Relationship between species richness and host-switching intensity (a-d) for empirical study ID. 2. Each *K* represents the population size tested. The lines refer to empirical information of parasite (continuous) and host (dotted). The colored dots are redundant with the x-axis scale of graphs, but are intended to guide the interpretation. For each configuration of the parameters of host-switching intensity, a total of 50 runs were performed for each carrying capacity, with the exception of K = 1000, which demanded more time for running. For this case, a total of 10 runs were performed.

### *Details for empirical database*

To test our model, the cases (communities) essentially need to have real phylogenies for hosts and parasites and their interactions. A literature search was performed using the phrase "*phylogeny host-parasite*" was carried out using Google Scholar between December 1, 2019 and January 2021, which identified more than 10,000 works. Among these, a total of 100 articles were selected for feasibility analyses for testing the model. Articles that did not contain phylogeny were immediately excluded. Studies focussing on the population level were also excluded. Studies that included less than six taxa were excluded because, as they have a low sampling effort, they can lead to misinterpretations. Additionally, studies with species that have asexual reproduction were excluded from consideration, as our model is sexed. Finally, for inclusion in our analyses, we extracted nine cases (Table 1 and Figure 2 in the main manuscript and Figure S5-S13) with  knowledge of the associations and phylogenies that exist between parasites and host tips. Then, we studied the effects of host-switching and host evolution signatures on parasite speciation patterns (phylogenetic trees and variation in species composition) only for surviving species. Extinct species were not included in the analyses. The interactions of all analysed cases are available at https://github.com/elviradbastiani/host_switching_model.

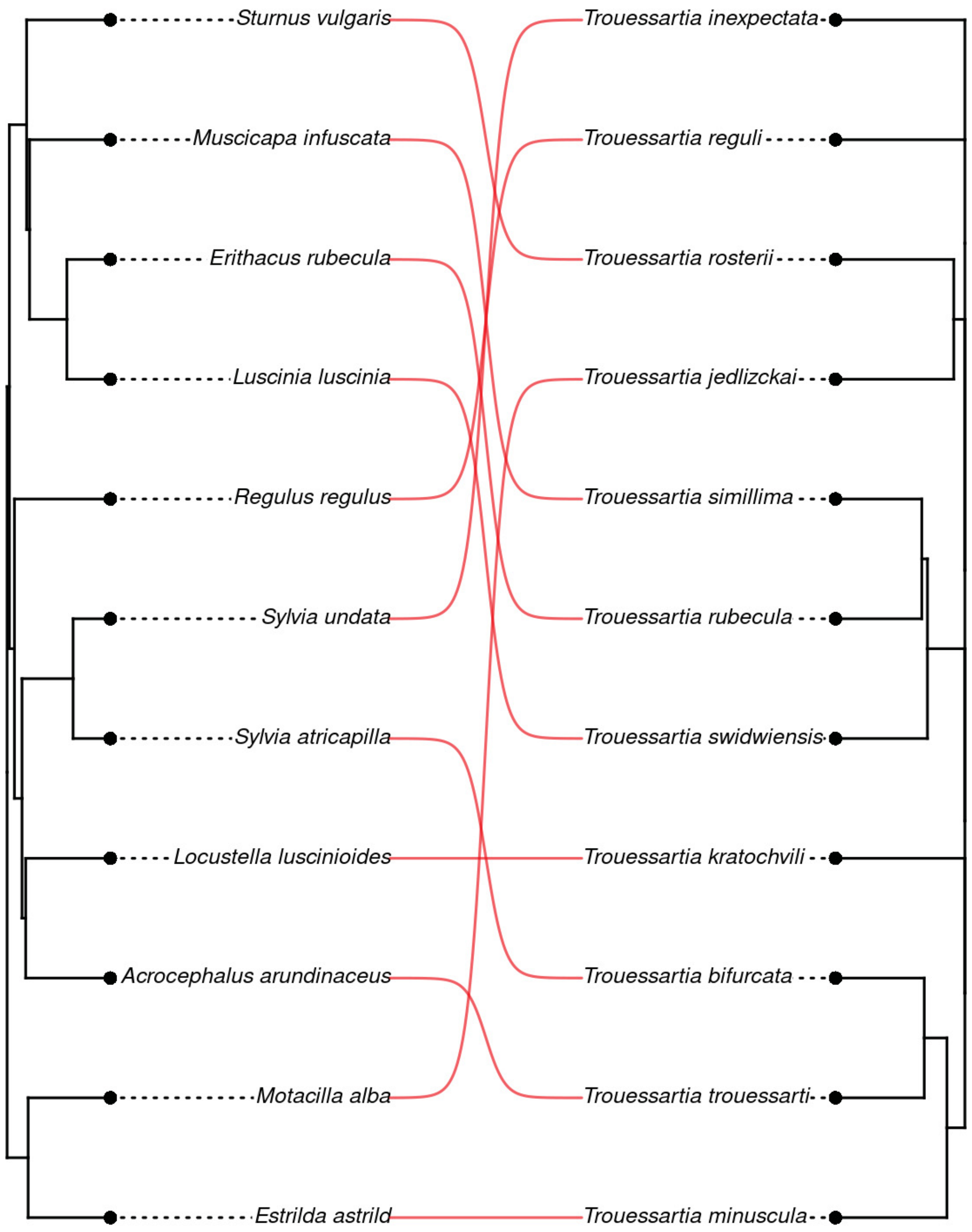


**Figure S5**. Phylogenetic trees that correspond to the empirical data of Bird and feather mites (*Trouessartia* spp.) corresponding to ID. 1 extracted from Donã et al. 2017.

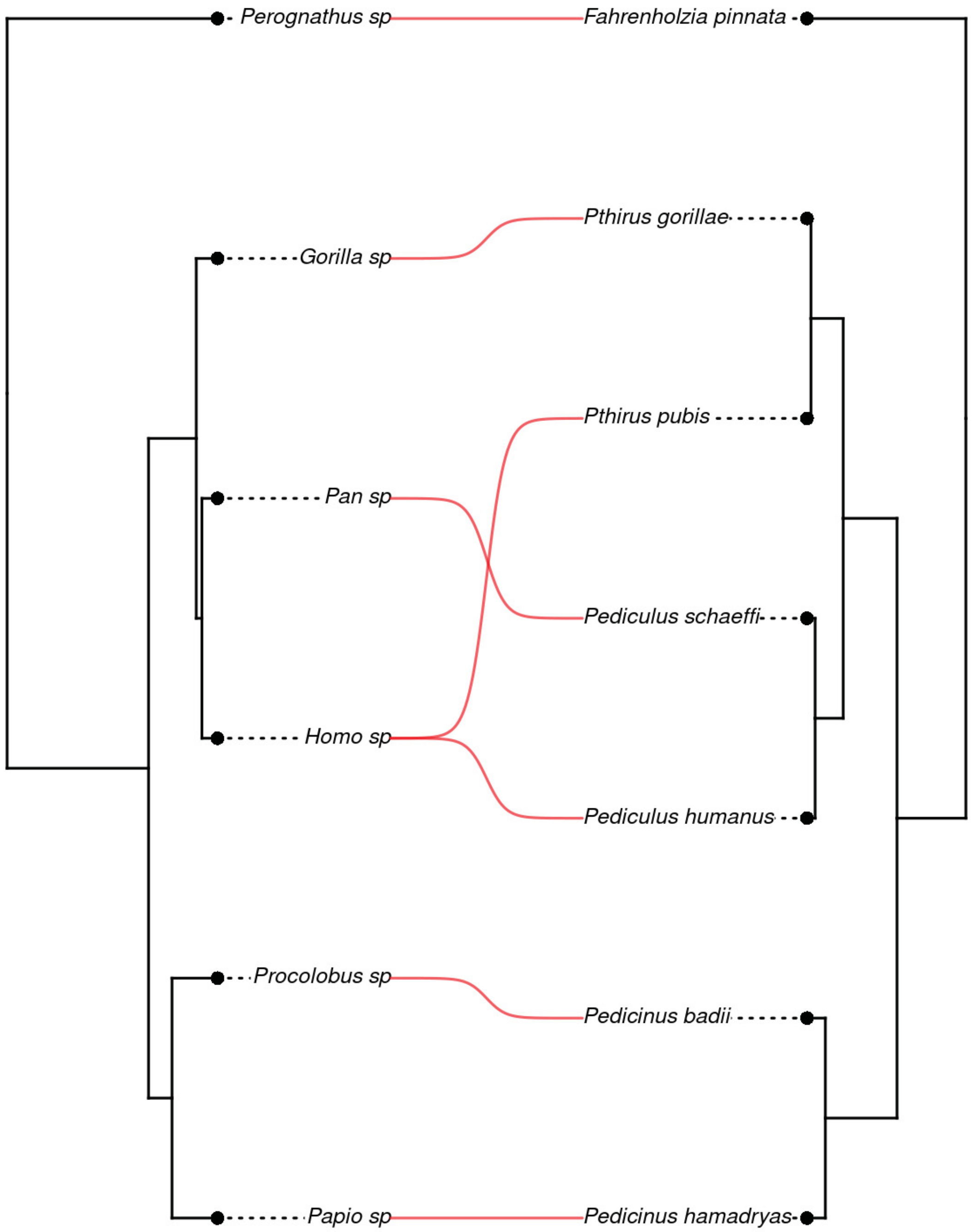


**Figure S6**. Phylogenetic trees that correspond to the empirical data of Mammals and Lice (*Pediculus* spp. and *Pthirus* spp.) corresponding to ID. 2 extracted from Reed et al. 2007.

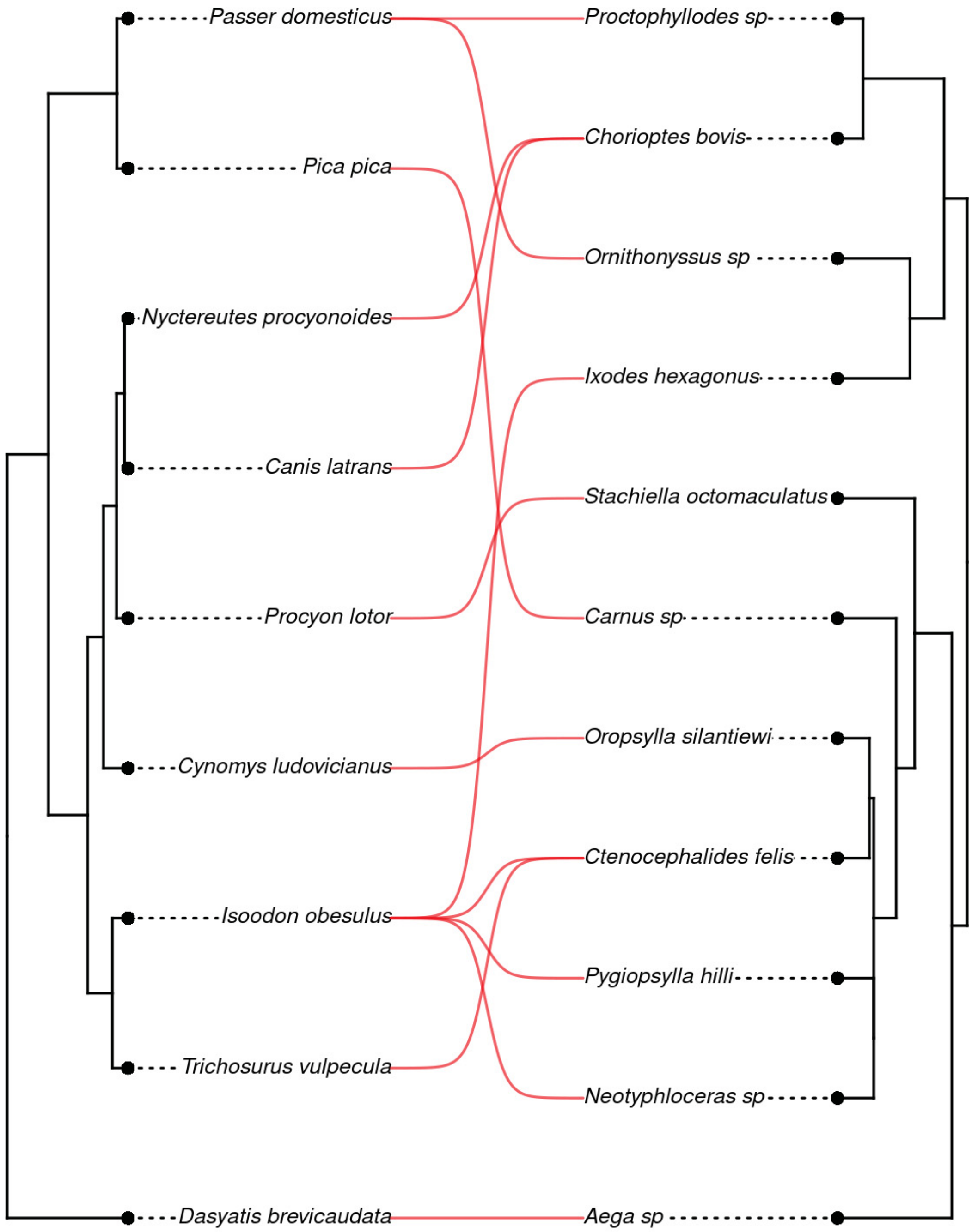


**Figure S7**. Phylogenetic trees that correspond to the empirical data of wildlife and arthropods corresponding to ID. 3 extracted from Becker et al. 2018.

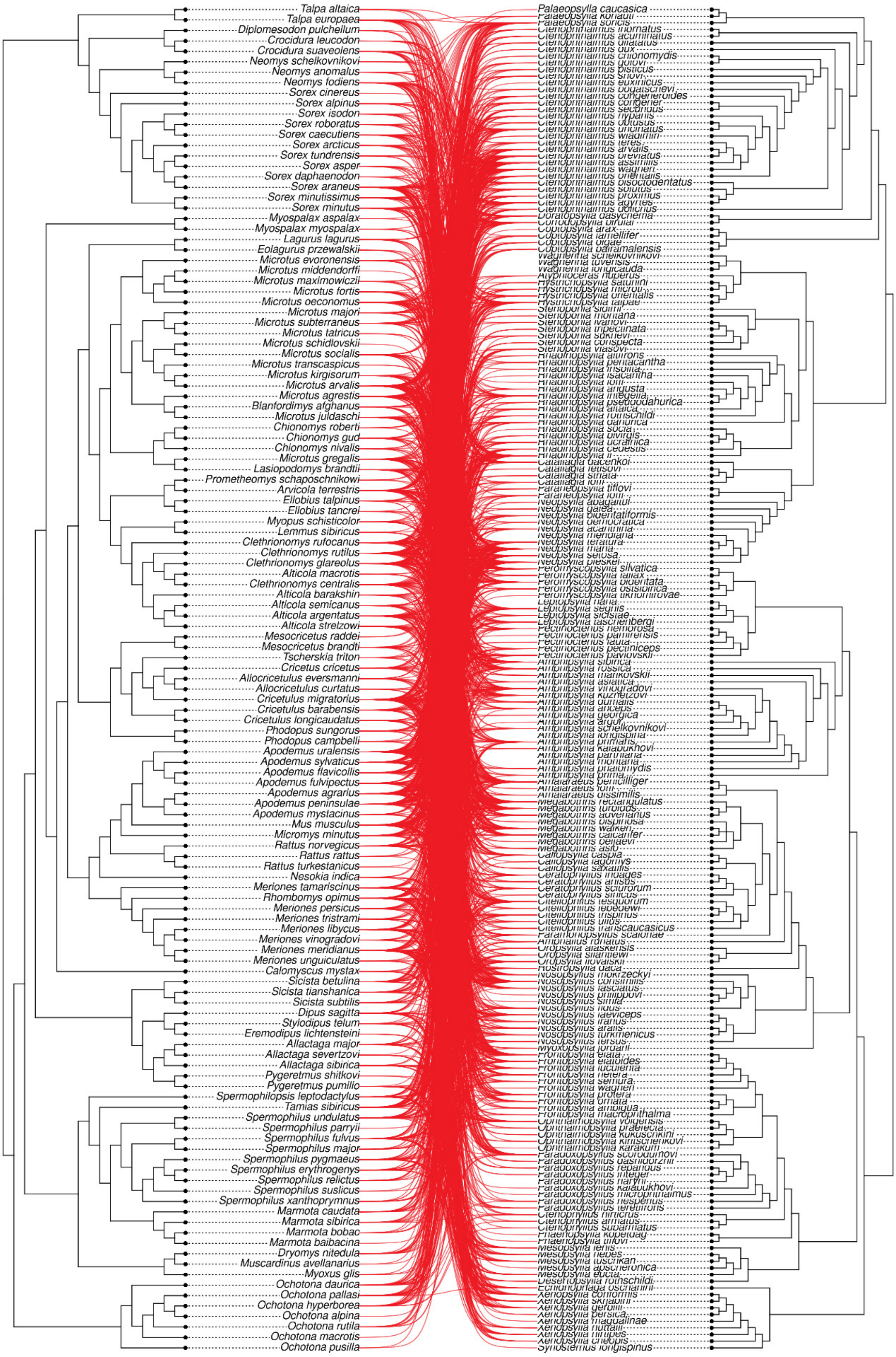


**Figure S8**. Phylogenetic trees that correspond to the empirical data of rodents and fleas corresponding to ID. 4 extracted from Krasnov et al. 2016.

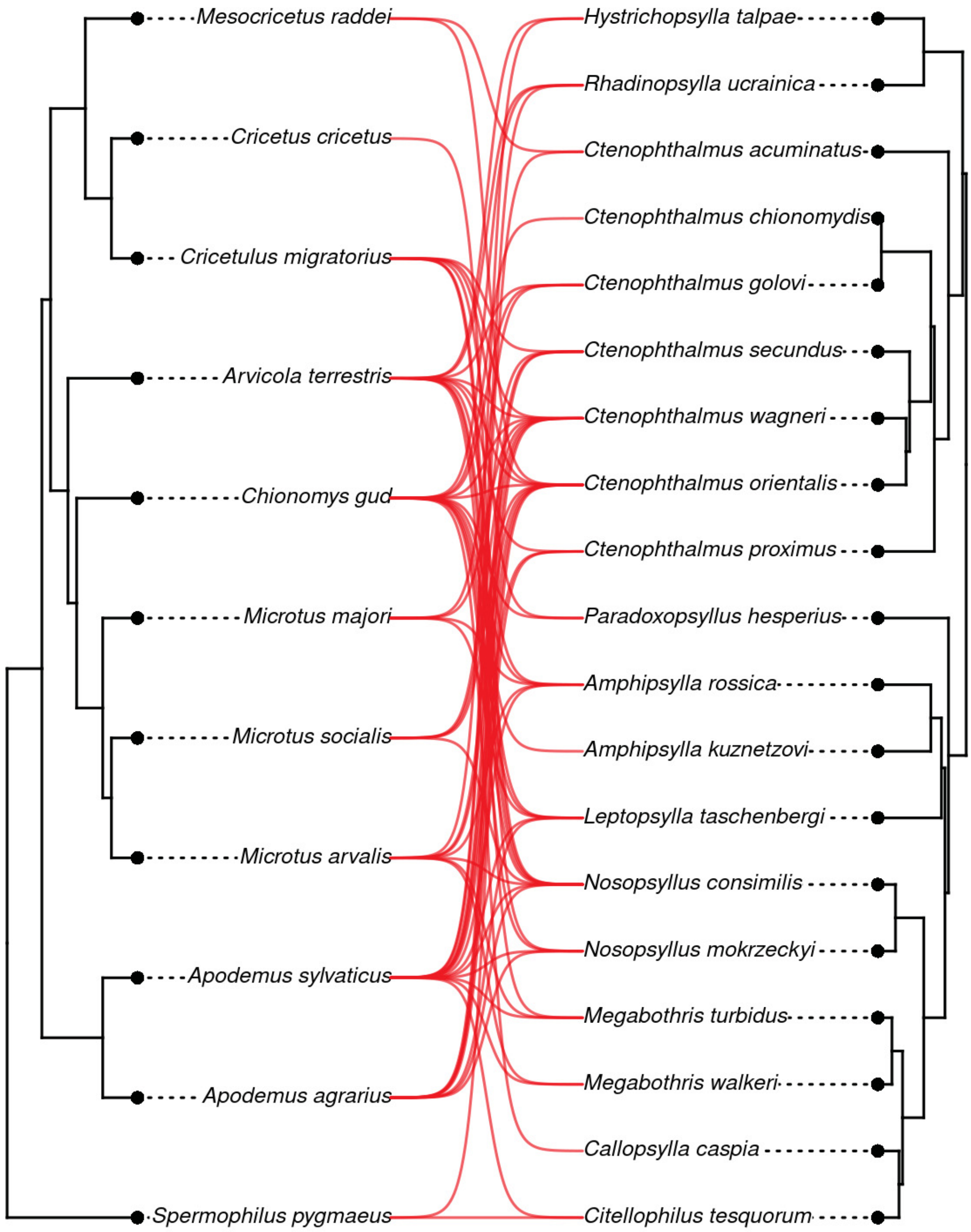


**Figure S9**. Phylogenetic trees that correspond to the empirical data of rodents and fleas corresponding to ID. 5 extracted from Krasnov et al. 2016.

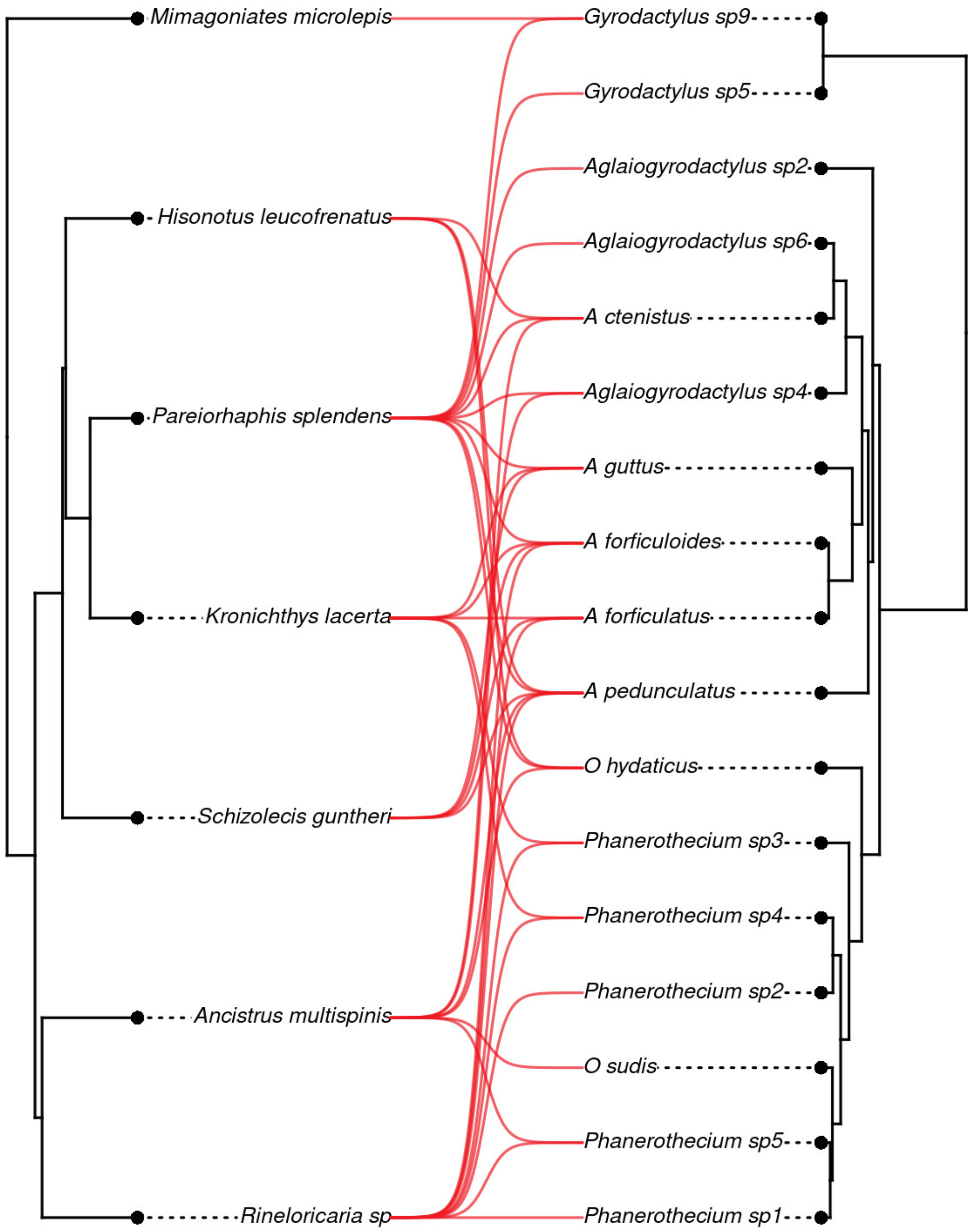


**Figure S10**. Phylogenetic trees that correspond to the empirical data of fish and platyhelminthes (Gyrodactylidae) corresponding to ID. 6 extracted from Patella et al. 2017.

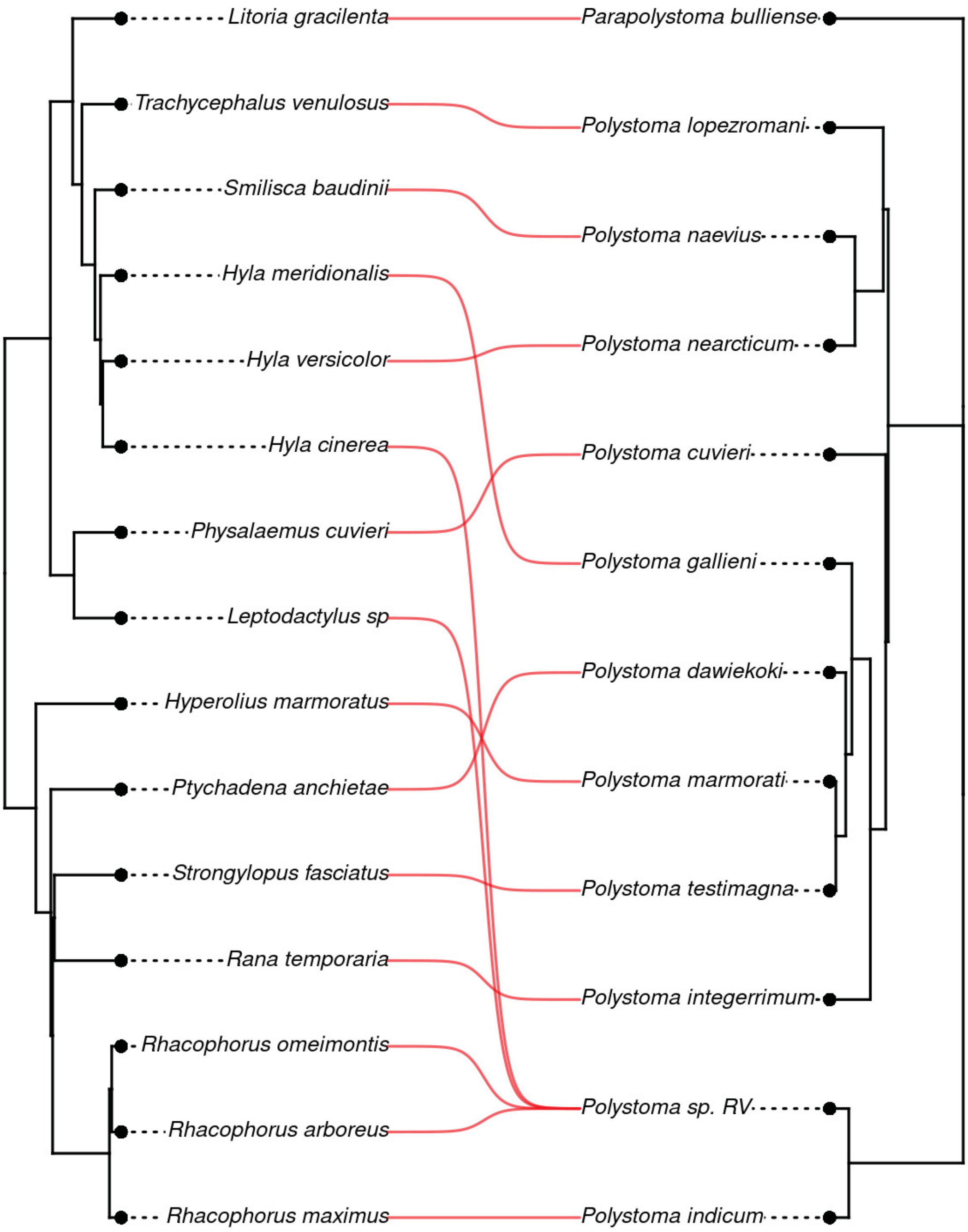


**Figure S11**. Phylogenetic trees that correspond to the empirical data of frogs and polystomes (Polystomatidae) corresponding to ID. 7 extracted from Badets et al. 2011.

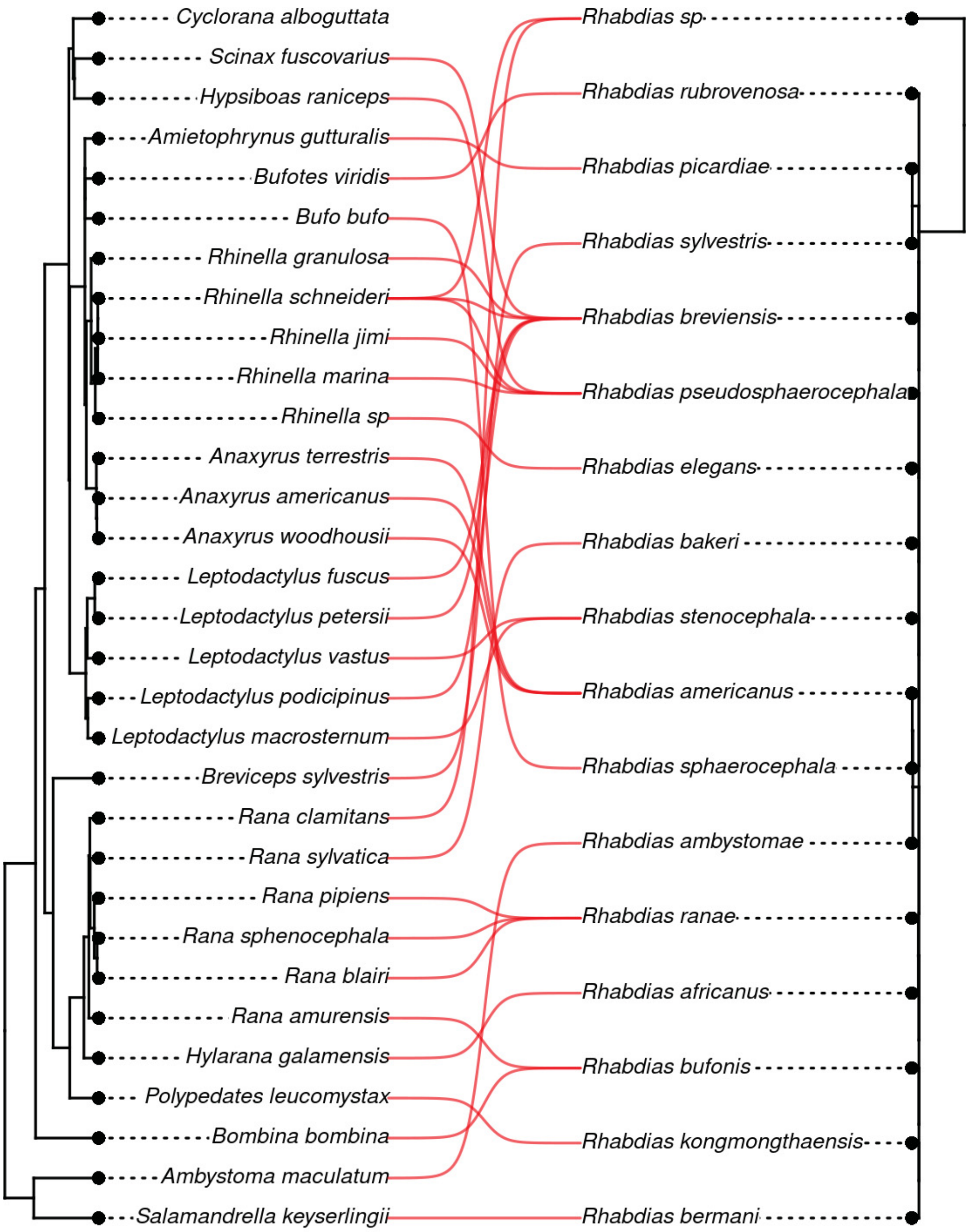


**Figure S12**. Phylogenetic trees that correspond to the empirical data of frogs and Nematodes (*Rhabdias* spp. ) corresponding to ID. 8 extracted from Müller et al. 2018.

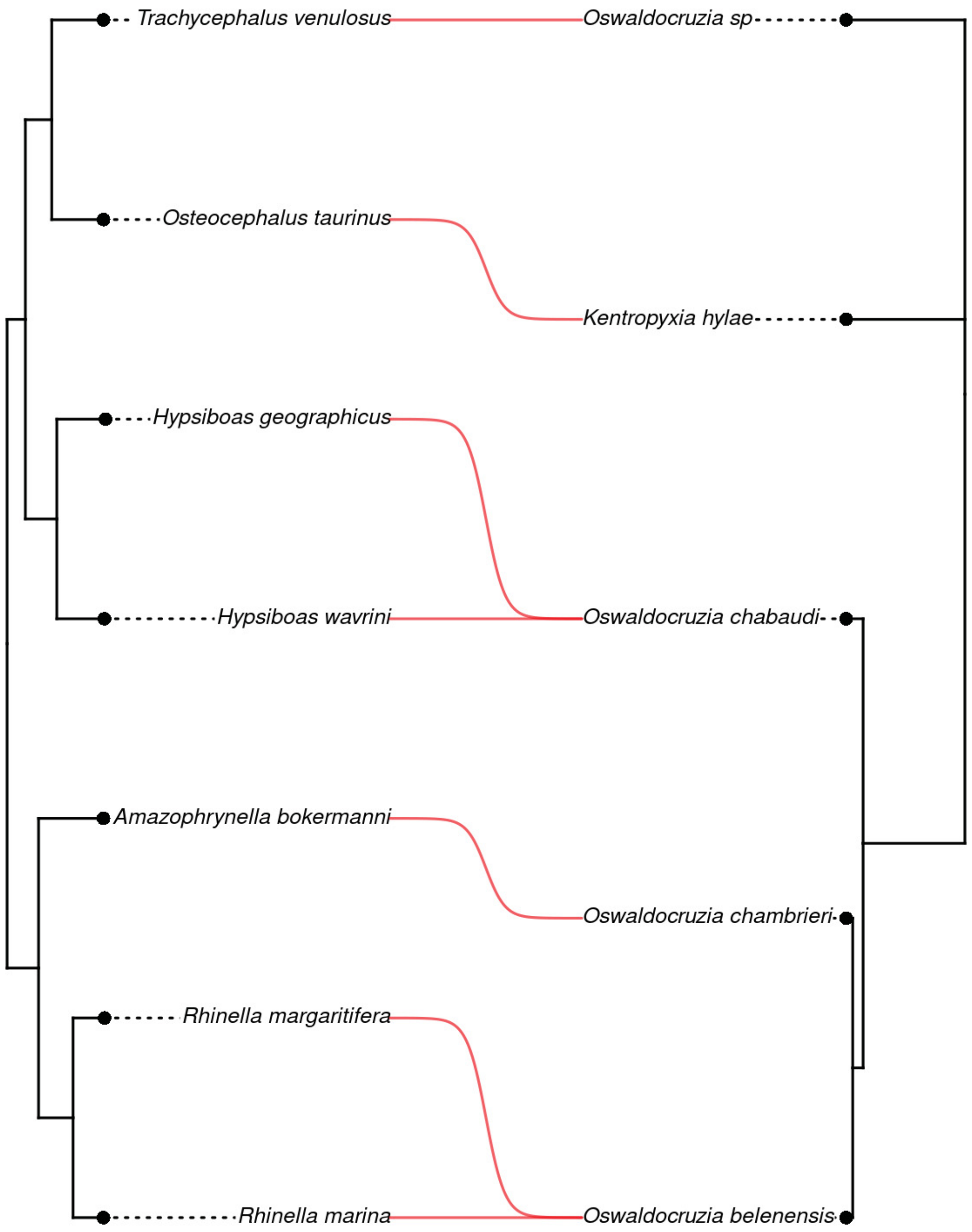


**Figure S13**. Phylogenetic trees that correspond to the empirical data of frogs and Nematodes (*Oswaldocruzia* spp. ) corresponding to ID. 8 extracted from Willkens et al. 2021.

### *Specific results*

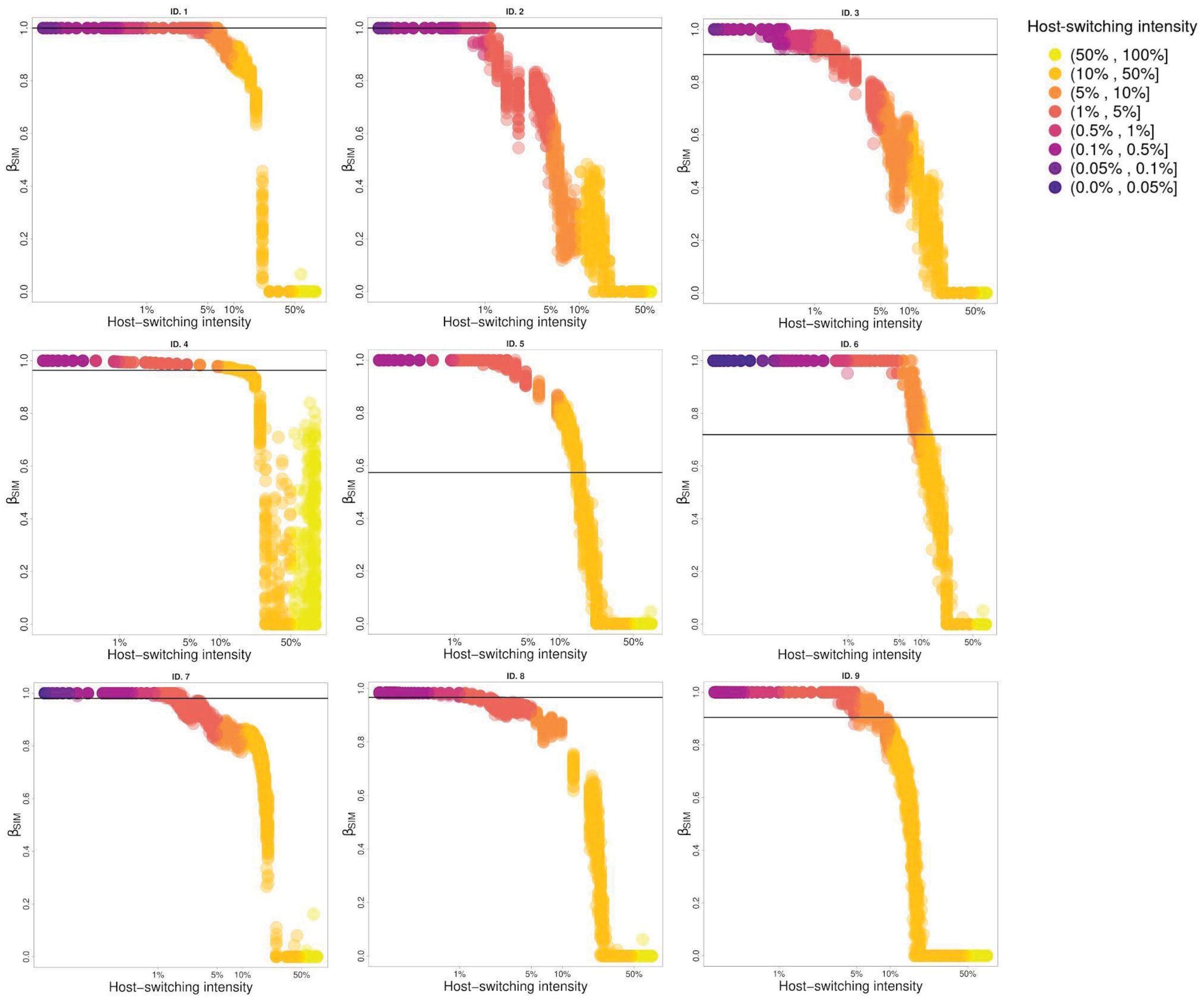


**Figure S14**. The relationship between variation in parasite composition (measured by the metric beta diversity - β - y-axis) and intensity of host-switching (x-axis and colours) for the nine empirical studies. A total of 50 runs were performed for each configuration of the parameter "host-switching intensity", with $K=250$ individuals. We present the results for endoparasites and ectoparasite empirical studies (continuous line refers to parasite information, and dotted line refers to hosts). To help distinguish the different intensities of the host switch, we make colour scales for each percentage interval.

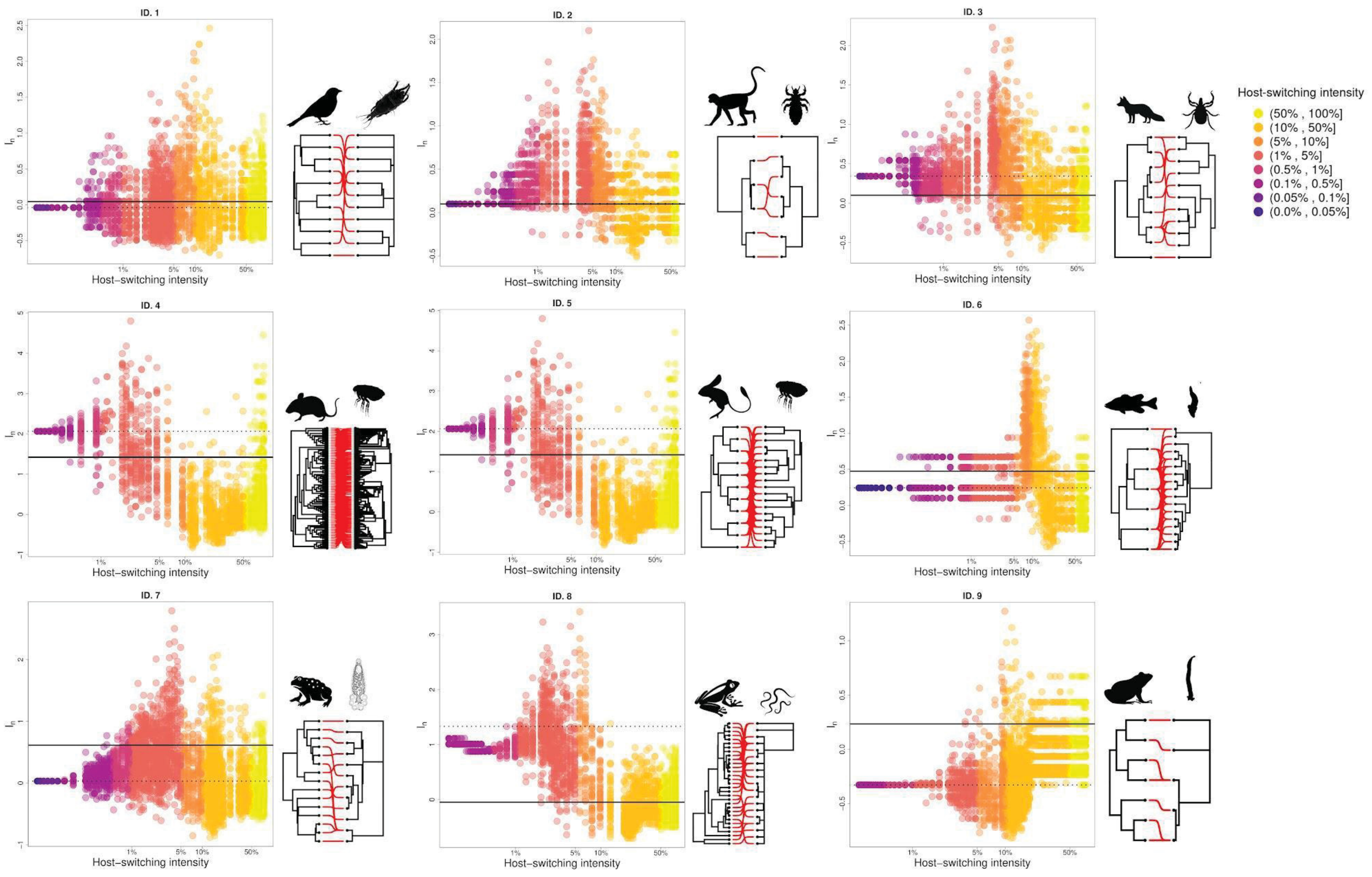


**Figure S15**. The relationship between variation in parasite composition (measured by the metric normalised Sackin index - $I_n$ - y-axis) and intensity of host-switching (x-axis and colours) for the nine empirical studies. A total of 50 runs were performed for each configuration of the parameter "host-switching intensity", with K=250. We present the results for endoparasites and ectoparasite empirical studies (continuous line refers to parasite information, and dotted line refers to hosts). To help distinguish the different intensities of the host switch, we make colour scales for each percentage interval.

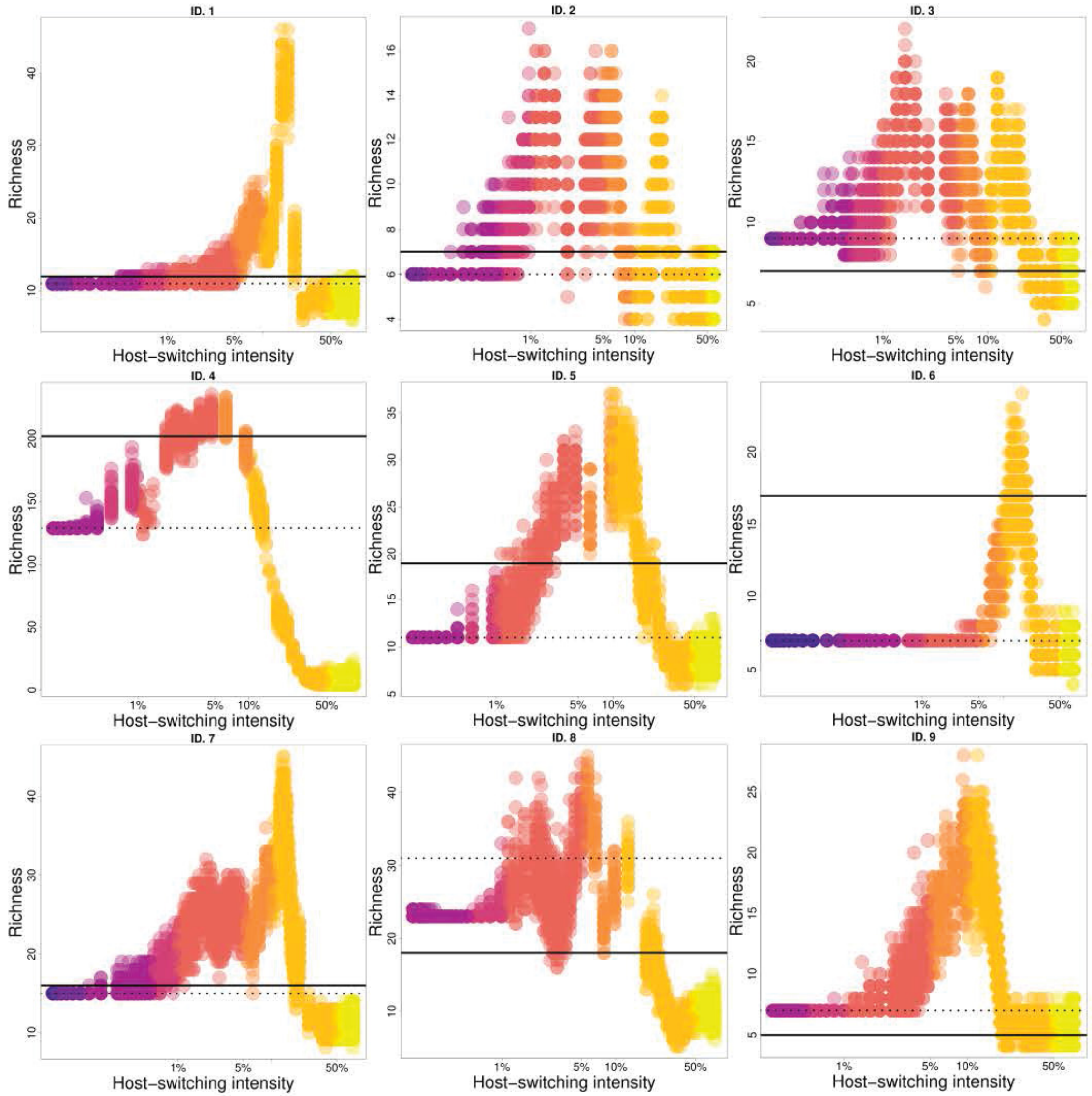

ID. 1
Richness
10
20
30
40
1%
5%
50%
Host–switching intensity
ID. 2
Richness
4
6
8
10
12
14
16
1%
5%
10%
50%
Host–switching intensity
ID. 3
Richness
5
10
15
20
1%
5%
10%
50%
Host–switching intensity
ID. 4
Richness
0
50
100
150
200
1%
5%
10%
50%
Host–switching intensity
ID. 5
Richness
5
10
15
20
25
30
35
1%
5%
10%
50%
Host–switching intensity
ID. 6
Richness
5
10
15
20
1%
5%
50%
Host–switching intensity
ID. 7
Richness
10
20
30
40
1%
5%
50%
Host–switching intensity
ID. 8
Richness
10
20
30
40
1%
5%
10%
50%
Host–switching intensity
ID. 9
Richness
5
10
15
20
25
1%
5%
10%
50%
Host–switching intensity

**Figure S16**. The relationship between variation in parasite composition (measured by the metric normalised Sackin index - $I_n$ - y-axis) and intensity of host-switching (x-axis and colours) for the nine empirical studies. A total of 50 runs were performed for each configuration of the parameter "host-switching intensity", with K=250. We present the results for endoparasites and ectoparasite empirical studies (continuous line refers to parasite information, and dotted line refers to hosts). To help distinguish the different intensities of the host switch, we make colour scales for each percentage interval.

*Example eco-evolutionary patterns over time*

Here we illustrated the complete temporal results (Fig. S17 and S18) only the empirical study of the feather mites associated with birds to explain the ecological and evolutionary trajectories over time. In the empirical study represented in Fig. 1 in the main document (feather mites associated with birds - ID. 1), all host species arose only in evolutionary time 1500. Only after this time, resource limitations become more evident and interactions start to become more restricted. For this case, as hosts diversify, they arrive at an end time (1812) with an eco-evolutionary pattern similar to the interactions in the empirical study. In the other empirical study, we observe similar patterns.

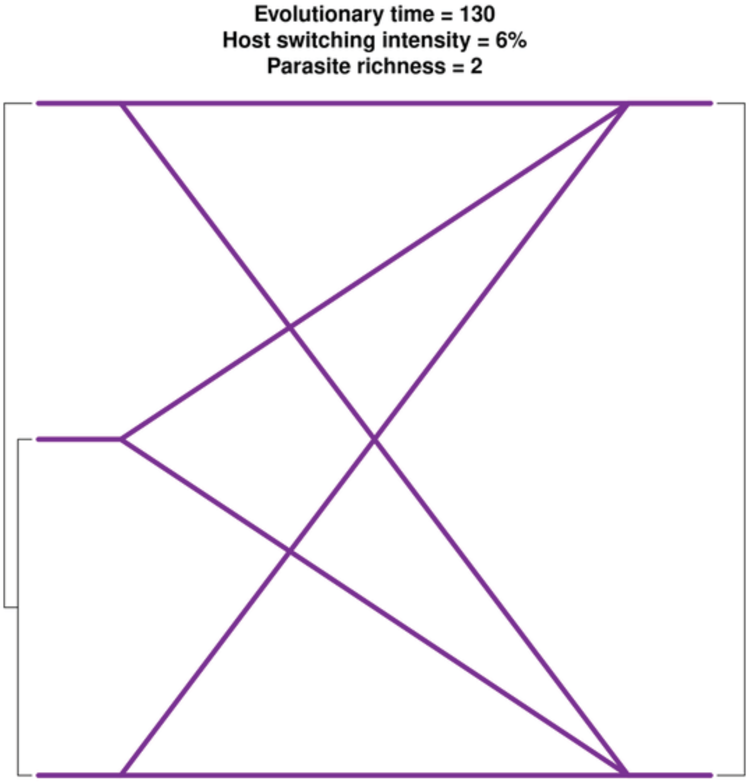


**Figure S17**. Complete temporal results (GIF) show the patterns of host-switching over evolutionary time for feather mites associated with birds. See the gif also at: https://github.com/elviradbastiani/host_switching_model).

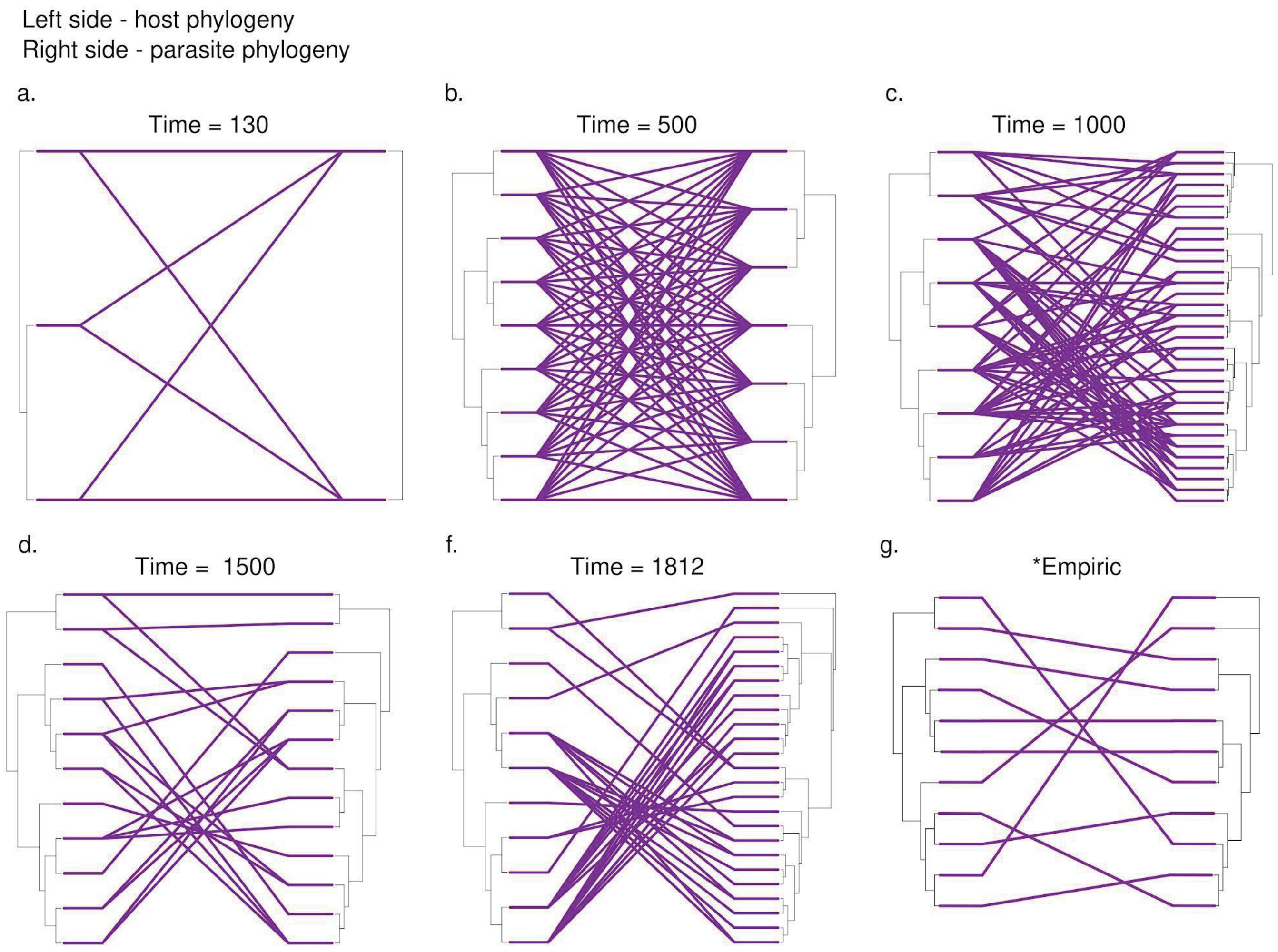


**Figure S18**. Ecological and evolutionary patterns of host and parasite to empirical study (case ID1 - feather mites associated with birds) over time (i-vi) with host-switching intensity between 1% - 5%. The end time has similar structures with case study 1. *empirical phylogeny host-parasite.

## REFERÊNCIAS

[Dataset] Badets, M., Whittington, I., Lalubin, F., Allienne, J.F., Maspimby, J.L., Bentz, S. & Verneau, O. (2011). Correlating early evolution of parasitic platyhelminths to Gondwana breakup. Systematic Biology, 60, 762-781. Accession number: EDB_10.1093/sysbio/syr078

[Dataset] Becker, D.J., Streicker, D.G. & Altizer, S. (2018). Using host species traits to understand the consequences of resource provisioning for host–parasite interactions. Journal of Animal Ecology, 87, 511-525. Accession number: EDB_10.1111/1365-2656.12765

[Dataset] Doña, J., Sweet, A.D., Johnson, K.P., Serrano, D., Mironov, S. & Jovani, R. (2017). Cophylogenetic analyses reveal extensive host-shift speciation in a highly specialized and host-specific symbiont system. Molecular phylogenetics and evolution, 115, 190-196. Accession number: EDB_10.1016/j.ympev.2017.08.005

Higgs, P. G., & Derrida, B. (1991). Stochastic models for species formation in evolving populations. Journal of Physics A: Mathematical and General, 24(17), L985.

[Dataset] Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S. & Degen, A.A. (2016). Trait-based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. Oikos, 125, 29-38. Accession number: EDB_10.1111/oik.02178

Manzo, F., & Peliti, L. (1994). Geographic speciation in the Derrida-Higgs model of species formation. Journal of Physics A: Mathematical and General, 27(21), 7079.

[Dataset] Mueller, M.I., Morais, D.H., Costa-Silva, G.J., Aguiar, A., Avila, R.W. & da Silva, R.J. (2018). Diversity in the genus *Rhabdias* (Nematoda, Rhabdiasidae): Evidence for cryptic speciation. Zoologica Scripta, 47, 595-607. Accession number: EDB_10.1111/zsc.12304

[Dataset] Patella, L., Brooks, D.R. & Boeger, W.A. (2017). Phylogeny and ecology illuminate the evolution of associations under the Stockholm paradigm: *Aglaiogyrodactylus* spp. (Platyhelminthes, Monogenoidea, Gyrodactylidae) and species of Loricariidae (Actinopterygii, Siluriformes). Vie Et Milieu, 67, 91-102. Accession number: EDB_20183235432

[Dataset] Reed, D.L., Light, J.E., Allen, J.M. & Kirchman, J.J. (2007). Pair of lice lost or parasites regained: the evolutionary history of anthropoid primate lice. Bmc Biology, 5, 1-11. Accession number: EDB_10.1186/1741-7007-5-7

[Dataset] Willkens, Y., Furtado, A.P., Dos Santos, J.N. & de Vasconcelos Melo, F.T. (2021). Do host habitat use and cospeciation matter in the evolution of *Oswaldocruzia* (Nematoda, Molineidae) from neotropical amphibians? Journal of Helminthology, 95, e33. Accession number: EDB_10.1017/S0022149X21000250

# CAPÍTULO 2

In progress - Journal of Animal Ecology

# Can host traits facilitate host-switching events by parasites?

[1*]Elvira D'Bastiani, [1,2]Karla M. Campião, [3]Débora Princepe, [4]André de Camargo Guaraldo, [5]Boris R. Krasnov,[1,6]Sabrina LB Araujo,

[1]Laboratório de Interações Biológicas, Universidade Federal do Paraná, UFPR, Curitiba, Paraná, Brazil

[2]Departamento de Zoologia, Universidade Federal do Paraná, UFPR, Curitiba, Paraná, Brazil

[3]Instituto de Física "Gleb Wataghin", Universidade Estadual de Campinas, UNICAMP, Campinas, São Paulo, Brazil

[4]Laboratório de Ecologia Comportamental e Ornitologia, Universidade Federal do Paraná, UFPR, Curitiba, Paraná, Brazil

[5]Mitrani Department of Desert Ecology, Swiss Institute for Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

[6]Departamento de Física, Universidade Federal do Paraná, UFPR, Curitiba, Paraná, Brazil

*Corresponding author: Elvira D'Bastiani

e-mail: elviradbastiani@gmail.com

**Abstract:** Traits of host species are important drivers of interspecific parasite transmission and can be informative to predict whether the addition or replacement of new species to a parasite host spectrum can occur. In this study, we explore how the predicted host-switching intensity varies among host communities; how the functional diversity and phylogenetic host variability are related to the host-switching intensities in host communities; and which host traits are related to the host-switching intensities among host species in each host community and among host species independent of the host community. We used an individual-based model to estimate the host-switching at two levels: community and species. The model considers that parasites can explore and colonise hosts under variable host-switching intensity, with parasite evolution driven by mutation, genetic drift and mating restriction. We hypothesised that the host-switching intensities by parasites vary among host communities and these intensities are related to some hosts’ traits. We found that the optimal range of predicted host-switching intensity by parasites varied between host communities; the optimal range for the host communities wasn't associated with the functional diversity and phylogenetic host variability nor with host traits. At host species level, host-switching was associated with species-specific adult body mass, diet breadth, home range, population density, and litter size, but varied between host communities. Our results suggest that host traits likely determine host-switching events and that these events are relatively frequent in communities at a local spatial scale. However, these events can vary substantially not only between host-parasite associations, but also spatially and, thus, alter the diversification of the parasite. This suggests that host-switching is a highly context-dependent phenomenon.

**Key-words**: ecological fitting; diversification of fleas; phylogenetic conservatism mechanism; rodent traits.

## INTRODUCTION

One of the most intriguing events observed during the evolutionary trajectory of many parasite lineages is host-switching. This  is a common event and refers to the dispersal of parasite individuals followed by colonisation of a new host lineage either closely or distantly related to the original host lineage (Page 2003; De Vienne et al. 2013; Araujo et al. 2015). A mechanism explaining the occurrence of host-switchings in nature (Agosta et al. 2010; Araujo et al. 2015) that has been adopted is the ecological fitting hypothesis, which predicts that pre-existing characteristics of a parasite may allow the organism to survive under different conditions and successfully colonise the new host (Agosta & Klemens 2008). The colonisation of a new host is not an end point, but a fundamental step in the processes of biological expansion and evolution in response to environmental changes (Hoberg & Brooks 2008; 2013; Brooks & Agosta 2012; Mácová 2018).

There are several ecological and evolutionary factors that may explain the intensity of host-switching events. The phylogenetic distance between the original and new host species, for example, can represent an adequate proxy for the nature of the resource, which is tracked by the parasite lineage (Charleston & Robertson 2002; Agosta & Klemmens 2008; Engelstädter & Fortuna 2019). Thus, the capability of the parasite to disperse and colonize new host species will be higher in related hosts, and this may influence the assembly of the parasite community within host communities. Indeed, there is evidence that hosts that are phylogenetically close hosts tend to harbour more similar parasite communities (Arneberg et al. 1998; Huang et al. 2014). Additionally, there are some ecological attributes that may potentially promote exposure to parasites, facilitating host-switching within host communities. In this sense, we expect a greater probability of switches in a community where host species share not only time and space but also morphological and ecological similarities. For example, host species that have overlapping diets would have a greater opportunity to become infected with the same species of parasite(s) due to a similar type of exposure. On the other hand, in a very heterogeneous community (high functional diversity), the probabilities of switches would be lower because, although there is time and space sharing, the low similarity between the host species reduces the opportunity of infection by the same parasite species.

Traits of host species, such as body mass, diet breadth, home range, population density, and litter size are important drivers of parasite transmission (Pilosof et al. 2015; Hayward et al. 2017; Dallas et al. 2019) and can be informative for predicting whether a new host species will be colonised. Thus, variation in these traits among different host species, and among different communities may contribute to our understanding of host-switching events, since they may restrict or facilitate colonisation of new host species by parasite species. For example, larger hosts may provide more resources (food and space) and may increase contact rates with different parasite species (Boyer et al. 2010; Kiffner et al. 2014). Likewise, the host diet may create opportunities for contact with different parasite species due to the foraging behaviour. Host home range and population density have also been positively correlated with parasite infection (Watve & Sukumar 1995; Bordes et al. 2009; Dallas et al. 2019). When hosts spatially overlap, or show some degree of similarity in these traits, the interaction opportunity for contact between host and parasite may increase.

Similarly, some elements of host reproductive biology may also increase parasite transmission. Higher litter size can also increase parasite transmission and contact rate between hosts (Boyer et al. 2010). Therefore, these factors affecting parasite transmission and host-switching events can substantially vary among host-parasite associations and also among host communities. Despite the known importance of these traits for parasite transmission, their relationship with the success of host-switchings is still not well understood.

D'Bastiani et al. (*In review*) proposed a host-switching model and observed that it is able to predict the ecological and evolutionary patterns of the empirical situations of different groups of parasites. This method uses the host phylogeny assuming that the phylogenetic conservatism of the host species is a proxy for resource similarity for parasites. The model considers parasite evolution over the host evolution and the probability of parasites switching hosts decreases with increasing divergence in the evolutionary time of the hosts. Then, during the simulated evolution time, host species emerge following an empirical host phylogeny, and a simulated parasite individuals can switch hosts and speciate. It was observed that the predicted intensity of host-switching, defined as the expected percentage of parasite individuals that switch host species in a community, varied between the empirical systems analysed. The authors showed that empirical studies of local spatial scale had a greater intensity of host-switching when compared to regional scale, but the difference in host-switching for a given spatial scale was not investigated due to the variation of investigated parasite associations (birds-ectoparasites, fishes-ectoparasites, for example). So, this leads to other questions: Is there variation in host-switching intensity among the same association and spatial scale? Do the hosts' traits associate the host-switching events? Then we hypothesised that the host-switching intensities by parasites vary among host communities and these intensities are related to some hosts' traits.

To answer these questions the flea-rodent system is a convenient biological model to explore how the addition or replacement of new host species occurs, and how these events are related to the traits of the host species. Flea species composition in rodent species results from multiple dispersal and migration events, with the rate of these events differing between biogeographic realms (i. e. the Nearctic biogeographic realm - Krasnov et al. 2015b). Flea communities in different realms have different evolutionary histories and these differences may affect the relative strength of ecological (= niche-based) drivers of flea species composition

(Gibert et al. 2021). Host-switching can occur frequently and is a highly context-dependent phenomenon, being a relevant factor in determining these associations (Stavtseva et al. 2021), which highlights the importance of disentangling which host traits may be related (Fig. 1). In this study, we applied the theoretical model proposed by D'Bastiani et al. (*In review*). We followed their methodology by measuring species turnover and the imbalance tree to identify the predicted host-switching intensity (community level). Besides that, we measured the predicted host-switching intensity at the species level. In this study we aimed to investigate: (i) how the predicted host-switching intensity varies among host communities; (ii) how the functional diversity and phylogenetic host variability are related to the host-switching intensities in host communities; (iii) which host traits are related to the host-switching intensities among host species in each host community; and (iv) which host traits are related to the host-switching intensities among species independent of the host community.

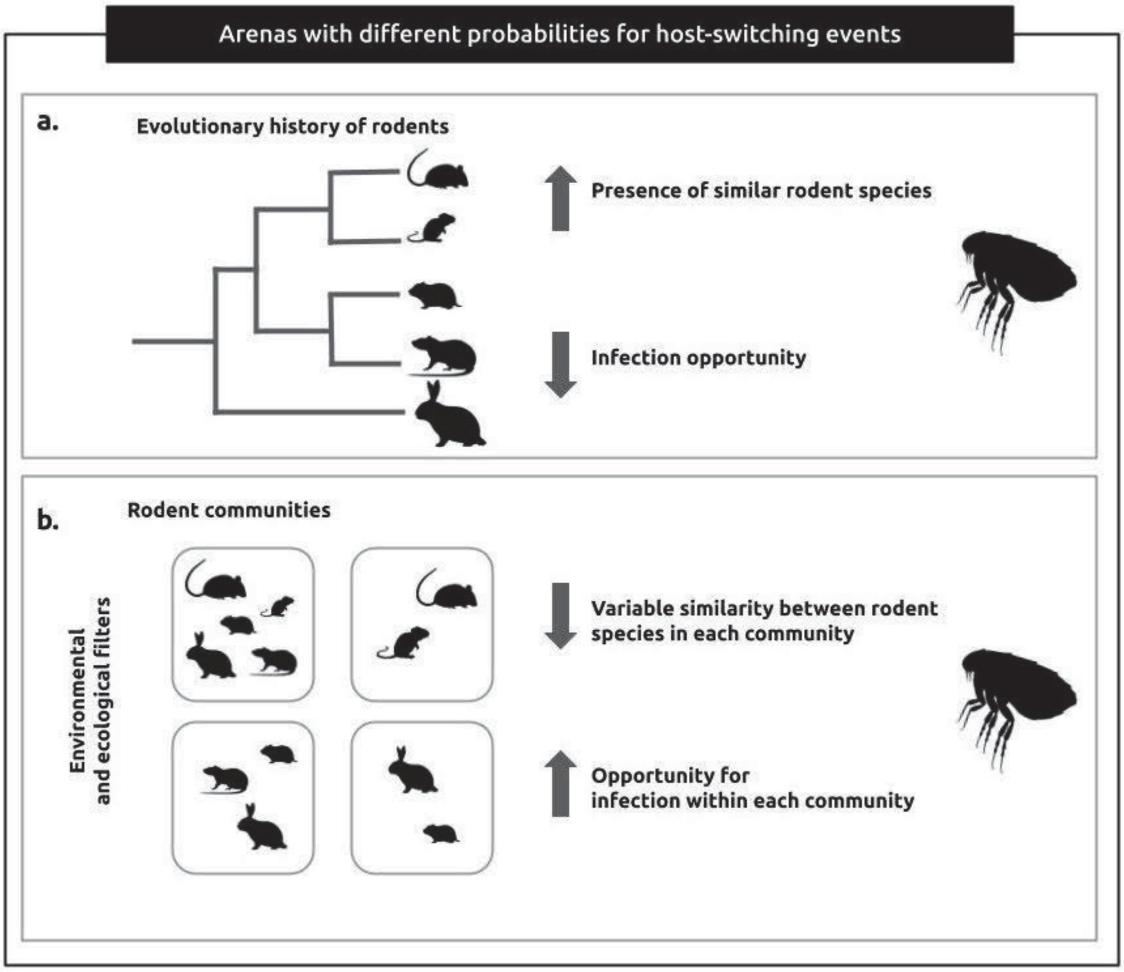


**Figure 1**. Schematic representation of two scenarios of host-switching. In scenario **a.** phylogeny with the species pool occurring on a regional spatial scale tends to have the largest similarity between rodent species, but the opportunity of infection is low since sister rodent species do not necessarily co-occur. In scenario **b.** species phylogenies from each local empirical study have less similarity between species when compared to the phylogeny of the regional pool, but the opportunity for interaction is higher within a community.

## MATERIAL AND METHODS

### Empirical data

We used ten empirical studies of flea-rodent associations in the Nearctic biogeographic realm (Table 1; Fig. S1-S10). All these studies include at least six species (of fleas and rodents) to avoid misinterpretations due to low sampling effort. The analysed communities comprise flea species associated with species of small mammals of the orders Soricomorpha, Rodentia, and Lagomorpha (Krasnov et al. 2019). The flea species *Nosopsyllus fasciatus*, *Xenopsylla cheopis*, and *Leptopsylla segnis* reported in the original studies were omitted from the analyses because they are associated with commensal rodents (*Mus musculus*, *Rattus norvegicus*, *Rattus rattus*) and have ubiquitous distributions (Krasnov et al. 2019).

To characterise the rodents' phylogenetic history, we constructed the host phylogeny based on a credible distribution of 1.000 trees obtained from http://vertlife.org/ for 61 rodent species (Upham et al. 2019). In addition, to characterise the flea phylogenetic history, we used phylogeny of the order proposed by Zhu et al. 2015. Both phylogenetic trees were ultrametrized for analyses. The phylogenetic trees and interactions for each community are presented in Fig. S1-S10, and the host phylogenetic tree from the Nearctic biogeographic realm in Fig. S11.

We characterised each host species by five traits: body mass (g), diet breadth, home range (km$^2$), population density (number of individuals per km$^2$), and litter size of the host species. The dataset includes 61 rodent species and when one species lacked information for any trait for (which happened for 36 of them), we assumed trait information of the phylogenetically closest species. These host trait values were extracted from the PanTHERIA database (Jones et al. 2009).

**Table 1**. Description of the rodent and flea richness for each host community, of which rodent phylogenies were used as model parameters and host-parasite association to validate the simulations. ID = represents the locality of each host community in different regions in the Nearctic biogeographic realm.

| ID | Rodent richness | Flea richness | Local | Reference |
|---|---|---|---|---|
| 1 | 14 | 14 | California Central | Linsdale & Davis 1956 |
| 2 | 8 | 16 | California South West | Davis et al. 2002 |

| | | | | |
|---|---|---|---|---|
| 3 | 11 | 10 | Connecticut | Main 1983 |
| 4 | 9 | 24 | Idaho | Allred 1968 |
| 5 | 20 | 17 | Indiana | Whitaker 1982 |
| 6 | 11 | 8 | Missouri | Kollars et al. 1997 |
| 7 | 8 | 12 | Montana | Holmes 2003 |
| 8 | 21 | 28 | New Mexico | Morlan 1955 |
| 9 | 19 | 15 | Tennessee | Durden & Kollars 1997 |
| 10 | 7 | 8 | Wisconsin | Amin 1976 |

In this study, each empirical study described in table 1 was called a host community. Since the empirical studies varied in the richness of host species and branch size, the total number of iterations of each host community also varied. These characteristics influence the variation of the $HSI_c$ (Fig. 2).

## The host-switching model

We performed simulations of parasite evolution to investigate the potential effect of host-switching events on the assembly of associations using the model proposed by D'Bastiani et al. *In review*. In this model, the eco-evolutionary trajectories of the parasites are influenced by the intensity of host-switching, which is mediated by their host evolutionary history (based on ultrametric empirical phylogeny). The model assumes that the evolutionary history of the hosts represents a proxy for resources used by the parasites and that the probability of host-switching decreases as the phylogenetic distance between the original and the new host species increases (D'Bastiani et al. *In review*). The probability of a parasite individual successfully migrates from one host to another host species, in a given generation *n*, is defined as:

$$P_{hs}(n)=exp[- r * (n - n_s)] , \qquad (1)$$

where $r$ is a positive parameter that controls the decay of the host-switching probability, and $n_s$ is the generation that the common host ancestor had speciated, then, $n-n_s$ is how long the two host species had diverged). If $r = 0$, these probabilities are equal to 1 regardless of the host divergence time, meaning that there is no restriction to host-switching. As a consequence, parasite gene flow is continuous and speciation is disfavored. At the other extreme, for sufficiently large $r$ values ($P_{hs}$~0), host-switching is absent, and cospeciation between hosts and parasites is expected. For intermediary $r$ values, some parasite individuals can eventually switch hosts (Fig. 2). This model enables speciation by host use isolation. The effect of the overall host-switching in a community does not depend only on $r$, but also on the particularities of each host phylogeny that is used as input for the calculation of the host-switching probability (Fig. 2).

Following D’ Bastiani et al. (*In review*), to compare the results between the communities over the complete temporal evolution (a entire simulation), we presented the expected percentage of parasite individuals that switch host species (average of all possible pairwise comparisons in the entire simulation) and called it **host-switching intensity of the community** ($HSI_C$) (Fig. 2a). Correspondingly, to interpret the host-switching among species, we calculated the expected percentage value of a parasite individual switching to a given host species $i$, only at the end time of the simulation, and called it **host-switching intensity by host species** ($HSI_S$) (Fig. 2a):

$$HSI_{Si} = \frac{1}{N}\sum_{j\neq i} Phs^{ij}(n_F). \qquad (2)$$

where $N$ is the richness of the host species and $n_F$ is end time, $P_{hs}^{ij}$ is the probability of host-switching (Eq. 1) between species $i$ and $j$.

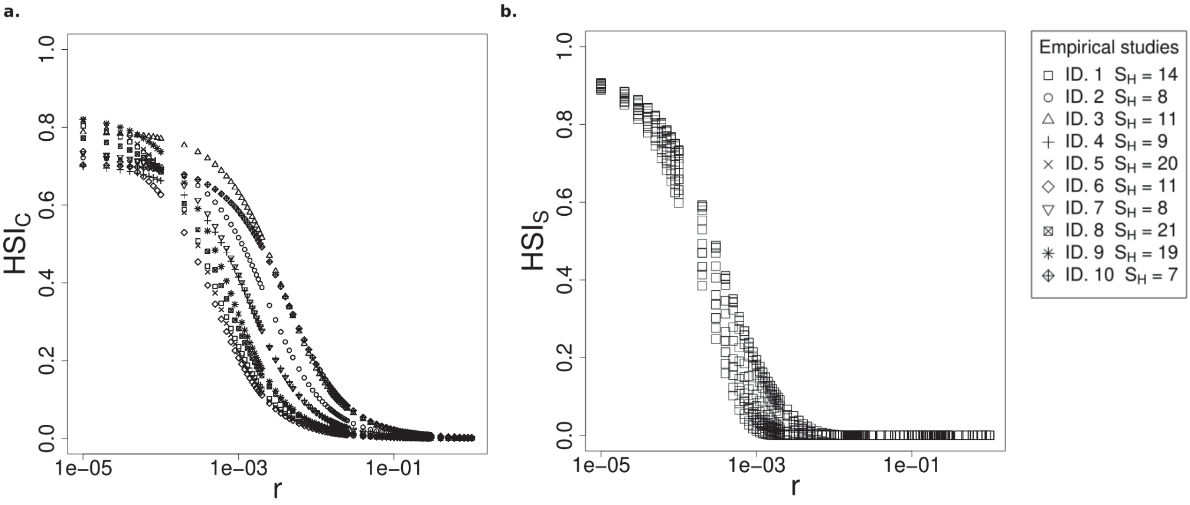


**Figure 2**. Relation between *r* (a parameter that defines the host-switching decay, Eq. 1) and the intensity of host-switching for host community (HSI$_C$) **(a)** and for host species (HSI$_S$) of the ID. 1 **(b)**. ID represents the locality of each host community in different regions in the Nearctic biogeographic realm and S$_H$ represents the host richness in each community: ID. 1 - California Central, ID. 2 - California South West, ID. 13 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri, ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin.

The host species are modelled as resources that impose a carrying capacity to parasite species, but in this model, the host species emerge (as a new host species that speciate) and the distance between them varies over time, according to a predetermined time of empirical diversification of hosts. The model does not consider the selection pressure imposed by parasites on the evolution of the hosts. Model parameters include the population size per host (*K* = 250), mutation probability per locus ($\mu$ = 0.025), and parameter *r* varying from 0 to 1. We ran 50 replicas for each scenario and each population size value is constant. See more model details in D'Bastiani et al. (In review).

The model outcome provides the host-switching intensity for different simulated scenarios, which can be compared with the empirical data of phylogenies and associations of parasites and their respective hosts. This requires information on species interaction and phylogenies for both hosts and parasites.

## Data analyses

Following D'Bastiani et al. (*In review*), we performed the simulations with a wide range of host-switching intensities for each empirical community. Then, we identified the optimum host-switching values that can reproduce the eco-evolutionary patterns of the empirical community, that is, the host-switching intensities that simultaneously reproduce the turnover ($\beta_{SIM}$ - Baselga et al. 2007; Baselga 2010; 2013a, b) and normalised Sacking Index ($I_n$ - Sackin 1972; Blum & François 2005; Marquitti et al. 2020) (both with ±5%  of confidence interval of the empirical data). Given the optimal range of host-switching intensity for each community, we calculated the host-switching intensity for each host species. These analyses were performed using 'ape' (Paradis & Schliep 2019), 'betapart' (Baselga et al. 2018) 'picante' (Kembel et al. 2010), 'phytools' (Revell 2012), and 'vegan' (Oksanen et al. 2013) R packages. Although the model also has information on species extinctions, they were not included in the analyses since there is no extinction information on the host communities. Although the model also has information on parasite species extinctions, they were not included in the analyses, as there is no information on extinctions in host communities.

### *Host community variables*

We calculated the phylogenetic species variability and functional diversity to understand the relationship with the variation in host-switching intensities among host communities. First, the relatedness among host species in each community was analysed with the host phylogenies. We calculated the phylogenetic species variability (PSVs) (Helmus et al. 2007) of each host community by using the phylogenetic distance among the host species. PSVs quantify the decrease in phylogenetic relatedness according to similarities shared by all species in a community, regardless of the number of species (see Fig. S12 - Helmus et al. 2007). PSVs is statistically independent of species richness. Values of PSVs range from 0 to 1, where 1 indicates that the sampled species are maximally unrelated.

Second, we described the ecological variation among host communities using the five traits (body mass, diet breadth, home range, population density and litter size) that represent different aspects of rodent life history. We scaled all continuous traits prior to calculating functional dispersion, which was conducted using the '*decostand*' function in "vegan" package in R. Based on these traits, we calculated pairwise similarities between all rodent species in each community with the Gower distance using the *'vegdist'* function in the "vegan" package in R. Then we calculated functional diversity index for each community using the '*pd'* function of the "picante" package. Because functional diversity is dependent on species richness, we standardised the effect size of richness in host communities with a null model approach, the standard effect sizes for every community, using the '*ses.pd'* function of the "picante" package (Kembel et al. 2010). Expected values for the metric are calculated for 1.000 draws of a random community from the species pool, each with equal SR to the observed community. SES, therefore, measures the difference between the observed values and null expectations.

### *Statistical analysis*

One-way analysis of variance (ANOVA) was used to determine if the optimal range of host-switching intensity among host communities varies. Generalised mixed-effect models (GLMM) were used to test the relationship between host-switching intensity and the explanatory variables. First, the intensity of each host community and the functional diversity and phylogenetic species variability of the hosts; second, the intensity for each host species and the mean of the host traits for each community; and third, the intensity for each host species and the mean of the traits independent from the community they belong. The models were performed using the *lmer* function of the 'lme 4' package (Bates et al. 2011). Statistically significant relationships were considered for p values equal or below 0.05.

Collinearity between fixed factors in the models was assessed using the variance inflation factor (VIF = 3 - Zuur et al. 2009, 2010; vif function in car package; Fox & Weisberg 2019). The first model didn't have variable collinearity. In the second and third models, when the traits were collinear, we kept the traits that we expected to have the most influence in terms of host-switching events, then sequentially deleted the variable that had less influence until all remaining VIFs were below 3. The predictors that were excluded were not shown in Tables 2 and 3.

For all GLMMs we normalised each variable using the mean value and standard deviation using the *scales* function of the 'base' package (Becker et al. 1988), except for SES_PD because we used the standard effect sizes. We empirically transformed each predictor to ensure the best model fit, visually determined (‘DHARMa’ package - Hartig & Hartig 2017). For the first GLMM, we square-root-transformed the variables host-switching intensity and PSVs. For the second GLMM of the variation of $HSI_S$, we square-root-transformed the variables host-switching intensity, diet breadth, home range and litter size and for log-transformed adult body mass. For the third GLMM we square-root-transformed the variables $HSI_S$, adult body mass, diet breadth, home range, and litter size.

In the first GLMM we assumed the optimal range of host-switching intensity in each host community [$HSI_C$] as the response variable, the SES.PD and PSVs as fixed variables, and the host communities (C) as random factor ($HSI_C$~SES.PD+PSVs+(1|C)). To analyse how the mean host's traits are associated with host-switching intensities within communities, in a second GLMM for each host community separately, we assumed the host-switching intensity for each host species [$HSI_S$] as the response variable, the mean adult body mass [BM], diet breadth [DB], population density [PD], home range [HR], and litter size [LS] as fixed variables, and host species (S) as random factor ($HSI_S$~BM+DB+PD+HR+LS+(1|S)). Finally, in the third GLMM, we assumed the host-switching intensity for each host species [$HSI_S$] as the response variable, the mean host's traits for each host species as fixed variables, and community-independent host species as random factor ($HSI_S$~BM+DB+HR+LS+(1|S)). We emphasise that each point in this model is an observation of the host-switching model. Each observation has its own host-switching intensity, and all of these reproduce the eco-evolutionary patterns of empirical flea communities.

Our main conclusions are based on the approach to model comparisons Burnham (1998). Models were ranked by importance based on weights calculated using Akaike's Information Criterion (AIC) (Table 3). We assessed the relative importance of each fixed-effect predictor variable by calculating the cumulative support for each predictor as the sum of weights of all models containing that predictor. All statistical analyses were performed in R v.4.0.0 (R Core Team 2020) and Rstudio v.1.3.959 (RStudio Team 2020).

## RESULTS

### Host-switching intensities among communities and among host species

We observed that the predicted host-switching intensities among host communities ($HSI_c$) ranged from 2.32% to 18.83% (Fig. S13-S15), and varied significantly among communities (ANOVA: F = 50.34, p = <0.001, Fig. 3; see the Tukey test results in Table S1). Within this range, the host community ID. 6 had the lowest host-switching intensity (2.32% - 9.04%), while the highest intensities of host-switching were observed for ID. 3 (16.56% - 18.02%). When we consider the $HSI_s$ irrespectively of the community they belong to, this range varies from <0.001% to 15% (Fig. 4 and Fig. S16).

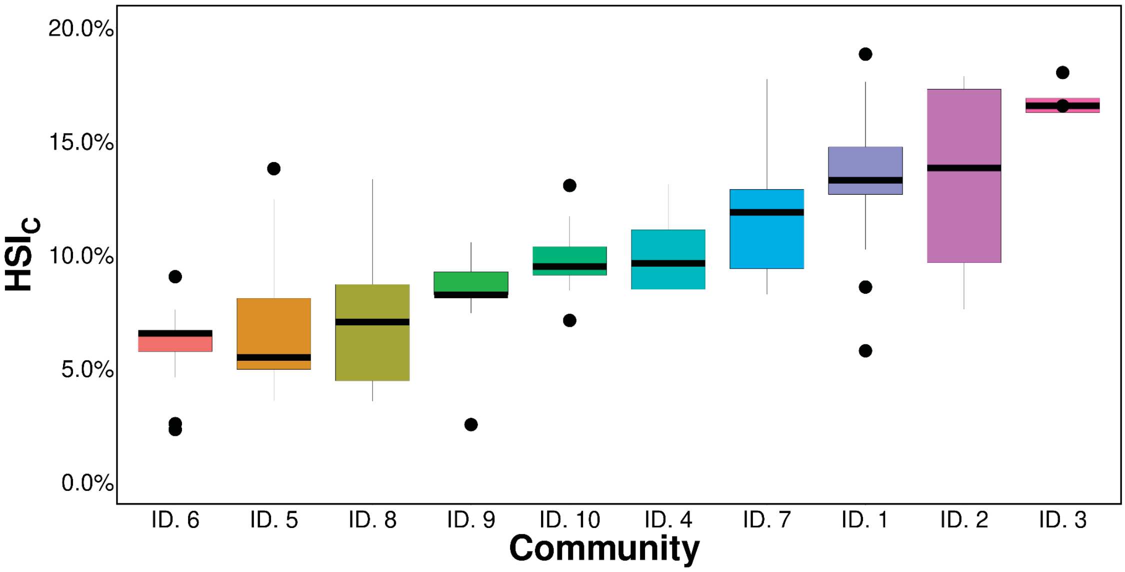


**Figure 3**. Variation in the host-switching intensity among host communities ($HSI_C$). The boxplots show the distributions of simulated host-switching intensities for each community. Axis x presents the host communities in different regions in the Nearctic biogeographic realm: ID. 1 - California Central, ID. 2 - California South West, ID. 3 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri,

ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin. The black circles are outliers.

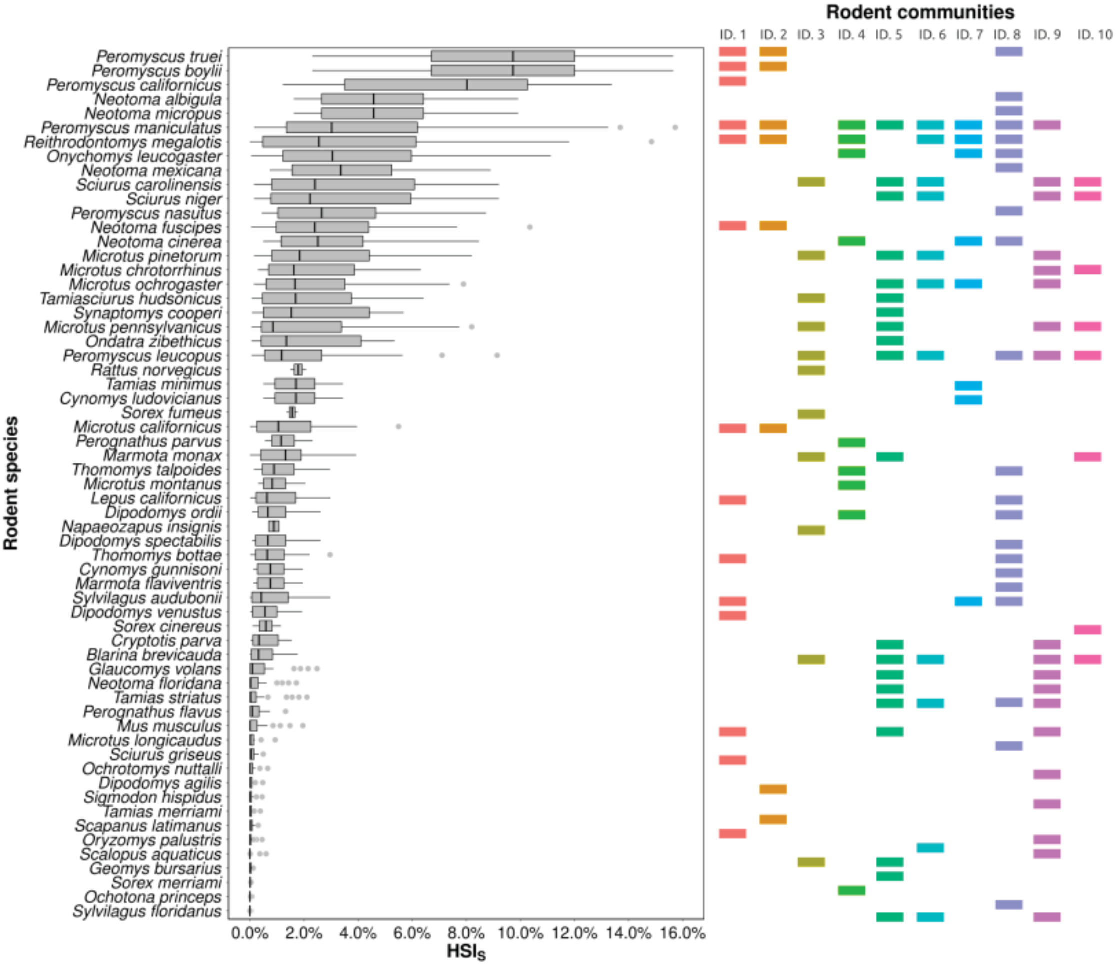


**Figure 4**. Variation in the host-switching intensity among host ($HSI_S$ - response variable) in the then empirical studies. The boxplots show the distributions of simulated host-switching intensities for each host species (predictors). Grey circles are outliers. The coloured rectangles represent the occurrence of the host species in the empirical study. ID represents each host community in different regions in the Nearctic biogeographic realm: ID. 1 - California Central, ID. 2 - California South West, ID. 13 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri, ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin.

## Can hosts' traits be related to host-switching intensities in communities and host species?

The optimal range of host-switching intensity in community ($HSI_c$) was not related by the functional diversity and phylogenetic species variability (Table 2 and Table S2). However, the host-switching intensity among host species ($HSI_s$) was correlated with particular host traits and varied according to each community (See details in Table 3 and Fig. S17-S36).

**Table 2**. Results of Linear mixed-effects models (GLMM) of host-switching intensity, functional diversity, phylogenetic species variability, and traits of host species infected by fleas. Legend: n represents the number of observations.

| Response (n) | Random variable | Predictor | Estimate±SE | df | t | p |
|---|---|---|---|---|---|---|
| Host-switching intensity in host communities (356) | Host communities | Functional diversity | 0.01±0.38 | 6.97 | 0.038 | 0.97 |
| | | Phylogenetic species variability | -0.0009±0.32 | 6.95 | -0.003 | 0.99 |

It is important to note that the model imposes that species with lower mean phylogenetic distance in relation to all other host species in a community will have greater $HSI_s$ (i. e. *Lepus californicus*, *Scapanus latimanus*, *Sciurus griseus*, and *Sylvilagus audubonii* in ID. 1). This occurs because host-switching events are mediated by the phylogenetic distance of the hosts in each host community (Eqs. 1 and 2).

In ID. 2, 4, 6, 7, 8, and 10, the hosts' traits had no significant relationship with $HSI_s$ (Table 3). However in ID. 1 (adult body mass - Fig. S27), ID. 3 (adult body mass and home range - Fig. S29), ID. 5 (diet breath and litter size - Fig. S31), and ID. 9 (diet breath, population density and litter size - Fig. S35), some traits were related (Table 3). So looking at significant cases also means looking at each host trait that might be facilitating host-switching events (Table 3; Fig. S15-S24).

**Table 3**. Results of Linear mixed-effects models (GLMM) of host-switching intensity by host species (**HSI$_s$**) and traits of host species infected by fleas. Legend: ID represents the local of each host community in different regions in the Nearctic biogeographic realm: ID. 1 - California Central, ID. 2 - California South West, ID. 13 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri, ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin; n represents the number of observations. Some variables were excluded from models due to collinearity: Body mass ID. 4; Home range - ID. 7 and 10; Litter size ID. 2, 3, and 10.

| **GLMM** | | | | | | |
|---|---|---|---|---|---|---|
| **Host community (n)** | **HSI$_s$** | **Predictor** | **Estimate±SE** | **df** | **t** | **p-value** |
| ID. 1 (182) | <0.001 - 14.96% | Adult body mass (g) | -0.08±0.02 | 8.00 | -3.06 | **0.01*** |
| | | Diet breadth | 0.04±0.02 | 8.00 | 1.80 | 0.10 |
| | | Population density (n km$^2$) | -0.006±0.03 | 8.00 | -0.26 | 0.79 |
| | | Home range (individual km$^2$) | 0.04±0.03 | 8.00 | 1.58 | 0.15 |
| | | Litter size | -0.01±0.02 | 8.00 | -0.65 | 0.53 |
| ID. 2 (80) | <0.001 - 21.00% | Adult body mass (g) | -0.05±0.05 | 3.00 | -1.10 | 0.35 |
| | | Diet breadth | -0.001±0.05 | 3.00 | -0.03 | 0.97 |
| | | Population density (n km$^2$) | -0.08±0.06 | 3.00 | -1.36 | 0.26 |
| | | Home range (individual km$^2$) | 0.05±0.06 | 3.00 | 0.84 | 0.46 |
| ID. 3 (22) | 0.36 - 8.20% | Adult body mass (g) | 0.06±0.02 | 3.00 | 2.40 | **0.05*** |
| | | Diet breadth | 0.03±0.03 | 3.00 | 1.24 | 0.26 |
| | | Population density (n km$^2$) | -0.01±0.02 | 3.00 | -0.68 | 0.51 |
| | | Home range (individual km$^2$) | -0.06±0.02 | 3.00 | -2.5 | **0.04*** |
| ID. 4 (32) | <0.001 - 7.34% | Diet breadth | 0.04±0.02 | 4.00 | 1.89 | 0.13 |
| | | Population density (n km$^2$) | 0.005±0.03 | 4.00 | 0.19 | 0.85 |

| GLMM | | | | | | |
|---|---|---|---|---|---|---|
| **Host community (n)** | **HSI$_s$** | **Predictor** | **Estimate±SE** | **df** | **t** | **p-value** |
| | | Home range (individual km$^2$) | 0.01±0.02 | 4.00 | 0.72 | 0.51 |
| | | Litter size | 0.03±0.03 | 4.00 | 1.09 | 0.33 |
| ID. 5 (228) | <0.001 - 7.89% | Adult body mass (g) | 0.005±0.01 | 14.00 | 0.41 | 0.68 |
| | | Diet breadth | 0.03±0.01 | 14.00 | 3.34 | **0.004*** |
| | | Population density (n km$^2$) | -0.00003±0.01 | 14.00 | -0.003 | 0.99 |
| | | Home range (individual km$^2$) | 0.01±0.01 | 14.00 | 1.41 | 0.17 |
| | | Litter size | 0.03±0.01 | 14.00 | 249 | **0.02*** |
| ID. 6 (121) | <0.001 - 5.19% | Adult body mass (g) | -0.01±0.02 | 5.00 | -0.60 | 0.57 |
| | | Diet breadth | 0.01±0.02 | 5.00 | 0.54 | 0.61 |
| | | Population density (n km$^2$) | -0.02±0.02 | 5.00 | -1.01 | 0.35 |
| | | Home range (individual km$^2$) | 0.01±0.03 | 5.00 | 0.46 | 0.66 |
| | | Litter size | 0.01±0.02 | 5.0 | 0.66 | 0.53 |
| ID. 7 (52) | <0.001 - 11.12%, | Adult body mass (g) | -0.04±0.02 | 4.00 | -2.26 | 0.08 |
| | | Diet breadth | 0.02±0.02 | 4.00 | 1.10 | 0.32 |
| | | Litter size | -0.02±0.01 | 4.00 | -1.48 | 0.21 |
| ID. 8 (176) | <0.001 - 0.62% | Adult body mass (g) | -0.0009±0.004 | 14.99 | -0.24 | 0.81 |
| | | Diet breadth | 0.003±0.003 | 14.99 | 0.87 | 0.39 |
| | | Population density (n km$^2$) | -0.0003±0.004 | 14.99 | 0.08 | 0.93 |
| | | Home range (individual km$^2$) | -0.006±0.003 | 14.99 | -1.79 | 0.09 |
| | | Litter size | 0.004±0.004 | 14.99 | 0.91 | 0.37 |
| ID. 9 (252) | <0.001 - 6.32% | Adult body mass (g) | -0.006±0.01 | 13.00 | -0.58 | 0.56 |
| | | Diet breadth | 0.03±0.01 | 13.00 | 2.89 | **0.01*** |

| GLMM | | | | | | |
|---|---|---|---|---|---|---|
| **Host community (n)** | **$HSI_s$** | **Predictor** | **Estimate±SE** | **df** | **t** | **p-value** |
| | | Population density (n $km^2$) | 0.04±0.01 | 13.00 | 3.90 | **<0.001*** |
| | | Home range (individual $km^2$) | 0.02±0.01 | 13.00 | 1.74 | 0.10 |
| | | Litter size | 0.02±0.01 | 13.00 | 2.63 | **0.02*** |
| ID. 10 (96) | 0.05 - 9.20% | Diet breadth | 0.05±0.03 | 3.00 | 1.39 | 0.25 |
| | | Population density (n $km^2$) | -0.008±0.03 | 3.00 | -2.40 | 0.09 |

The litter size was the only variable related to host-switching intensities when analysed independently of the host community, revealing that the higher host-switching predicted by the model can be associated with the host species with small litter size (see details in Table 4).

**Table 4**. Results of Linear mixed-effects models (LMM) of host-switching intensity, functional diversity, phylogenetic species variability, and traits of host species infected by fleas. Legend: n represents the number of observations.

| **Response (n)** | **Random variable** | **Predictor** | **Estimate±SE** | **df** | **t** | **p** |
|---|---|---|---|---|---|---|
| Host-switching intensity in host species (1.245) | All host species | Adult body mass (g) | -0.01±0.01 | 53.57 | -1.18 | 0.24 |
| | | Diet breadth | 0.003±0.009 | 57.16 | 0.43 | 0.66 |
| | | Home range (individual $km^2$) | 0.004±0.01 | 52.52 | 0.40 | 0.68 |
| | | Litter size | -0.01±0.005 | 634.51 | -2.02 | **0.04*** |

## DISCUSSION

Here, we use an individual based model to predict the intensity of host-switching in community and species levels. We show that: (i) the predicted range of host-switching intensity by parasites for host communities varied; (ii) this variation wasn't associated with the functional diversity and phylogenetic host variability; (iii) the host-switching among host species in a community was associated with the hosts' traits, varying according to each host community; (iv) the litter size was the only trait associated with host-switching intensities compared among rodents of the entire species pool. These results are consistent with our hypothesis that host-switching events can be related to some host traits and it can facilitate new associations.

Phylogenetic species variability (PSVs) was not related to host-switching intensity. The sorting of the regional species pool (gamma diversity) in local communities (alfa diversity) is determined by the dispersal capability of each species and by environmental filters (Cornell & Harrison 2014; Cadotte & Tucker 2017; Pärtel et al. 2013) and this leads to variation in PSVs among local communities. The higher the PSVs the greater the diversity of evolutionary lineages is (Helmus et al. 2007). Because in our model the host-switching intensity decreases as the phylogenetic distance increases, we expected lower host-switching intensity as a response of high PSVs. Thus, the lack of such a relationship indicates that other factors may be driving the switches of flea species between the rodent hosts.

Our results pointed to some particular traits shared among phylogenetically close species that may be related to the variation in host-switching intensity. The parameter *r* in the model (Eq. 1) controls the decay of the host-switching probability over time but does not differ among hosts (in a given simulation). Then, the probability of host-switching will always be higher between closely related species. The average of this probability for a given species in relation to all other species, HSIs, will be necessarily higher for the species with a smaller average of phylogenetic distance in relation to all other species. Then, when discussing the significance of host-switching with a trait, we need to keep in mind that we only identify which trait follows our model's proxy. For example, in the empirical study ID. 5 phylogeny seems to be a good proxy to describe the similarities in host diet breadth and litter size, indicating that hosts with higher diet breadth and litter size have greater host-switching intensities (Fig. S17). Thus, the species that have a shorter average of divergence time are those with greater diet breadth and litter size. In fact, it is expected that these two traits favour host-switching and our results support that these two traits are important drivers of host-switching.

Other traits were also good predictors, following an expected tendency, such as  body mass, diet breadth, population density and litter size (ID. 3 and 9). However, not all relationships had a positive tendency, such as the body mass and home range in DI. 1 and ID 3. respectively. Here, we still need to think more about what this means and how best to discuss these results. This part is under construction. We expected that the increase in the size of host home ranges might be positively related to host-switching as it can lead to a higher probability of encounters with multiple parasite species (Boyer et al. 2010), and increased rates of intraspecific and interspecific contact among hosts, which creates opportunity for host host-switching (Jetz et al. 2004; Clay et al. 2009; Previtali et al. 2010), but this was not what we observed. This was not expected because interindividual variability in the home range size of rodents is mainly characteristic of the breeding period of rodents (Schwarzenberger & Klingel 1994; Lott 1991). Males increase their mobility and expand their home ranges for the sake of increasing mating chances (Schwarzenberger & Klingel 1994; Waterman 2007). In contrast, reproductive females decreased mobility, so they may occupy a specific burrow for parturition (Wolff 1993). As a result, highly mobile males have higher chances to encounter ectoparasites (Clay et al. 2009), while these chances are obviously lower for territorial females, consequently this can influence the host-switching. One example of the importance of host home range in host-switching events is the association between wing lice and pigeons/doves (Boyd et al. 2022). In wing lice (Insecta: Phthiraptera: Columbicola) of pigeons and doves (hereafter doves; Aves: Columbiformes) the long-distance dispersal was central to parasite diversification. The host dispersal provided new ecological opportunities for parasites leading to adaptive radiation of these species. In local communities, it is expected that ecological barriers are lower and the opportunity for interaction is greater. It appears that ecological fit is more important than association with specific host species (Brooks & Hoberg 2007). When examining flea-rodent associations, our results show that the hosts' home range, if related to phylogeny, can trigger novel host-switching events because the host dispersal provides new ecological opportunities for parasite species.

Despite finding these results, our model has some limitations. The ecological opportunity can be given due to the traits of the hosts and our model is limited in this sense, as it does not separate the capacity for interaction and opportunity for interaction. So a next step for the model to be more realistic is to vary our parameter *r* according to each host species trait, and separate what is due to ecological opportunity in addition to the interaction capacity. Also, because in our model the host-switching intensity is mediated by the phylogeny, it is not possible to infer about host traits that are phylogenetically conserved.

With natural environments constantly changing, many flea species that were once restricted to specific areas are now expanding their distribution to new regions and changing the composition of native communities. Ecological and evolutionary studies of fleas are usefulful tools for understanding the spread of zoonotic diseases and can provide a theoretical basis for control and prevention. Our study has implications for understanding how host-switching events are related to rodent species traits. Our study shows evidence that it is possible to predict the uptake of new hosts by parasites in empirical communities, but it also raises important questions. These questions include: (i) how are parasite species distributed in the geographic distribution areas of their hosts, and how are the events of host-switching by parasites influenced by these distributions?; (ii) how does our model parameter $r$, associated with phylogeny and also with the attributes of each host species, influence host-switching events?; and (iii) how do these host-switching events influence the structures of host parasite interaction networks?

In summary, the intensity of host-switching varies among species and host communities. The host-switching events by fleas seem to be related with traits of host species that are shared between phylogenetically close species such as diet breadth, the home range and litter size. We suggest that host-switching events mediated by phylogenetic conservatism are likely to be determined by hosts' traits and these events are relatively frequent in communities with a local spatial scale. However, these events can vary substantially not only between host-parasite associations, but also spatially and, thus, alter the diversification of the parasite. Due to the pre-existing capacity and the opportunity for interaction, parasites can perform switches and establish an association with new hosts.

## ACKNOWLEDGEMENTS

We thank the researchers who collected and reported the field data, our institutions, and the many colleagues who helped us in different ways during this project for their comments and suggestions.

## FINANCIAL SUPPORT

EDB was supported by Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES). DP was supported by the São Paulo Research Foundation (FAPESP), grants #2018/11187-8, #2019/24449-3, and #2016/01343-7 (ICTP-SAIFR). SBLA was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq: #11284/2021-3).

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA ACCESSIBILITY STATEMENT

The phylogenies and interactions of all analysed studies are available at https://github.com/elviradbastiani/host-switching_localscale_hostraits.

## REFERENCES

Agosta, S. J., & Klemens, J. A. (2008). Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. Ecology Letters, 11(11), 1123-1134.

Agosta, S. J., Janz, N., & Brooks, D. R. (2010). How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. Zoologia (Curitiba), 27(2), 151-162.

Araujo, S. B., Braga, M. P., Brooks, D. R., Agosta, S. J., Hoberg, E. P., von Hartenthal, F. W., & Boeger, W. A. (2015). Understanding host-switching by ecological fitting. PLoS One, 10(10), e0139225.

Allred, D. M. (1968) Fleas of the National Reactor Testing Station. Great Basin Naturalist, 28, 73-87.

Amin, O. M. (1976). Host Associations and Seasonal Occurrence of Fleas from Southeastern Wisconsin Mammals, with Observations on Morphologic Variations1. Journal of Medical Entomology, 13(2), 179–192. doi:10.1093/jmedent/13.2.179

Arneberg, P., Skorping, A., Grenfell, B., & Read, A. F. (1998). Host densities as determinants of abundance in parasite communities. Proceedings of the Royal Society of London. Series B: Biological Sciences, 265(1403), 1283-1289.

Baselga A., Jiménez-Valverde A., Niccolini G. 2007. A multiple-site similarity measure independent of richness. Biology Letters, 6, 642-645.

Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global ecology and biogeography, 19, 134-143.

Baselga A. 2013a. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. Methods in Ecology and Evolution, 4, 552-557.

Baselga A. 2013b. Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. Ecography, 36, 124-128.

Baselga A., Orme D., Villéger S., De Bortoli J., Leprieur F., Logez M., Henriques-Silva R. 2018. Partitioning beta diversity into turnover and nestedness components. Package ‘betapart’. Version, 1(1).

Bates D., Maechler M., Bolker B., Walker S., Christensen R. H. B., Singmann H. Grothendieck G. 2011. Package ‘lme4’. Linear mixed-effects models using S4 classes. R package version, 1(6).

Becker, R. A., Chambers, J. M. and Wilks, A. R. (1988) The New S Language. Wadsworth & Brooks/Cole.

Blum M. G.  François O. 2005. On statistical tests of phylogenetic tree imbalance: the Sackin and other indices revisited. Mathematical biosciences, 195, 141-153.

Bordes, F., Morand, S., Kelt, D. A., & Van Vuren, D. H. (2009). Home range and parasite diversity in mammals. The American Naturalist, 173(4), 467-474.

Boyd, B. M., Nguyen, N. P., Allen, J. M., Waterhouse, R. M., Vo, K. B., Sweet, A. D., ... & Johnson, K. P. (2022). Long-distance dispersal of pigeons and doves generated new ecological opportunities for host-switching and adaptive radiation by their parasites. Proceedings of the Royal Society B, 289(1970), 20220042.

Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks Tamias sibiricus. Journal of Animal Ecology, 79(3), 538-547.

Brooks, D. R., & Agosta, S. J. (2012). Children of time: The extended synthesis and major metaphors of evolution. Zoologia (Curitiba), 29, 497-514.

Brooks, D. R., & Hoberg, E. P. (2007). How will global climate change affect parasite–host assemblages?. Trends in parasitology, 23(12), 571-574.

Burnham, K. P. (1998). Model selection and multimodel inference. A practical information-theoretic approach.

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned?. Trends in ecology & evolution, 32(6), 429-437.

Charleston, M. A., & Robertson, D. L. (2002). Preferential host switching by primate lentiviruses can account for phylogenetic similarity with the primate phylogeny. Systematic biology, 51(3), 528-535.

Clay, C. A., Lehmer, E. M., Previtali, A., St. Jeor, S., & Dearing, M. D. (2009). Contact heterogeneity in deer mice: implications for Sin Nombre virus transmission. Proceedings of the Royal Society B: Biological Sciences, 276(1660), 1305-1312.

Cornell, H. V., & Harrison, S. P. (2014). What are species pools and when are they important?. Annual Review of Ecology, Evolution, and Systematics, 45, 45-67.

D’Bastiani, E., Princepe, D., Campião, K. M., Marquitti, F. M., Boeger, W. A., & Araujo, S. L. (2022). Effect of host-switching on the eco-evolutionary patterns of parasites. *In review*.

Dallas, T. A., Han, B. A., Nunn, C. L., Park, A. W., Stephens, P. R., & Drake, J. M. (2019). Host traits associated with species roles in parasite sharing networks. Oikos, 128(1), 23-32.

Davis, R.M., Smith, R.T., Madon, M.B. & Sitko-Cleugh, E. (2002) Flea, rodent and plague ecology at Chichupate Campground, Ventura County, California. Journal of Vector Ecology, 27, 107-127.

De Vienne D. M., Refrégier G., López-Villavicencio M., Tellier A., Hood M. E. Giraud T. 2013. Cospeciation *vs* host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytologist, 198, 347-385.

Durden, L. A., & Kollars Jr, T. M. (1997). The fleas (Siphonaptera) of Tennessee. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(1), 13-22.

Engelstädter J. Fortuna N. Z. 2019. The dynamics of preferential host switching: Host phylogeny as a key predictor of parasite distribution. Evolution, 73, 1330-1340.

Fox J. Weisberg S. 2019. Nonlinear Regression, Nonlinear Least Squares, and Nonlinear Mixed Models in R. population, 150, 200.

Gibert, C., Shenbrot, G. I., Stanko, M., Khokhlova, I. S., & Krasnov, B. R. (2021). Dispersal-based versus niche-based processes as drivers of flea species composition on small mammalian hosts: inferences from species occurrences at large and small scales. Oecologia, 197(2), 471-484.

Hartig, F., & Hartig, M. F. (2017). Package 'DHARMa'. R package.

Hayward, A., Tsuboi, M., Owusu, C., Kotrschal, A., Buechel, S. D., Zidar, J., ... & Kolm, N. (2017). Evolutionary associations between host traits and parasite load: insights from Lake Tanganyika cichlids. Journal of Evolutionary Biology, 30(6), 1056-1067.

Helmus, M. R., Bland, T. J., Williams, C. K., & Ives, A. R. (2007). Phylogenetic measures of biodiversity. The American Naturalist, 169(3), E68-E83.

Hoberg, E. P., & Brooks, D. R. (2008). A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. Journal of Biogeography, 35(9), 1533-1550.

Hoberg, E. P., & Brooks, D. R. (2013). 14 Episodic processes, invasion and faunal mosaics in evolutionary and ecological time. The balance of nature and human impact, 199.

Holmes, B. E. (2003). Ecology and persistence of sylvatic plague in Phillips County Montana.

Huang, S., Bininda‐Emonds, O. R., Stephens, P. R., Gittleman, J. L., & Altizer, S. (2014). Phylogenetically related and ecologically similar carnivores harbour similar parasite assemblages. Journal of Animal Ecology, 83(3), 671-680.

Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. (2004). The scaling of animal space use. Science, 306(5694), 266-268.

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A. (2009). PanTHERIA: a species‐level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090‐184. Ecology, 90(9), 2648-2648.

Kembel, S. W., & Kembel, M. S. W. (2014). Package ‘picante’. R Foundation for Statistical Computing, Vienna, Austria: https://cran. r-project. org/web/packages/picante/picante. pdf.[Google Scholar].

Kiffner, C., Stanko, M., Morand, S., Khokhlova, I. S., Shenbrot, G. I., Laudisoit, A., ... & Krasnov, B. R. (2014). Variable effects of host characteristics on species richness of flea infracommunities in rodents from three continents. Parasitology Research, 113(8), 2777-2788.

Kollars Jr, T. M., Durden, L. A., & Oliver Jr, J. H. (1997). Fleas and lice parasitizing mammals in Missouri. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(2), 125-132.

Krasnov, B. R., Shenbrot, G. I., & Khokhlova, I. S. (2015b). Historical biogeography of fleas: the former Bering Land Bridge and phylogenetic dissimilarity between the Nearctic and Palearctic assemblages. Parasitology research, 114(5), 1677-1686.

Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S. & Degen, A.A. (2016). Trait‐based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. Oikos, 125, 29-38. Accession number: EDB_10.1111/oik.02178

Krasnov, B. R., Shenbrot, G. S., van der Mescht, L., Warburton, E. M., & Khokhlova, I. S. (2019). Phylogenetic and compositional diversity are governed by different rules: a study of fleas parasitic on small mammals in four biogeographic realms. Ecography, 42(5), 1000-1011.

Linsdale, J. M., Davis, B. S., & Davis, B. S. (1956). Taxonomic Appraisal and Occurence of Fleas at the Hastings Reservation in Central California, by Jean M. Linsdale and Betty S. Davis. University of California Press.

Lott, D. F. (1991). Intraspecific variation in the social systems of wild vertebrates (Vol. 2). Cambridge University Press.

Mácová, A., Hoblíková, A., Hypša, V., Stanko, M., Martinů, J., & Kvičerová, J. (2018). Mysteries of host switching: Diversification and host specificity in rodent-coccidia associations. Molecular phylogenetics and evolution, 127, 179-189.

Main, A. J. (1983). Fleas (Siphonaptera) on small mammals in Connecticut, USA. Journal of Medical Entomology, 20(1), 33-39.

Marquitti F. M. D., Fernandes L. D., de Aguiar M. A. M. 2020. Allopatry increases the balance of phylogenetic trees during radiation under neutral speciation. Ecography, 43(10), 1487-1498.

Morlan, H. B. (1955). Mammal fleas of Santa Fe County, New Mexico. Texas Reports on Biology and Medicine, 13(1), 93-125.

Oksanen J., Blanchet F. G., Kindt R., Legendre P., Minchin P. R., O'hara R. B. Oksanen M. J. 2013. Package 'vegan'. Community ecology package, version, 2, 1-295.

Page, R. D. (Ed.). (2003). Tangled trees: phylogeny, cospeciation, and coevolution.

University of Chicago Press.

Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics, 35(3), 526-528.

Pärtel, M., Szava-Kovats, R., & Zobel, M. (2013). Community completeness: linking local and dark diversity within the species pool concept. Folia Geobotanica, 48(3), 307-317.

Pilosof, S., Morand, S., Krasnov, B. R., & Nunn, C. L. (2015). Potential parasite transmission in multi-host networks based on parasite sharing. PloS one, 10(3), e0117909.

Previtali, M. A., Lehmer, E. M., Pearce-Duvet, J. M., Jones, J. D., Clay, C. A., Wood, B. A., ... & Dearing, M. D. (2010). Roles of human disturbance, precipitation, and a pathogen on the survival and reproductive probabilities of deer mice. Ecology, 91(2), 582-592.

Team R. 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. Available at: https://www.rstudio.com/. Last accessed 05 april 2022.

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). Methods in ecology and evolution, (2), 217-223.

Team R. C. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria: Available at: https://www. R-project. org/. Last accessed 05 april 2022.

Sackin M. J. 1972. “Good” and “bad” phenograms. Systematic Biology, 21(2), 225-226.

Schwarzenberger, T., & Klingel, H. (1995). Telemetrische Untersuchungen zur Raumnutzung und Aktivitätsrhythmik freilebender Gelbhalsmäuse Apodemus flavicollis Melchior, 1834. Zeitschrift für Säugetierkunde, 60(1), 20-32.

Stavtseva, N. A., Fielden, L. J., Khokhlova, I. S., Warburton, E. M., van der Mescht, L., & Krasnov, B. R. (2021). Colonization of a novel host by fleas: changes in egg production and egg size. Parasitology Research, 120(2), 451-459.

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS biology, 17(12), e3000494.

Watve, M. G., & Sukumar, R. (1995). Parasite abundance and diversity in mammals: correlates with host ecology. Proceedings of the National Academy of Sciences, 92(19), 8945-8949.

Whitaker, J. O. (1982). Ectoparasites of mammals of Indiana. Monograph/Indiana Academy of Science (USA).

Wolff, J. O. (1993). Why are female small mammals territorial?. Oikos, 364-370.

Zhu, Q., Hastriter, M. W., Whiting, M. F., & Dittmar, K. (2015). Fleas (Siphonaptera) are Cretaceous, and evolved with Theria. Molecular Phylogenetics and Evolution, 90, 129-139.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R (Vol. 574). New York: Springer.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. Methods in ecology and evolution, 1(1), 3-14.

[Dataset] Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. Ecology, 90(9), 2648-2648.

[Dataset] Linsdale, J. M., Davis, B. S., & Davis, B. S. (1956). Taxonomic Appraisal and Occurence of Fleas at the Hastings Reservation in Central California, by Jean M. Linsdale and Betty S. Davis. University of California Press.

[Dataset] Davis, R.M., Smith, R.T., Madon, M.B. & Sitko-Cleugh, E. (2002) Flea, rodent and plague ecology at Chichupate Campground, Ventura County, California. Journal of Vector Ecology, 27, 107-127.

[Dataset] Main, A. J. (1983). Fleas (Siphonaptera) on small mammals in Connecticut, USA. Journal of Medical Entomology, 20(1), 33-39.

[Dataset] Allred, D. M. (1968) Fleas of the National Reactor Testing Station. Great Basin Naturalist, 28, 73-87.

[Dataset] Whitaker, J. O. (1982). Ectoparasites of mammals of Indiana. Monograph/Indiana Academy of Science (USA).

[Dataset] Kollars Jr, T. M., Durden, L. A., & Oliver Jr, J. H. (1997). Fleas and lice parasitizing mammals in Missouri. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(2), 125-132.

[Dataset] Holmes, B. E. (2003). Ecology and persistence of sylvatic plague in Phillips County Montana.

[Dataset] Morlan, H. B. (1955). Mammal fleas of Santa Fe County, New Mexico. Texas Reports on Biology and Medicine, 13(1), 93-125.

[Dataset] Durden, L. A., & Kollars Jr, T. M. (1997). The fleas (Siphonaptera) of Tennessee. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(1), 13-22.

[Dataset] Amin, O. M. (1976). Host Associations and Seasonal Occurrence of Fleas from Southeastern Wisconsin Mammals, with Observations on Morphologic Variations1. Journal of Medical Entomology, 13(2), 179–192. doi:10.1093/jmedent/13.2.179

# SUPPLEMENTARY MATERIAL

## MATERIAL AND METHODS

### Details for empirical database

To test the model, we used ten empirical studies of flea-rodent associations in the Nearctic biogeographic realm. The phylogenies and networks are available at https://github.com/elviradbastiani/host-switching_localscale_hostraits.

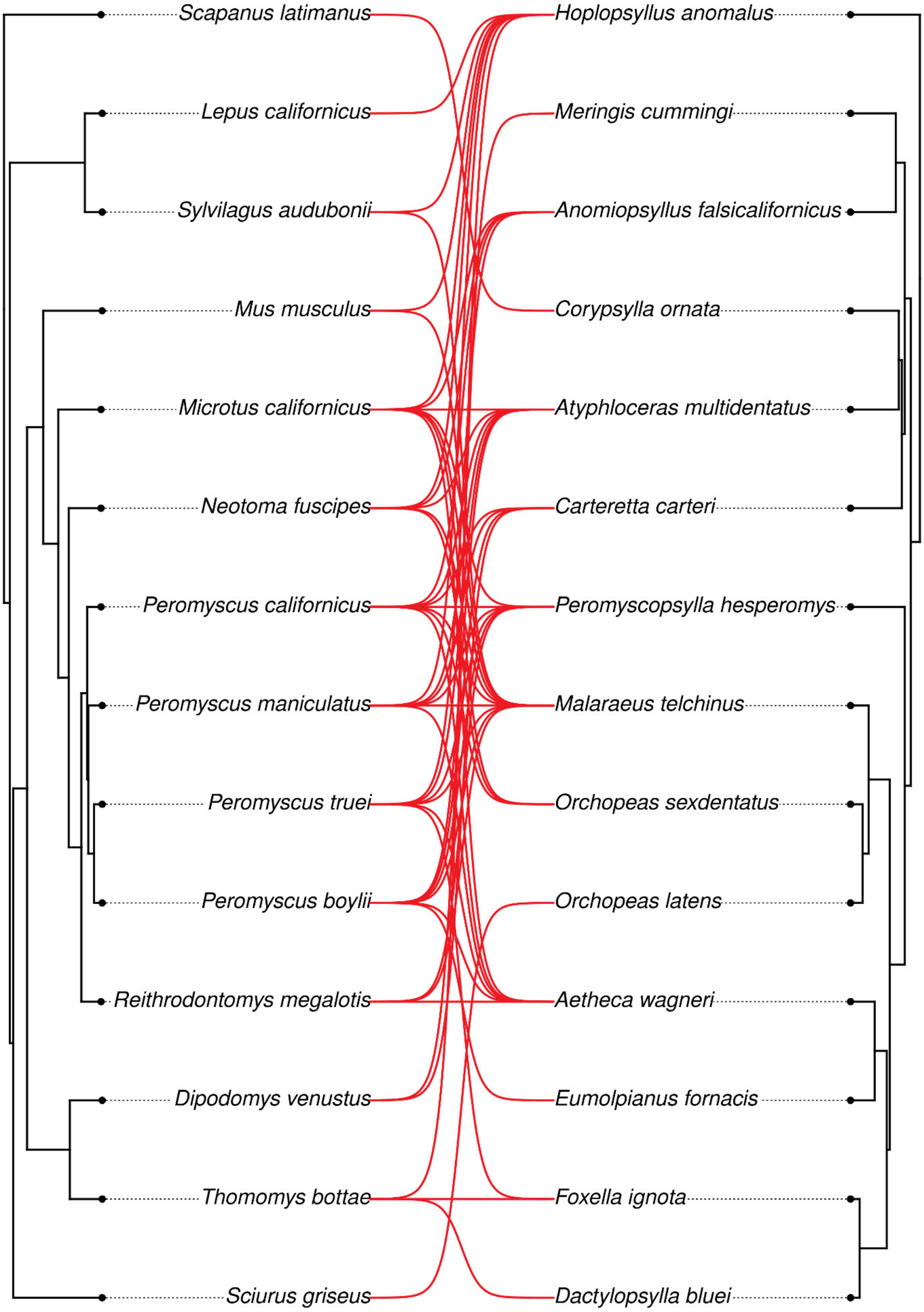


**Figure S1**. Phylogenetic tree and associations that correspond to the empirical study ID. 1 extracted from Linsdale & Davis 1956.

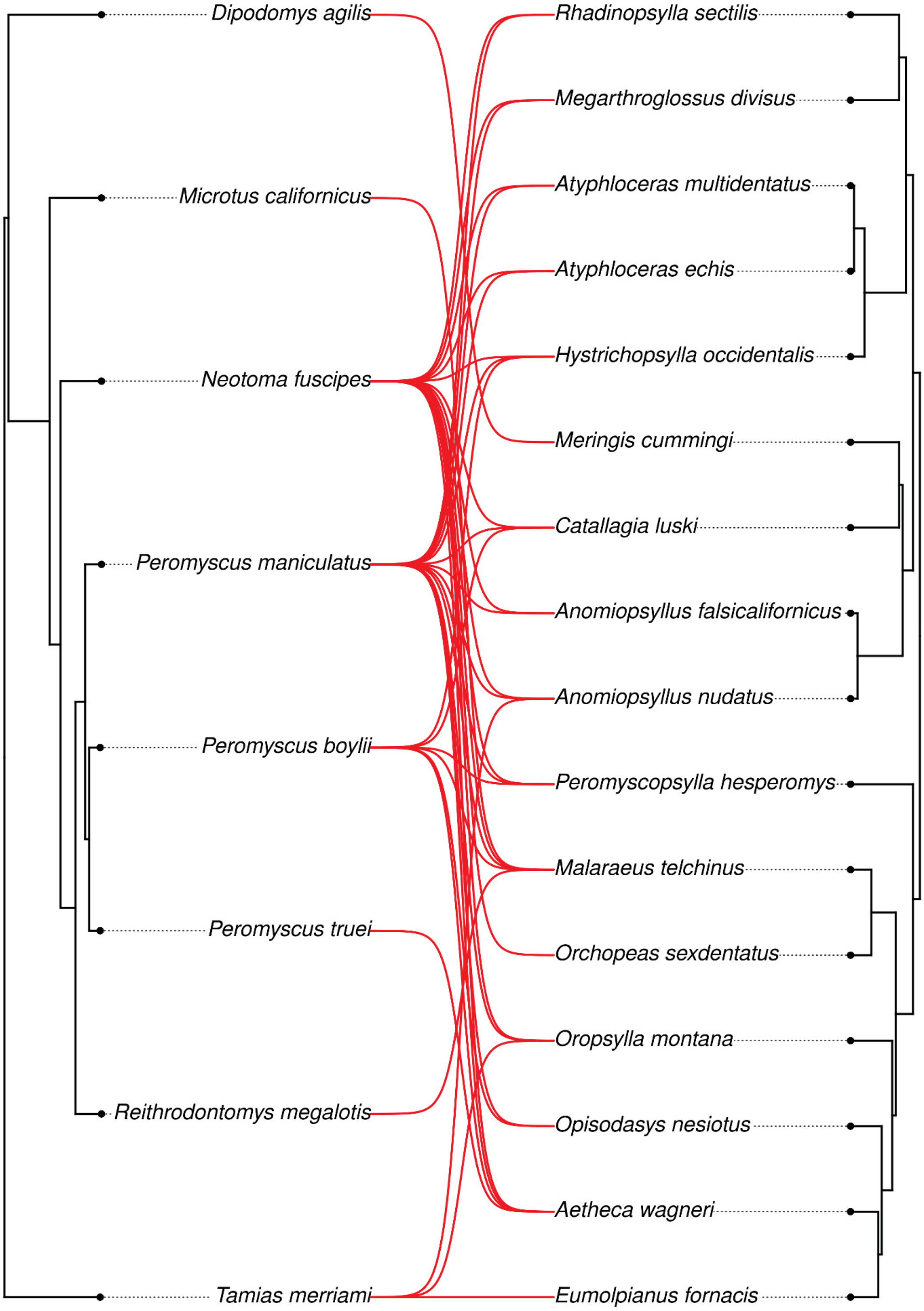


**Figure S2**. Phylogenetic tree and associations that correspond to the empirical study ID. 2 extracted from Davis et al. 2002.

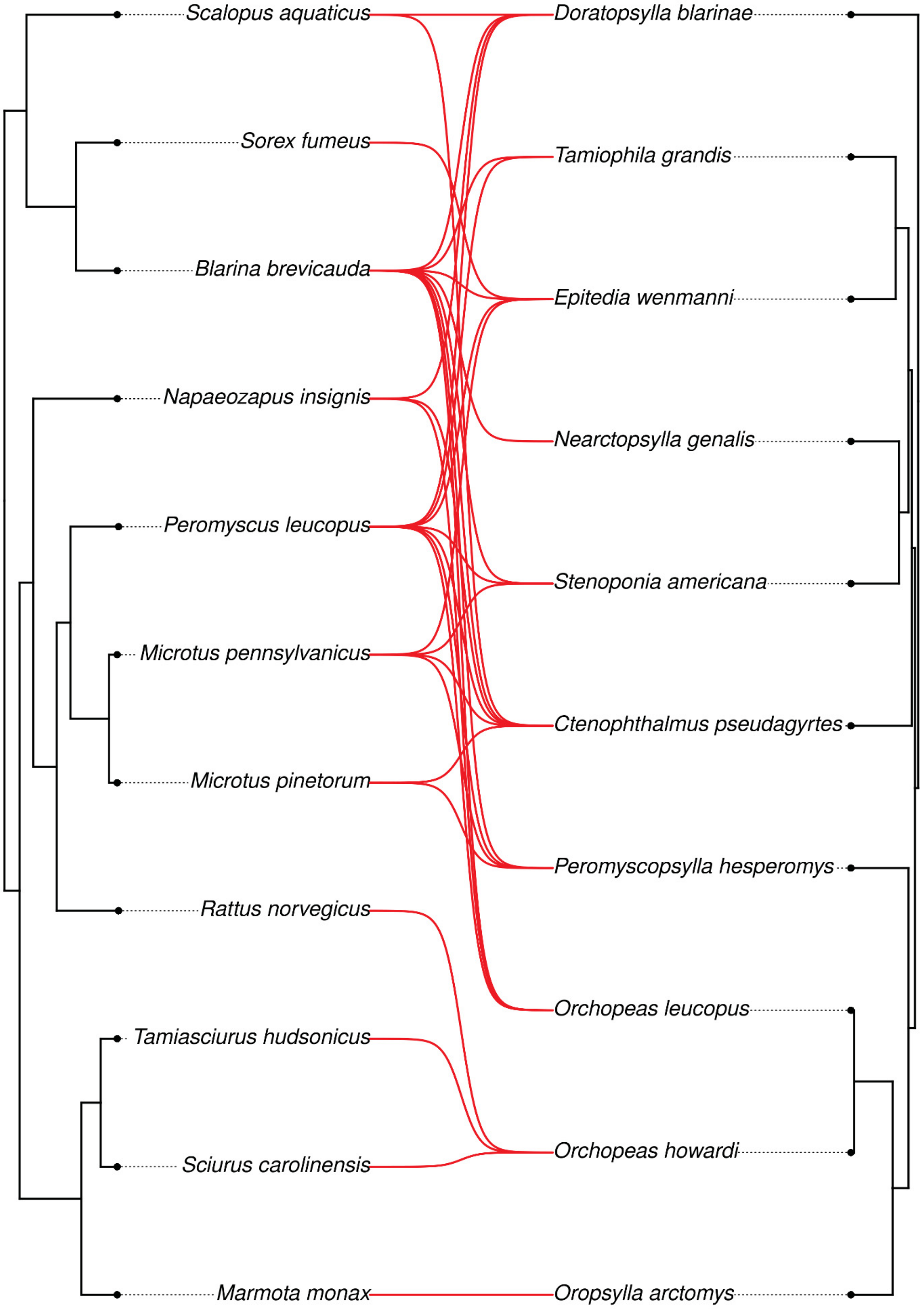


**Figure S3**. Phylogenetic tree and associations that correspond to the empirical study ID. 3 extracted from Main 1983.

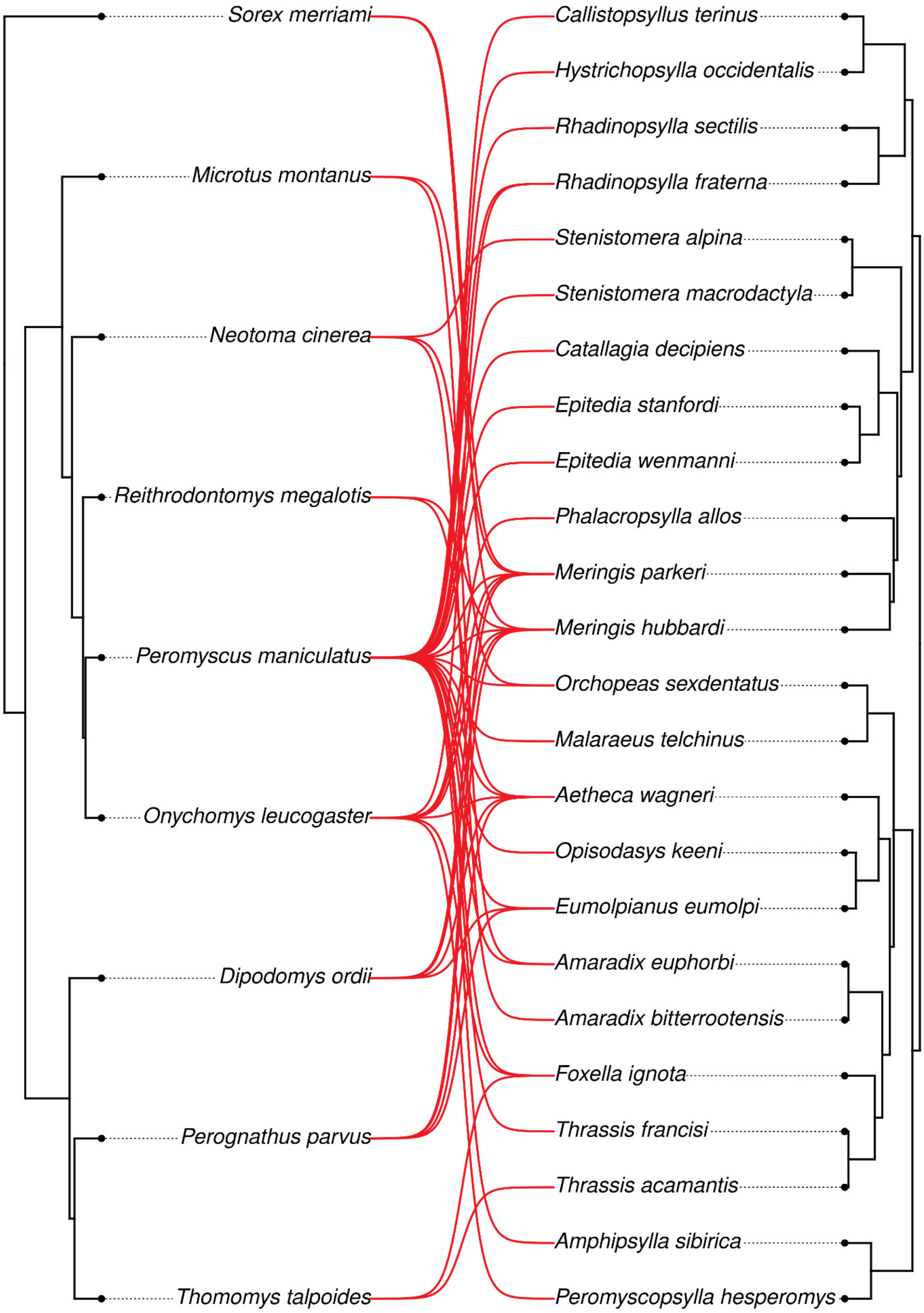


**Figure S4**. Phylogenetic tree and associations that correspond to the empirical study ID. 4 extracted from Allred 1968.

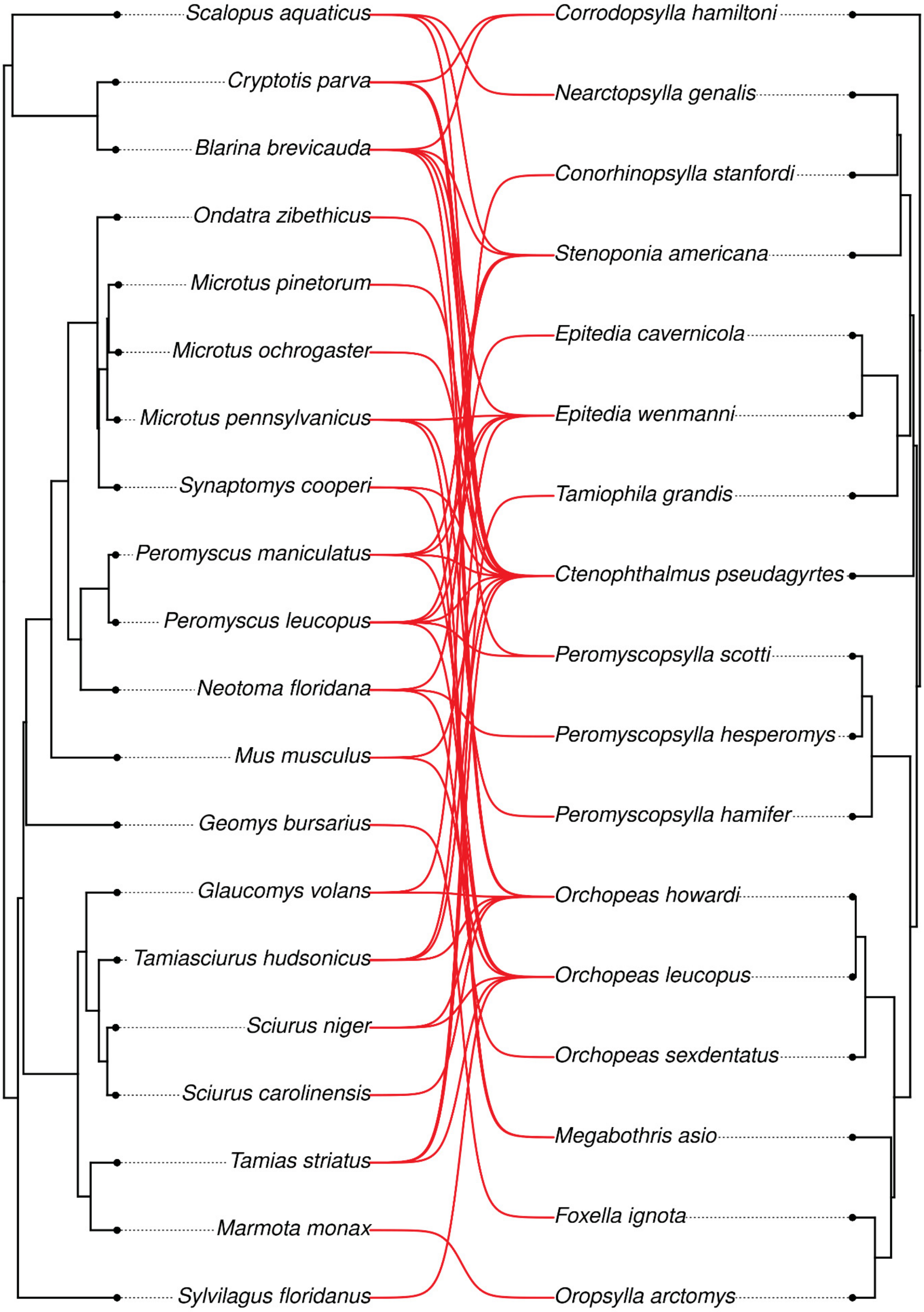


**Figure S5**. Phylogenetic tree and associations that correspond to the empirical study ID. 5 extracted from Whitaker 1982.

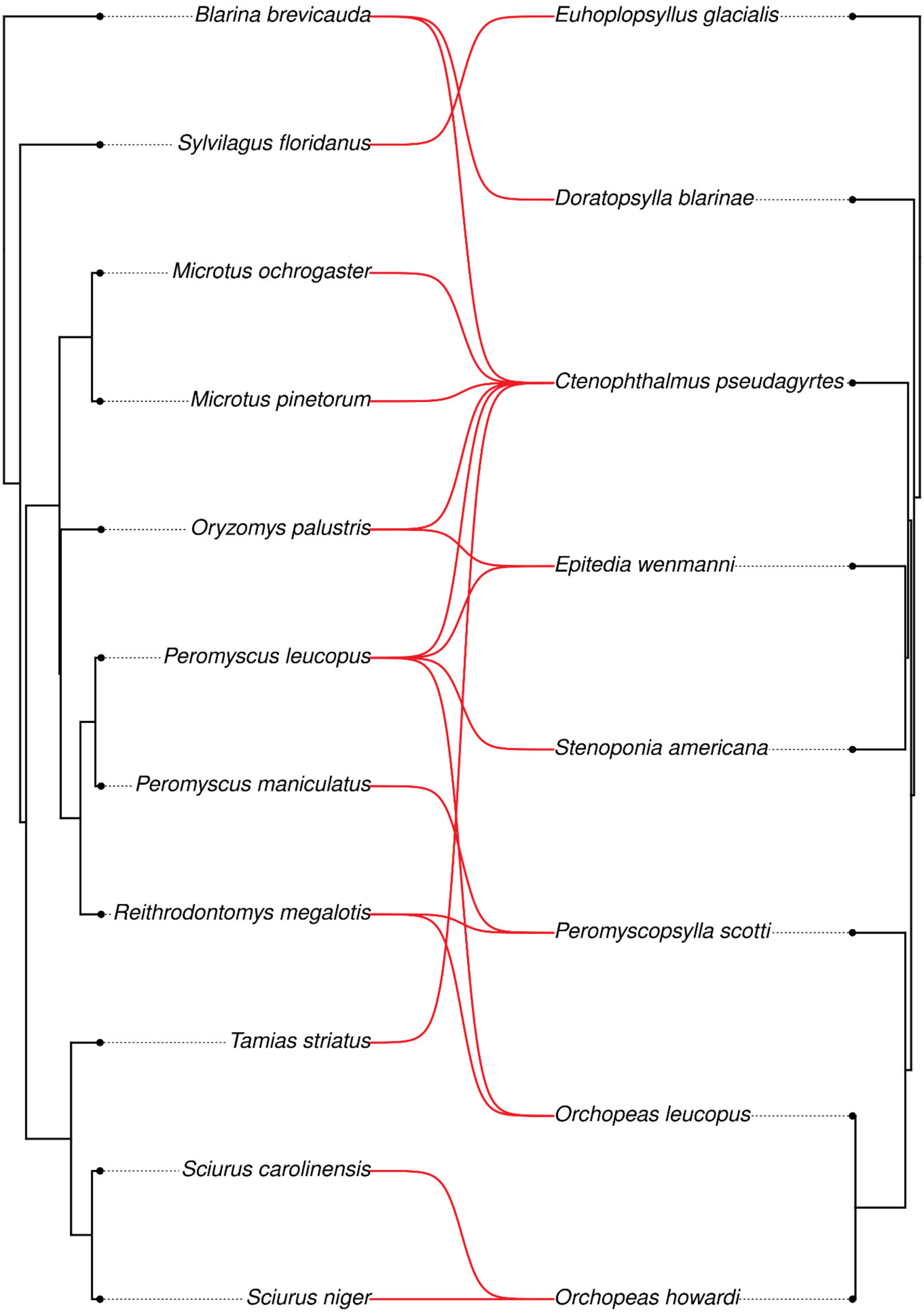


**Figure S6**. Phylogenetic tree and associations that correspond to the empirical study ID. 6 extracted from Kollars et al. 1997.

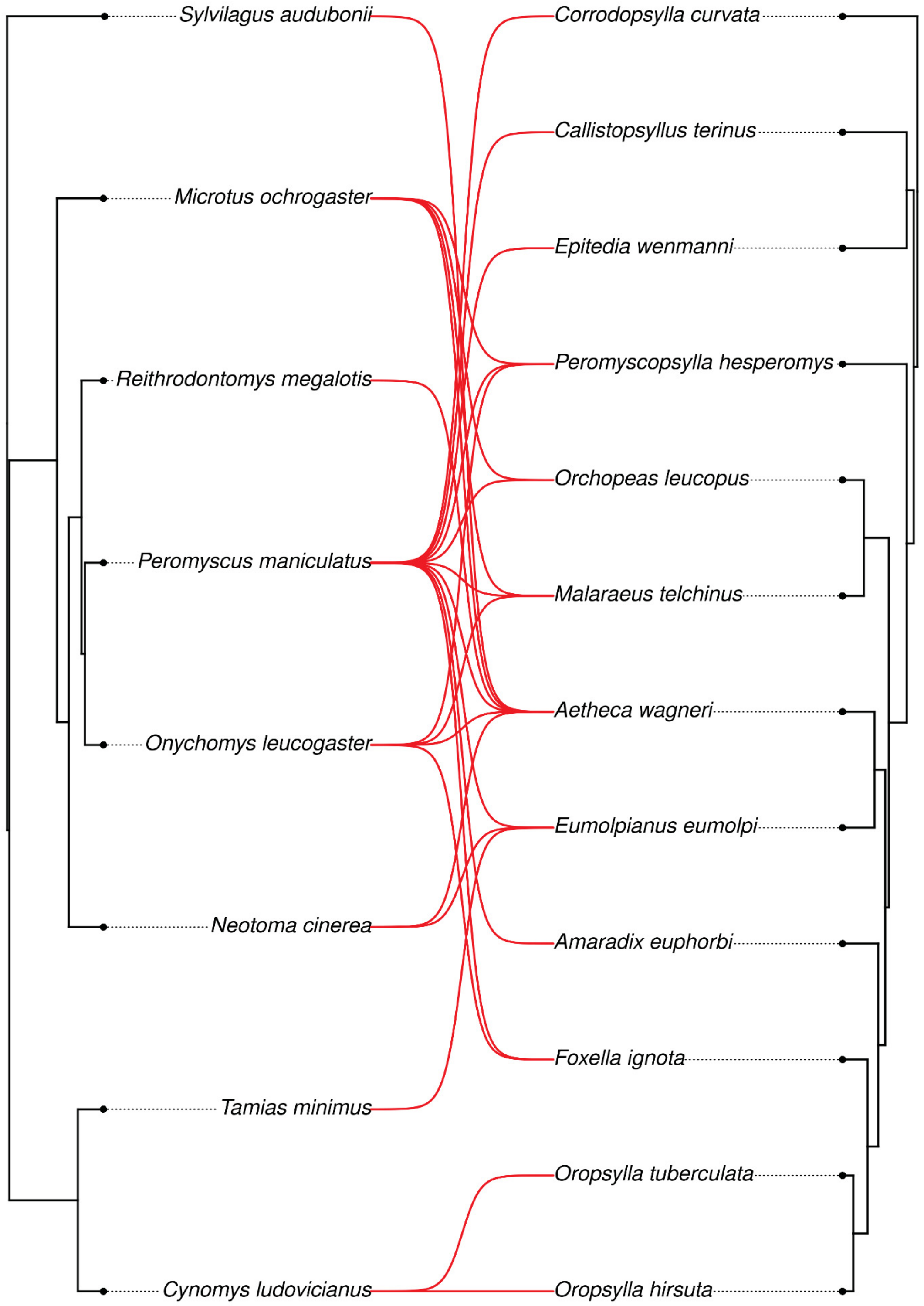


**Figure S7**. Phylogenetic tree and associations that correspond to the empirical study ID. 7 extracted from Holmes 2003.

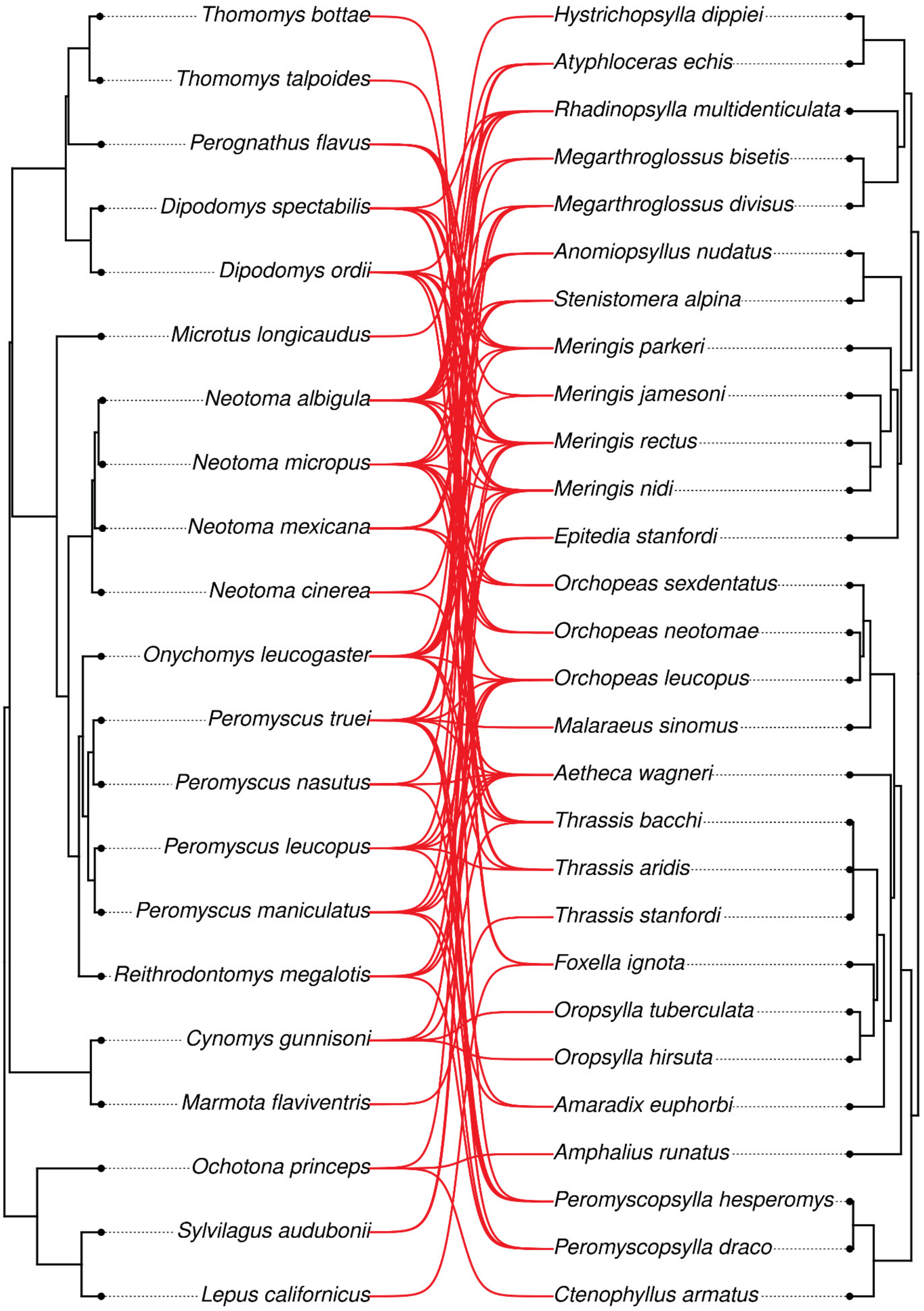


**Figure S8**. Phylogenetic tree and associations that correspond to the empirical study ID. 8 extracted from Morlan 1955.

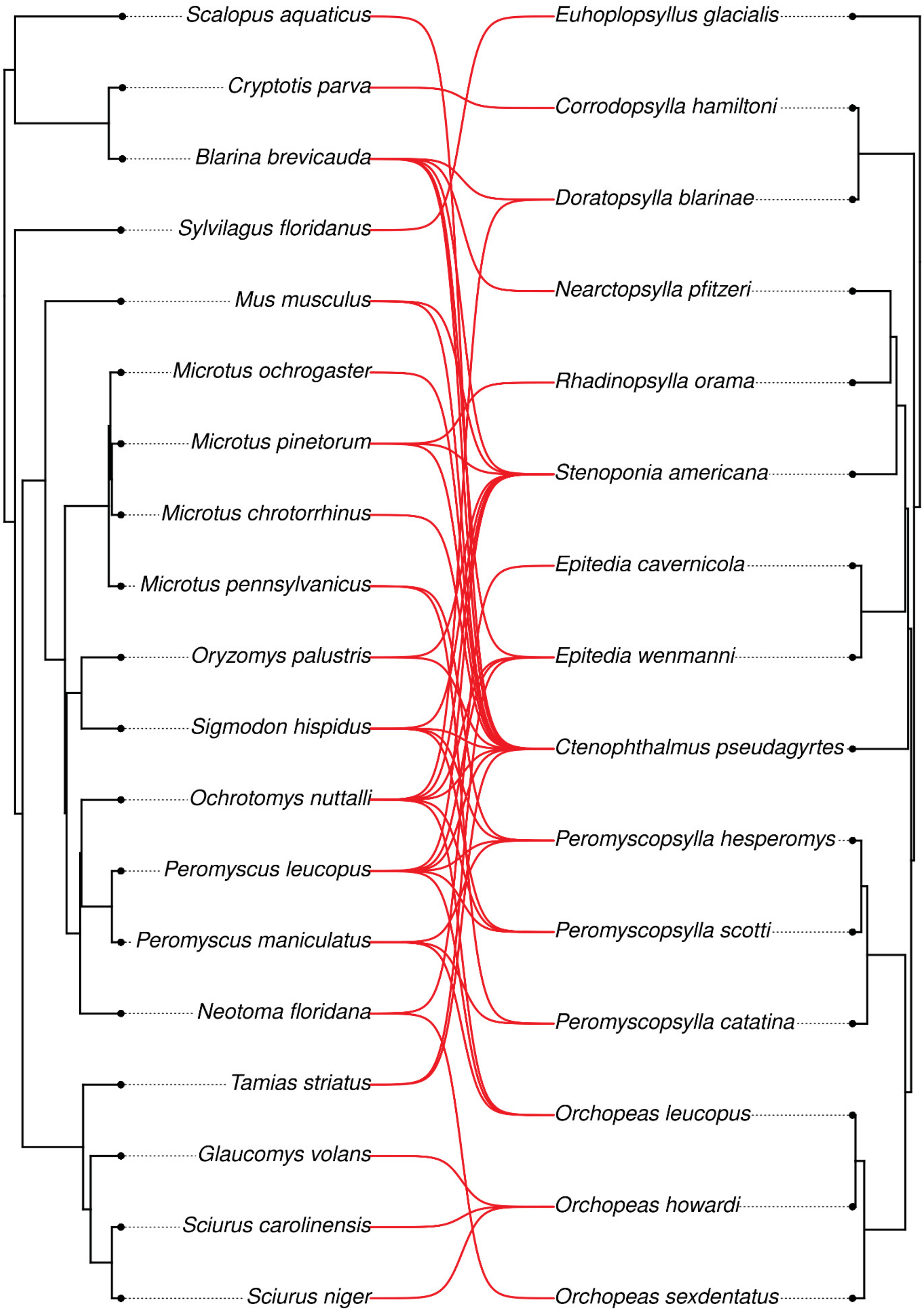


**Figure S9**. Phylogenetic tree and associations that correspond to the empirical study ID. 9 extracted from Durden & Kollars 1997.

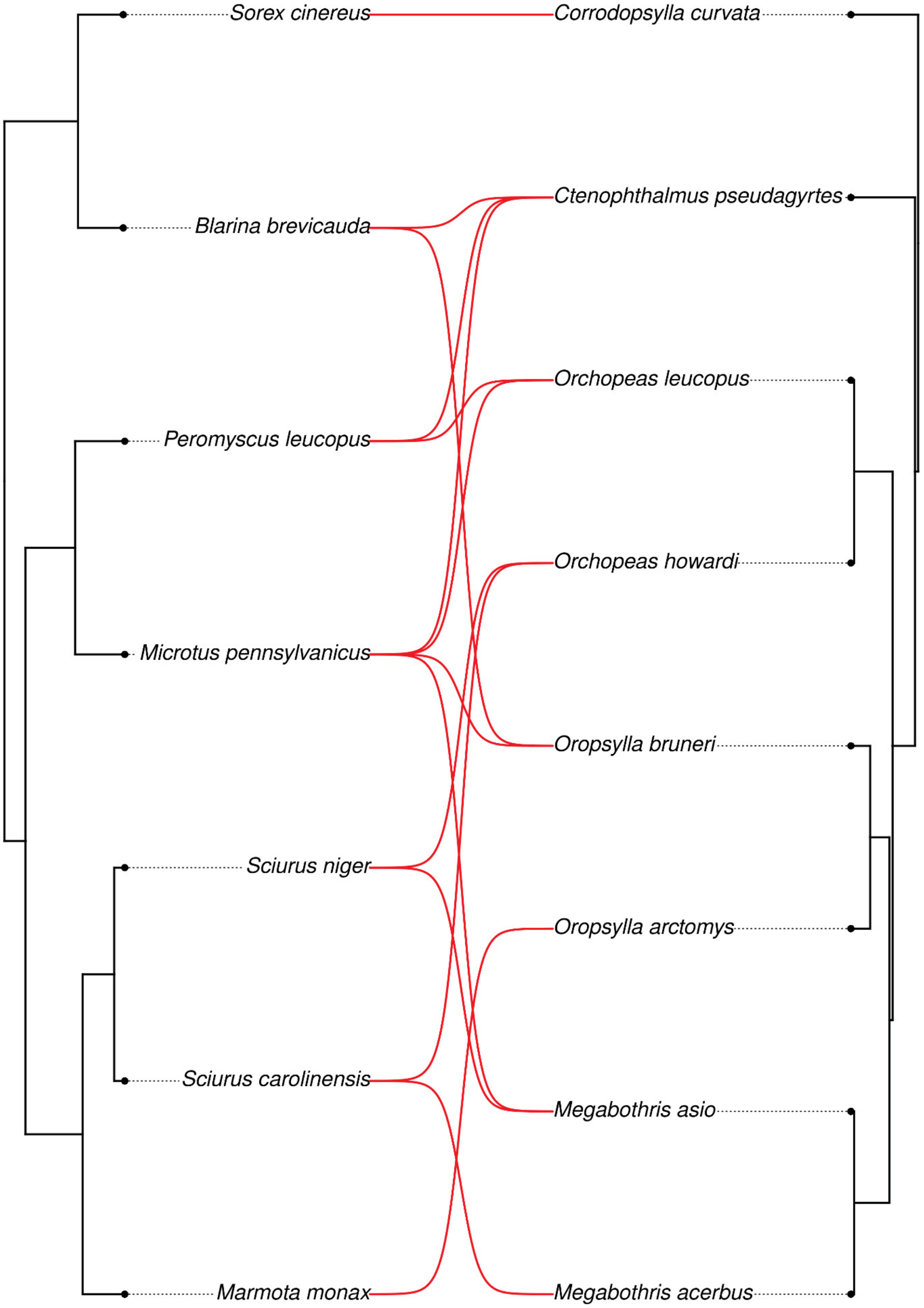


**Figure S10**. Phylogenetic tree and associations that correspond to the empirical study ID. 10 extracted from Amin 1976.

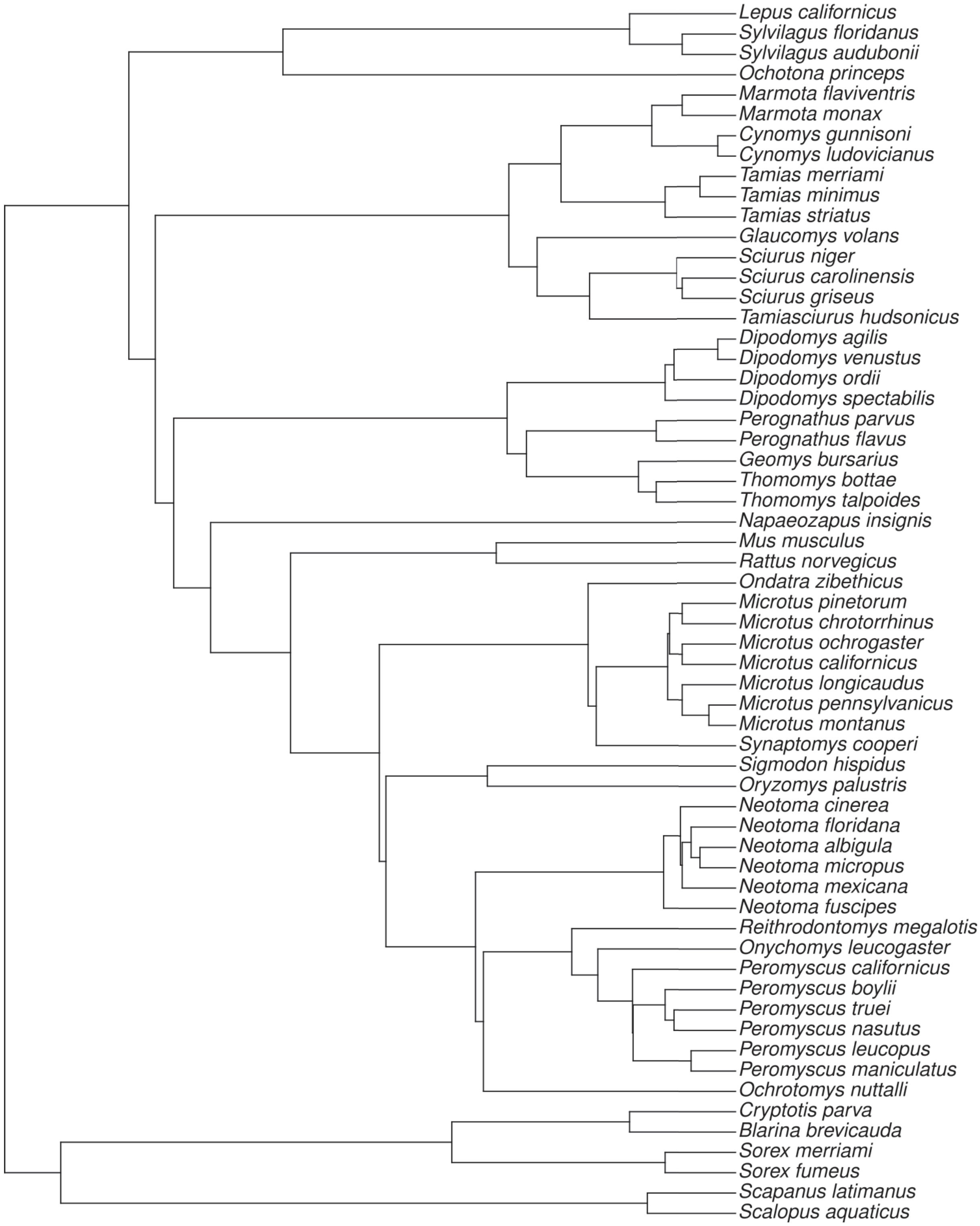


**Figure S11**. Phylogenetic tree of rodents from the Nearctic biogeographic realm.

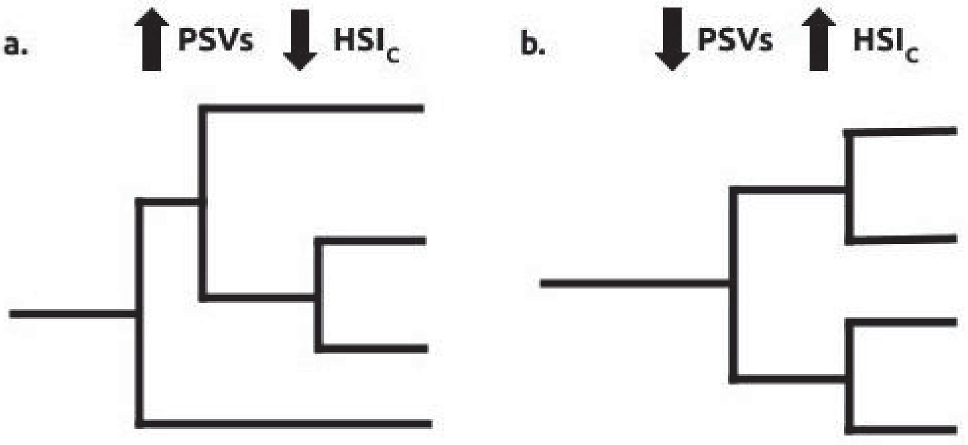


**Figure S12**. Phylogenetic species variability (PSVs) in two different **a**. host phylogeny with greater variability and **b**. host phylogeny with less variability.

## RESULTS

**Table S1**. Tukey multiple comparisons of means 95% family-wise confidence level. optimum host-switching intensities among host communities.

| Comparisons | diff | wr | upr | p |
|---|---|---|---|---|
| ID. 10-ID. 1 | -0.0072773536 | -0.015452801 | 0.0008980939 | 0.12 |
| ID. 3-ID. 1 | 0.0031474527 | -0.012218186 | 0.0185130917 | 0.99 |
| ID. 4-ID. 1 | -0.0102759085 | -0.022693114 | 0.0021412973 | 0.19 |
| ID. 5-ID. 1 | -0.0174745391 | -0.024165639 | -0.0107834397 | <0.001 |
| ID. 6-ID. 1 | -0.0238845116 | -0.031869522 | -0.0158995008 | <0.001 |
| ID. 7-ID. 1 | -0.0007611707 | -0.011163757 | 0.0096414160 | 0.99 |
| ID. 8-ID. 1 | -0.0328666631 | -0.039131967 | -0.0266013595 | <0.001 |
| ID. 9-ID. 1 | -0.0257353096 | -0.032283858 | -0.0191867608 | <0.001 |
| ID. 3-ID. 10 | 0.0104248063 | -0.005450226 | 0.0262998387 | 0.51 |
| ID. 4-ID. 10 | -0.0029985549 | -0.016040824 | 0.0100437146 | 0.99 |
| ID. 5-ID. 10 | -0.0101971856 | -0.017987218 | -0.0024071530 | <0.001 |
| ID. 6-ID. 10 | -0.0166071581 | -0.025533198 | -0.0076811179 | <0.001 |
| ID. 7-ID. 10 | 0.0065161828 | -0.004625074 | 0.0176574398 | 0.67 |
| ID. 8-ID. 10 | -0.0255893095 | -0.033016814 | -0.0181618049 | <0.001 |
| ID. 9-ID. 10 | -0.0184579560 | -0.026125895 | -0.0107900171 | <0.001 |
| ID. 4-ID. 3 | -0.0134233612 | -0.031845243 | 0.0049985201 | 0.36 |
| ID. 5-ID. 3 | -0.0206219919 | -0.035786079 | -0.0054579052 | <0.001 |
| ID. 6-ID. 3 | -0.0270319644 | -0.042809769 | -0.0112541600 | <0.001 |
| ID. 7-ID. 3 | -0.0039086235 | -0.021037328 | 0.0132200812 | 0.99 |
| ID. 8-ID. 3 | -0.0360141158 | -0.050995195 | -0.0210330363 | <0.001 |
| ID. 9-ID. 3 | -0.0288827623 | -0.043984491 | -0.0137810338 | <0.001 |

| | | | | |
|---|---|---|---|---|
| ID. 5-ID. 4 | -0.0071986307 | -0.019365539 | 0.0049682779 | 0.65 |
| ID. 6-ID. 4 | -0.0136086032 | -0.026532351 | -0.0006848556 | 0.03 |
| ID. 7-ID. 4 | 0.0095147377 | -0.005027499 | 0.0240569749 | 0.52 |
| ID. 8-ID. 4 | -0.0225907546 | -0.034528798 | -0.0106527112 | <0.001 |
| ID. 9-ID. 4 | -0.0154594011 | -0.027548501 | -0.0033703009 | <0.001 |
| ID. 6-ID. 5 | -0.0064099725 | -0.013999904 | 0.0011799592 | 0.17 |
| ID. 7-ID. 5 | 0.0167133684 | 0.006610870 | 0.0268158669 | <0.001 |
| ID. 8-ID. 5 | -0.0153921240 | -0.021145444 | -0.0096388036 | <0.001 |
| ID. 9-ID. 5 | -0.0082607704 | -0.014321311 | -0.0022002294 | <0.001 |
| ID. 7-ID. 6 | 0.0231233409 | 0.012121066 | 0.0341256162 | <0.001 |
| ID. 8-ID. 6 | -0.0089821515 | -0.016199511 | -0.0017647918 | <0.001 |
| ID. 9-ID. 6 | -0.0018507979 | -0.009315364 | 0.0056137679 | 0.99 |
| ID. 8-ID. 7 | -0.0321054924 | -0.041931157 | -0.0222798273 | <0.001 |
| ID. 9-ID. 7 | -0.0249741388 | -0.034982793 | -0.0149654848 | <0.001 |
| ID. 9-ID. 8 | 0.0071313535 | 0.001544460 | 0.0127182466 | <0.001 |

## Relationship between turnover and host-switching intensity in each community

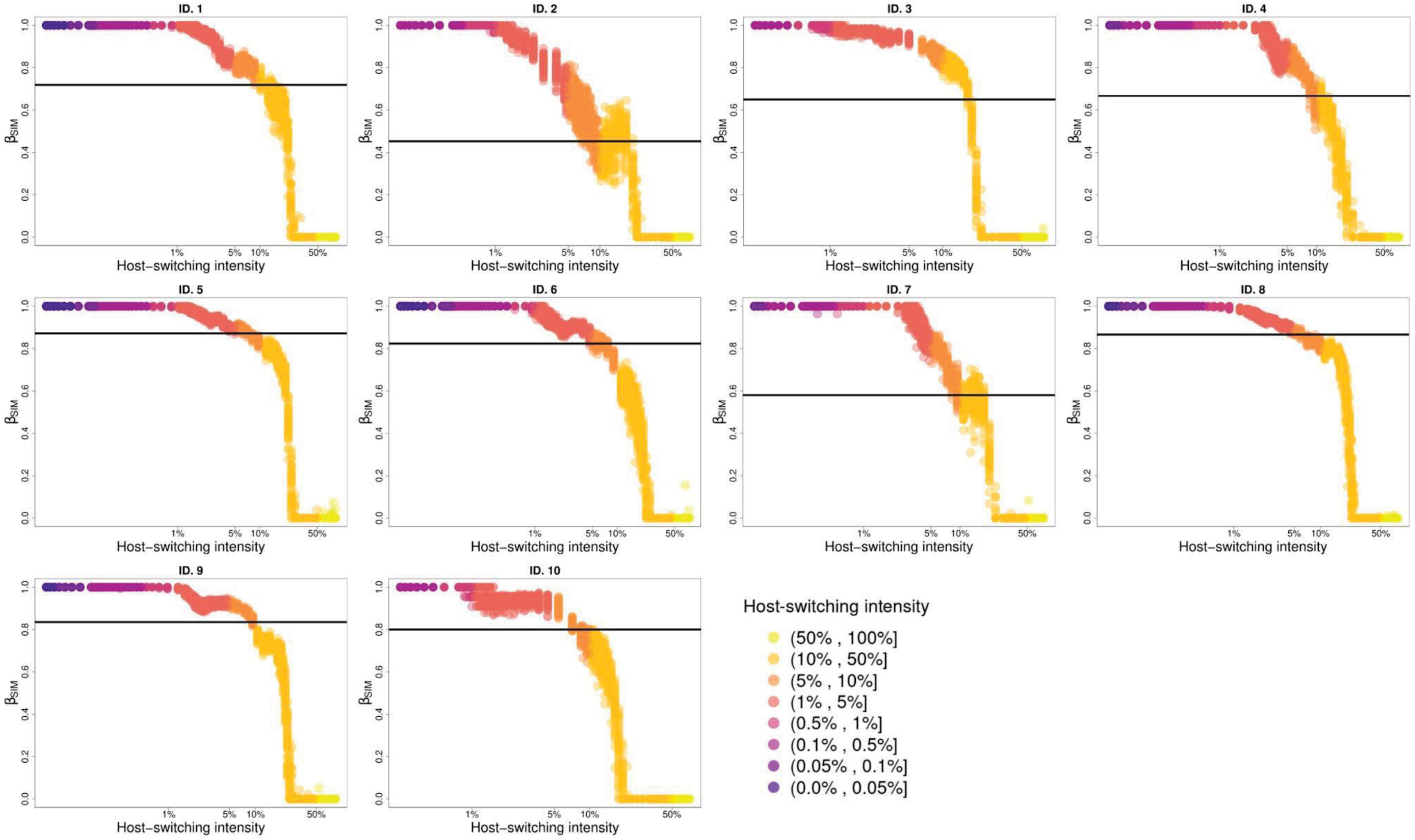


**Figure S13**. The relationship between turnover of parasite species among host species (measured by the metric beta diversity - $\beta_{SIM}$ - y-axis) and intensity of host-switching (x-axis and colours) for ten empirical studies. A total of 50 runs were performed for each configuration of the parameter host-switching intensity, with $K=250$ individuals. We present the results for empirical studies: the continuous line refers to parasite information, and the dotted line refers to hosts. To help distinguish the different intensities of the host switch, we make colour scales for each percentage interval. ID represents the each host community in different regions in the Nearctic biogeographic realm: ID. 1 - California Central, ID. 2 - California South West, ID. 13 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri, ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin.

# Relationship between the imbalance tree and host-switching intensity in each community

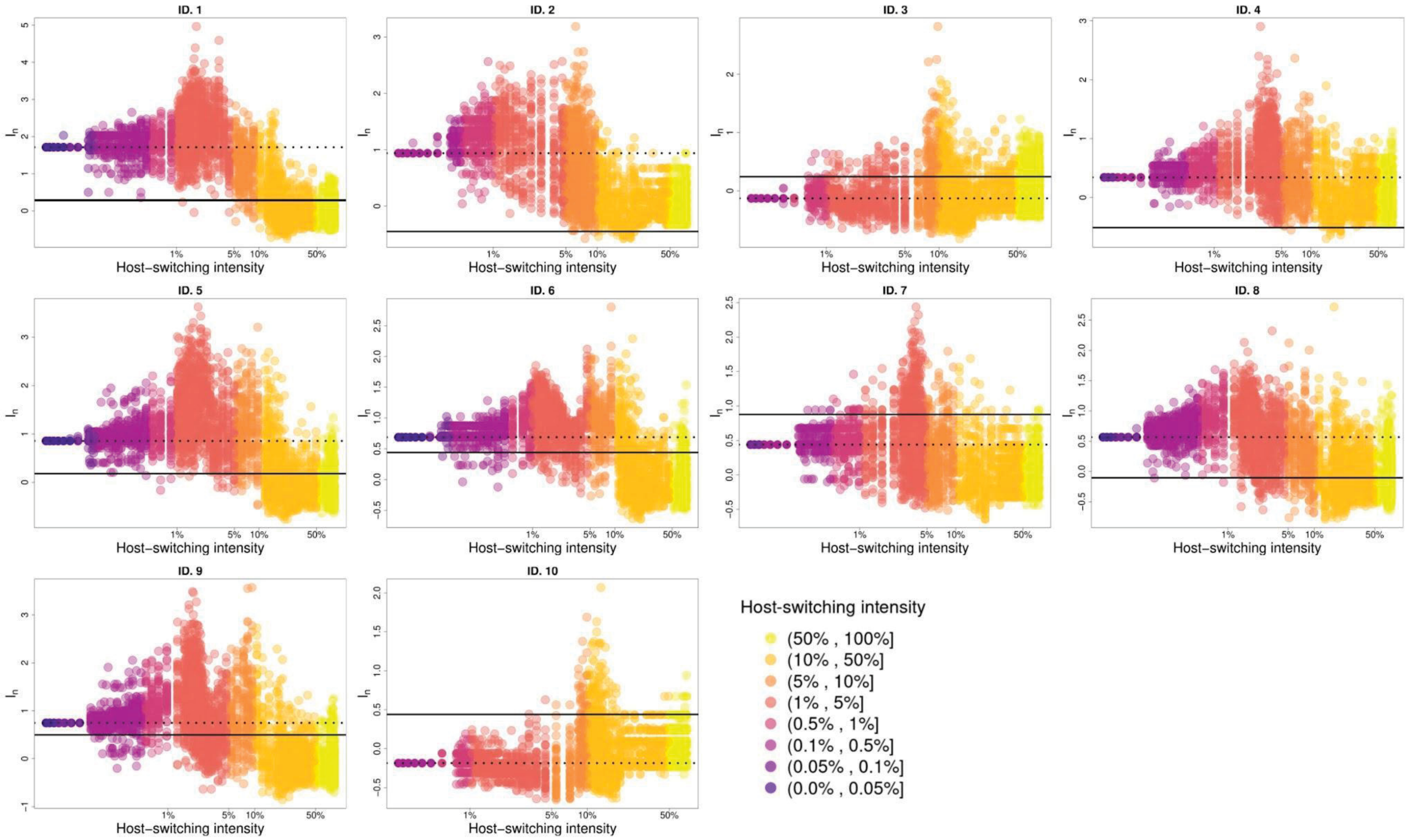


**Figure S14**. The relationship between the parasite imbalance tree (measured by the metric normalised Sackin index - $I_n$ - y-axis) and intensity of host-switching (x-axis and colours) for ten empirical studies. A total of 50 runs were performed for each configuration of the parameter host-switching intensity, with K=250 individuals. We present the results for empirical studies: the continuous line refers to parasite information, and the dotted line refers to hosts. To help distinguish the different intensities of the host switch, we make colour scales for each percentage interval. ID represents the each host community in different regions in the Nearctic biogeographic realm: ID. 1 - California Central, ID. 2 - California South West, ID. 13 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri, ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin.

## Relationship between turnover and imbalance tree according to the host-switching intensity in each communit

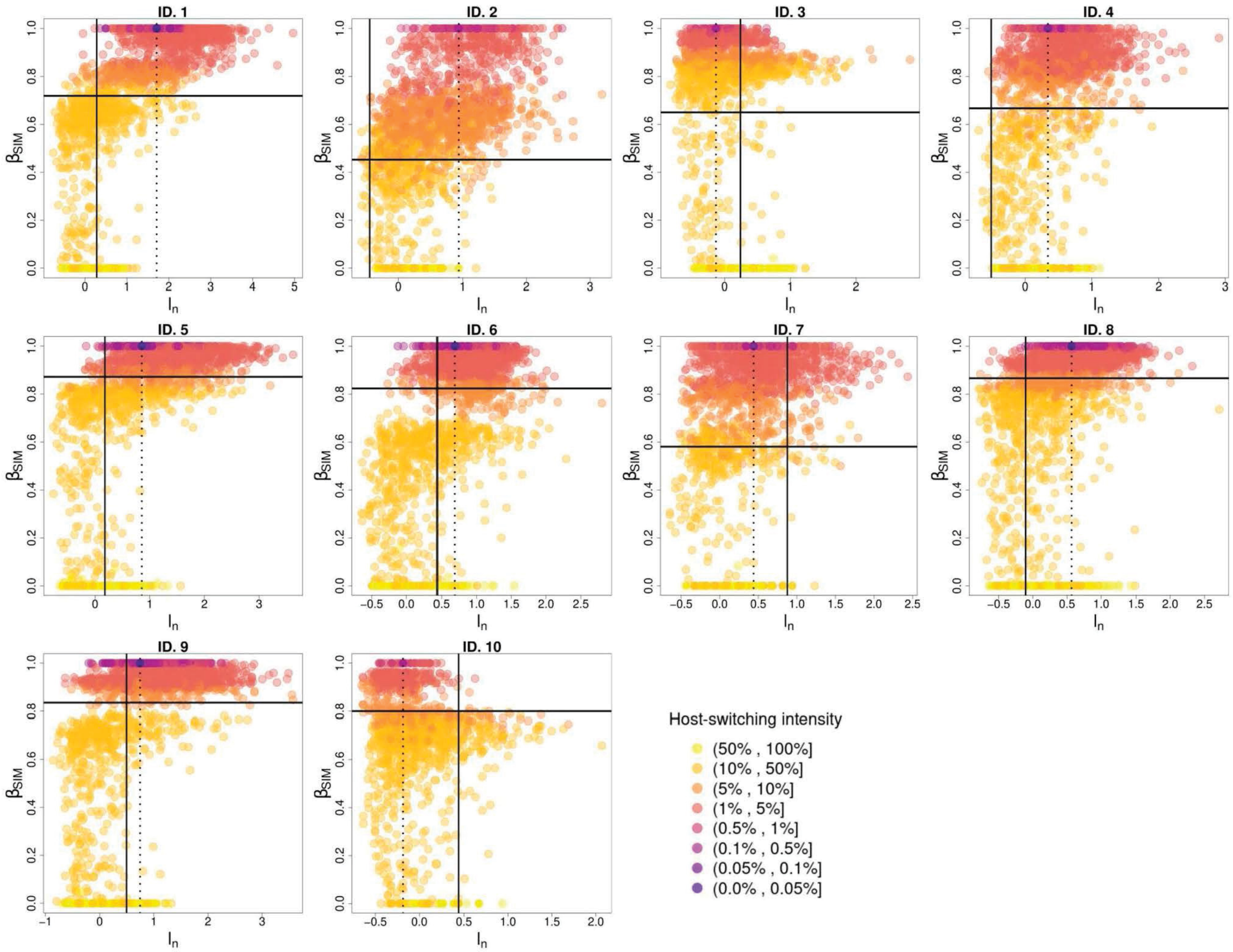

ID. 1
ID. 2
ID. 3
ID. 4
ID. 5
ID. 6
ID. 7
ID. 8
ID. 9
ID. 10
$\beta_{SIM}$
$I_n$
Host-switching intensity
(50% , 100%]
(10% , 50%]
(5% , 10%]
(1% , 5%]
(0.5% , 1%]
(0.1% , 0.5%]
(0.05% , 0.1%]
(0.0% , 0.05%]

**Figure S15**. The relationship between turnover of parasite species among host species normalised Sackin index of parasite species, and host-switching intensity for ten empirical studies: the parasites’ turnover, measured by the metric turnover($\beta_{SIM}$) on the y-axis and the normalised Sackin index ($I_n$) on the x-axis. Each ID represents an empirical study. The lines refer to empirical information of parasite (continuous) and host (dotted). Colour scales represent each percentage interval of host-switching intensity. A total of 50 runs were performed with 250 individuals of carrying capacity, for each configuration of the parameters of host-switching intensity. ID represents the each host community in different regions in the Nearctic biogeographic realm: ID. 1 - California Central, ID. 2 - California South West, ID. 13 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri, ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin.

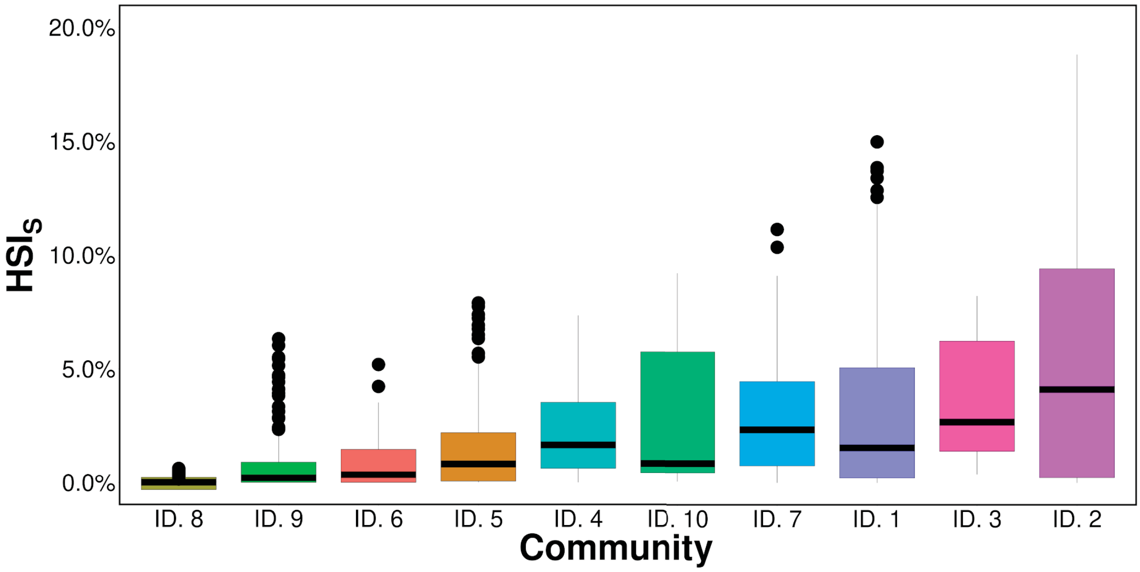


**Figure S16**. Variation in the host-switching intensity among host species ($HSI_S$). The boxplots show the distributions of simulated host-switching intensities for each community. Axis x presents the rodent communities in different regions in the Nearctic biogeographic realm: ID. 1 - California Central, ID. 2 - California South West, ID. 3 - Connecticut, ID. 4 - Idaho, ID. 5 - Indiana, ID. 6 - Missouri, ID. 7 - Montana, ID. 8 - New Mexico, ID. 9 - Tennessee and ID. 10 - Wisconsin. The black circles are outliers.

**Table S2.** Results of functional diversity and phylogenetic variability of host species for each empirical study (host community).

| Empirical study | PD | SR | pd.obs | pd.rand.mean | pd.rand.sd | Pd.Obs.rank | Pd.Obs.z | Pd.Obs.p | runs | PSV | SR.1 | vars |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ID.1 | 1.12 | 14 | 1.12 | 0.93 | 0.12 | 933 | 1.58 | 933 | 999 | 0.68 | 14 | 0.002 |
| ID.2 | 0.58 | 8 | 0.58 | 0.65 | 0.10 | 261.5 | -0.65 | 0.2615 | 999 | 0.53 | 8 | 0.005 |
| ID.3 | 0.81 | 11 | 0.81 | 0.80 | 0.11 | 581 | 0.12 | 581 | 999 | 0.81 | 11 | 0.003 |
| ID.4 | 0.60 | 9 | 0.60 | 0.70 | 0.10 | 159 | -0.93 | 159 | 999 | 0.66 | 9 | 0.004 |
| ID.5 | 1.23 | 20 | 1.23 | 1.17 | 0.13 | 688 | 0.46 | 688 | 999 | 0.73 | 20 | 0.001 |
| ID.6 | 0.76 | 11 | 0.76 | 0.79 | 0.11 | 417 | -0.29 | 417 | 999 | 0.69 | 11 | 0.003 |
| ID.7 | 0.49 | 8 | 0.49 | 0.65 | 0.09 | 43 | -1.59 | 43 | 999 | 0.62 | 8 | 0.005 |
| ID.8 | 1.24 | 21 | 1.24 | 1.21 | 0.13 | 608 | 0.25 | 608 | 999 | 0.63 | 21 | 0.001 |
| ID.9 | 1.02 | 19 | 1.02 | 1.13 | 0.13 | 224 | -0.80 | 224 | 999 | 0.72 | 19 | 0.001 |
| ID.10 | 0.69 | 7 | 0.69 | 0.59 | 0.08 | 856 | 1.13 | 856 | 999 | 0.77 | 7 | 0.006 |

## Generalised mixed-effects model (GLMM)

In the third GLMM, we assumed the host-switching intensity for each host species [$HSI_S$] as the response variable, the mean for adult body mass (g) [BM], diet breadth [DB], home range (individual km2)[HR], and litter size [LS] for each host species as fixed variables, and community-independent host species as random variables ($HSI_S$~BM+DB+HR+LS+(1|S)) (See the mean of traits for each host in each community in S15-S24).

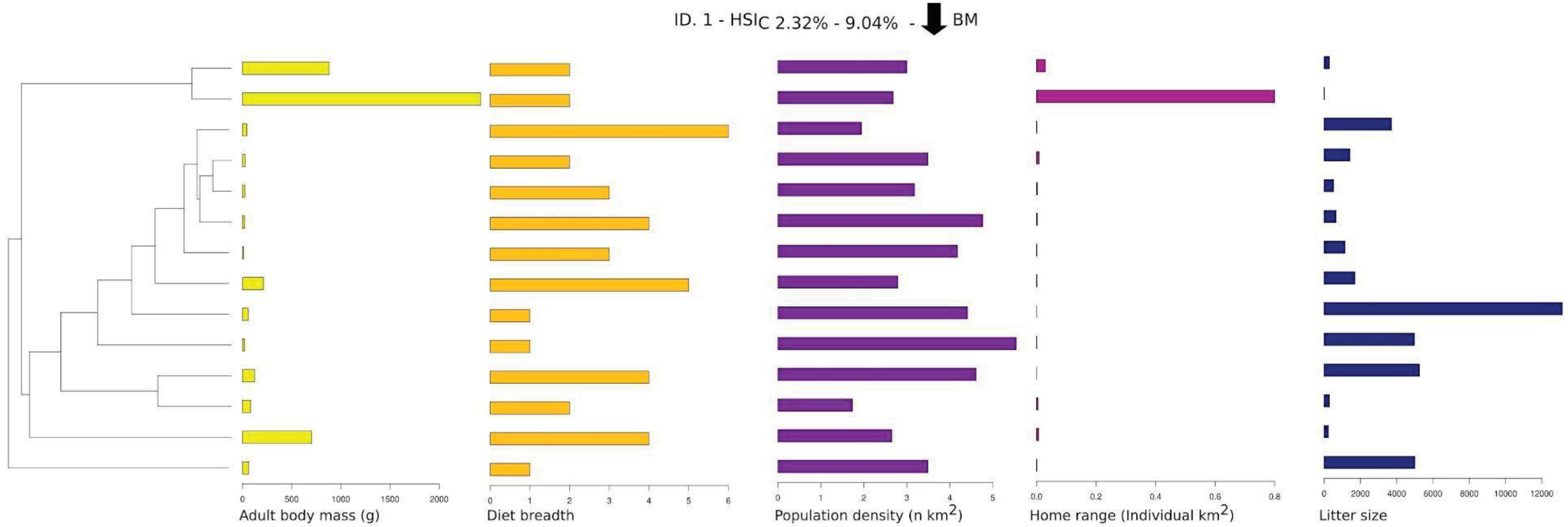


**Figura S17** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID.1 extracted from Linsdale & Davis 1956. Only body mass (BM) is related (negatively) to the host-switching among host species. Hosts' traits were extracted from Jones et al. (2009).

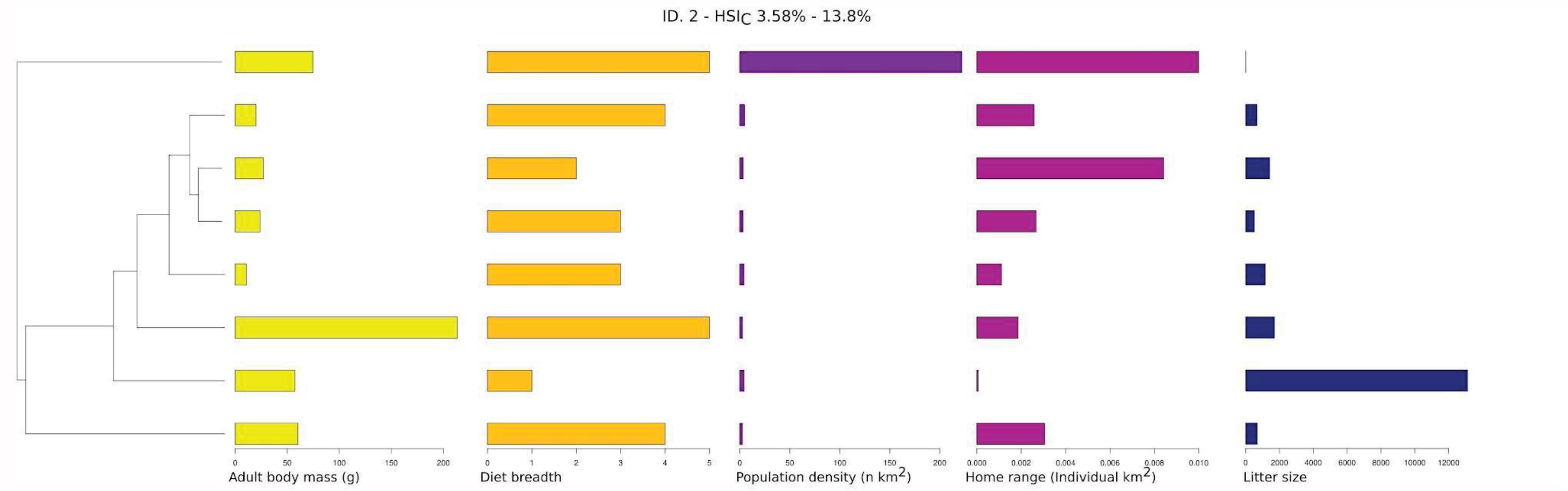


**Figura S18** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 2 extracted from Davis et al. 2002. Hosts' traits were extracted from Jones et al. (2009).

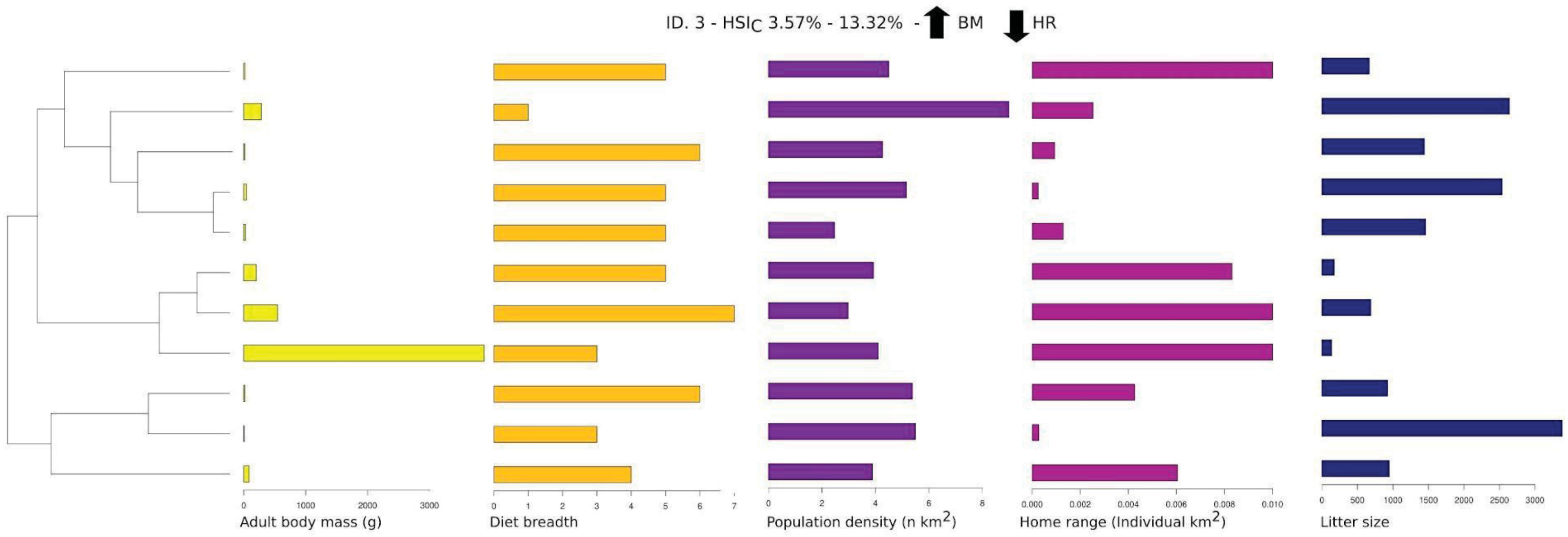


**Figura S19** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 3 extracted from Main 1983. Hosts' traits were extracted from Jones et al. (2009).

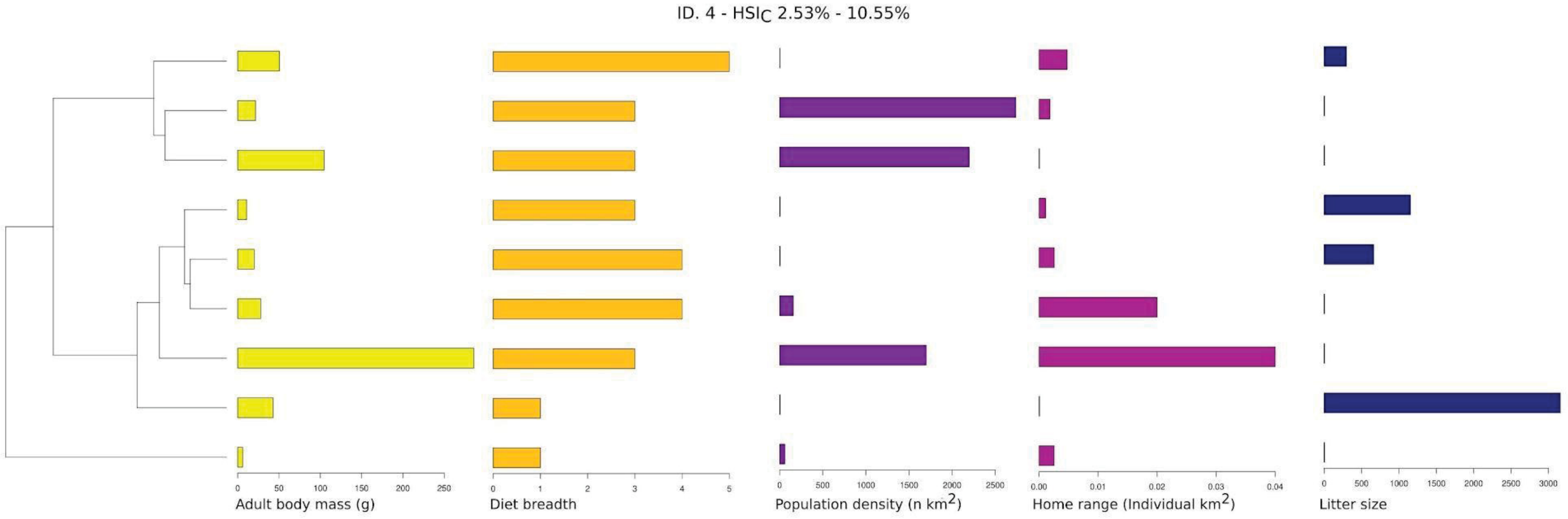


**Figura S20** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 4 extracted from Allred 1968. Hosts' traits were extracted from Jones et al. (2009).

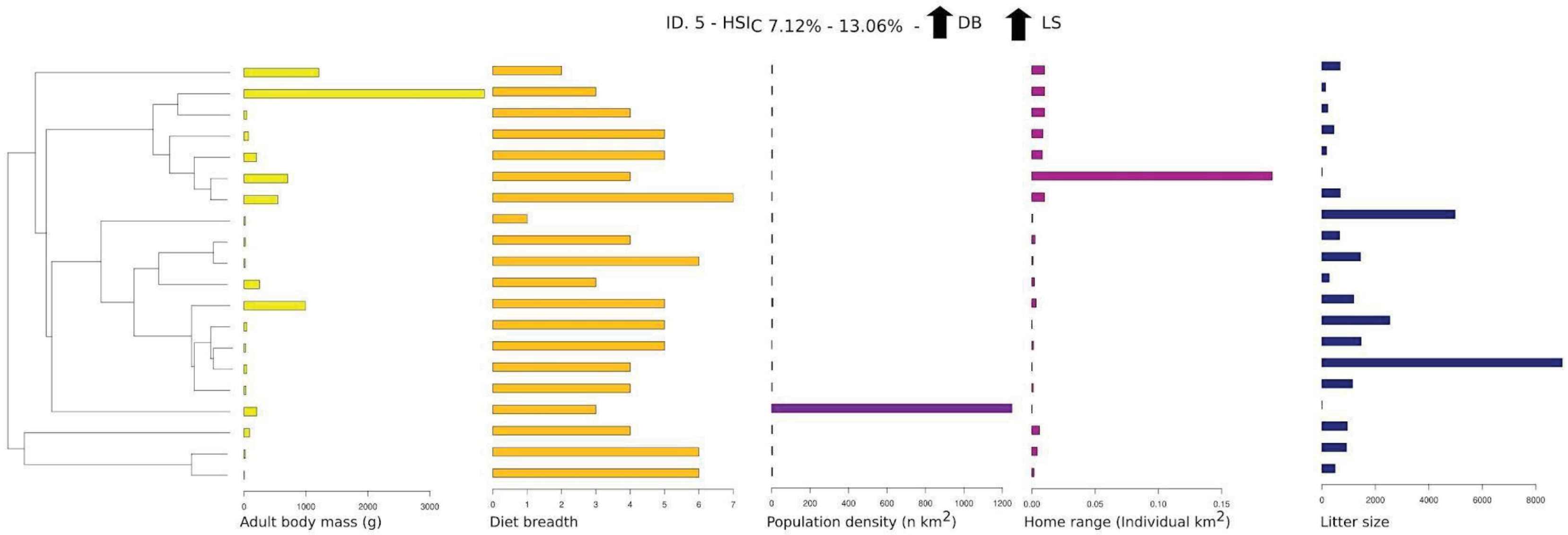


**Figura S21** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 5 extracted from Whitaker 1982. Hosts' traits were extracted from Jones et al. (2009).

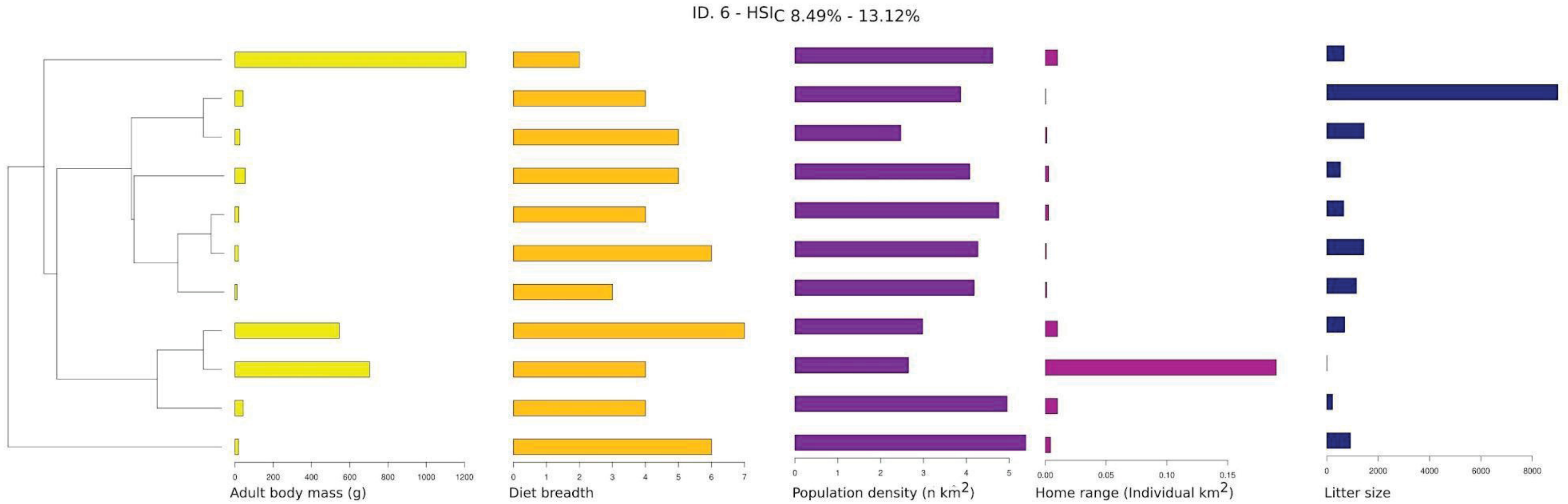


**Figura S22** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 6 extracted from Kollars et al. 1997. Hosts' traits were extracted from Jones et al. (2009).

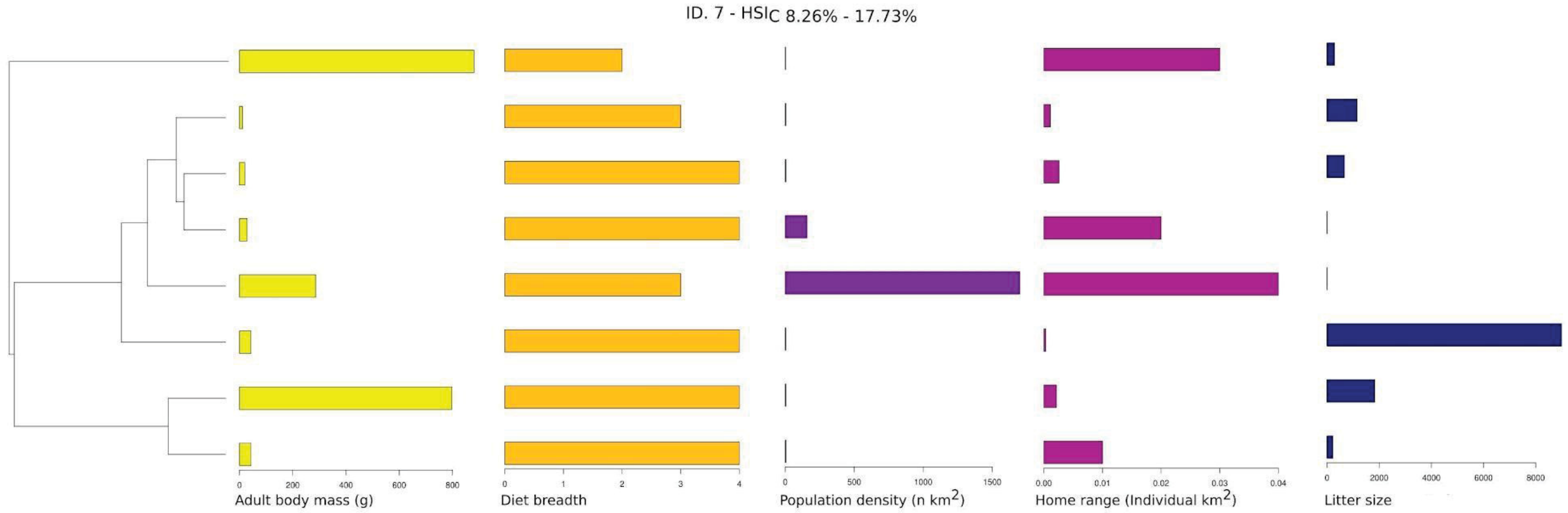


**Figura S23**- Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 7 extracted from Holmes 2003. Hosts' traits were extracted from Jones et al. (2009).

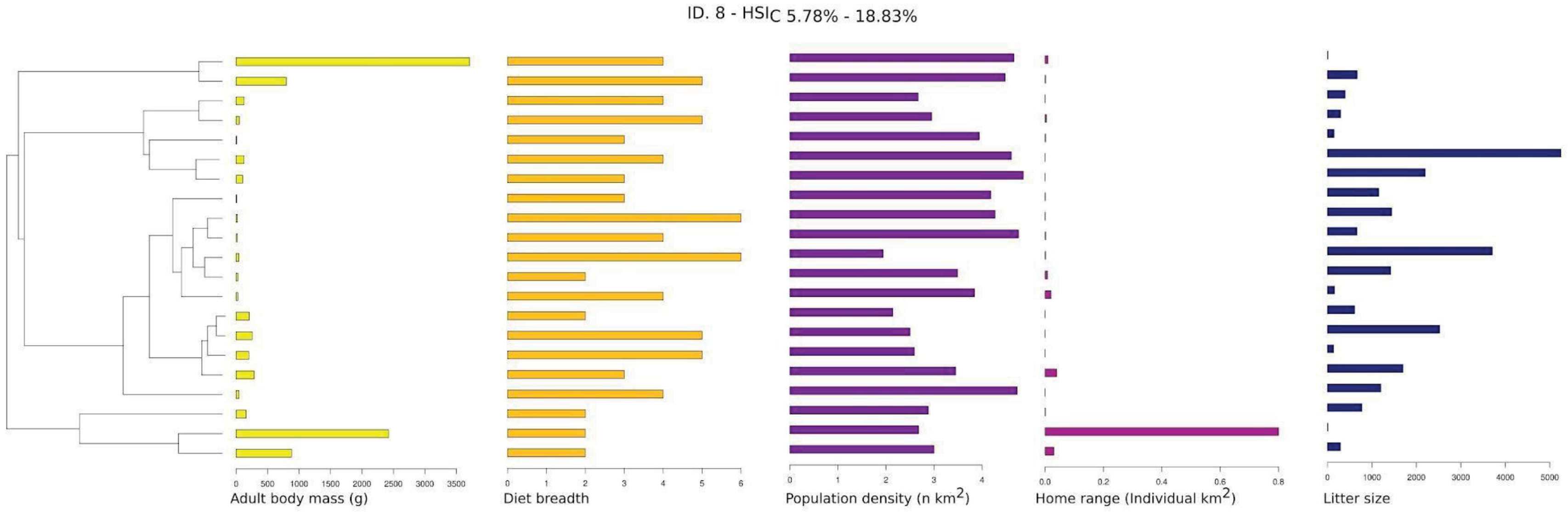


**Figura S24** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 8 extracted from Morlan 1955. Hosts' traits were extracted from Jones et al. (2009).

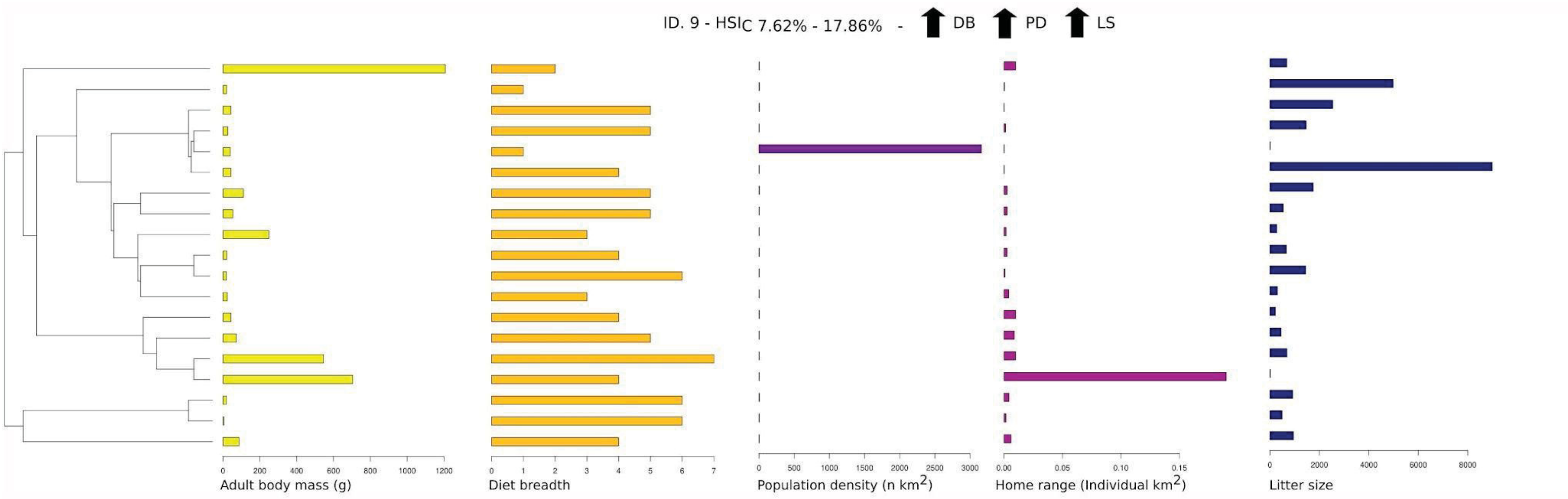


**Figura S25**- Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 9 extracted from Durden & Kollars 1997. Hosts' traits were extracted from Jones et al. (2009).

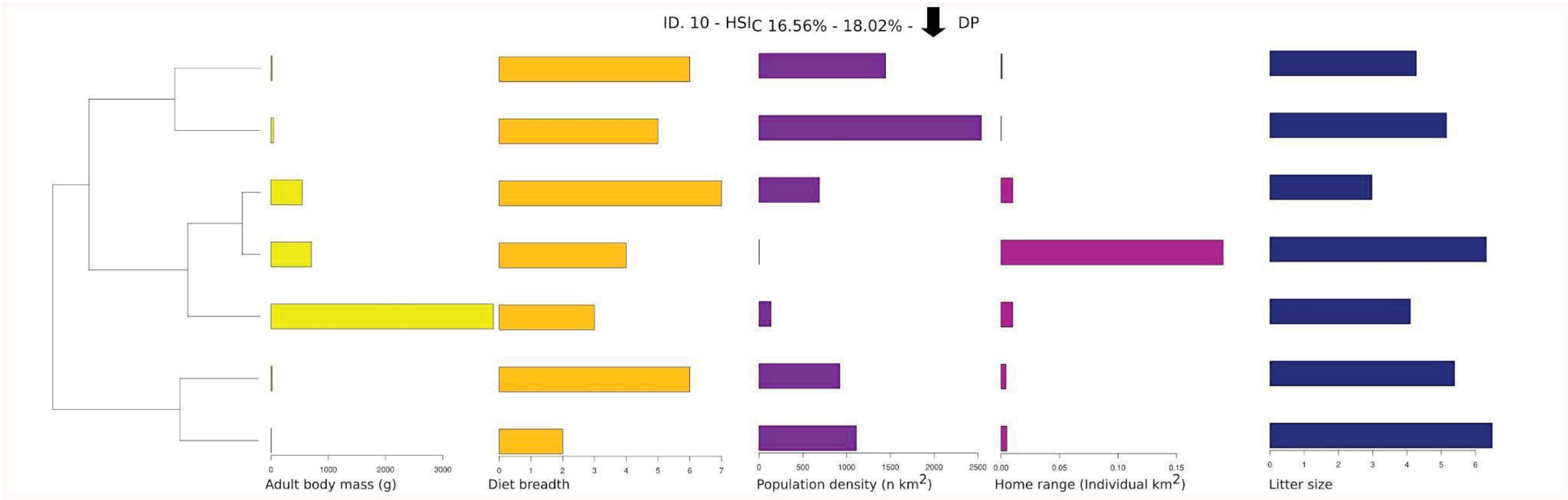


**Figura S26** - Relationship of the distribution of branches of rodent species (phylogeny) with the mean of each host trait of the empirical study ID. 10 extracted from Amin 1976. Hosts’ traits were extracted from Jones et al. (2009).

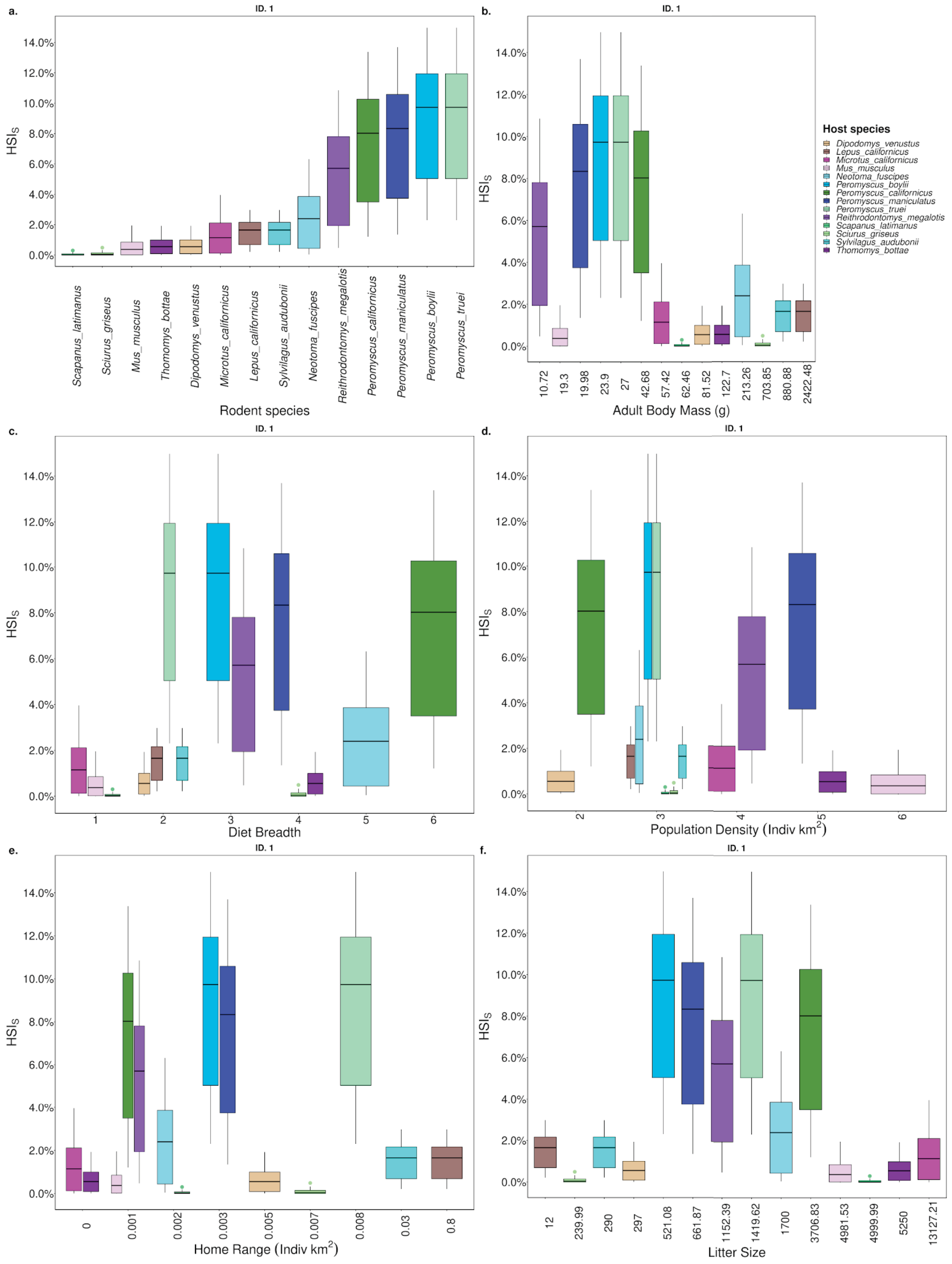


**Figure S27**. Relation of the host-switching intensity by host species in empirical study ID. 1 (extracted from Linsdale & Davis 1956). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the 14 host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

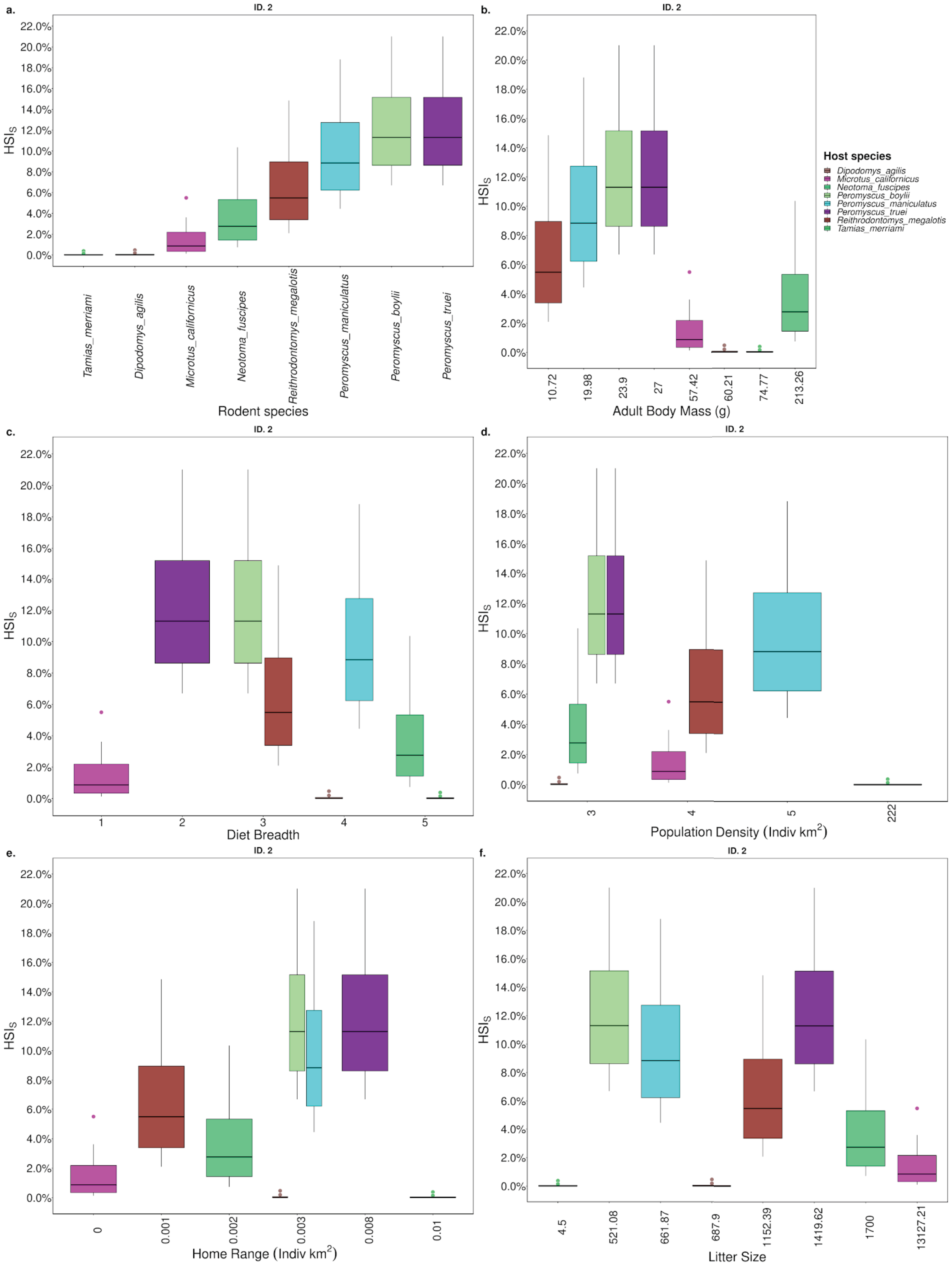


**Figure S28**. Relation of the host-switching intensity by host species in empirical study ID. 2 (extracted from Davis et al. 2002). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the eight host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

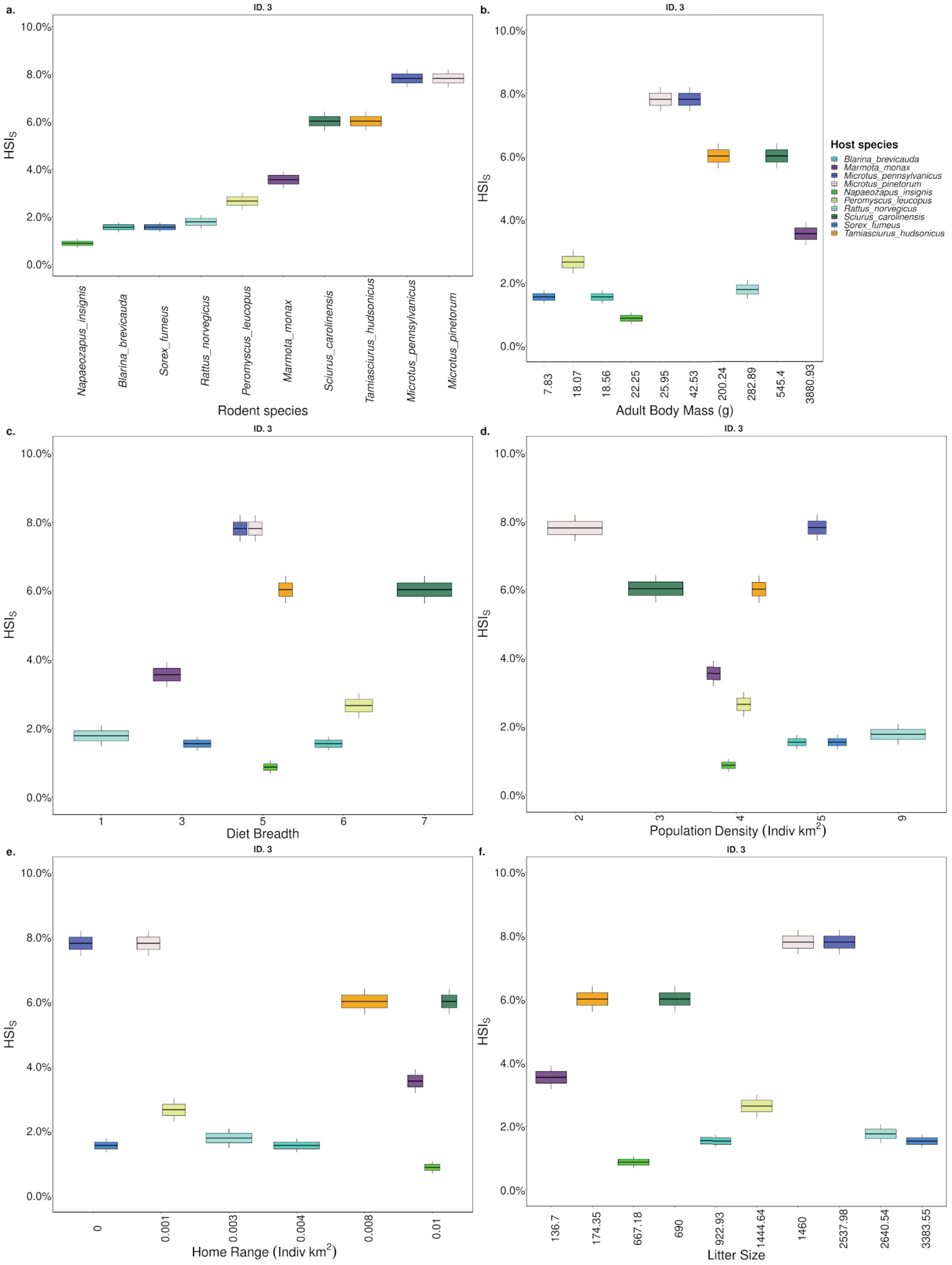


**Figure S29**. Relation of the host-switching intensity by host species in empirical study ID. 3 (extracted from Main 1983). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the 11 host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

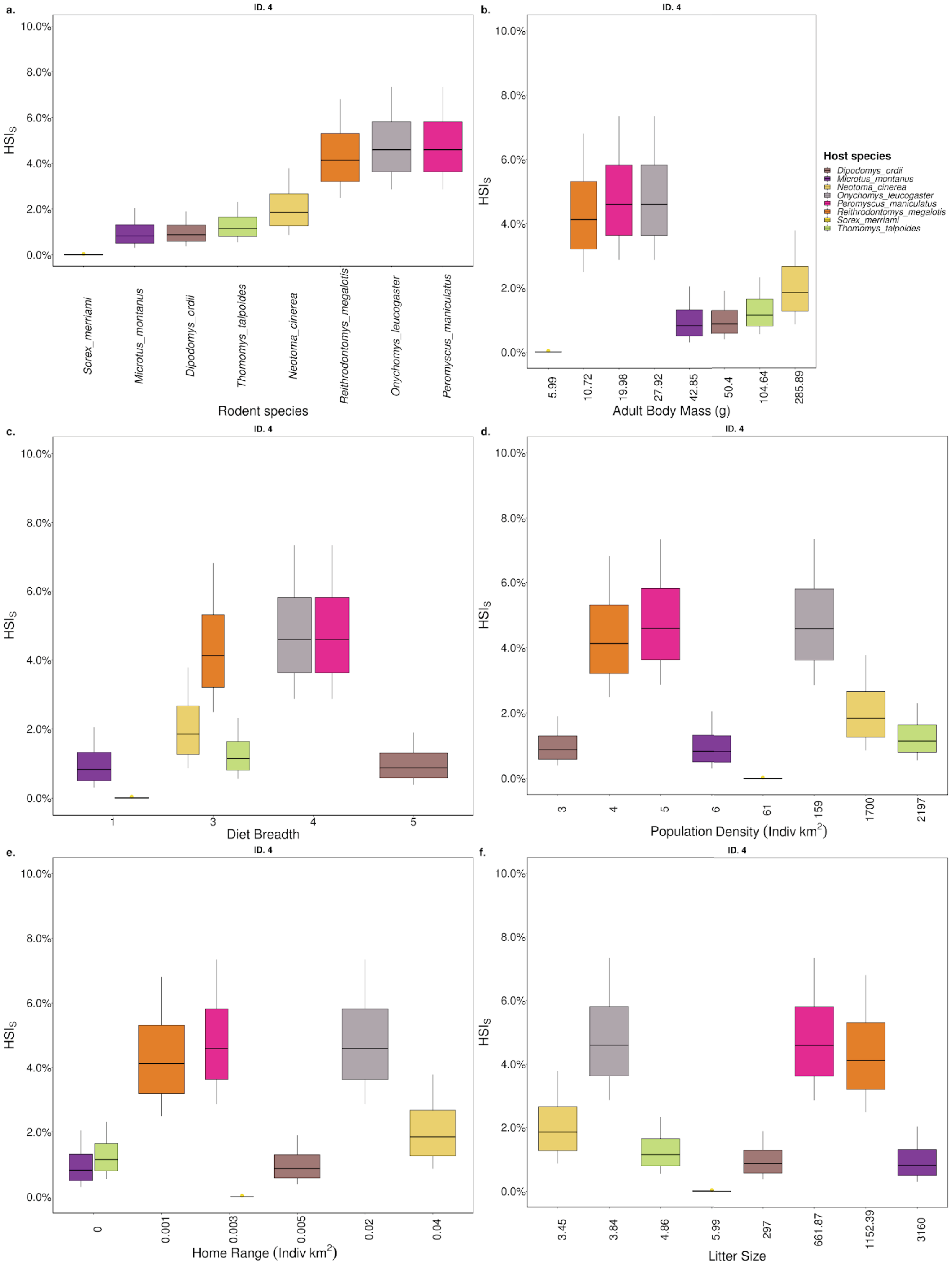


**Figure S30**. Relation of the host-switching intensity by host species in empirical study ID. 4 (extracted from Allred 1968). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the nine host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

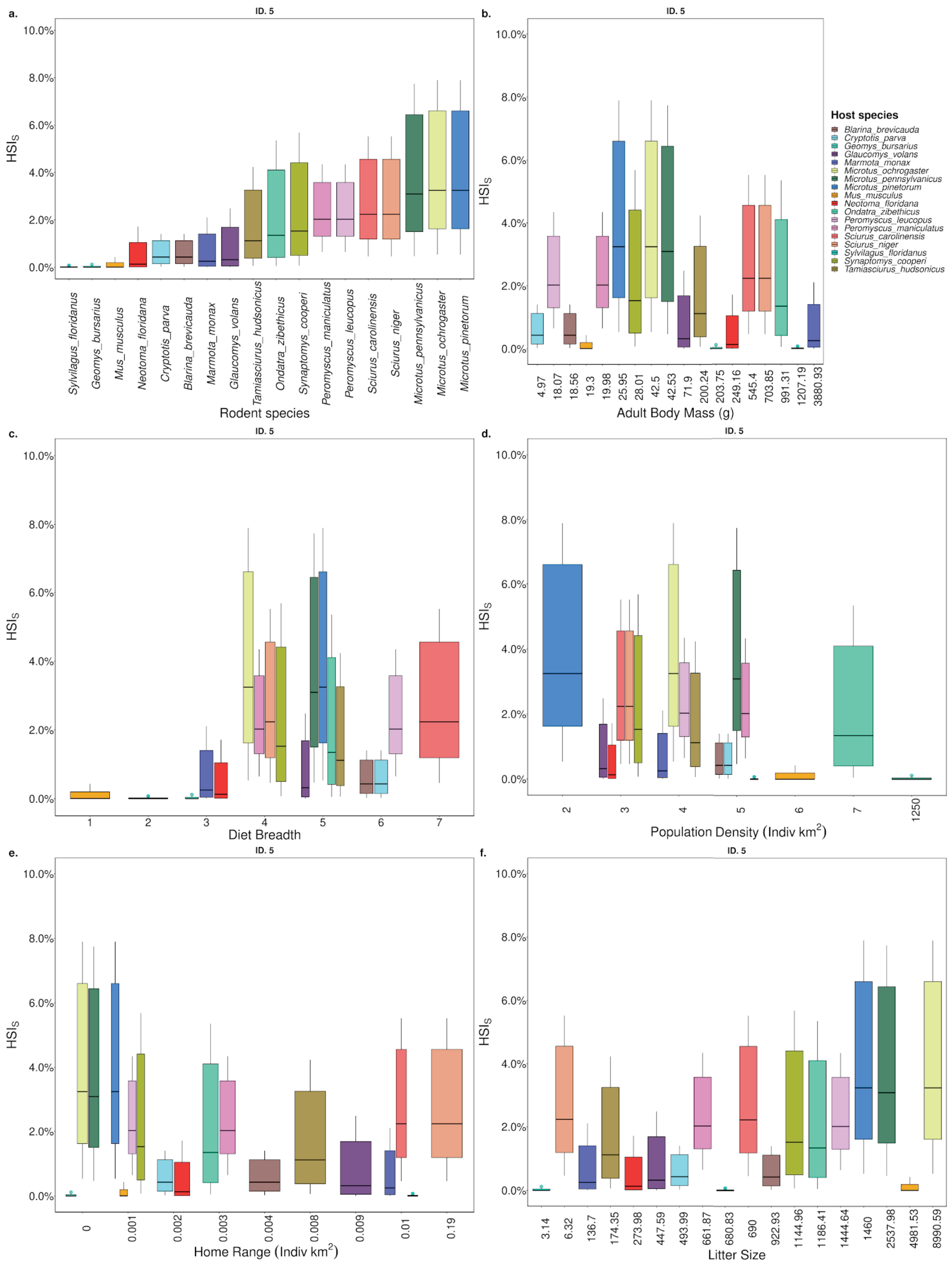


**Figure S31**. Relation of the host-switching intensity by host species in empirical study ID. 5 (extracted from Whitaker 1982). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the 20 host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

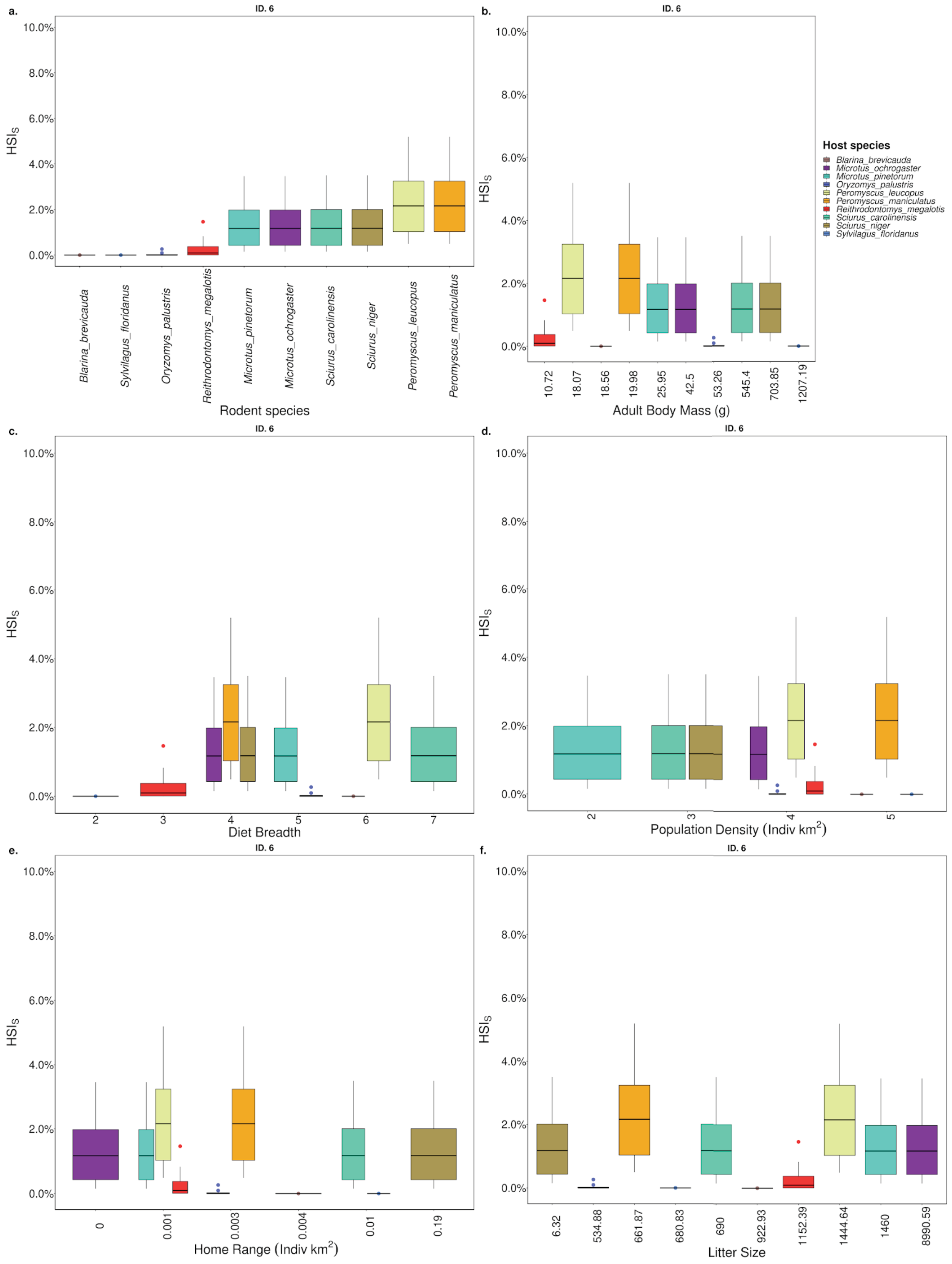


**Figure S32**. Relation of the host-switching intensity by host species in empirical study ID. 6 (extracted from Kollars et al. 1997). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the 11 host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

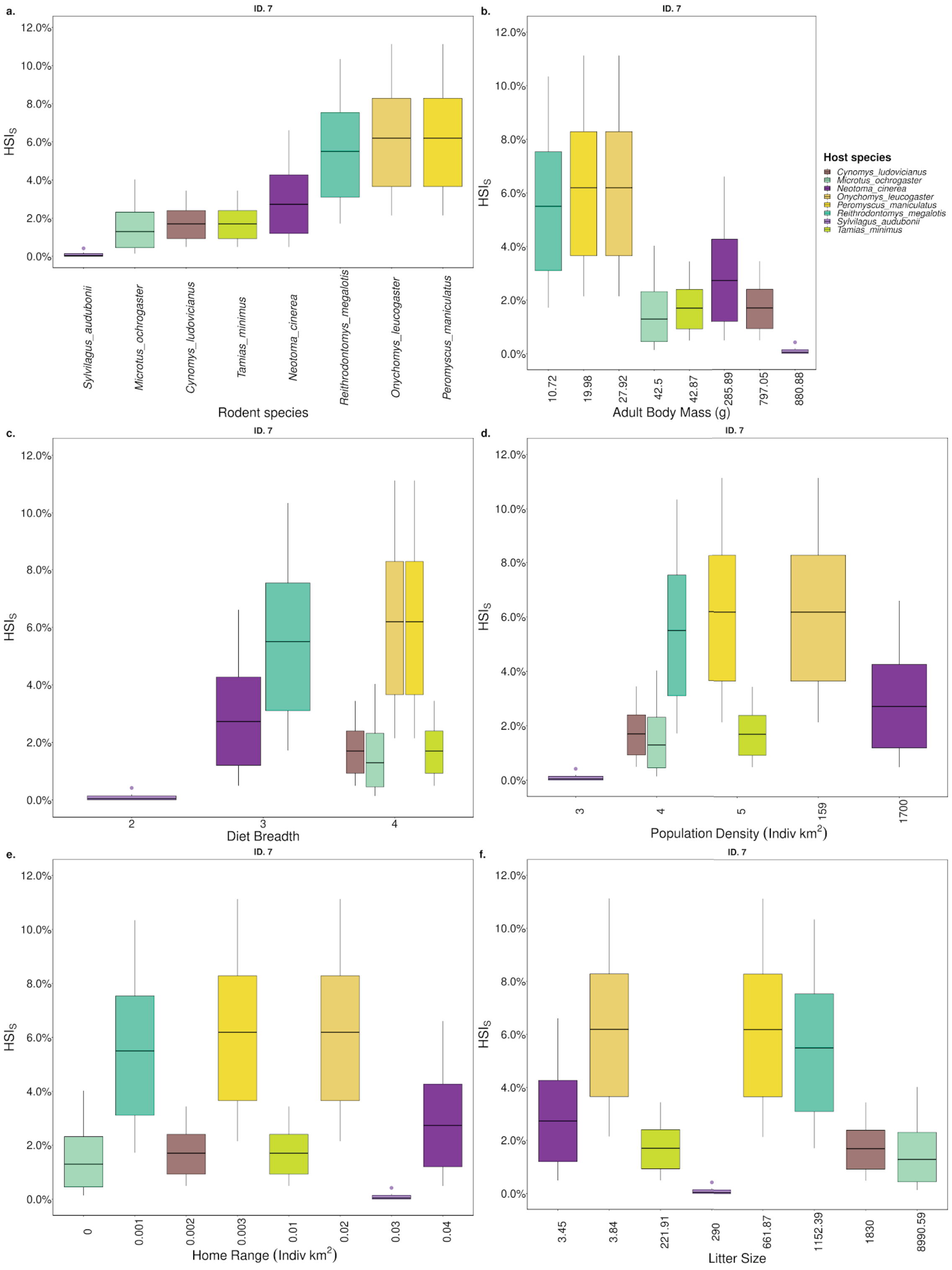


**Figure S33**. Relation of the host-switching intensity by host species in empirical study ID. 7 (extracted from Holmes 2003). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the eight host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

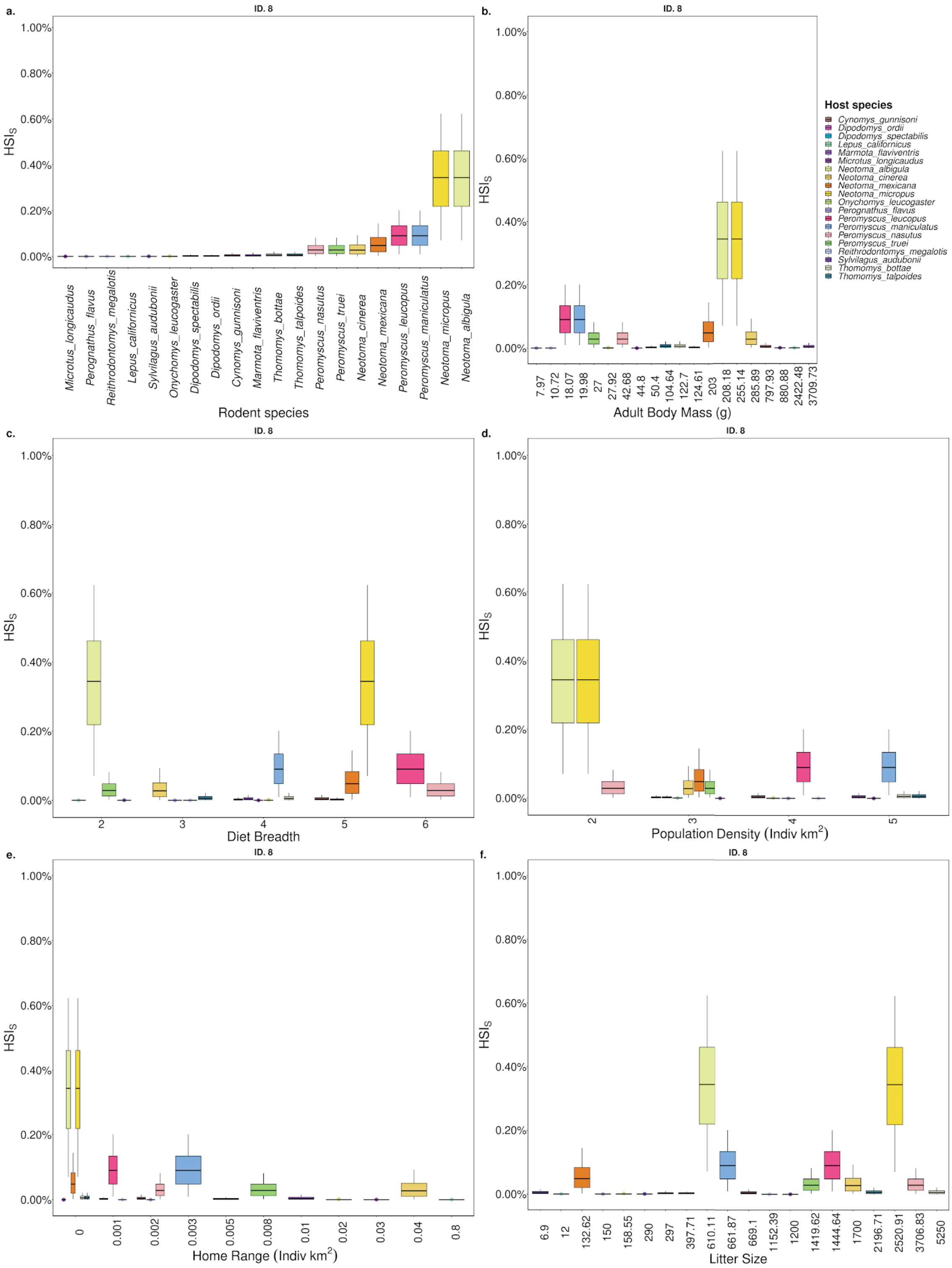


**Figure S34**. Relation of the host-switching intensity by host species in empirical study ID. 8 (extracted from Morlan 1955). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the 21 host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

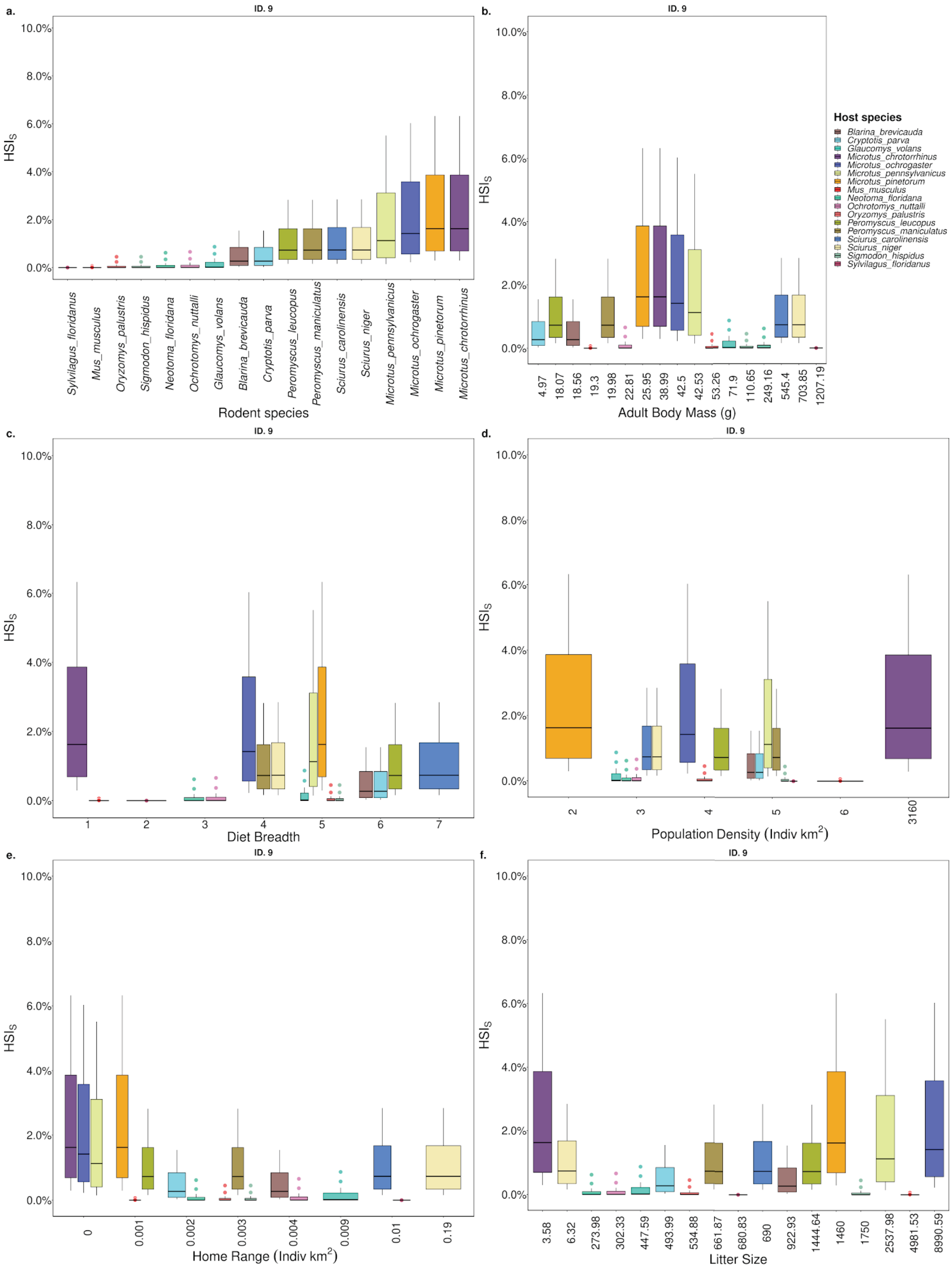


**Figure S35**. Relation of the host-switching intensity by host species in empirical study ID. 9 (extracted from Durden & Kollars 1997). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the 19 host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

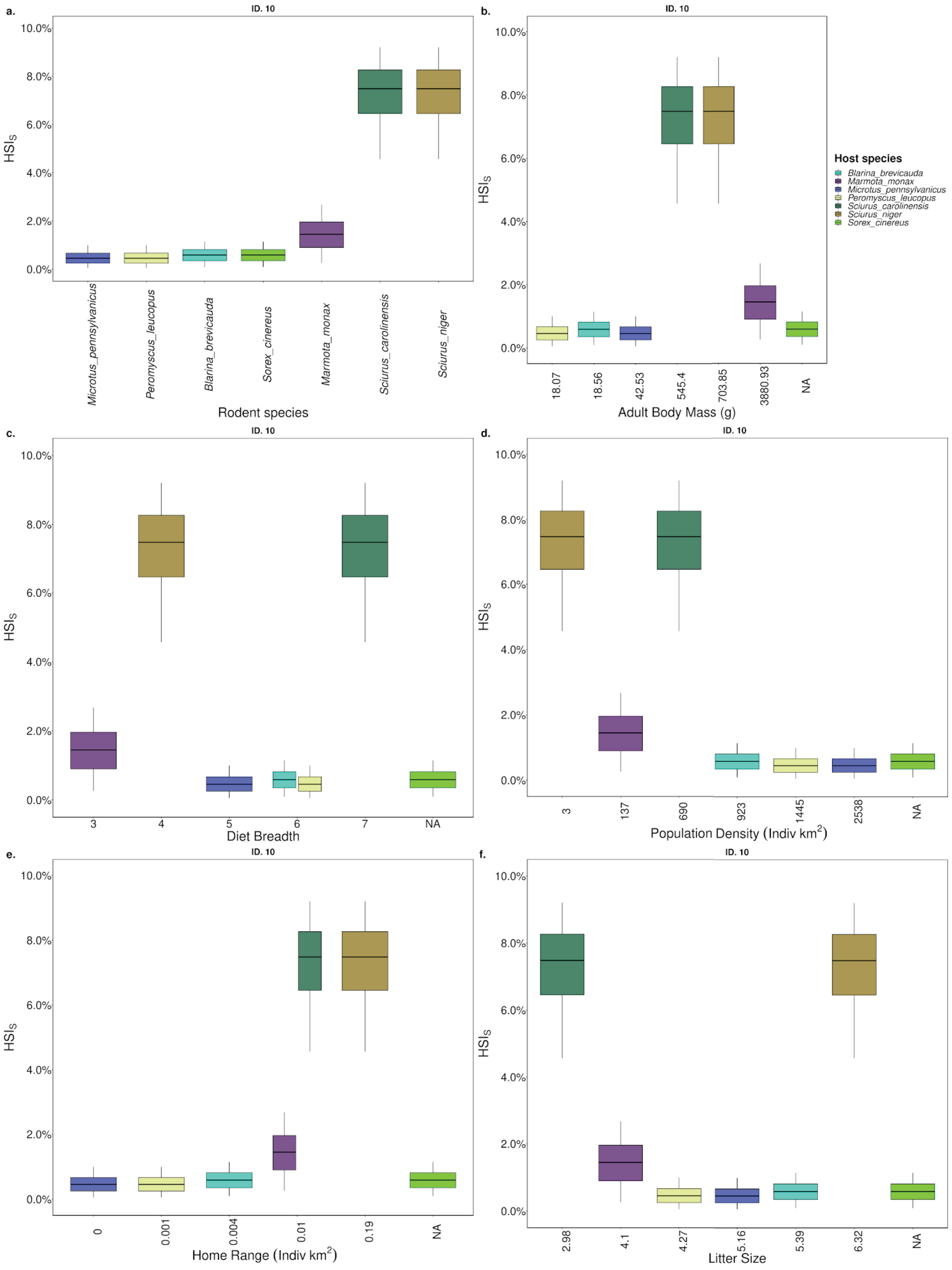


**Figure S36**. Relation of the host-switching intensity by host species in empirical study ID. 10 (extracted from Amin 1976). The boxplots show the distributions of simulated host-switching intensities by host species for each variation of hosts' traits. For this analysis, we showed the seven host species. The colours represent the information for each host species and the x-axis is categorical according to the range of variation of hosts' traits for each host species. Hosts' traits were extracted from Jones et al. (2009).

## REFERENCES

[Dataset] Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. Ecology, 90(9), 2648-2648.

[Dataset] Linsdale, J. M., Davis, B. S., & Davis, B. S. (1956). Taxonomic Appraisal and Occurence of Fleas at the Hastings Reservation in Central California, by Jean M. Linsdale and Betty S. Davis. University of California Press.

[Dataset] Davis, R.M., Smith, R.T., Madon, M.B. & Sitko-Cleugh, E. (2002) Flea, rodent and plague ecology at Chichupate Campground, Ventura County, California. Journal of Vector Ecology, 27, 107-127.

[Dataset] Main, A. J. (1983). Fleas (Siphonaptera) on small mammals in Connecticut, USA. Journal of Medical Entomology, 20(1), 33-39.

[Dataset] Allred, D. M. (1968) Fleas of the National Reactor Testing Station. Great Basin Naturalist, 28, 73-87.

[Dataset] Whitaker, J. O. (1982). Ectoparasites of mammals of Indiana. Monograph/Indiana Academy of Science (USA).

[Dataset] Kollars Jr, T. M., Durden, L. A., & Oliver Jr, J. H. (1997). Fleas and lice parasitizing mammals in Missouri. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(2), 125-132.

[Dataset] Holmes, B. E. (2003). Ecology and persistence of sylvatic plague in Phillips County Montana.

[Dataset] Morlan, H. B. (1955). Mammal fleas of Santa Fe County, New Mexico. Texas Reports on Biology and Medicine, 13(1), 93-125.

[Dataset] Durden, L. A., & Kollars Jr, T. M. (1997). The fleas (Siphonaptera) of

Tennessee. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(1), 13-22.

[Dataset] Amin, O. M. (1976). Host Associations and Seasonal Occurrence of Fleas from Southeastern Wisconsin Mammals, with Observations on Morphologic Variations1. Journal of Medical Entomology, 13(2), 179–192. doi:10.1093/jmedent/13.2.179

# CAPÍTULO 3

*Parasitology*

**cambridge.org/par**

**Research Article**

**Cite this article:** D'Bastiani E, Campião KM (2020). Disentangling the beta-diversity in anuran parasite communities. *Parasitology* 1–6. https://doi.org/10.1017/S0031182020002061

Received: 18 June 2020
Revised: 12 October 2020
Accepted: 15 October 2020

**Key words:**
Community structure; functional diversity; helminth diversity; opportunity for interaction; phylogenetic species variability

**Author for correspondence:**
Elvira D'Bastiani,
E-mail: elviradbastiani@gmail.com

# Disentangling the beta-diversity in anuran parasite communities

Elvira D'Bastiani[1] and Karla M. Campião[2]

[1]Postgraduate Program in Ecology and Conservation, Federal University of Paraná, Laboratory of Biological Interaction – Biological Sciences, Caixa Postal (P.O. Box) 19031, CEP (Postal Code) 81531-990, Curitiba, PR, Brazil and [2]Department of Zoology, Federal University of Paraná, Laboratory of Biological Interaction – Biological Sciences, Caixa Postal (P.O. Box) 19031, CEP (Postal Code) 81531-990, Curitiba, PR, Brazil

## Abstract

There is great heterogeneity in parasite communities among hosts, understanding the nature and drivers of such variations is still a great scientific quest. Here, we analyse the variation in parasite communities by addressing the following questions: (i) What is the beta-diversity component (nestedness or turnover) that most contributes to beta diversity in parasite communities among anuran species? (ii) Does the beta diversity of parasite communities follow a non-random pattern? (iii) Is the dissimilarity in composition of parasite communities related to the phylogenetic or functional dissimilarity among hosts? We found that turnover in parasite assemblages was the main component of beta diversity, but the variation observed both in the total beta diversity and in its components did not differ from the respective null models. The dissimilarity among parasite communities was not related to the phylogenetic species variability or functional dissimilarity among anuran species for most localities. In short, our findings may indicate a process of resource tracking by the parasite species, in which the resource may not necessarily be conserved phylogenetically in their hosts.

## Introduction

Ecologists are always pursuing to unveil mechanisms that generate variations in the assemblage and functionality of biological communities. An ubiquitous pattern is the temporal and spatial shift in the composition and abundance of these communities, which can be described as beta diversity. Beta diversity may be decomposed into two components: nestedness and turnover. These components reflect mechanisms underneath the differences in species composition among communities (Harrison *et al*., 1992; Baselga *et al*., 2007; Baselga, 2017). Nestedness occurs when communities with a lower number of species are subsets of richer communities, and may reflect processes of species loss (Wright and Reeves, 1992; Ulrich and Gotelli, 2007; Baselga, 2010). Turnover implies the replacement of some species, and generally reflects species sorting by environmental or dispersal processes, stochastic events, geographic barriers or historical constraints (Qian *et al*., 2005; Baselga, 2010, 2012, 2017). Disentangling the components of beta diversity can help us understand the processes underlying the variation in community composition (Baselga, 2012, 2013*a*; Baselga and Leprieur, 2015).

Spatial and environmental determinants of beta diversity have been studied in a variety of communities, including plant (Condit *et al*., 2002; Svenning and Skov, 2007), and animal communities in terrestrial (Baselga, 2008; Maestri and Patterson, 2016; Maestri *et al*., 2017), marine (Thrush *et al*., 2010) and freshwater environments (Pool *et al*., 2014; Maestri *et al*., 2017). Parasite organisms have received less attention, although they represent a substantial proportion of global biodiversity (Poulin and Morand, 2000). Parasites are good models to study beta-diversity patterns because their habitat can be easily and discretely defined as a set of exploited hosts. Differences in host species characteristics such as habitat, geographic distribution, diet and body size, will be reflected in the extent they are exposed to different parasite species (e.g. Fontenot and Font, 1996; Lile, 1998; Campião *et al*., 2015). Thus, each host individual is considered a habitat patch for colonization by any species within the local pool of parasite species, and sympatric host species can represent a natural experiment, where the analysis of their characteristics may explain the differences among their parasite communities.

Similarity between parasite communities can result from both historical and contemporary determinants (Poulin and Morand, 2000). A shared evolutionary history among host species contributes to the similarities in the composition of parasite communities. This may reflect conservatism of specific traits tracked by parasite species and may create phylogenetic congruences in species interactions. However, species present traits that are not preserved phylogenetically, such as aspects of host ecology that are shared among non-related hosts may also explain the absence of phylogenetic patterns. Phylogenetically conserved or not, traits are related to essential aspects of the host's natural history, such as the feeding and reproduction strategies and habitat use, these traits act as filters for the establishment of parasites. Each host trait can affect parasite species differently, resulting in differences among communities. Understanding the influence of these host traits is essential to direct studies beyond the pure number of parasite species towards a more inclusive approach.

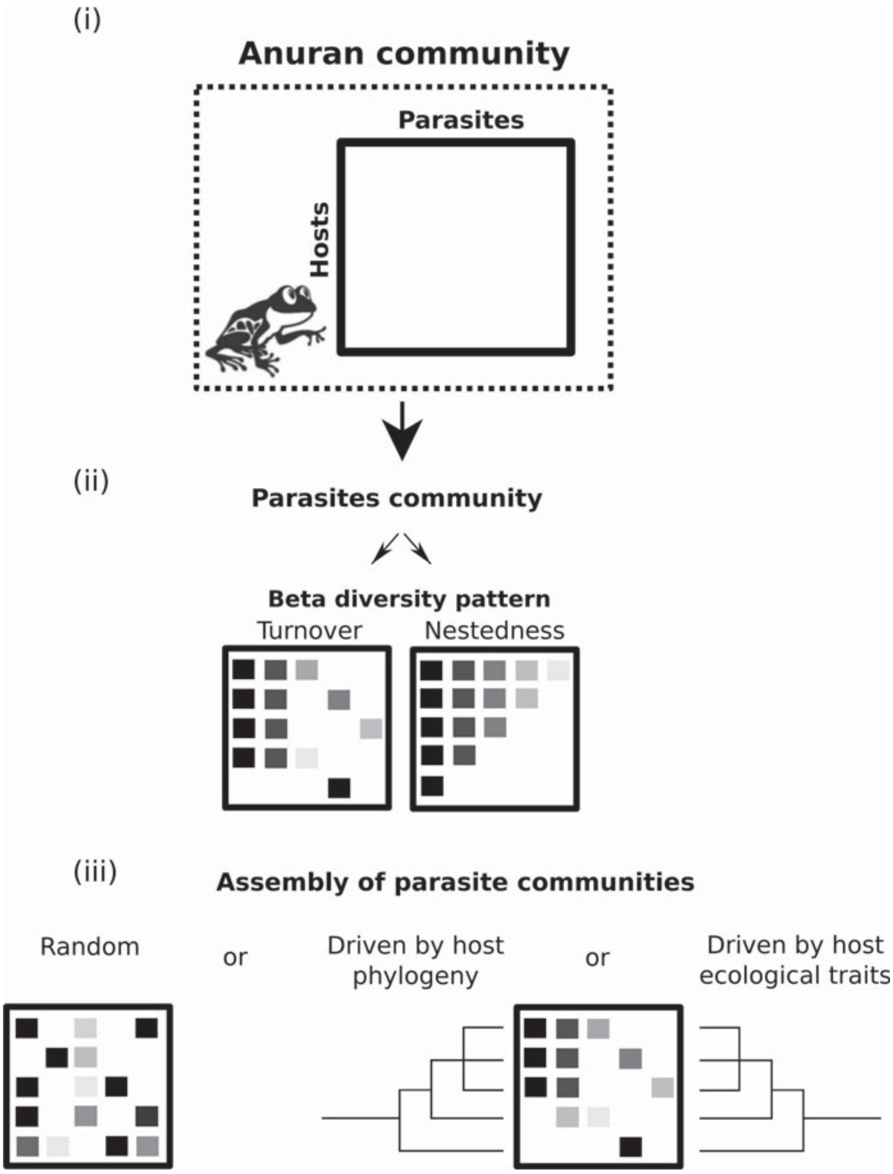


**Fig. 1.** Schematic representation of our study hypothesis, where we analysed the anuran host community (dotted box) and the local pool of parasite species: (i) each host species (lines) is a habitat patch for colonization by the local pool of parasite species (columns); (ii) there is a variation in the composition of parasite communities among host species, that can be partitioned into two components: turnover and nestedness; (iii) the dissimilarity in the composition of parasite communities among host species may be random or determined by the phylogenetic or functional dissimilarity of anurans host species.

In this study, we analysed the variation in the parasite communities (Fig. 1) by addressing the following questions: (i) What is the beta-diversity component (nestedness or turnover) that most contribute to beta diversity in parasite communities among anuran species? (ii) Does the beta diversity of parasite communities follow a non-random pattern? (iii) Is the dissimilarity in composition of parasite communities related to the phylogenetic or functional dissimilarity among hosts?

## Materials and methods

### *Data on parasites and anuran host species composition*

We compiled data on parasite species of anuran hosts from published surveys. All possible combinations with key-words 'amphibians', 'parasites', 'helminth' and 'Anura' were used to search for anuran-parasite empirical studies conducted from 1 January 1925 to 20 April 2020. These data were collected using online database platforms such as BioOne, Isi JSTOR, PubMed, SciELO, Scopus and Web of Science. We updated the amphibian's nomenclature according to Frost (2020). Parasite communities included species of the phyla Acanthocephala, Nematoda and Platyhelminthes (monogenean, digenean trematodes and monogenean). It is known that the composition of parasite species may be inaccurate for small samples (Poulin, 2007). Therefore, we used data from the surveys that (i) examined at least six individuals for each species of host, and (ii) at least six host species in each anuran community. Details on each selected study are given in Table 1 and Supplementary material S1.

### *Phylogenetic and functional variables*

To analyse anuran communities, similarities among anuran species were considered in the phylogenetic and functional dimensions. The relatedness among anuran species in each community was analysed with the phylogeny proposed by Jetz and Pyron (2018) (Supplementary material S2). We calculated the phylogenetic species variability (PSV) of each anuran community by using the phylogenetic distance among the host species (Helmus *et al.*, 2007). PSV quantifies the decrease in phylogenetic relatedness according to similarities shared by all species in a community, regardless of the number of species (Helmus *et al.*, 2007). Values of PSV range from 0 to 1, where 1 indicates that the sampled species are maximally unrelated (overdispersed).

The ecological variation among anurans was described by four different traits that represent different aspects of their life history. We calculated the functional diversity (FD) considering anuran body size, type of habitat used and aspects of the reproductive behaviour. Anuran habitat was classified as terrestrial, arboreal, aquatic, cryptozoic, fossorial and rheophilic. The reproductive

**Table 1.** Description of the anuran host communities analysed.

| Location | Latitude | Longitude | PSV host | FD host | *P* | Host species richness | Host sample size | Parasite species richness | Parasite sample size | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| ANC | −45.05 | −23.75 | 0.76 | 1.11 | 0.33 | 8 | 194 | 8 | 2058 | Aguiar *et al.* (2014) |
| CAS | −49.94 | −9.36 | 0.17 | 0.63 | 0.98 | 6 | 107 | 8 | 363 | Goldberg *et al.* (2009) |
| DIN | −22.60 | −52.87 | 0.61 | 0.52 | 0.07 | 6 | 140 | 15 | – | da Graça *et al.* (2017) |
| PAN | −56.65 | −18.98 | 0.47 | 0.78 | 0.12 | 11 | 229 | 16 | – | Campião *et al.* (2016) |
| PER | −35.19 | −8.04 | 0.36 | 0.57 | 0.03 | 9 | 218 | 11 | 781 | Martins-Sobrinho *et al.* (2017) |
| PAR | −45.31 | −23.22 | 0.48 | 0.69 | 0.35 | 13 | 168 | 12 | 1422 | Toledo *et al.* (2018) |

Legend: Locations- ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; and PAR, Paraitinga. Description of the phylogenetic species variability (PSV) and functional diversity (FD) of hosts. *P* value refers to the observed functional diversity (FD) compared with random expectations.

behaviour was described based on the oviposition site for tadpole development, which can be aquatic with or without a nest, terrestrial with or without a nest (Haddad and Prado, 2005; Haddad *et al*., 2013; Crump, 2015) (Supplementary material S3). In addition to describing the FD of anuran communities, these characteristics reflect different levels of exposure to the parasitic infective stages and can act as filters in the assembly of parasite communities.

### *Data analyses*

We tested whether the variables used to describe anuran communities were collinear by calculating pairwise differences between host species richness and PSV, and FD. For these comparisons, we used the Kruskal–Wallis test, once our data did not meet all assumptions of parametric tests.

Using the approach proposed by Baselga (2010, 2013*a*, *b*) we calculated total beta diversity ($\beta$) among host populations for each local community and then partitioned it into turnover and nestedness components. Total beta diversity is calculated by using the Sorensen dissimilarity measure ($\beta_{\text{SOR}}$), whereas the Simpson dissimilarity measure ($\beta_{\text{TUR}}$) calculates the turnover component; nestedness ($\beta_{\text{NES}}$) is calculated by subtracting total beta diversity and turnover (R Core Team, 2020). We used a resampling procedure computing 1000 random samples and calculated the average, standard deviation and *P* values for each local community (Baselga, 2017).

To test the relation between both phylogenetic and functional distances among host species and the similarity of their parasite communities we used a Mantel test (*r*) with the Spearman method. After that, for each location we generated 10 000 matrices to create a null sampling distribution of the Mantel statistic, and calculated a *Z*-score. This was calculated as $Z_{\text{score}} = [r_{\text{obs}} - \text{mean}(r_{\text{sim}})]/\sigma(r_{\text{sim}})$, where $r_{\text{obs}}$ is the observed value of correlation and $r_{\text{sim}}$ represents the values of correlation in the randomized matrices. We report correlation coefficients (*r*), *Z*-score and *P* value.

All statistical analyses were performed using R software (R Core Team, 2020), with the 'betapart' (Baselga *et al*., 2018), 'picante' (Kembel *et al*., 2010) and 'vegan' (Oksanen *et al*., 2019) packages. For all tests, we assumed significance of $P < 0.05$.

## Results

### *Characterization of host communities*

We found six studies on anuran communities that met the criteria for analyses. These communities were distributed in different ecosystems in Brazil, which included forested areas in the northern and southern Atlantic Forest (ANC – Anchieta, DIN – Diamante do Norte, PER – Pernambuco, PAR – Paraitinga), Cerrado areas – i.e. the Brazilian savanna (CAS – Caseara) and wetland areas (PAN – Pantanal) (Table 1). A total of 48 anuran species belonging to eight families were sampled: 22 species of Hylidae, 14 Leptodactylidae, three Bufonidae, three Microhylidae, two Brachycephalidae, one Craugastoridae, one Hemiphractidae, one Odontophrynidae and one Phyllomedusidae. The number of anuran species studied in each local community ranged from 6 to 13 (Table 1), and these communities varied in PSV and FD.

Anuran communities from CAS and DIN were the least diverse, with six anuran species and the lowest values of PSV and FD (Table 1). The anuran community in PAN had the highest species richness, but showed intermediate values of PSV and FD. The anuran community of ANC had the most diverse anuran community in the phylogenetic and functional dimensions, even though their taxonomic species richness was not the highest. There was no significant relationship between the observed PSV and species richness (Kruskal–Wallis chi-squared = 2.57, df = 3, *P* value = 0.46), neither between observed anuran FD and species richness (Kruskal–Wallis chi-squared = 3.71, df = 4, *P* value = 0.44).

### *Characterization of the parasite communities and their beta diversity*

The six anuran communities comprised 54 helminth taxa and included four undetermined acanthocephalans, 37 nematodes and 12 platyhelminthes (11 digenetic trematodes and 1 monogenean). Parasite species richness was the highest in PAN, followed by DIN (Table 1). For all the parasite compound communities (all host species combined) the total beta diversities varied between 0.68 in PER and 0.90 in CAS (Table 2). The variation in the composition of the parasite among anurans for all the communities indicated the turnover ($\beta_{\text{TUR}}$) as the component with a greater contribution than nestedness (Table 2 and Fig. 2). The variation observed both in the total beta diversity and in its components did not differ from the respective null models (Table 2, $P > 0.05$ in all cases), except for the PER community, where the difference between the observed total parasite beta diversity and the null models was marginally significant (Table 2). In short, for all parasite communities, turnover contributes more to the observed beta diversity, and the differences in the parasite communities among anuran species did not differ from random distributions.

### *Relationship between parasite communities and host traits*

To investigate deterministic factors that could drive parasite occurrence among hosts, we tested whether host phylogeny and

**Table 2.** Beta diversity of parasite communities in six communities of anuran hosts

| Location | Beta diversity | Obs | Null model | | |
|---|---|---|---|---|---|
| | | | Mean | SD | $P$ |
| ANC | $\beta_{SOR}$ | 0.64 | 0.44 | 0.27 | 0.28 |
| | $\beta_{TUR}$ | $0.44^a$ | 0.25 | 0.34 | 0.36 |
| | $\beta_{NES}$ | 0.20 | 0.18 | 0.15 | 0.43 |
| CAS | $\beta_{SOR}$ | 0.70 | 0.23 | 0.23 | 0.32 |
| | $\beta_{TUR}$ | $0.48^a$ | 0.38 | 0.38 | 0.45 |
| | $\beta_{NES}$ | 0.22 | 0.62 | 0.23 | 0.34 |
| DIN | $\beta_{SOR}$ | 0.90 | 0.92 | 0.13 | 0.73 |
| | $\beta_{TUR}$ | $0.84^a$ | 0.85 | 0.27 | 0.73 |
| | $\beta_{NES}$ | 0.06 | 0.06 | 0.15 | 0.20 |
| PAN | $\beta_{SOR}$ | 0.88 | 0.79 | 0.23 | 0.51 |
| | $\beta_{TUR}$ | $0.82^a$ | 0.68 | 0.36 | 0.38 |
| | $\beta_{NES}$ | 0.06 | 0.10 | 0.17 | 0.51 |
| PER | $\beta_{SOR}$ | 0.68 | 0.38 | 0.17 | 0.06 |
| | $\beta_{TUR}$ | $0.56^a$ | 0.26 | 0.21 | 0.12 |
| | $\beta_{NES}$ | 0.12 | 0.11 | 0.09 | 0.47 |
| PAR | $\beta_{SOR}$ | 0.70 | 0.54 | 0.21 | 0.31 |
| | $\beta_{TUR}$ | $0.38^a$ | 0.12 | 0.23 | 0.18 |
| | $\beta_{NES}$ | 0.32 | 0.42 | 0.28 | 0.59 |

Legend: Locations - ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; PAR, Paraitinga. $\beta_{SOR}$, stands for the overall beta diversity; $\beta_{TUR}$, for turnover; $\beta_{NES}$, for nestedness. Obs, refers toobserved. sd, refers to standard deviation. *P* value refers to the observed beta diversity (β) compared with random expectations.
$^a$Major component.

life-history traits could be related to the variation in parasite community composition by comparing distance matrices. For most anuran communities, the dissimilarity in the composition of parasite communities did not relate to the phylogenetic or functional dissimilarity among anuran species (Table 3). However, for the anuran community from PAR, there was a significant correlation between parasite community dissimilarity and the phylogenetic distance among their hosts (Mantel statistic $r = 0.32$, $Z$-score = 2.14, $P = 0.01$).

## Discussion

We described beta-diversity patterns in parasite communities and examined underlying factors that could drive the helminth parasite assemblages of anurans. Our analyses demonstrate that the turnover component had a greater contribution in the variation of the composition of parasite community among species of sympatric anurans. However, the beta-diversity pattern observed in parasite communities seems random, as it did not differ from the null model expectations. Also, the taxonomic dissimilarity among parasite communities was not related to the host PSV or host FD. We found only one anuran community with a significant correlation between the dissimilarity in the composition of the parasite communities and the phylogenetic among their hosts.

The turnover in parasite species, as we observed here, may reflect patterns of parasite species dispersion, and additionally, how these species recognize the available hosts as resources. Local environmental filters may have selected a very heterogeneous pool of host species, which, in addition to parasite resource specialization, may constrain the interactions. Indeed, helminth species have environmental tolerances that restrict their spatial distribution, and often specialize on a subset of available host species (Cooper *et al*., 2012). In other words, this pattern may be a result of the parasites tracking and exploiting specific resources within the available pool of hosts.

The pattern of parasite beta diversity observed in this study did not differ from that expected by null models, which assumes that species are ecologically equivalent (Hubbell, 2001; Ulrich and Gotelli, 2007). This non-differentiation indicates that the parasite species can be randomly assembled from the local pool to the communities analysed here. This pattern can occur when the abundance of species is the most important factor driving the association (Hubbell, 2001; Mouritsen and Poulin, 2002; Poulin, 2004). When a species is more abundant, it is more likely to colonize and establish itself in a new environment. Particularly, due to the low specificity observed in many species of parasites, being abundant would be enough for the establishment of the interaction. As we did not have data on the abundance of species, we suggest that this relationship needs to be verified in future studies. The random pattern in assemblies of parasites is commonly observed at local scales, in which species are probably more susceptible to stochastic factors (Korallo-Vinarskaya *et al*., 2013; Van Der Mescht *et al*., 2016). However, studies on larger scales may reveal a non-random pattern, describing the mechanisms we are searching for.

The composition of parasite communities was not related to the host PSV or host FD. Distantly related hosts can provide the same resource for parasites if this resource is any characteristic that evolved in parallel. In this case, the interaction can be mediated by factors such as contact opportunity. For example, two terrestrial frog species that are phylogenetically distant but share the same habitat would have similar parasite communities. This has been frequently observed in many host–parasite systems, including anurans, where we see the same parasite species associated with host species that are very distant phylogenetically (Aguiar *et al*., 2014; Campião *et al*., 2016). The commonness of these 'not expected' host–parasite associations confound predictions based on species phylogenies.

Anuran species have considerable diversity in ways of life (terrestrial, arboreal, aquatic, cryptozoic, fossorial and rheophilic), and may promote differential infection opportunity by several parasites. The similarities in the biological attributes of the hosts may predict similarity in the composition of their parasite communities. Thus, our results are surprising since we expected that the higher the phylogenetic and functional similarity among hosts, the lower the taxonomic dissimilarity in parasite species (Krasnov *et al*., 2012; Campião *et al*., 2015; Cuthill and Charleston, 2019).

A limitation in our study is that the anuran communities, as well as the phylogenetic and functional trees in each location, are not complete, as there were species present in the environment that were not studied, and could change the results if they had been included. In this sense, our findings could be affected by the reduced statistical power of small host sampling size in each community. Still, we were able to observe some congruences among communities in the different localities analysed. Moreover, studies on parasite communities, as those we analysed here, generally target the most common and abundant host species, and may therefore be helpful models to access community assembly patterns.

In summary, our study supports the idea that a parasite is likely to be tracking specific resources. This would indicate that the assembly of the parasite species depends on the type of resource that the parasite can use. The influence of host traits and evolutionary history on parasite community composition

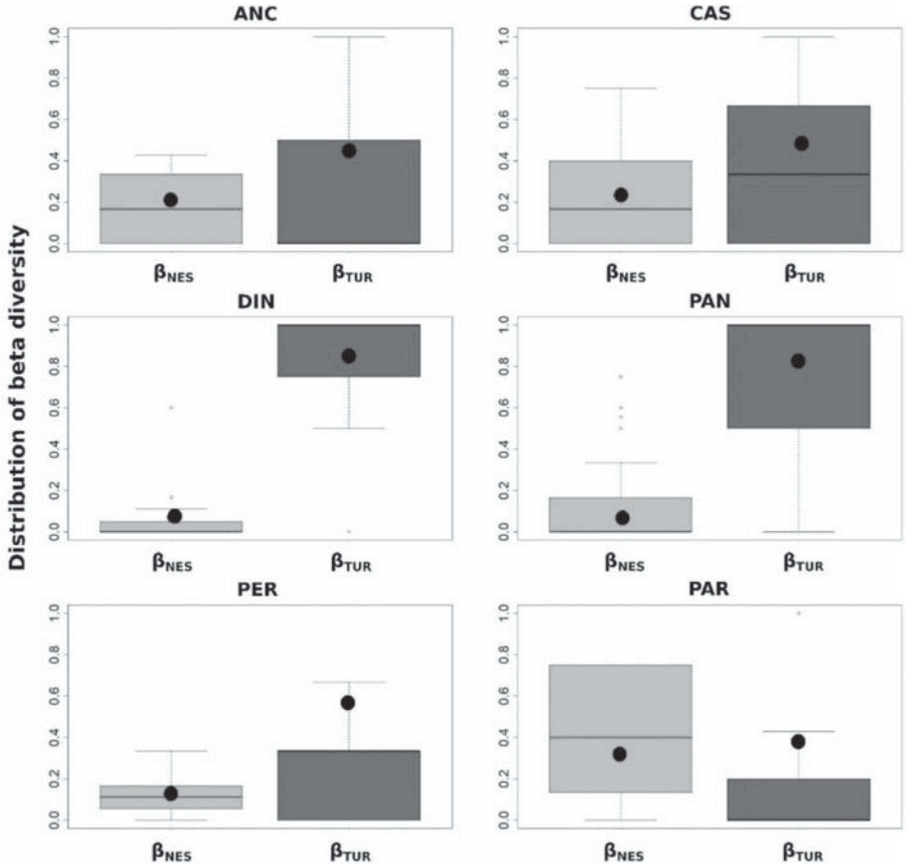


**Fig. 2.** Simulated and observed values of the two beta-diversity (β) components calculated for parasite communities of six communities of anuran hosts ( Locations: ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; PAR, Paraitinga). The black dots represent the observed values and the boxplots show the null model distributions, where the light grey box is the nestedness component ($\beta_{NES}$) and the dark grey box is the turnover ($\beta_{TUR}$) component. The smaller grey dots correspond to the outliers, and the bars to the standard error of the null models.

**Table 3.** Results of Mantel tests used to test whether the taxonomic dissimilarity of parasite communities is more related to the phylogenetic or functional dissimilarity of the anuran hosts

| Location | Correlation | Mantel statistic, *r* | $Z_{score}$ | *P* |
|---|---|---|---|---|
| ANC | Taxonomic – phylogenetic | 0.03 | 0.10 | 0.43 |
| | Taxonomic – functional | −0.35 | −1.38 | 0.91 |
| CAS | Taxonomic – phylogenetic | −0.17 | −0.59 | 0.68 |
| | Taxonomic – functional | 0.06 | 0.25 | 0.41 |
| DIN | Taxonomic – phylogenetic | 0.26 | 0.92 | 0.17 |
| | Taxonomic – functional | 0.05 | 0.20 | 0.45 |
| PAN | Taxonomic – phylogenetic | −0.11 | −0.85 | 0.80 |
| | Taxonomic – functional | −0.04 | −0.30 | 0.57 |
| PER | Taxonomic – phylogenetic | 0.24 | 0.99 | 0.17 |
| | Taxonomic – functional | −0.09 | −0.47 | 0.65 |
| PAR | Taxonomic – phylogenetic | 0.32 | 2.14 | **0.01** |
| | Taxonomic – functional | 0.27 | 1.85 | **0.02** |

Legend: Locations - ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; PAR, Paraitinga. We report on the correlation coefficient (*r*), the $Z_{score}$ of the comparison between the observed correlation and that of the null model, and the associated significant *P* (*P* value) for each location.

may be masked by other forces structuring communities, but most certainly influences community structure to some degree. Our study integrates different approaches from ecology and parasitology, and may also contribute to understanding the structure of parasites among populations of hosts in other antagonistic systems. The analysis of different dimensions of diversity, which is a tradition in the study of free-living organisms, has become an important baseline to the understanding of parasite assemblages, and in this sense our study adds data to this increasing body of evidence.

**Supplementary material.** The supplementary material for this article can be found at https://doi.org/10.1017/S0031182020002061.

**Acknowledgements.** We thank the researchers from the Neotropical region who collected and reported the field data, our institutions and the many colleagues who helped us in different ways during this project, especially Sabrina L.B. Araujo, Walter A. Boeger and Gabriel de La Torre for their comments and suggestions. EDB is grateful for the Ph.D. degree scholarship provided by Capes (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior).

**Author contributions.** Conceived and designed the experiments: EDB and KMC. Performed the experiments: EDB. Analysed the data: EDB and KMC. Wrote the paper: EDB and KMC.

**Financial support.** This study was supported by Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES).

**Conflict of interest.** The authors declare that they have no conflict of interests.

## References

**Aguiar A, Morais DH, Cicchi PJP and Da Silva RJ** (2014) Evaluation of helminths associated with 14 amphibian species from a Neotropical island near the southeast coast of Brazil. *Herpetological Review* **45**, 227–236.

**Baselga A** (2008) Determinants of species richness, endemism and turnover in European longhorn beetles. *Ecography* **31**, 263–271.

**Baselga A** (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143.

**Baselga A** (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **21**, 1223–1232.

**Baselga A** (2013a) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography* **36**, 124–128.

**Baselga A** (2013b) Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs abundance gradients. *Methods in Ecology and Evolution* **4**, 552–557.

**Baselga A** (2017) Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution* **8**, 799–808.

**Baselga A and Leprieur F** (2015) Comparing methods to separate components of beta diversity.

**Baselga A, Jiménez-Valverde A and Niccolini G** (2007) A multiple-site similarity measure independent of richness. *Biology Letters* **3**, 642–645.

**Baselga A, Orme D, Villeger S, De Bortoli J and Leprieur F** (2018) betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1.

**Campião KM, Aquino Ribas AC, Morais DH, Silva RJ and Tavares LER** (2015) How many parasites species a frog might have? Determinants of parasite diversity in South American anurans. *PLoS One* **10**, e0140577.

**Campião KM, Silva ICO, Dalazen GT, Paiva F and Tavares LER** (2016) Helminth parasites of 11 anuran species from the Pantanal Wetland, Brazil. *Comparative Parasitology* **83**, 92–100.

**Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Núñez P, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E and Hubbell SP** (2002) Beta-diversity in tropical forest trees. *Science (New York, N.Y.)* **295**, 666–669.

**Cooper N, Griffin R, Franz M, Omotayo M and Nunn CL** (2012) Phylogenetic host specificity and understanding parasite sharing in primates. *Ecology Letters* **15**, 1370–1377.

**Crump ML** (2015) Anuran reproductive modes: evolving perspectives. *Journal of Herpetology* **49**, 1–16.

**Cuthill J and Charleston M** (2019) A simple model explains the dynamics of preferential host switching among mammal RNA viruses. *Evolution: International Journal of Organic Evolution* **67**, 980–990.

**da Graça RJ, Oda FH, Lima FS, Guerra V, Gambale PG and Takemoto RM** (2017) Metazoan endoparasites of 18 anuran species from the mesophytic semideciduous Atlantic Forest in southern Brazil. *Journal of Natural History* **51**, 705–729.

**Fontenot LW and Font WF** (1996) Helminth parasites of four species of aquatic snakes from two habitats in southeastern Louisiana. *Journal-Helminthological Society Washington* **63**, 66–75.

**Frost DR** (2020) *Amphibian species of the World 6.0, an Online Reference.* New York: Darrel Frost and the American Museum of Natural History.

**Goldberg SR, Bursey CR, Caldwell JP and Shepard DB** (2009) Gastrointestinal helminths of six sympatric species of Leptodactylus from Tocantins State, Brazil. *Comparative Parasitology* **76**, 258–266.

**Haddad CF and Prado CP** (2005) Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *BioScience* **55**, 207–2017.

**Haddad CF, Toledo LF, Prado CP, Loebmann D, Gasparini JL and Sazima I** (2013) *Guia dos anfíbios da Mata Atlântica: diversidade e biologia*. São Paulo, Brazil: Anolis Books.

**Harrison S, Ross SJ and Lawton JH** (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* **1**, 151–158.

**Helmus MR, Bland TJ, Williams CK and Ives AR** (2007) Phylogenetic measures of biodiversity. *The American Naturalist* **169**, E68–E83.

**Hubbell SP** (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press (MPB-32).

**Jetz W and Pyron RA** (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology & Evolution* **2**, 850–858.

**Kembel S, Cowan P, Helmus M, Cornwell W, Morlon H, Ackerly D, Blomberg SP and Webb C** (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics (Oxford, England)* **26**, 1463–1464.

**Korallo-Vinarskaya NP, Vinarski MV, Khokhlova IS and Krasnov BR** (2013) Body size and coexistence in gamasid mites parasitic on small mammals: null model analyses at three hierarchical scales. *Ecography* **36**, 508–517.

**Krasnov B, Fortuna M, Mouillot D, Khokhlova I, Shenbrot G and Poulin R** (2012) Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *The American Naturalist* **179**, 501–511.

**Lile NK** (1998) Alimentary tract helminths of four pleuronectid flatfish in relation to host phylogeny and ecology. *Journal of Fish Biology* **53**, 945–953.

**Maestri R and Patterson BD** (2016) Patterns of species richness and turnover for the South American rodent fauna. *PLoS One* **11**, e0151895.

**Maestri R, Shenbrot GI and Krasnov BR** (2017) Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. *Journal of Biogeography* **44**, 1880–1890.

**Martins-Sobrinho PM, Silva WGDO, Santos EGD, Moura GJBD and Oliveira JBD** (2017) Helminths of some tree frogs of the families Hylidae and Phyllomedusidae in an Atlantic rainforest fragment, Brazil. *Journal of Natural History* **51**, 1639–1648.

**Mouritsen K and Poulin R** (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* **124**, 101–117.

**Oksanen J, Guillaume Blanchet F, Friendly F, Kindt R, Legendre P, McGlinn D, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens H, Szoecs E and Wagner H** (2019) vegan: Community Ecology Package. R package version 2.5-6.

**Pool TK, Grenouillet G and Villéger S** (2014) Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. *Diversity and Distributions* **20**, 1235–1244.

**Poulin R** (2004) Parasites and the neutral theory of biodiversity. *Ecography* **27**, 119–123.

**Poulin R** (2007) Are there general laws in parasite ecology?.

**Poulin R and Morand S** (2000) The diversity of parasites. *The Quarterly Review of Biology* **75**, 277–293.

**Qian H, Ricklefs RE and White PS** (2005) Beta diversity of angiosperms in temperate floras of Eastern Asia and eastern North America. *Ecology Letters* **8**, 15–22.

**R Core Team** (2020) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

**Svenning J-C and Skov F** (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters* **10**, 453–460.

**Thrush SF, Hewitt JE, Cummings VJ, Norkko A and Chiantore M** (2010) $\beta$-Diversity and species accumulation in Antarctic coastal benthos: influence of habitat, distance and productivity on ecological connectivity. *PLoS One* **5**, e11899.

**Toledo GM, Schwartz HO, Nomura HAQ, Aguiar A, Velota RAMV, Da Silva RJ and Anjos LA** (2018) Helminth community structure of 13 species of anurans from Atlantic rainforest remnants, Brazil. *Journal of Helminthology* **92**, 438–444.

**Ulrich W and Gotelli NJ** (2007) Null model analysis of species nestedness patterns. *Ecology* **88**, 1824–1831.

**Van Der Mescht L, Krasnov BR, Matthee CA and Matthee S** (2016) Community structure of fleas within and among populations of three closely related rodent hosts: nestedness and beta-diversity. *Parasitology* **143**, 1268–1278.

**Wright DH and Reeves JH** (1992) On the meaning and measurement of nestedness of species assemblages. *Oecologia* **92**, 416–428.

## Considerações finais

Abordagens que combinam teorias evolutivas e ecológicas com dados empíricos são fundamentais para o avanço da compreensão dos mecanismos que governam a origem, as mudanças e a manutenção das comunidades ecológicas. No capítulo 1, encontramos uma faixa ótima de intensidade de troca de hospedeiro que pode prever padrões ecológicos e evolutivos semelhantes aos observados nas situações empíricas. Nossos resultados mostraram que o *turnover* de parasitos entre as espécies de hospedeiros diminuiu à medida que a intensidade de troca de hospedeiro aumentou e observamos uma baixa variação entre as repetições do modelo. Por outro lado, o balanço das árvores filogenéticas não teve uma tendência monotônica e observamos uma ampla variação. Esses resultados revelaram que, embora o balanço das árvores filogenéticas seja uma métrica sensível a eventos estocásticos, o turnover pode ser um *proxy* para troca de hospedeiro. Além disso, estudos empíricos locais parecem ter uma maior intensidade de troca de hospedeiros quando comparados a estudos regionais, destacando que a escala espacial é provavelmente uma limitação crucial da troca de hospedeiros. Por fim, neste capítulo concluímos que o nosso modelo no qual a troca de hospedeiro é mediada pela proximidade evolutiva entre as espécies de hospedeiros é um bom preditor para associações parasitárias, bem como para as origens da diversidade parasitária. Vemos isso como um passo importante em nossa compreensão sobre os processos de diversificação dos parasitos.

No capítulo 2, utilizando o modelo desenvolvido no capítulo 1, descobrimos que a faixa ótima de intensidade de troca de hospedeiro por parasitos prevista para comunidades varia; essa faixa ótima nas comunidades de hospedeiros não foi associada à diversidade funcional e nem com a variabilidade filogenética do hospedeiro; A faixa ótima de intensidade de troca de hospedeiro nas espécies de hospedeiros foi associada à média de cada atributo das espécies de hospedeiros (massa corporal adulta, amplitude da dieta, área de vida , densidade populacional e tamanho da ninhada), mas isso variou de acordo com cada comunidade de hospedeiro. Por fim, neste capítulo concluímos que as características do hospedeiro provavelmente influenciam os eventos de troca de hospedeiros. Isso sugere que a troca de hospedeiro é um fenômeno altamente dependente do contexto.

No capítulo 3, utilizando dados de interações anuros-endoparasitos, descobrimos que a rotatividade de espécies de parasitos entre as espécies de hospedeiros foi o principal componente da diversidade beta. Porém, a variação observada tanto na diversidade beta total como em seus componentes não diferiram dos respectivos modelos nulos. Observamos também que a dissimilaridade entre as comunidades parasitárias não foi relacionada com a variabilidade filogenética  dos hospedeiros e nem com a dissimilaridade funcional das hospedeiros para a maioria das localidades analisadas. Nossos resultados indicam um processo de rastreamento de recursos pelas espécies de parasitos.

Considerando os estudos desenvolvidos nos três capítulos da minha tese, de forma geral os padrões ecológicos e evolutivos dos parasitos podem variar devido aos eventos de troca de hospedeiros e estes padrões variam substancialmente entre as comunidades, podendo assim, ser um importante determinante da diversificação de espécies de parasitos. Nossos resultados sugerem que os eventos de troca de hospedeiros e a diversificação das espécies de parasitos são processos altamente dependentes do contexto ecológico e evolutivo das espécies associadas. O próximo passo é entender como a intensidade de troca de hospedeiros influencia a estrutura de redes de interação ao longo do tempo evolutivo. Um segundo passo, seria modificar o modelo alterando o parâmetro *r* e diferenciar que é a capacidade de interação e o que é oportunidade ecológica sob perspectiva das espécies de parasitos.

## Referências Geral

Agosta S. J., Janz N., Brooks D. R. (2010). How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. Zoologia (Curitiba), 27(2), 151-162.

Agosta, S. J., & Brooks, D. R. (2020). The Major Metaphors of Evolution. Series in Evolutionary Biology: New Perspectives in Its Development. Cham: Springer Nature Switzerland.

Agosta, S. J., & Klemens, J. A. (2008). Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. Ecology Letters, 11(11), 1123-1134.

Agosta, S. J., Janz, N., & Brooks, D. R. (2010). How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. Zoologia (Curitiba), 27(2), 151-162.

Aguiar A, Morais DH, Cicchi PJP and Da Silva RJ (2014) Evaluation of helminths associated with 14 amphibian species from a Neotropical island near the southeast coast of Brazil. Herpetological Review 45, 227–236.

Aldous D. J. (2001). Stochastic models and descriptive statistics for phylogenetic trees, from Yule to today. Statistical Science, 16, 23-34.3

Allred, D. M. (1968) Fleas of the National Reactor Testing Station. Great Basin Naturalist, 28, 73-87.

Amin, O. M. (1976). Host Associations and Seasonal Occurrence of Fleas from Southeastern Wisconsin Mammals, with Observations on Morphologic Variations1. Journal of Medical Entomology, 13(2), 179–192. doi:10.1093/jmedent/13.2.179

Anderson, P. K., Cunningham, A. A., Patel, N. G., Morales, F. J., Epstein, P. R., & Daszak, P. (2004). Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. Trends in ecology & evolution, 19(10), 535-544.

Araujo, S. B., Braga, M. P., Brooks, D. R., Agosta, S. J., Hoberg, E. P., von Hartenthal, F. W., & Boeger, W. A. (2015). Understanding host-switching by ecological fitting. PLoS One, 10(10), e0139225.

Arneberg, P., Skorping, A., Grenfell, B., & Read, A. F. (1998). Host densities as determinants of abundance in parasite communities. Proceedings of the Royal Society of London. Series B: Biological Sciences, 265(1403), 1283-1289.

Baselga A (2008) Determinants of species richness, endemism and turnover in European longhorn beetles. Ecography 31, 263–271.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134–143.

Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography 21, 1223–1232.

Baselga A (2013a) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. Ecography 36, 124–128.

Baselga A (2013b) Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs abundance gradients. Methods in Ecology and Evolution 4, 552–557.

Baselga A (2017) Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. Methods in Ecology and Evolution 8, 799–808.

Baselga, A., & Leprieur, F. (2015). Comparing methods to separate components of beta diversity. Methods in Ecology and Evolution, 6(9), 1069-1079.

Baselga A, Jiménez-Valverde A and Niccolini G (2007) A multiple-site similarity measure independent of richness. Biology Letters 3, 642–645.

Baselga A, Orme D, Villeger S, De Bortoli J and Leprieur F (2018) betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1.

Baselga A., Gómez-Rodríguez C., Araújo M. B., Castro-Insua A., Arenas M., Posada D., Vogler A. P. (2022). Joint analysis of species and genetic variation to quantify the role of dispersal and environmental constraints in community turnover. Ecography, e05808.

Bates D., Maechler M., Bolker B., Walker S., Christensen R. H. B., Singmann H. Grothendieck G. (2011). Package 'lme4'. Linear mixed-effects models using S4 classes. R package version, 1(6).

Becker, R. A., Chambers, J. M. and Wilks, A. R. (1988) The New S Language. Wadsworth & Brooks/Cole.

Blum M. G.  François O. (2005). On statistical tests of phylogenetic tree imbalance: the Sackin and other indices revisited. Mathematical biosciences, 195, 141-153.

Boeger, W. A., Brooks, D. R., Trivellone, V., Agosta, S. J., & Hoberg, E. P. (2022). Ecological super-spreaders drive host-range oscillations: Omicron and risk-space for emerging infectious disease. Transboundary and Emerging Diseases.

Bordes, F., Morand, S., Kelt, D. A., & Van Vuren, D. H. (2009). Home range and parasite diversity in mammals. The American Naturalist, 173(4), 467-474.

Boyd, B. M., Nguyen, N. P., Allen, J. M., Waterhouse, R. M., Vo, K. B., Sweet, A. D., ... & Johnson, K. P. (2022). Long-distance dispersal of pigeons and doves generated new ecological opportunities for host-switching and adaptive radiation by their parasites. Proceedings of the Royal Society B, 289(1970), 20220042.

Boyer, N., Réale, D., Marmet, J., Pisanu, B., & Chapuis, J. L. (2010). Personality, space use and tick load in an introduced population of Siberian chipmunks Tamias sibiricus. Journal of Animal Ecology, 79(3), 538-547.

Braga M. P.  Janz N. 2021. Host repertoires and changing insect–plant interactions. Ecological Entomology, 46, 1241–1253.

Brooks D. R., Hoberg E. P., Boeger W. A., Gardner S. L., Galbreath K. E., Herczeg D. Dursahinhan A. T. (2014). Finding them before they find us: informatics, parasites, and environments in accelerating climate change. Comparative Parasitology, 81, 155-164.

Brooks D. R., McLennan D. A. (2002). The nature of diversity. University of Chicago Press.

Brooks, D. R., & Agosta, S. J. (2012). Children of time: The extended synthesis and major metaphors of evolution. Zoologia (Curitiba), 29, 497-514.

Brooks, D. R., & Hoberg, E. P. (2006). Systematics and emerging infectious diseases: from management to solution. Journal of Parasitology, 92(2), 426-429.

Brooks, D. R., & Hoberg, E. P. (2007). How will global climate change affect parasite–host assemblages?. Trends in parasitology, 23(12), 571-574.

Brooks, D. R., Hoberg, E. P., & Boeger, W. A. (2019). The Stockholm paradigm: climate change and emerging disease. University of Chicago Press.

Burnham, K. P., & Anderson, D. R. (1998). Practical use of the information-theoretic approach. In Model selection and inference (pp. 75-117). Springer, New York, NY.

Bush S. E., Sohn E. Clayton D. H. (2006). Ecomorphology of parasite attachment: experiments with feather lice. Journal of Parasitology, 92, 25-31.

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned?. Trends in ecology & evolution, 32(6), 429-437.

Campião KM, Aquino Ribas AC, Morais DH, Silva RJ and Tavares LER (2015) How many parasites species a frog might have? Determinants of parasite diversity in South American anurans. PLoS One 10, e0140577.

Campião KM, Silva ICO, Dalazen GT, Paiva F and Tavares LER (2016) Helminth parasites of 11 anuran species from the Pantanal Wetland, Brazil. Comparative Parasitology 83, 92–100.

Cardona G., Mir A., Rosselló F. (2013). Exact formulas for the variance of several balance indices under the Yule model. Journal of Mathematical Biology, 67(6), 1833-1846.

Charleston, M. A., & Robertson, D. L. (2002). Preferential host switching by primate lentiviruses can account for phylogenetic similarity with the primate phylogeny. Systematic biology, 51(3), 528-535.

Clay, C. A., Lehmer, E. M., Previtali, A., St. Jeor, S., & Dearing, M. D. (2009). Contact heterogeneity in deer mice: implications for Sin Nombre virus transmission. Proceedings of the Royal Society B: Biological Sciences, 276(1660), 1305-1312.

Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Núñez P,- Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E and Hubbell SP (2002) Beta-diversity in tropical forest trees. Science (New York, N.Y.) 295, 666–669.

Cooper N, Griffin R, Franz M, Omotayo M and Nunn CL (2012) Phylogenetic host specificity and understanding parasite sharing in primates. Ecology Letters 15, 1370–1377.

Cornell, H. V., & Harrison, S. P. (2014). What are species pools and when are they important?. Annual Review of Ecology, Evolution, and Systematics, 45, 45-67.

Costa C. L., Lemos-Costa P., Marquitti F. M., Fernandes L. D., Ramos, M. F., Schneider D. M. de Aguiar M. A. (2019). Signatures of microevolutionary processes in phylogenetic patterns. Systematic biology, 68, 131-144.

Crump ML (2015) Anuran reproductive modes: evolving perspectives. Journal of Herpetology 49, 1–16.

Cuthill J. H. Charleston M. A. (2013). A simple model explains the dynamics of preferential host switching among mammal RNA viruses. Evolution: International Journal of Organic Evolution, 67, 980-990.

D’Bastiani, E., Princepe, D., Campião, K. M., Marquitti, F. M., Boeger, W. A., & Araujo, S. L. (2022). Effect of host-switching on the eco-evolutionary patterns of parasites. *In review*.

da Graça RJ, Oda FH, Lima FS, Guerra V, Gambale PG and Takemoto RM (2017) Metazoan endoparasites of 18 anuran species from the mesophytic semideciduous Atlantic Forest in southern Brazil. Journal of Natural History 51, 705–729.

Dallas, T. A., Han, B. A., Nunn, C. L., Park, A. W., Stephens, P. R., & Drake, J. M. (2019). Host traits associated with species roles in parasite sharing networks. Oikos, 128(1), 23-32.

Damas J., Hughes G. M., Keough K. C., Painter C. A., Persky N. S., Corbo M. Lewin H. A. 2020. Broad host range of SARS-CoV-2 predicted by comparative and structural analysis of ACE2 in vertebrates. Proceedings of the National Academy of Sciences, 117, 22311-22322.

Davis, R.M., Smith, R.T., Madon, M.B. & Sitko-Cleugh, E. (2002) Flea, rodent and plague ecology at Chichupate Campground, Ventura County, California. Journal of Vector Ecology, 27, 107-127.

De Vienne D. M., Refrégier G., López-Villavicencio M., Tellier A., Hood M. E.  Giraud T. (2013). Cospeciation *vs* host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytologist, 198, 347-385.

Dearlove B. L., Frost S. D. (2015). Measuring asymmetry in time-stamped phylogenies. PLoS computational biology, 11(7), e1004312.

Diamond, J. (2002). Evolution, consequences and future of plant and animal domestication. Nature, 418(6898), 700-707.

Dominguez, M., de la Colina, M. A., Di Giacomo, A. G., Reboreda, J. C., & Mahler, B. (2015). Host switching in cowbird brood parasites: how often does it occur?. Journal of evolutionary biology, 28(6), 1290-1297.

Dowton M.  Austin A. D. (1995). Increased genetic diversity in mitochondrial genes is correlated with the evolution of parasitism in the Hymenoptera. Journal of Molecular Evolution, 41, 958-965.

Durden, L. A., & Kollars Jr, T. M. (1997). The fleas (Siphonaptera) of Tennessee. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(1), 13-22.

Ehrlich, P. R., & Raven, P. H. (1964). Butterflies and plants: a study in coevolution. Evolution, 586-608.

Engelstädter J.  Fortuna N. Z. (2019). The dynamics of preferential host switching: Host phylogeny as a key predictor of parasite distribution. Evolution, 73, 1330-1340.

Erwin, T. L. (1985). The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. Taxonomy, phylogeny, and zoogeography of beetles and ants, 437-472.

Fallon S. M., Ricklefs R. E., Latta S. C., Bermingham E. (2004). Temporal stability of insular avian malarial parasite communities. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271(1538), 493-500.

Fecchio A., Wells K., Bell, J.A., Tkach V. V., Lutz H. L., Weckstein J. D. Clark N. J. (2019). Climate variation influences host specificity in avian malaria parasites. Ecology Letters, 22, 547-557.

Fenner, F., & Fantini, B. (1999). Biological control of vertebrate pests. CABI publishing.

Filion A., Doherty J. F., Poulin R., Godfrey S. S. (2022). Building a comprehensive phylogenetic framework in disease ecology. Trends in Parasitology.

Fontenot LW and Font WF (1996) Helminth parasites of four species of aquatic snakes from two habitats in southeastern Louisiana. Journal-Helminthological Society Washington 63, 66–75.

Fox J. Weisberg S. (2019). Nonlinear Regression, Nonlinear Least Squares, and Nonlinear Mixed Models in R. population, 150, 200.

Frost DR (2020) Amphibian species of the World 6.0, an Online Reference. New York: Darrel Frost and the American Museum of Natural History.

Frost S. D., Volz E. M. (2013). Modelling tree shape and structure in viral phylodynamics. Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1614), 20120208.

Gavrilets S. Hastings A. (1996). Founder effect speciation: a theoretical reassessment. The American Naturalist, 147, 466-491.

Gibert, C., Shenbrot, G. I., Stanko, M., Khokhlova, I. S., & Krasnov, B. R. (2021). Dispersal-based versus niche-based processes as drivers of flea species composition on small mammalian hosts: inferences from species occurrences at large and small scales. Oecologia, 197(2), 471-484.

Goldberg SR, Bursey CR, Caldwell JP and Shepard DB (2009) Gastrointestinal helminths of six sympatric species of Leptodactylus from Tocantins State, Brazil. Comparative Parasitology 76, 258–266.

Habermannová J., Bogusch P., Straka J. (2013). Flexible host choice and common host switches in the evolution of generalist and specialist cuckoo bees (Anthophila: Sphecodes). PLoS One, 8(5), e64537.

Habermannová, J., Bogusch, P., & Straka, J. (2013). Flexible host choice and common host switches in the evolution of generalist and specialist cuckoo bees (Anthophila: Sphecodes). PLoS One, 8(5), e64537.

Haddad CF and Prado CP (2005) Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. BioScience 55, 207–2017.

Haddad CF, Toledo LF, Prado CP, Loebmann D, Gasparini JL and Sazima I (2013) Guia dos anfíbios da Mata Atlântica: diversidade e biologia. São Paulo, Brazil: Anolis Books.

Hahn, B. H., Shaw, G. M., De, K. M., Cock, & Sharp, P. M. (2000). AIDS as a zoonosis: scientific and public health implications. Science, 287(5453), 607-614.

Harrison S, Ross SJ and Lawton JH (1992) Beta diversity on geographic gradients in Britain. Journal of Animal Ecology 1, 151–158.

Hartig, F., & Hartig, M. F. (2017). Package ‘DHARMa’. R package.

Harvey, J. A., Ximénez de Embún, M. G., Bukovinszky, T., & Gols, R. (2012). The roles of ecological fitting, phylogeny and physiological equivalence in understanding realized and fundamental host ranges in endoparasitoid wasps. Journal of Evolutionary Biology, 25(10), 2139-2148.

Hay E. M., Poulin R., Jorge F. 2020. Macroevolutionary dynamics of parasite diversification: A reality check. Journal of Evolutionary Biology, 33(12), 1758-1769.

Hayward A., Poulin R. Nakagawa S. (2021). A broadscale analysis of host-symbiont cophylogeny reveals the drivers of phylogenetic congruence. Ecology Letters, 24, 1681–1696.

Hayward, A., Tsuboi, M., Owusu, C., Kotrschal, A., Buechel, S. D., Zidar, J., ... & Kolm, N. (2017). Evolutionary associations between host traits and parasite load: insights from Lake Tanganyika cichlids. Journal of Evolutionary Biology, 30(6), 1056-1067.

Helmus, M. R., Bland, T. J., Williams, C. K., & Ives, A. R. (2007). Phylogenetic measures of biodiversity. The American Naturalist, 169(3), E68-E83.

Higgs, P. G., & Derrida, B. (1991). Stochastic models for species formation in evolving populations. Journal of Physics A: Mathematical and General, 24(17), L985.

Hoberg, E. P., & Brooks, D. R. (2008). A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. Journal of Biogeography, 35(9), 1533-1550.

Hoberg, E. P., & Brooks, D. R. (2010). Beyond vicariance: integrating taxon pulses, ecological fitting, and oscillation in evolution and historical biogeography. The biogeography of host-parasite interactions, 7, 20.

Hoberg, E. P., & Brooks, D. R. (2013). 14 Episodic processes, invasion and faunal mosaics in evolutionary and ecological time. The balance of nature and human impact, 199.

Holmes, B. E. (2003). Ecology and persistence of sylvatic plague in Phillips County Montana.

Holmes, E. C. (2022). COVID-19—lessons for zoonotic disease. Science. Vol 375(6585) 1114-1115.

Huang, S., Bininda-Emonds, O. R., Stephens, P. R., Gittleman, J. L., & Altizer, S. (2014). Phylogenetically related and ecologically similar carnivores harbour similar parasite assemblages. Journal of Animal Ecology, 83(3), 671-680.

Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press (MPB-32).

Hudson, P. J., Rizzoli, A., Grenfell, B. T., Heesterbeek, H., & Dobson, A. P. (Eds.). (2002). The ecology of wildlife diseases (pp. 1-5). Oxford: Oxford University Press.

Imrie R. M., Roberts K. E. Longdon B. (2021). Between virus correlations in the outcome of infection across host species: Evidence of virus by host species interactions. Evolution letters, 5, 472-483.

Janz, N., & Nylin, S. (2008). The oscillation hypothesis of host-plant range and speciation. Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects, 2008, 203-215.

Janzen, D. H. (1985). On ecological fitting.

JANZEN, Daniel H. When is it coevolution? 1980.

Jaramillo M. Rivera-Parra J. L. 2018. Host-Switching: How It Starts. In Disease Ecology. Springer, Cham, pp. 139-156.

Jetz W and Pyron RA (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life.

Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. (2004). The scaling of animal space use. Science, 306(5694), 266-268.

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. Ecology, 90(9), 2648-2648.

Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. Nature, 451(7181), 990-993.

Kembel S, Cowan P, Helmus M, Cornwell W, Morlon H, Ackerly D, Blomberg SP and Webb C (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics (Oxford, England) 26, 1463–1464.

Kembel, S. W., & Kembel, M. S. W. (2014). Package ‘picante’. R Foundation for Statistical Computing, Vienna, Austria: https://cran. r-project. org/web/packages/picante/picante. pdf.[Google Scholar].

Kiffner, C., Stanko, M., Morand, S., Khokhlova, I. S., Shenbrot, G. I., Laudisoit, A., ... & Krasnov, B. R. (2014). Variable effects of host characteristics on species richness of flea infracommunities in rodents from three continents. Parasitology Research, 113(8), 2777-2788.

Kolbe J. J., Glor R. E., Rodríguez Schettino L., Lara A. C., Larson A., Losos J. B. (2004). Genetic variation increases during biological invasion by a Cuban lizard. Nature, 431(7005), 177-181.

Kollars Jr, T. M., Durden, L. A., & Oliver Jr, J. H. (1997). Fleas and lice parasitizing mammals in Missouri. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(2), 125-132.

Korallo-Vinarskaya NP, Vinarski MV, Khokhlova IS and Krasnov BR (2013) Body size and coexistence in gamasid mites parasitic on small mammals: null model analyses at three hierarchical scales. Ecography 36, 508–517.

Krasnov B, Fortuna M, Mouillot D, Khokhlova I, Shenbrot G and Poulin R (2012) Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. The American Naturalist 179, 501–511.

Krasnov B. R., Burdelova N. V., Khokhlova I. S., Shenbrot G. I., Degen A. (2005). Larval interspecific competition in two flea species parasitic on the same rodent host. Ecological Entomology, 30(2), 146-155.

Krasnov B. R., Spickett A., Junker K., Van der Mescht L., Matthee S. (2021). Functional and phylogenetic uniqueness of helminth and flea assemblages of two South African rodents. International journal for parasitology, 51(10), 865-876.

Krasnov, B. R., Shenbrot, G. I., & Khokhlova, I. S. (2015b). Historical biogeography of fleas: the former Bering Land Bridge and phylogenetic dissimilarity between the Nearctic and Palearctic assemblages. Parasitology research, 114( 5), 1677-1686.

Krasnov, B. R., Shenbrot, G. S., van der Mescht, L., Warburton, E. M., & Khokhlova, I. S. (2019). Phylogenetic and compositional diversity are governed by different rules: a study of fleas parasitic on small mammals in four biogeographic realms. Ecography, 42(5), 1000-1011.

Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S. & Degen, A.A. (2016). Trait-based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. Oikos, 125, 29-38. Accession number: EDB_10.1111/oik.02178

Kuzmin Y., de Vasconcelos Melo F. T.  Dos Santos J. N. (2014). A new species of *Serpentirhabdias* Tkach, Kuzmin Snyder, 2014 (Nematoda: Rhabdiasidae) parasitic in the brown ground snake *Atractus major* Boulenger (Reptilia: Serpentes: Dipsadidae) in Brazil. Systematic Parasitology, 89, 101-106.

Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. Evolution, 1210-1226.

Light J. E.  Hafner M. S. (2007). Cophylogeny and disparate rates of evolution in sympatric lineages of chewing lice on pocket gophers. Molecular phylogenetics and evolution, 45, 997-1013.

Lile NK (1998) Alimentary tract helminths of four pleuronectid flatfish in relation to host phylogeny and ecology. Journal of Fish Biology 53, 945–953.

Linsdale, J. M., Davis, B. S., & Davis, B. S. (1956). Taxonomic Appraisal and Occurence of Fleas at the Hastings Reservation in Central California, by Jean M. Linsdale and Betty S. Davis. University of California Press.

Lott, D. F. (1991). Intraspecific variation in the social systems of wild vertebrates (Vol. 2). Cambridge University Press.

Mácová, A., Hoblíková, A., Hypša, V., Stanko, M., Martinů, J., & Kvičerová, J. (2018). Mysteries of host switching: Diversification and host specificity in rodent-coccidia associations. Molecular phylogenetics and evolution, 127, 179-189.

Maestri R and Patterson BD (2016) Patterns of species richness and turnover for the South American rodent fauna. PLoS One 11, e0151895.

Maestri R, Shenbrot GI and Krasnov BR (2017) Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. Journal of Biogeography 44, 1880–1890.

Main, A. J. (1983). Fleas (Siphonaptera) on small mammals in Connecticut, USA. Journal of Medical Entomology, 20(1), 33-39.

Manzo F., Peliti L. (1994). Geographic speciation in the Derrida-Higgs model of species formation. Journal of Physics A: Mathematical and General, 27(21), 7079.

Marquitti F. M. D., Fernandes L. D., de Aguiar M. A. M. (2020). Allopatry increases the balance of phylogenetic trees during radiation under neutral speciation. Ecography, 43(10), 1487-1498.

Martins-Sobrinho PM, Silva WGDO, Santos EGD, Moura GJBD and Oliveira JBD (2017) Helminths of some tree frogs of the families Hylidae and Phyllomedusidae in an Atlantic rainforest fragment, Brazil. Journal of Natural History 51, 1639–1648.

Mayr E. 1999. Systematics and the origin of species, from the viewpoint of a zoologist. Harvard University Press, pp. 372.

McLennan, D. A., & Brooks, D. R. (2002). Complex histories of speciation and dispersal in communities: a re‐analysis of some Australian bird data using BPA. Journal of Biogeography, 29(8), 1055-1066.

Meinilä, M., Kuusela, J., Ziętara, M. S., & Lumme, J. (2004). Initial steps of speciation by geographic isolation and host switch in salmonid pathogen Gyrodactylus salaris (Monogenea: Gyrodactylidae). International Journal for Parasitology, 34(4), 515-526.

Milgroom, M. G., Wang, K., Zhou, Y., Lipari, S. E., & Kaneko, S. (1996). Intercontinental population structure of the chestnut blight fungus, Cryphonectria parasitica. Mycologia, 88(2), 179-190.

Moran, N. A. (1988). The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. The American Naturalist, 132(5), 681-706.

Morlan, H. B. (1955). Mammal fleas of Santa Fe County, New Mexico. Texas Reports on Biology and Medicine, 13(1), 93-125.

Mouritsen K and Poulin R (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. Parasitology 124, 101–117.

Müller, M.I., Morais, D.H., Costa‐Silva, G.J., Aguiar, A., Avila, R.W. & da Silva, R.J. (2018). Diversity in the genus Rhabdias (Nematoda, Rhabdiasidae): Evidence for cryptic speciation. Zoologica Scripta, 47, 595-607.

Nylin S., Agosta S., Bensch S., Boeger W. A., Braga M. P., Brooks D. R. Janz, N. (2018). Embracing colonizations: a new paradigm for species association dynamics. Trends in ecology evolution, 33, 4-14.

Nylin, S., Slove, J., & Janz, N. (2014). Host plant utilization, host range oscillations and diversification in nymphalid butterflies: a phylogenetic investigation. Evolution, 68(1), 105-124.

Oksanen J, Guillaume Blanchet F, Friendly F, Kindt R, Legendre P, McGlinn D, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens H, Szoecs E and Wagner H (2019) vegan: Community Ecology Package. R package version 2.5-6.

Oksanen J., Blanchet F. G., Kindt R., Legendre P., Minchin P. R., O'hara R. B. Oksanen M. J. (2013). Package 'vegan'. Community ecology package, version, 2, 1-295.

Olival, K. J., Hosseini, P. R., Zambrana-Torrelio, C., Ross, N., Bogich, T. L., & Daszak, P. (2017). Host and viral traits predict zoonotic spillover from mammals. Nature, 546(7660), 646-650.

Page, R. D. (Ed.). (2003). Tangled trees: phylogeny, cospeciation, and coevolution. University of Chicago Press. Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics, 35(3), 526-528.

Pärtel, M., Szava-Kovats, R., & Zobel, M. (2013). Community completeness: linking local and dark diversity within the species pool concept. Folia Geobotanica, 48(3), 307-317.

Pilosof, S., Morand, S., Krasnov, B. R., & Nunn, C. L. (2015). Potential parasite transmission in multi-host networks based on parasite sharing. PloS one, 10(3), e0117909.

Pool TK, Grenouillet G and Villéger S (2014) Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. Diversity and Distributions 20, 1235–1244.

Poulin R (2004) Parasites and the neutral theory of biodiversity. Ecography 27, 119–123.

Poulin R (2007) Are there general laws in parasite ecology? Poulin R and Morand S (2000) The diversity of parasites. The Quarterly Review of Biology 75, 277–293.

Poulin R., Morand S. (2000). The diversity of parasites. The quarterly review of biology, 75(3), 277-293.

Previtali, M. A., Lehmer, E. M., Pearce-Duvet, J. M., Jones, J. D., Clay, C. A., Wood, B. A., ... & Dearing, M. D. (2010). Roles of human disturbance, precipitation, and a pathogen on the survival and reproductive probabilities of deer mice. Ecology, 91(2), 582-592.

Qian H, Ricklefs RE and White PS (2005) Beta diversity of angiosperms in temperate floras of Eastern Asia and eastern North America. Ecology Letters 8, 15–22.

R Core Team (2020) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). Methods in ecology and evolution, (2), 217-223.

Sackin M. J. (1972). “Good” and “bad” phenograms. Systematic Biology, 21(2), 225-226.

Sanaei E., Charlat S., Engelstädter J. (2021). *Wolbachia* host shifts: routes, mechanisms, constraints and evolutionary consequences. Biological Reviews, 96(2), 433-453.

Schwarzenberger, T., & Klingel, H. (1995). Telemetrische Untersuchungen zur Raumnutzung und Aktivitätsrhythmik freilebender Gelbhalsmäuse Apodemus flavicollis Melchior, 1834. Zeitschrift für Säugetierkunde, 60(1), 20-32.

Stavtseva, N. A., Fielden, L. J., Khokhlova, I. S., Warburton, E. M., van der Mescht, L.,& Krasnov, B. R. (2021). Colonization of a novel host by fleas: changes in egg production and egg size. Parasitology Research, 120(2), 451-459.

Streicker D. G., Turmelle A. S., Vonhof M. J., Kuzmin I. V., McCracken G. F. Rupprecht C. E. (2010). Host phylogeny constrains cross-species emergence and establishment of rabies virus in bats. Science, 329, 676-679.

Svenning J-C and Skov F (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10, 453–460.

Team R. (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. Available at: https://www.rstudio.com/. Last accessed 05 april 2022.

Team R. C. (2020). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria: Available at: https://www. R-project. org/. Last accessed 05 april 2022.

Thompson, J. N. (2005). The geographic mosaic of coevolution. University of Chicago Press.

Thrush SF, Hewitt JE, Cummings VJ, Norkko A and Chiantore M (2010) β-Diversity and species accumulation in Antarctic coastal benthos: influence of habitat, distance and productivity on ecological connectivity. PLoS One 5, e11899.

Toledo GM, Schwartz HO, Nomura HAQ, Aguiar A, Velota RAMV, Da Silva RJ and Anjos LA (2018) Helminth community structure of 13 species of anurans from Atlantic rainforest remnants, Brazil. Journal of Helminthology 92, 438–444.

UlrichWand Gotelli NJ (2007) Null model analysis of species nestedness patterns. Ecology 88, 1824–1831.

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS biology, 17(12), e3000494.

Van Der Mescht L, Krasnov BR, Matthee CA and Matthee S (2016) Community structure of fleas within and among populations of three closely related rodent hosts: nestedness and beta-diversity. Parasitology 143, 1268–1278. Wright DH and Reeves JH (1992) On the meaning and measurement of nestedness of speciesassemblages. Oecologia 92, 416–428.

Watve, M. G., & Sukumar, R. (1995). Parasite abundance and diversity in mammals: correlates with host ecology. Proceedings of the National Academy of Sciences, 92(19), 8945-8949.

Whitaker, J. O. (1982). Ectoparasites of mammals of Indiana. Monograph/Indiana Academy of Science (USA).

Wiegmann, B. M., Mitter, C., & Farrell, B. (1993). Diversification of carnivorous parasitic insects: extraordinary radiation or specialized dead end? The American Naturalist, 142(5), 737-754.

Wille, M., Geoghegan, J. L., & Holmes, E. C. (2021). How accurately can we assess zoonotic risk?. PLoS biology, 19(4), e3001135.

Wolff, J. O. (1993). Why are female small mammals territorial? Oikos, 364-370. Woolhouse, M. E., Haydon, D. T., & Antia, R. (2005). Emerging pathogens: the epidemiology and evolution of species jumps. Trends in ecology & evolution, 20(5), 238-244.

Yule U. G. (1925). A mathematical theory of evolution, based on the conclusions of Dr. JC Willis, FRS. Philosophical Transactions of the Royal Society of London Series B, 213, 21-87.

Zhu, Q., Hastriter, M. W., Whiting, M. F., & Dittmar, K. (2015). Fleas (Siphonaptera) are Cretaceous, and evolved with Theria. Molecular Phylogenetics and Evolution, 90, 129-139.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. Methods in ecology and evolution, 1(1), 3-14.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R (Vol. 574). New York: Springer.

[Dataset] Allred, D. M. (1968) Fleas of the National Reactor Testing Station. Great Basin Naturalist, 28, 73-87.

[Dataset] Amin, O. M. (1976). Host Associations and Seasonal Occurrence of Fleas from Southeastern Wisconsin Mammals, with Observations on Morphologic Variations1. Journal of Medical Entomology, 13(2), 179–192. doi:10.1093/jmedent/13.2.179.

[Dataset] Badets M., Whittington I., Lalubin F., Allienne J. F., Maspimby J. L., Bentz S. Verneau O. (2011). Correlating early evolution of parasitic platyhelminths to Gondwana breakup. Systematic Biology, 60, 762-781. Accession number: EDB_10.1093/sysbio/syr078.

[Dataset] Becker, D.J., Streicker, D.G. & Altizer, S. (2018). Using host species traits to understand the consequences of resource provisioning for host–parasite interactions. Journal of Animal Ecology, 87, 511-525. Accession number: EDB_10.1111/1365-2656.12765.

[Dataset] Davis, R.M., Smith, R.T., Madon, M.B. & Sitko-Cleugh, E. (2002) Flea, rodent and plague ecology at Chichupate Campground, Ventura County, California. Journal of Vector Ecology, 27, 107-127.

[Dataset] Doña, J., Sweet, A.D., Johnson, K.P., Serrano, D., Mironov, S. & Jovani, R. (2017). Cophylogenetic analyses reveal extensive host-shift speciation in a highly specialized and host-specific symbiont system. Molecular phylogenetics and evolution, 115, 190-196. Accession number: EDB_10.1016/j.ympev.2017.08.005.

[Dataset] Durden, L. A., & Kollars Jr, T. M. (1997). The fleas (Siphonaptera) of Tennessee. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(1), 13-22.

[Dataset] Holmes, B. E. (2003). Ecology and persistence of sylvatic plague in Phillips County Montana.

[Dataset] Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A. (2009). PanTHERIA: a species‐level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090‐184. Ecology, 90(9), 2648-2648.

[Dataset] Kollars Jr, T. M., Durden, L. A., & Oliver Jr, J. H. (1997). Fleas and lice parasitizing mammals in Missouri. Journal of Vector Ecology: Journal of the Society for Vector Ecology, 22(2), 125-132.

[Dataset] Krasnov, B.R., Shenbrot, G.I., Khokhlova, I.S. & Degen, A.A. (2016). Trait-based and phylogenetic associations between parasites and their hosts: a case study with small mammals and fleas in the Palearctic. Oikos, 125, 29-38. Accession number: EDB_10.1111/oik.02178.

[Dataset] Linsdale, J. M., Davis, B. S., & Davis, B. S. (1956). Taxonomic Appraisal and Occurence of Fleas at the Hastings Reservation in Central California, by Jean M. Linsdale and Betty S. Davis. University of California Press.

[Dataset] Main, A. J. (1983). Fleas (Siphonaptera) on small mammals in Connecticut, USA. Journal of Medical Entomology, 20(1), 33-39.

[Dataset] Morlan, H. B. (1955). Mammal fleas of Santa Fe County, New Mexico. Texas Reports on Biology and Medicine, 13(1), 93-125.

[Dataset] Müller M. I., Morais D. H., Costa-Silva G. J., Aguiar A., Avila R.W. da Silva R. J. (2018). Diversity in the genus Rhabdias (Nematoda, Rhabdiasidae): Evidence for cryptic speciation. Zoologica Scripta, 47, 595-607. Accession number: EDB_10.1111/zsc.12304.

[Dataset] Patella, L., Brooks, D.R. & Boeger, W.A. (2017). Phylogeny and ecology illuminate the evolution of associations under the Stockholm paradigm: Aglaiogyrodactylus spp. (Platyhelminthes, Monogenoidea, Gyrodactylidae) and species of Loricariidae (Actinopterygii, Siluriformes). Vie Et Milieu, 67, 91-102. Accession number: EDB_20183235432.

[Dataset] Reed, D.L., Light, J.E., Allen, J.M. & Kirchman, J.J. (2007). Pair of lice lost or parasites regained: the evolutionary history of anthropoid primate lice. Bmc Biology, 5, 1-11. Accession number: EDB_10.1186/1741-7007-5-7.

[Dataset] Whitaker, J. O. (1982). Ectoparasites of mammals of Indiana. Monograph/Indiana Academy of Science (USA).

[Dataset] Willkens, Y., Furtado, A.P., Dos Santos, J.N. & de Vasconcelos Melo, F.T. (2021). Do host habitat use and cospeciation matter in the evolution of Oswaldocruzia

(Nematoda, Molineidae) from neotropical amphibians? Journal of Helminthology, 95, e33. Accession number: EDB_10.1017/S0022149X21000250.

# Apêndice I

## Atividades complementares a tese

Para mais informações sobre as atividades realizadas durante o meu doutorado acesse: https://elviradbastiani.wixsite.com/ecoevo (aba meu doutorado).