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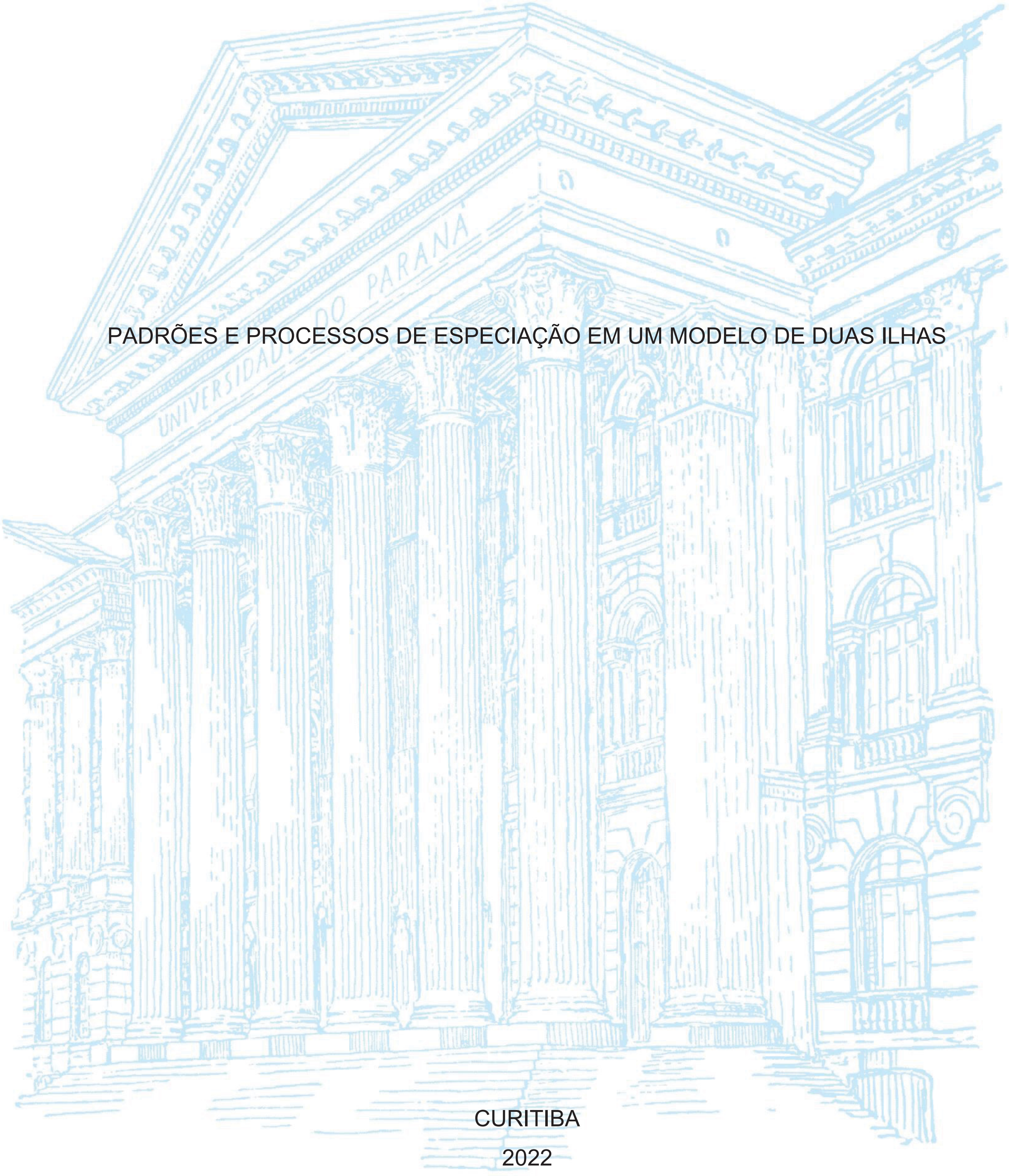

PADRÕES E PROCESSOS DE ESPECIAÇÃO EM UM MODELO DE DUAS ILHAS

CURITIBA
2022

SIMONE CZARNOBAI

PADRÕES E PROCESSOS DE ESPECIAÇÃO EM UM MODELO DE DUAS ILHAS

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: Profª. Drª. Sabrina Borges Lino Araujo

Coorientador: Prof. Dr. Walter Antonio Boeger

CURITIBA

2022

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

Czarnobai, Simone.
Padrões e processos de especiação em um modelo de duas ilhas. / Simone Czarnobai. – Curitiba, 2022.
1 recurso on-line : PDF.

Orientadora: Sabrina Borges Lino Araújo.
Coorientador: Walter Antônio Boeger.

Tese (Doutorado) – Universidade Federal do Paraná, Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação.

1. Migração. 2. Especiação Genética. 3. Habitat (Ecologia). 4. Espécies. 5. Nível do mar. 6. Geografia ambiental. I. Título. II. Araújo, Sabrina Borges Lino. III. Boeger, Walter Antônio. IV. Universidade Federal do Paraná. Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação.

Bibliotecária: Rosilei Vilas Boas CRB-9/939

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SETOR DE CIÊNCIAS BIOLÓGICAS
UNIVERSIDADE FEDERAL DO PARANÁ
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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 **SIMONE CZARNOBAI** intitulada: **Padrões e processos de especiação em um modelo de duas ilhas**, 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.

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CURITIBA, 26 de Abril de 2022.

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29/04/2022 15:14:16.0
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Avaliador Interno (UNIVERSIDADE FEDERAL DO PARANÁ)

Dedico essa tese aos meus pais, que não tiveram outra escolha a não ser renunciar aos estudos para se dedicar ao trabalho, filhos e casa e que não mediram esforços para que eu conseguisse chegar até aqui.

AGRADECIMENTOS

À minha orientadora professora Sabrina Araujo, pela oportunidade que me deu, por me orientar com tanta dedicação e paciência ao longo desses 5 anos, pela compreensão e apoio em situações particulares, por todo incentivo – essencial para que eu não desistisse – e por me receber tão bem na sua casa. Meus sinceros agradecimentos. Um ser humano incrível, uma pesquisadora de alta performance e mãe da Anita e do Pedro. Será sempre exemplo e inspiração pra mim.

Ao meu coorientador professor Walter Borges, pela essencial contribuição no desenvolvimento da base conceitual dessa Tese e pelas pertinentes discussões sobre evolução.

Ao professor Rodrigo Caetano por guiar meus primeiros passos na programação com toda dedicação e paciência do mundo.

Ao professor Marcus de Aguiar e seu grupo de pesquisa: Flávia Marquitti, Thiago Pradella e, em especial, à Débora Princepe, pela inestimável contribuição no desenvolvimento dessa Tese, principalmente no Capítulo I.

Aos professores do PPGECO, por todo conhecimento compartilhado, importante para minha formação como Ecóloga.

Aos colegas de turma, pela amizade, convivência e trocas, em especial à Raquel Rodrigues, Vanessa Vlnieska, Daiane Pilatti por terem me acolhido em suas casas quando eu não tinha lugar para ficar em Curitiba.

Aos amigos Mariana Martello, Tobias de Morais e Luciana Colombo pelo companheirismo, incentivo e apoio ao longo desses anos tanto na vida acadêmica quanto pessoal. Tenho boas histórias para contar às minhas filhas. Mari, muito obrigada por sempre me fazer lembrar das minhas qualidades e potencialidades, você é luz.

Aos colegas do Laboratório de Interações Biológicas, pelas trocas de experiência e conhecimento. Especialmente aos amigos Marcelo Borges, Angie Souza e Elvira de Bastiani, sou muito grata por toda ajuda e suporte que me deram, principalmente com os scripts do R e com os infinitos erros do FORTRAN.

Aos meus pais, Sonia e Rafael, por me mostrarem o valor e o poder de transformação da educação e por todo o esforço que fizeram para que eu pudesse me dedicar aos estudos e chegar até aqui. Essa conquista é mérito de vocês também.

Aos meus familiares Edson, Vanilde e Daniel e à minha amiga Keli Risso, por torcerem tanto por mim. Como foi importante, recarregar as energias na companhia de vocês e receber tanto carinho em cada passagem por Beltrão durante essa jornada.

Ao meu companheiro de vida Antony, por todos esses anos de parceria e por sempre segurar as pontas para que eu conseguisse chegar até aqui.

Às minhas filhas gêmeas Laura e Antonella, que chegaram no meio do doutorado e início da pandemia, por me acompanharem, ainda na barriga, em simpósios e reuniões, e pelas incontáveis mamadas que passamos assistindo a aulas e a palestras online e escrevendo essa Tese. Queridas, mamãe é muito, muito grata por tê-las como filhas. Amo vocês duas, infinitamente e incondicionalmente.

À Universidade Federal do Paraná e ao Programa de Pós-Graduação em Ecologia e Conservação, pelo apoio ao projeto e, em especial, ao Colegiado do Programa, sempre solícito com os estudantes, incluindo eu, principalmente depois que descobri a gravidez.

E, finalmente, à CAPES, pelo imprescindível auxílio financeiro durante o desenvolvimento da Tese.

Há uma força motriz mais poderosa que o vapor, a eletricidade e a energia atômica:

a VONTADE.

(Albert Einstein)

RESUMO

O isolamento geográfico é um mecanismo central na especiação. No entanto, o completo isolamento entre as populações é uma condição nem sempre atendida devido à escassez de características geográficas capazes de interromper totalmente o fluxo gênico pelo tempo necessário para se completar a especiação. Embora a migração possa dificultar a especiação porque mantém o fluxo gênico, ela promove a colonização de novas áreas podendo aumentar a especiação devido a introdução de novidades genéticas nas populações semi-isoladas. Assim, o papel da migração na especiação é controverso e o objetivo deste estudo foi entender como a migração contínua e intermitente afetam a especiação. O primeiro capítulo usou um modelo neutro de especiação de duas ilhas com migração contínua e avaliou padrões de diversidade em função da probabilidade de migração, tamanho da população e número de genes envolvidos no isolamento reprodutivo (tamanho do genoma). Para genomas pequenos, baixos níveis de migração induzem especiação nas ilhas que de outra forma não ocorreriam. A diversidade, no entanto, cai drasticamente para uma única espécie que habita as duas ilhas à medida que a probabilidade de migração aumenta. Para genomas grandes, a especiação simpátrica ocorre mesmo quando as ilhas estão estritamente isoladas. Então a riqueza de espécies por ilha aumenta com a probabilidade de migração, mas o número total de espécies diminui à medida que se tornam cosmopolitas. Para cada tamanho de genoma e população existe uma intensidade de migração ótima que maximiza o número de espécies. Discutimos os modos observados de especiação induzidos pela migração e como eles aumentam a riqueza de espécies no sistema insular enquanto promovem a assimetria entre as ilhas e dificultam o endemismo. O segundo capítulo também usou um modelo neutro de especiação de duas ilhas, mas neste a migração não foi contínua, e sim periódica, com fases cíclicas de isolamento e conexão (barreiras intermitentes), que seguem a flutuação histórica do nível do mar. Os resultados revelaram que barreiras intermitentes promovidas por ciclos de isolamento e conexão potencializaram os eventos de especiação. E, ainda, as migrações de baixa intensidade durante as fases de conexão são responsáveis por introduzir novidades genéticas e acelerar o processo de especiação, aumentando a riqueza de espécies. Mostramos pulsos de diversificação condizentes com a teoria de pulso de táxon e discutimos nossos resultados com estudos empíricos de diferentes grupos de espécies que também tiveram histórico de barreiras intermitentes durante sua evolução e que apesar de terem passado pelas mesmas oscilações climáticas globais, a taxa de diversificação não foi a mesma para todos eles.

Palavras-chave: Isolamento geográfico. Migração. Especiação. Riqueza de espécies. Flutuação do nível do mar.

ABSTRACT

Geographic isolation is a central mechanism in speciation. However, complete isolation between populations is a condition not always met due to the scarcity of geographic features capable of completely interrupting gene flow for the time necessary to complete speciation. Although migration can make speciation difficult because it maintains gene flow, it promotes the colonization of new areas and can increase speciation due to the introduction of genetic novelties in semi-isolated populations. Thus, the role of migration in speciation is controversial and the aim of this study was to understand how continuous and intermittent migration affect speciation. The first chapter used a two-island neutral model of speciation with continuous migration and study diversity patterns as a function of the migration probability, population size, and the number of genes involved in reproductive isolation (genome size). For small genomes, low levels of migration induce speciation on the islands that otherwise would not occur. Diversity, however, drops sharply to a single species inhabiting both islands as the migration probability increases. For large genomes, sympatric speciation occurs even when the islands are strictly isolated. Then species richness per island increases with the probability of migration, but the total number of species decreases as they become cosmopolitan. For each genome and population size, there is an optimal migration intensity for each population size that maximizes the number of species. We discuss the observed modes of speciation induced by migration and how they increase species richness in the insular system while promoting asymmetry between the islands and hindering endemism. The second chapter also used a two-island neutral model of speciation, but in this one the migration was not continuous, but periodic, with cyclic phases of isolation and connection (intermittent barriers), which follow the historical of sea-level fluctuation. The results revealed that intermittent barriers promoted by isolation and connection cycles potentiated speciation events. Furthermore, low-intensity migrations during the connection phases are responsible for introducing genetic novelties and accelerating the speciation process, increasing species richness. We show diversification pulses consistent with the taxon pulse theory and discuss our results with empirical studies of different groups of species that also had a history of intermittent barriers during their evolution and that despite having gone through the same global climatic oscillations, the rate of diversification was not the same for all of them.

Keywords: Geographic isolation. Migration. Speciation. Species richness. Sea-level fluctuation.

SUMÁRIO

INTRODUÇÃO GERAL

Considerando o contexto geográfico, a especiação tradicionalmente é dividida em três categorias: alopátrica, parapátrica e simpátrica. Esses diferentes modos de especiação estão associados a diferentes níveis de fluxo gênico entre as populações durante o processo de divergência (Coyne e Orr, 2004). Na especiação alopátrica, o fluxo gênico entre as populações é totalmente interrompido devido a alguma barreira que impede a migração. Então, as populações originais ficam subdivididas e isoladas podendo acumular diferenças genéticas e, eventualmente, levar à especiação. Se as diferenças genéticas acumuladas durante o isolamento forem suficientes, o isolamento reprodutivo será completo e as populações não se fundirão caso restabelecerem o contato (Mayr, 1963). Esse é o clássico caso que Bush (1975) denominou de especiação alopátrica por subdivisão. No entanto, a especiação alopátrica pode ocorrer também por efeito fundador (Bush, 1975). Nesse caso, uma nova população é estabelecida por um pequeno número de indivíduos fundadores provenientes de uma grande população que colonizam a nova área (Mayr, 1963). Na especiação parapátrica, a sobreposição parcial de populações resulta em uma redução, mas não na eliminação da migração. Ela ocorre sempre que as espécies evoluem como populações contínuas, gerando um padrão de isolamento por distância, o que pode resultar em populações em diferentes lados dos clines evoluindo para espécies isoladas reprodutivamente (Bush, 1975; Endler, 1973). Na especiação simpátrica, o fluxo gênico é mantido ao longo do processo de divergência. Neste caso, a seleção divergente de base ecológica associada a condições ambientais bióticas ou abióticas ou seleção sexual é maior (mais forte) do que o nível de fluxo gênico, permitindo que as populações se diferenciem na ausência de isolamento geográfico (Bush, 1975; Mayr, 1963).

Embora a especiação alopátrica seja a mais comum e mais documentada na natureza (Coyne e Orr, 2004; Fitzpatrick et al 2009), ela exige o completo isolamento geográfico entre as populações. No entanto, essa condição nem sempre é atendida devido a escassez de características geográficas capazes de interromper totalmente o fluxo gênico pelo tempo necessário para se completar a especiação (Ziwen et al 2019). Contudo, é comum haver populações semi-isoladas, que apresentam algum grau de fluxo gênico por meio da migração. Nesses casos, o papel da migração na especiação é controverso: promove a colonização de novas áreas, favorecendo a diferenciação, mas, ao mesmo tempo, também promove o fluxo gênico, o qual atua inibindo a divergência da população (Winker, 2000). Já foi visto que a migração de um ou poucos indivíduos por geração entre duas populações é indicado como suficiente para manter o fluxo gênico e evitar a diversificação genética (Slatkin, 1987) e, por isso, tem sido reportada como um impedimento para a especiação (Montgomery, 1985). No entanto, tem sido mostrado que uma rápida especiação é possível mesmo quando subpopulações trocam vários indivíduos por geração (Gavrilets et al 2000). Adicionalmente, migrações intermitentes podem ocorrer quando barreiras geográficas são quebradas, por exemplo quando o nível do mar baixou mais de 120m na última máxima glacial do Pleistoceno e conectou populações insulares previamente isoladas por meio de pontes terrestres (Hewitt, 2000). Eventos cíclicos de isolamento e conexão são componentes dos pulsos de táxons.

Os pulsos de táxon contam a história adaptativa e geográfica de uma linhagem (Erwin, 1985). Os pulsos compreendem episódios alternados de expansão e isolamento bióticos, responsáveis por distribuições geográficas complexas (Erwin, 1979; 1985). Existem dois tipos de pulsos de táxons: os ecopulsos e os "*choropulsos"*. Os ecopulsos ocorrem em ambientes instáveis e são desencadeados por fatores ecológicos como a competição (antagonismo ou por recursos) e climáticos, que agem com rapidez e dureza sobre os táxons. Já os "*choropulsos"* são definidos como mudanças adaptativas lentas causadas por mudanças genéticas acumuladas devido à vicariância em habitats estáveis (Erwin, 1979). Os eventos climáticos do Pleistoceno são exemplos de ecopulsos enquanto o *rifting* da África e da América do Sul (separação das placas tectônicas destas regiões), que levou milhões de anos, ocasionou os "*choropulsos*" (Erwin, 1979).

Foi Erwin que, em 1979, utilizou pela primeira vez o termo pulso de táxon no seu trabalho com carabídeos. Essa ideia de pulsos já havia sido sugerida por outros autores que utilizaram outras denominações e, em seu trabalho, Erwin (1979) menciona Darlington (1943) como precursor da ideia e mais tarde o próprio Darlington (1970) refere-se aos pulsos como "turnos". De acordo com Erwin (1979), os pulsos também receberam as seguintes denominações: epacme por Haeckel (1866), anástrofes por Walther (1908), evolução quântica por Simpson (1944), mega-evolução por Carter (1951) e fases explosivas por Rensch (1959). Erwin (1979, 1985) também reconhece o pulso de táxon no trabalho de Eldredge e Gould (1972) sob o nome de equilíbrio pontuado. Apesar de antiga, a ideia dos pulsos ganhou destaque com as publicações de Erwin (1979; 1981; 1985). No entanto, poucos trabalhos posteriores fizeram referência à teoria de pulso de táxon na década de 1980. Na década de 90, destaca-se o trabalho de Liebherr e Hajek (1990), o qual fez uma importante revisão dos conceitos e testou a teoria de pulso de táxon. No entanto, os resultados não suportaram as ideias de Erwin e a teoria de pulso de táxon caiu em esquecimento, implicando baixo número de trabalhos publicados naquela década. O trabalho de Halas, Zamparo e Brooks (2005) fez ressurgir a discussão sobre a diversificação por pulso de táxon. Nesse trabalho, os autores propõem um protocolo para distinguir diversificação biótica por pulso de táxon da diversificação via vicariância. A partir de então, outros autores aplicam esse protocolo em seus estudos (e.g. Baggio et al 2017; Folinsbee e Brooks, 2007; Brooks e Ferrao, 2005). Além disso, o Paradigma de Estocolmo retomou fortemente as discussões acerca do pulso de táxon (Brooks e Hoberg, 2007).

Esta tese é resultado de um trabalho envolvendo modelagem matemática aplicada ao estudo de processos ecológicos e evolutivos ligados à especiação. O objetivo é compreender quais os fatores estão por trás do processo de especiação e como a migração contínua e intermitente afetam a especiação. Para alcançar este objetivo, criamos um modelo computacional capaz de combinar, de diferentes maneiras, um conjunto de parâmetros que atuam como nossas variáveis preditoras. Como variável resposta, temos o número de espécies geradas para cada cenário simulado computacionalmente. Esta tese está dividida em dois capítulos. No primeiro capítulo, usamos modelo neutro de especiação de duas ilhas com migração contínua para avaliar padrões de diversidade em função da probabilidade de migração, tamanho da população e número de genes envolvidos no isolamento reprodutivo (tamanho do genoma). O segundo capítulo também usamos um modelo neutro de especiação de duas ilhas, mas neste a migração não foi contínua, e sim periódica, com fases cíclicas de isolamento e conexão (barreiras intermitentes), que seguem a flutuação histórica do nível do mar.

REFERÊNCIAS

Albert, J. S., Schoolmaster, D. R., Tagliacollo, V., & Duke-Sylvester, S. M. (2017). Barrier displacement on a neutral landscape: Toward a theory of continental biogeography. *Systematic Biology*, *66*(2), 167–182. https://doi.org/10.1093/sysbio/syw080

Baggio, Rafael A., Stoiev, S. B., Spach, H. L., & Boeger, W. A. (2017). Opportunity and taxon pulse: the central influence of coastal geomorphology on genetic diversification and endemism of strict estuarine species. *Journal of Biogeography*, *44*(7), 1626–1639. https://doi.org/10.1111/jbi.12934

Baggio, R. A. (2016). *Desvendando a história antiga e recente de peixes neotropicais usando marcadores moleculares*. 129. https://doi.org/10.13140/RG.2.2.10627.91686

Baptestini, E. M., de Aguiar, M. A. M., & Bar-Yam, Y. (2013). Conditions for neutral speciation via isolation by distance. *Journal of Theoretical Biology*, *335*, 51–56. https://doi.org/10.1016/J.JTBI.2013.06.011

Bird MI, Taylor D, Hunt C. (2005). Palaeoenvironments of insu- lar Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? Quaternary Science Reviews, 24, 2228– 2242.

Bolnick, D. I., & Fitzpatrick, B. M. (2007). Sympatric Speciation: Models and Empirical Evidence. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 459–487. https://doi.org/10.1017/S1743921310002723

Costa, C. L. N., Lemos-Costa, P., Marquitti, F. M. D., Fernandes, L. D., Ramos, M. F., Schneider, D. M., Martins, A. B., & de Aguiar, M. A. M. (2018). Signatures of Microevolutionary Processes in Phylogenetic Patterns. *Systematic Biology*, *June*, 1–14. https://doi.org/10.1093/sysbio/syy049

Costa, C. L. N., Schneider, D. M., Ramos, M. F., & de Aguiar, M. A. M. (2017). *Constructing phylogenetic trees in individual based models*. http://arxiv.org/abs/1709.04416

Coyne J. A., Orr H. A. (2004). Speciation. Sunderland, MA: Sinauer Assoc. 545 pp.

Darwin C. (1859). The Origin of Species. John Murray, London

de Aguiar, M. A M, Baranger, M., Baptestini, E. M., Kaufman, L., & Bar-Yam, Y. (2009). Global patterns of speciation and diversity. *Nature*, *460*(7253), 384–387. https://doi.org/10.1038/nature08168

de Aguiar, Marcus A.M. (2017). Speciation in the Derrida-Higgs model with finite genomes and spatial populations. *Journal of Physics A: Mathematical and Theoretical*, *50*(8). https://doi.org/10.1088/1751-8121/aa5701

Erwin, T. L. (1979). Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In T. L. Erwin, G. E. Ball, & D. R. Whitehead (Eds.), *Carabid beetles: their evolution, natural history, and classification* (pp. 539–592). Dr W. Junk Publishers.

Erwin, T. L. (1981). Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. In G. Nelson & D. E. Rosen (Eds.), *Vicariance Biogeography: a critique* (pp. 159–196). New York, Columbia University Press.

Erwin, T. L. (1985). The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In *Taxonomy, phylogeny and zoogeography of beetles and ants* (Issue 1). https://doi.org/10.2165/11207260-000000000-00000

Fitzpatrick, B. M., Fordyce, J. A., & Gavrilets, S. (2009). Pattern, process and geographic modes of speciation. *Journal of Evolutionary Biology*, *22*(11), 2342–2347. https://doi.org/10.1111/j.1420-9101.2009.01833.x

Gavrilets, S. (2003). Perspective: Models of speciation - What have we learned in 40 years? *Evolution*, *57*(10), 2197–2215. https://doi.org/10.1111/j.0014-3820.2003.tb00233.x

Gavrilets, S. (2014). Models of speciation: Where are we now? *Journal of Heredity*, *105*(S1), 743–755. https://doi.org/10.1093/jhered/esu045

Gavrilets, S., Li, H., & Vose, M. D. (2000). Patterns of {Parapatric} {Speciation}. *Evolution*, *54*(4), 1126–1134. http://www.jstor.org.ezproxy.lib.uh.edu/stable/2640611

Guo, Y. Y., Luo, Y. B., Liu, Z. J., & Wang, X. Q. (2015). Reticulate evolution and sea-level fluctuations together drove species diversification of slipper orchids (Paphiopedilum) in South-East Asia. *Molecular Ecology*, *24*(11), 2838–2855. https://doi.org/10.1111/mec.13189

Higgs, P. G., & Derrida, B. (1991). Stochastic models for species formation in evolving populations. *Journal of Physics A: Mathematical and General*, *24*(17). https://doi.org/10.1088/0305-4470/24/17/005

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. https://doi.org/10.1111/j.1365-2699.2008.01951.x

Song, G., Qu, Y., Yin, Z., Li, S., Liu, N., & Lei, F. (2009). Phylogeography of the Alcippe morrisonia (Aves: Timaliidae): Long population history beyond late Pleistocene glaciations. *BMC Evolutionary Biology*, *9*(1), 1–11. https://doi.org/10.1186/1471-2148-9-143

Tschá, M. K., Baggio, R. A., Marteleto, F. M., Abilhoa, V., Bachmann, L., & Boeger, W. A. (2017). Sea-level variations have influenced the demographic history of estuarine and freshwater fishes of the coastal plain of Paraná, Brazil. *Journal of Fish Biology*, *90*(3), 968–979. https://doi.org/10.1111/jfb.13211

Turelli, M., Barton, N. H., & Coyne, J. A. (2001). Theory of Speciation. *Trends in Ecology & Evolution*, *16*(7), 330–343. http://tree.trends.com0169

You, Y., Sun, K., Xu, L., Wang, L., Jiang, T., Liu, S., Lu, G., Berquist, S. W., & Feng, J. (2010). Pleistocene glacial cycle effects on the phylogeography of the Chinese endemic bat species, Myotis davidii. *BMC Evolutionary Biology*, *10*(1). https://doi.org/10.1186/1471-2148-10-208

Zhang, H., Yan, J., Zhang, G., & Zhou, K. (2008). Phylogeography and demographic history of Chinese black-spotted frog populations (Pelophylax nigromaculata): Evidence for independent refugia expansion and secondary contact. *BMC Evolutionary Biology*, *8*(1), 1–16. https://doi.org/10.1186/1471-2148-8-21

CAPÍTULO I

Padrões de diversidade e processos de especiação em um sistema de duas ilhas com migração contínua

(Diversity patterns and speciation processes in a two-island system with continuous migration[1])

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[1] Os resultados apresentados aqui são parte do trabalho aceito para publicação na revista *Evolution.*

ABSTRACT

Geographic isolation is a central mechanism of speciation, but perfect isolation of populations is rare. Although speciation can be hindered if gene flow is large, intermediate levels of migration can enhance speciation by introducing genetic novelty in the semi-isolated populations or founding small communities of migrants. Here we consider a two-island neutral model of speciation with continuous migration and study diversity patterns as a function of the migration probability, population size, and the number of genes involved in reproductive isolation (genome size). For small genomes, low levels of migration induce speciation on the islands that otherwise would not occur. Diversity, however, drops sharply to a single species inhabiting both islands as the migration probability increases. For large genomes, sympatric speciation occurs even when the islands are strictly isolated. Then species richness per island increases with the probability of migration, but the total number of species decreases as they become cosmopolitan. For each genome size, there is an optimal migration intensity for each population size that maximizes the number of species. We discuss the observed modes of speciation induced by migration and how they increase species richness in the insular system while promoting asymmetry between the islands and hindering endemism.

Keywords: Continuous migration, speciation with gene flow, neutral model, island biogeography.

INTRODUCTION

Geography plays a central role in speciation. The isolation of populations imposed by geographic barriers, allopatry, is indeed the most straightforward process of diversification (Coyne and Orr 2004; Fitzpatrick et al. 2009): when isolation is complete, gene flow is interrupted, and mutations accumulated in individuals of one group are not shared with individuals of the other group, increasing the genetic discrepancies between the populations and eventually leading to reproductive isolation. Speciation in the presence of gene flow, however, is also very frequent, occurring when isolation is partial or even when geographic barriers are completely absent (Gavrilets 2003; Hey 2006; Smadja and Butlin 2011). For instance, speciation with restricted gene flow in spatially structured populations, called parapatry, has been studied in different contexts (Gavrilets et al. 1998; Gavrilets 2000; Gavrilets et al. 2000; de Aguiar et al. 2009; Yamaguchi and Iwasa 2017a). Likewise, populations inhabiting a single geographic area, with no restriction to gene flow, can also split into different species, a process termed sympatry. The possibility of sympatric speciation has been theoretically demonstrated for populations under disruptive selection (Smith 1966; Gavrilets 2006; Bolnick and Fitzpatrick 2007), strong competition (Dieckmann and Doebeli 1999), mating preference (Caetano et al. 2020) and even in neutral scenarios (Higgs and Derrida 1991), but its occurrence in nature is rare and still controversial (Fitzpatrick et al. 2009; Bolnick 2004).

Migration between groups is a common behavior that prevents complete isolation of populations (Winker 2000; Nosil 2008; Chaine and Clobert 2012; Turbek et al. 2018). For instance, estuarine-river environments and tide pools are systems under pulse-driven biotic events (Halas et al. 2005). These environments are cyclically isolated and expanded as a consequence of the water levels (Baggio et al. 2017). Thus, the system behaves like islands subject to periodic exchanges of migrants from neighboring sites. Similarly, species that have seasonal migration behavior are constantly mixing in a common area nesting or breeding place and irradiating after to other sites (Cooper and Uy 2017; Manthey et al. 2020; Winker and Pruett 2006; Everson et al. 2019). In this case, the migration itself (associated with dispersal abilities and spatial structure of the landscape) plays the role of an intermittent geographic barrier (Hey 2006; Claramunt et al. 2012; Agnarsson et al. 2014; Pinheiro et al. 2014; Linck and Battey 2019; Ashby et al. 2020). Such intermediate geographic situations can affect the process of speciation in complex ways since diversification in the presence of migration depends on a balance between colonization, local selection, and the homogenizing effects of gene flow (Garant et al. 2007). On the one hand, high levels of migration can constrain diversification via maintenance of gene flow (Mayr 1963; von Rönn et al. 2016) and hinder speciation (Fitzpatrick et al. 2009; Claramunt et al. 2012). It has been suggested that even one or a few migrants should be sufficient to avoid genetic diversification altogether (Slatkin 1987). On the other hand, migration between partially isolated populations can foster speciation by increasing genetic variation (Smadja and Butlin 2011; Cowie and Holland 2006) and by promoting founder events (Spurgin et al. 2014), which is the establishment of a small number of migrants in a new area, favoring rapid genetic changes and eventual diversification into a new species (Barton and Charlesworth 1984; Templeton 1980; Gavrilets and Hastings 1996; Templeton 2008). Understanding how migration increases diversity in semi-isolated populations has become increasingly important in a world of fragmented environments (Hagen et al. 2012; Mills and Allendorf 1996).

Investigation of the role of migration on speciation has mainly focused on the time to speciation and the influence of population structure on the rate of species creation, with evolution essentially driven by mutation and genetic drift (Manzo and Peliti 1994; Yamaguchi and Iwasa 2013). Notably, migration increases the time for speciation (Gavrilets 2000), but species divergence can be favored by subdivision of the population, even in the absence of local adaptation (Gavrilets et al. 1998, 2000). When considering isolated populations under rare but recurrent migration, optimal intermediate migration intensities maximize the rate of species creation in two-islands systems (Yamaguchi and Iwasa 2013, 2017b, 2016). Still, some patterns are yet to be addressed and discussed in more detail, such as the distribution of species richness, endemism, and species persistence. In this aspect, models can help elucidate and differentiate processes from patterns. Furthermore, current advances in obtaining genome-wide datasets provide robust estimates of gene flow and demographic history (Hey 2010; Gyllenhaal et al. 2020), evincing that speciation with gene flow in insular systems is common and may rise even in the absence of ecological divergence (Gyllenhaal et al. 2020). Therefore, understanding how migration and diversification are related can provide a better interpretation of speciation events in these intermediary geographic configurations that are not fully sympatric or allopatric.

In the present study, we focus on how migration intensity affects speciation and species richness in insular communities. We consider a neutral model for two islands subject to frequent exchange of individuals, where mating occurs locally and is only restricted by genetic similarity. The model is based on the work of Manzo & Peliti (Manzo and Peliti 1994), who considered a similar dynamic process of local reproduction and migration between two islands in the limit of infinitely large genomes, and investigated the possibility of allopatric speciation in the presence of gene flow. Here we show that population size and genetic features, particularly the number of loci involved in reproductive isolation, are key to determine not only the total number of species in the system but also the fraction of species that are endemic or cosmopolitan. Our simulations show that migration promotes the appearance of new species through two distinct processes: founding populations and sympatry. In the first case, the small but continuous flow of migrants creates a sub-population that differentiates from the residents. In the second case, the migrants mix with the residents, creating a genetically diverse population that eventually splits into species.

METHODS

Model overview

Our model for insular populations is based on the theory proposed by Manzo & Peliti (Manzo and Peliti 1994), which is itself based on the sympatric speciation model by Higgs & Derrida (Higgs and Derrida 1991). In these models, each individual is characterized by a string of infinite biallelic genes that represents the loci involved in reproductive isolation, dubbed as the individual's genome. Using infinite genes allows the derivation of several analytic results by mean-field calculations. However, important features of the infinite genes model disappear if the genome size is small, including the possibility of sympatric speciation (de Aguiar 2017). Here restrict out model to finite genomes (de Aguiar et al. 2009; Costa et al. 2018). We shall see that genome length plays a key role in the diversification process.

We consider two identical spatial regions (hereafter called islands) occupied by populations that can migrate and evolve through mutations and recombination. Each individual α is represented by a binary string of independent *B* genes, $\{S_1^\alpha, S_2^\alpha, ..., S_B^\alpha\}$, where each locus S_i^α can assume the alleles ±1. Individuals are hermaphroditic and reproduction is sexual. Population size is kept constant at the carrying capacity *M* in each island, except during the migration period when small fluctuations are allowed. The dynamics starts with *M* clonal individuals on each island and goes through cyclical events of migration, reproduction, and species identification (see Fig. 1), as detailed below:

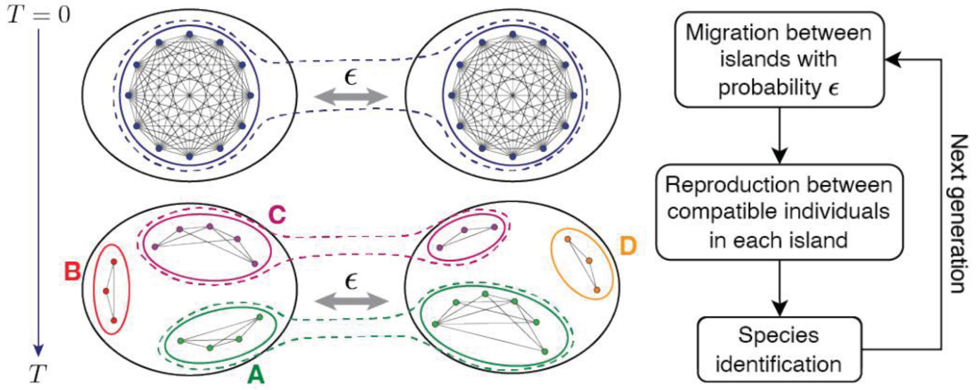

Figure 1. Schematic of the model dynamics. We consider two insular populations of initially identical individuals, represented by dots. At each time step, the islands exchange individuals with a probability ε. Generations are non-overlapping and sexual reproduction occurs between individuals in the same island having a minimal genetic similarity. Species are identified at the end of each cycle based on the possibility of gene flow, illustrated by links and enclosed in ellipses. The ellipses A, B, C and D (full lines) correspond to species classification within each island. Species can be exclusive to an island (B and D), or can be common to both (A and C, dashed lines).

Migration: at each generation, each individual has a probability ε of migrating to the other island. Thus, the population size in each island can vary right after migration, but the total remains 2*M* individuals. We refer to this process as continuous migration, as opposed to rare migrations of larger groups (Yamaguchi and Iwasa 2013).

Reproduction: reproduction occurs after migration only between individuals on the same island. On each island, *M* offspring are born and replace the previous population, compensating for fluctuations in populations size that may have occurred after migration. Generations do not overlap, and offspring are generated as follows: a first parent P_1 (focal parent) is chosen at random. A second parent P_2 is selected, also at random, among the remaining individuals. Reproduction between these two individuals will only occur if they are genetically compatible, i.e., if they have a minimal genetic similarity, as defined below. If the selected P_2 is not compatible with P_1, another second parent is randomly selected until this condition is met. If after M trials 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. The offspring's genome is also subjected to a mutation rate μ per loci. Reproduction is restricted by the genetic compatibility of the mating pair. Two individuals α and β can reproduce only if their genetic similarity, defined by $q_{min} = 1 - 2G/B$.

Species identification: speciation occurs when the gene flow between groups of individuals is disrupted. The population maps to a network where the individuals (nodes) are connected if they are genetically compatible. Species correspond to the components of the network. Not all individuals of a species need to be compatible since the genetic flow can be established through intermediary individuals. In network terms, there is a path connecting them within the component, as illustrated in Figure 1. We identify species considering local and global classifications. In the first case, only individuals from the same island are considered (components circled by continuous lines in Fig. 1), while in the second, the genetic compatibility network is built regardless of which island individuals belong (components circled by dashed lines in Fig. 1).

Numerical simulations and data analysis

We performed simulations with finite genomes to evaluate how migration probability (ε), population size per island (M) and amount of loci involved in reproductive isolation (B) affects patterns of diversity in a two-island system. The mutation rate per locus and the genetic threshold for reproduction were fixed for all simulations, $\mu = 0.001$ and $G = 0.05B$, respectively. The parameters of interest were varied with the following values: B = 1000, 2000, 3000, 10000; M from 25 to 500 individuals; and ε from 0 to 0.5. Populations were evolved during 2000 generations, with observation of species richness at T = 500, 1000, and 2000 generations. We ran 50 simulations for each set of parameters, unless stated otherwise (see apêndice A, Fig. S1).

When probing the species richness, we considered both local and global classifications (see *Species identification* in previous section). In the local classification, the species richness per island were designated by N_{L1} and N_{L2}. Under the global classification, the species richness in each island was N_1 and N_2, and the total number of species was N_T. Local and global classifications differed when individuals in one island, say island 1, could establish gene flow with two species of island 2 that would otherwise be reproductively isolated, a configuration that resembles the ring species assemblage (Martins et al. 2013). In this case these two species that contributed to N_{L2} would count as one for N_2. We quantified these events, named here "ring-like species", by calculating $N_{ring} = (N_{L1} - N_1) + (N_{L2} - N_2)$ (the local classification was exclusively employed for this analysis).

We also evaluated the asymmetry ∆N between the islands as the proportion of unbalance in species richness (under the global classification) in respect to the average,

$$\frac{\Delta N = \sqrt{(N_1 - N_2)^2}}{\bar{N}}, \tag{1}$$

where $\bar{N} = (N_1 + N_2)/2$. The diversity between the islands was measured based on the Jaccard distance index, whereas we calculate the number of exclusive species given by $(N_T - N_1) + (N_T - N_2)$. We call here the beta-diversity index β_I the normalization of this quantity, defined as

$$\beta_I = \frac{2N_T - N_1 - N_2}{N_T}. \tag{2}$$

If species are exclusive to each island, $N_T = N_1 + N_2$ and $\beta_I = 1$, indicating maximum endemism. In the other hand, if species are all common to both islands, we have $N_T = N_1 = N_2$ and $\beta_I = 0$, i.e., all species are cosmopolitan.

RESULTS

We first explored how migration probability, genome size, and population size affected diversity at the end of the simulations ($T = 2000$) for genome lengths $B = 1000$, 2000, and 3000 with varying migration probability, $0 \leq \varepsilon \leq 0.08$. When the islands were completely isolated from each other, $\varepsilon = 0$, speciation did not occur within the islands for the smallest genome size, $B = 1000$ (Fig. 2, upper left). In this case, the populations differentiated only through the accumulation of mutations in each island (allopatry), and each island had a unique exclusive species (indicated by $\beta_I = 1$ in Fig. 2, bottom left). This inter-island divergence was limited by the population size (M <~ 350 individuals), as larger M required longer times for speciation (see Fig. S2). For $B = 2000$, sympatric speciation in isolated islands was rare, occurring scarcely only for small values of M (Fig. 2, upper center). On the other hand, for $B = 3000$, isolated islands presented sympatric speciation for all M >~ 50 (Fig. 2, upper right). Increasing B also led to an increase in the maximum population size that supported $\beta_I = 1$, the maximum endemism (Fig. 2, middle). Strict allopatry ($\varepsilon = 0$) represented the peak of endemism for all scenarios (see Fig. 2, middle).

Migration even at low levels was sufficient to increase the number of species on each island. However, the beta-diversity decreased with migration, as expected, with a slower decay the larger the genome size. Therefore, although species in each island were more numerous, they were more likely to be shared. Regardless of the genome size, a curve depending on population size and migration probability maximized the per island and total species richness, with peak values increasing with B (Fig. 2, top; for the values of the total species richness, N_T, see Fig. S2, S3 and S4). The increase of the average number of species per island, $\overline{N}$, was followed by the formation of ring-like species (Fig. 2, middle), that is, groups of individuals with disrupted gene flow in the same island but with the possibility of gene flow when individuals from the other island were considered. The increase in N_{ring} was simultaneous to the loss of endemism, indicating the genetic homogenization due to more intense migration. Those patterns were consistent over time, with a direct dependence on the time for allopatry with M (see Fig. S2, S3 and S4).

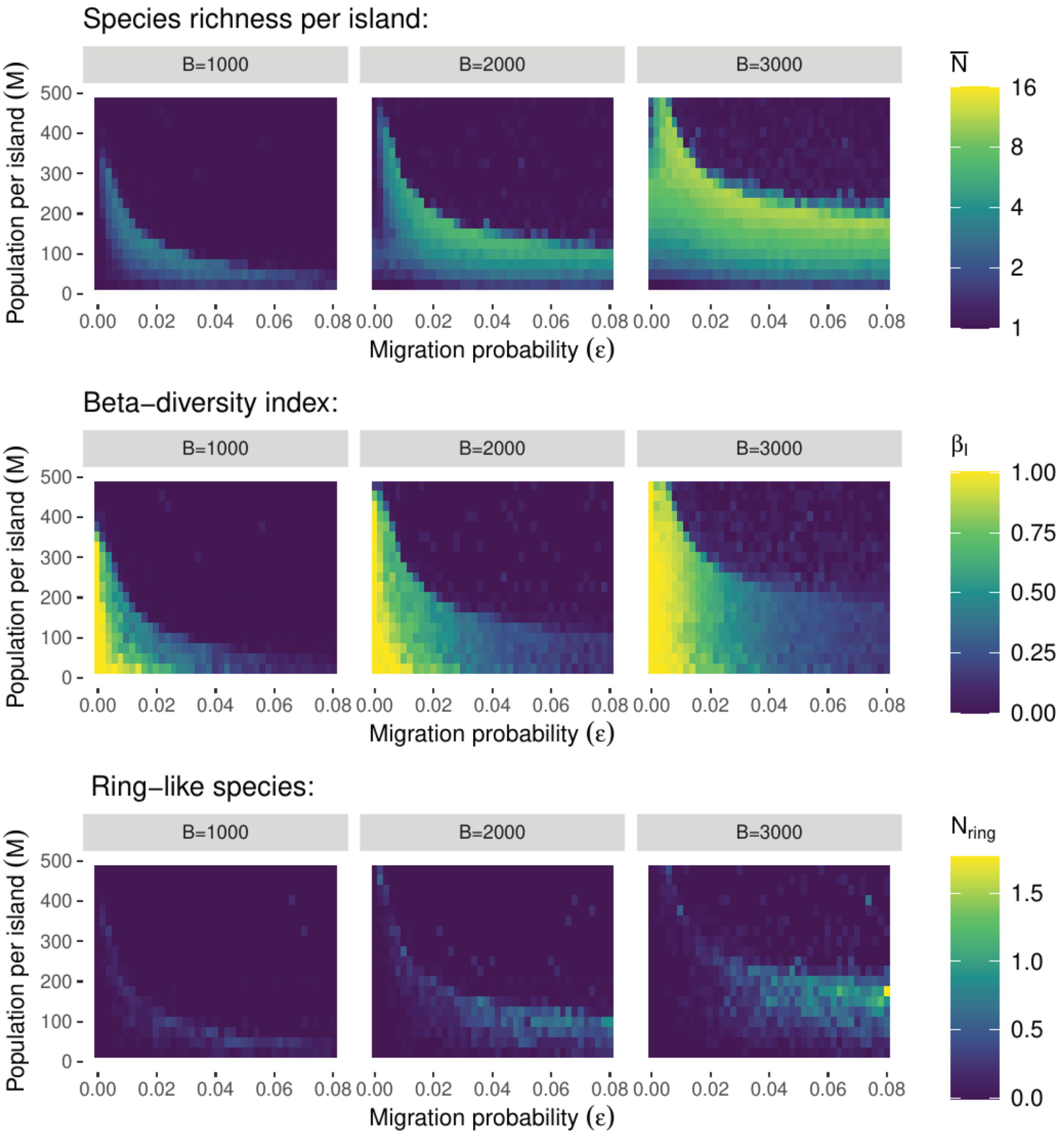

Figure 2. Diversity patterns in the islands as function of population size (M) and migration probability (ε) for genome lengths B = 1000, 2000 and 3000 at T = 2000: average species richness per island, $\overline{N} = (N_1 + N_2)/2$ (first row); the proportion of species that is exclusive of an island, measured by the beta-diversity index β_I (second row); and the number of ring-like species, N_{ring} (third row). Migration increases the species richness in each island but reduces the beta-diversity, followed by the formation of ring-like species. There are optimal combinations of population size and migration probability that favor speciation for each genome length B. The patterns are similar through the values of B, with larger B sustaining a higher number of species.

For large genomes (B = 10000), the population split into several species even in strict isolation (sympatric speciation), and migration increased species richness further. However, intense migration, ranging from ε = 0.1 to 0.5, led to the homogenization of the populations that evolved effectively as contiguous $2M$ individuals. For small genomes, B = 1000 and 2000, migration was essential to increment species richness, as seen before. However, here we observe that this effect was limited to low levels of migration: above a critical point, the number of species within the island collapsed to a single one shared by the two islands (ε ≥ 0.014 for *B* = 1000 and ε ≥ 0.03 for *B* = 2000). *B* = 3000 had an intermediary behavior, presenting several species for ε = 0, but also collapsed for high levels of migration (ε ≥ 0.2) with a continuous transition. The increment in total species richness (N_T) beyond the number of total species in strict allopatry (ε = 0) showed that migration induced some form of speciation in the insular community, and the effect was more intense for small genome lengths (Fig. 3b).

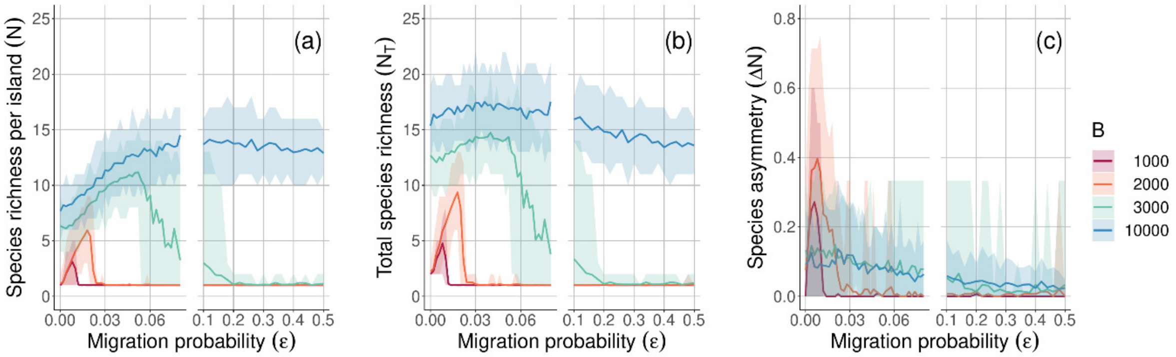

Figure 3. Species richness and asymmetry between the islands at *T* = 2000 for varying migration probability (*ε*) and genome sizes *B* (colors) with fixed population size (*M* = 200). Results are shown for 50 independent simulations. The solid lines represent the average value of all realizations, and the shadowed areas show a confidence interval of 90%. (a) Average number of species per island, $\bar{N} = (N_1 + N_2)/2$. (b) Total number of species, N_T. (c) Species asymmetry Δ*N*. The higher asymmetry occurs for values of *B* for which migration is essential for speciation.

Although the migration probability was symmetric between islands, the number of species in each one was asymmetric, especially for low and intermediary migration intensities, 0 ≤ ε ≤ 0.03 (Fig. 3c). This asymmetry occurred most of the time but was ephemeral, as we observed an alternation of the island with more species and fluctuation of the species richness on both islands (videos included in the apêndice A). Comparing to a null model of random distribution of the species between the two islands with equal probability (see the apêndice A, section S2 D), we verified that some of the asymmetry results from inherent stochasticity of the system, but the highest asymmetry, beyond the expected by chance, occurred for values of *B* and ε for which migration was the essential mechanism for the speciation. We inferred that asymmetry occurred when speciation induced by migration enhanced random imbalances between the number of species on each island. For instance, when one island was composed of a single species, migrants were likely to establish a new species on the arrival island as they were genetically compatible. On the other hand, as the other island then had more than one species, its migrants had a reduced chance of being conspecific and were more likely to go extinct on the island of arrival for lack of compatible mates, keeping the first island with a single species.

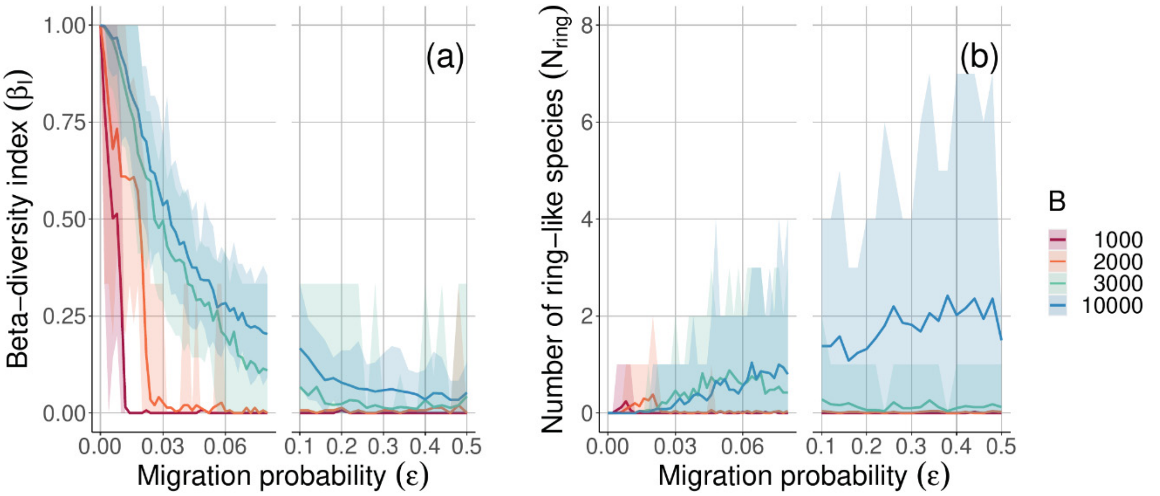

Figure 4. Beta-diversity index of the insular community and ring-like species at *T* = 2000 for varying migration probability (*ε*) and genome sizes *B* (colors), with fixed population size (*M* = 200). (a) The beta-diversity index β_I decreases monotonically with migration from full allopatry (*ε* = 0 and *β* = 1) to the mixed populations sharing most of the species (ε ≈ 0.5 and *β* ≈ 0). (b) As migration increases, gene flow disrupted within one island can be re-established by individuals from the other island, in a configuration similar to ring species.

Analysis of the beta-diversity index in the insular community shows that, as expected, increasing the migration probability led to a decline in β_I (Fig. 4a), from the complete endemism when islands were isolated (ε = 0 and β_I = 1) to the mixed populations, having most of the species in common (ε ≈ 0.5 and $\beta_I \approx 0$). Large genomes were more resilient, with slow decay, while the small genomes presented a sharp drop, following the collapse in the number of per island and total species to a single one. Although the proportion of exclusive species in the system always decreased, the absolute number of exclusive species increased with migration for small genomes (Fig.

S6). The increase in the migration probability also caused the appearance of ring-like species (Fig. 4b). Figure 4c illustrates how it occurred during the simulations. In this example, using the local referential, the island at the left had one species and the other two species, $N_{L1} = 1$ and $N_{L2} = 2$. However, the two species in the second island were, in fact, a single one in the global classification, with gene flux between the two groups reconnected by individuals of island one, then $N_1 = N_2 = 1$. This assemblage is similar to ring species (Martins et al. 2013) on a much smaller scale and longing only through a few generations, although appearing throughout the dynamics and even at $T = 2000$, as shown in Fig. 4b. Such a configuration either preceded speciation (when the disrupted gene flow later led to the formation of species) or disappeared with the subsequently re-establishment of gene flow by the arrival of migrants or due to mutation. Therefore, we classified them as “ring-like species”. For small genomes, they occurred in a small number, restricted to the range of migration intensity that made $N_i > 1$. For large genomes, they were recurrent and appeared in significant numbers under intense migration.

Finally, we investigated the processes by which migration leads to speciation. Using genetic compatibility networks, we observed two speciation modes induced by migration, illustrated in Figure 5. *Speciation by founding populations* occurred when migrants arriving on an island could not reproduce with the resident population for being of a different species and, when they were able to accumulate through several generations and establish a population, ended up founding a new species (Fig. 5, left panel). We hypothesize that this was the dominant mode for low migration probabilities based on the examples observed with videos. The second mode, recognized as a *sympatric speciation induced by migration* (shown in the right panel), seems to occur more frequently under slightly larger migration probabilities. Here the islands presented common species, then migrants could reproduce with the resident population, and their incorporated genetic novelties promoted speciation. The described effects can be observed in detail in the videos included with the apêndice A.

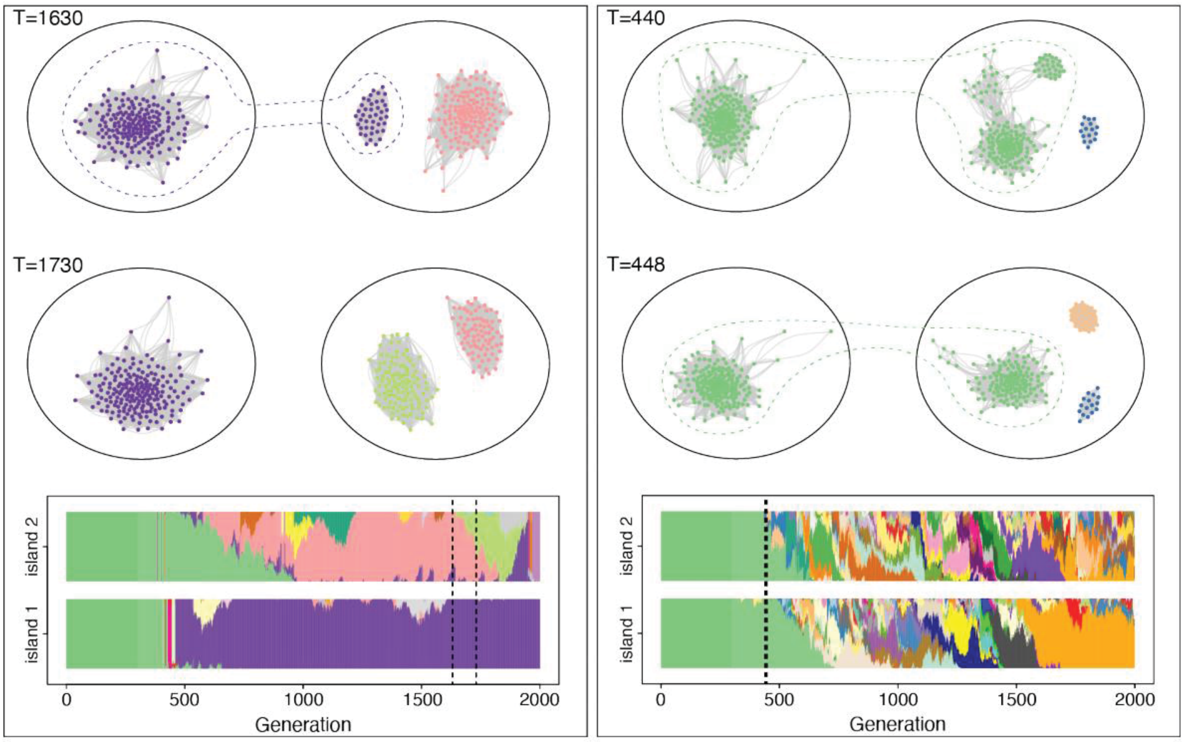

Figure 5. Evolution of the populations for B = 1000 and ε = 0.004 (left) and B = 2000 and ε = 0.02 (right) exemplifying the speciation modes induced by migration. Bars on the bottom indicate the distribution of species abundances in each island over time. Individuals of the same species have the same color and are connected by links or dashed lines when they belong to different islands. In the speciation through founder populations (left panel), a portion of migrants differentiates into a new species without mixing with the native population. In the second mode (right panel), migrants can incorporate into the resident population, then differentiation between islands is hindered, but migration promotes sympatric speciation.

DISCUSSION

Strict allopatry with one species per island was only maintained for small genomes (B = 1000 and 2000) in the absence of migration with M = 200. Even a few migrants were sufficient to promote speciation. For instance, with ε = 0.004 (equivalent to an average number of σ = 0.8 migrants per generation), speciation by founding populations already occurred (see Fig. 5 left panel and videos in the apêndice A). This mode was mainly related to low migration intensity and benefited from the slow dynamics of those genomes size (Fig. S5). When the two islands still had the same species, the migrants were genetically similar and, in a small number, did not bring sufficient novelties to cause a break in gene flow. After the islands differentiated from each other (around $T > 400$ generations), recently arriving migrants in each island could not reproduce with the resident population and either accumulated through several generations or went extinct. When a population was established in the arrival island, they differentiated into a new species (Fig. 5, left panel). No sympatry was observed in those cases, in the sense that the island's resident species did not branch. Therefore, the ancestry of the new species was always fully connected to migrants, i.e., they did not share common ancestors with the former (native) species.

With a slightly higher level of migration, the islands had more than one species and shared some of them. Although there was a loss of endemism, sympatry induced by migration was favored: migrants could reproduce with residents, and their mixing led to speciation. Remarkably, despite the higher proportion of shared species, the absolute number of exclusive species increased with migration for small genomes (Fig. S6). This connection between high species richness with low endemism or low species richness and high endemism in insular systems has been observed in Darwin finches, for instance (Hamilton and Rubinoff 1963), and explained by the spatial structure of the islands (Gascuel et al. 2016). Low levels of migration can be understood as a great physical distance between the islands, while a moderate level indicates islands closer to each other, establishing an analogy between our results and previous findings. Also, an intermediary level of migration seemed to optimize the evolution of diversity, which has been suggested in different contexts (Yamaguchi and Iwasa 2013; Garant et al. 2007), for instance, in the intermediate dispersal model (Agnarsson et al. 2014; Ashby et al. 2020). Based on the theory of island biogeography and associating migration with dispersal abilities, it proposes that colonization promotes speciation at the same time that may increase the probability of extinction; therefore, moderate levels of migration optimize species richness in islands (Agnarsson et al. 2014; Ashby et al. 2020). Our model reproduces this effect while also providing a mechanistic view of the processes by which migration promotes speciation.

Small genome sizes were positively correlated to the asymmetry in species richness between the islands beyond the expected by chance (i.e., if the given total number of species was randomly distributed between the islands with equal probability). The effect was more significant for low levels of migration (Fig. 3c, also S7 and S8), and we hypothesized it was related to speciation by founding populations that, as mentioned before, enhanced random imbalances of species richness. When sympatric speciation took place, increasing the number of species, asymmetry was less observed. Asymmetry in the geographic range of recently branched sister species is expected under peripatric speciation and is more likely to occur in small populations (Barraclough and Vogler 2000). Here asymmetry in species richness resulted from gene flow in a symmetric setup (same number of individuals and migration probability in both islands) with a small number of species and not from landscape heterogeneity or different species ranges. Further investigation might address how such imbalances affect species abundances and the structure of the phylogenies.

Diversity under high migration could only be sustained with large genomes, which can be explained by the trade-off between population size and genome length. In this model, when considering a single island, sympatric speciation does not occur if the genome is too small due to the low genetic variability and the slow accumulation of mutations (de Aguiar 2017). The required variability is readily provided by low and moderate migration. However, under higher exchange of migrants, the populations evolve as contiguous, and then the time to speciation increases for finite genomes (see (de Aguiar 2017) and Fig. S2, S3 and S4), hindering speciation. Large genomes, however, can sustain higher variability and present fast dynamics. Nevertheless, the robustness of large genomes made their response to migration less compelling.

Along the whole dynamics, we observed the formation of ring-like species, but they were more important for large genomes under high migration intensity, indicating how gene flow was actively connecting the populations. Previous models for islands with migration predicted the occurrence of ring species but in larger chains of patches (Gavrilets et al. 1998); here we find a similar effect with only two islands. However, they do not resemble the observed ring species (Martins et al. 2013), for having a much smaller extension and low durability, but can be later used as an indicative or step of the speciation process.

Finally, we note that the results presented here are conditioned to the regime of continuous migration and relatively large mutation probability ($\mu M \approx 0.1$). Rare migrations of larger groups can lead to different outcomes if the time between migrations is larger than M and $\mu \ll 1/M$, allowing fixation of migrants alleles between migrations (Yamaguchi and Iwasa 2016; Yamaguchi et al. 2021). Hence, diversity in island systems depends on a large number of factors that include periodicity of migration, number of individuals, mutation probability and number of loci and alleles involved in reproductive isolation. Therefore, comparing models with data requires careful analysis of the situation at hand.

APÊNDICE A – Supporting Material

A. Number of simulations

Figure S1 shows the number of simulations performed for each genome size, population size, and migration probability to compose Figure 2 of the main text. For parameter values resulting in a small number of species (≈ 1), we could make fewer realizations to calculate the average value since fluctuations were small. It was convenient for simulations of finite genomes that demand high computational costs. Notice that, after the migration intensity for which the number of species collapses to a single one shared, a few realizations are sufficient. For the analysis with fixed population size M = 200 (Fig. 3 and 4 of the main text), we ran 50 simulations in all cases.

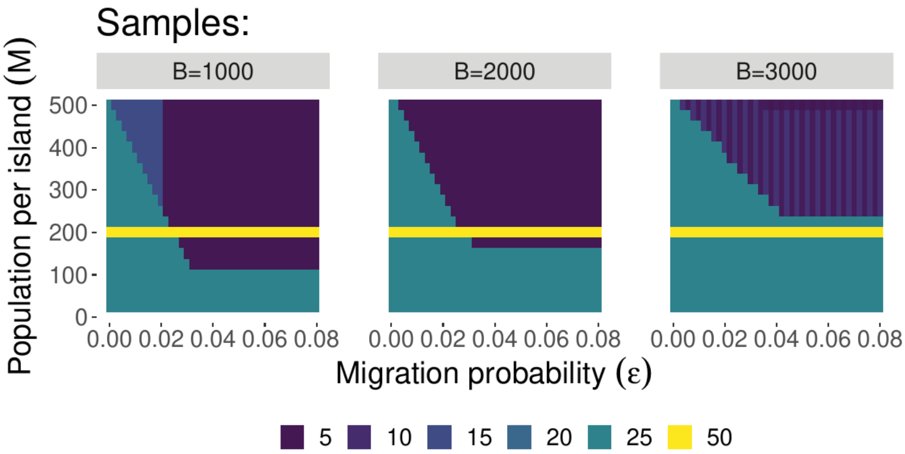

Figure S1. Number of simulations (color scale) performed to compose Figure 2 of the main text.

B. Evolution of diversity for B = 1000, 2000, and 3000

Here we present additional results to support our analysis in the manuscript. Figures S2, S3 and S4 show the patterns of diversity for the genome sizes B = 1000, 2000, and 3000 respectively, similarly to Figure 2 in the main text, in different time steps: T = 500, 1500 and 2000 generations. In each figure, the columns represent the time of the observation. From top to bottom, the plots represent the average values of the total number of species in the insular system (N_T), the number of species per island $\overline{N} = (N_1 + N_2)/2$, the ratio of the total number of species that are exclusive to an island (β_I), the number of ring-like species (N_{ring}), and the asymmetry in species richness ($\Delta N = | N_1 - N_2|/\overline{N}$). The numbers of simulations utilized follow the indicated in Figure S1. The diversity patterns were consistent over time, but larger populations took longer to speciate in allopatry or with migration, i.e., the time to speciation depends on M for finite genomes. Figure S5 depicts the dynamics in the two islands for some values of migration probability and fixed population size $M = 200$. The colors identify species, and the height is proportional to the species abundance. In allopatry ($\varepsilon = 0$), we observe that sympatric speciation occurred only for $B = 3000$. Also, differentiation between islands took longer the shorter the genome size. Migration induced speciation up to a critical value of ε that collapsed the populations to a single shared species. Longer genomes supported higher migration flux before collapsing.

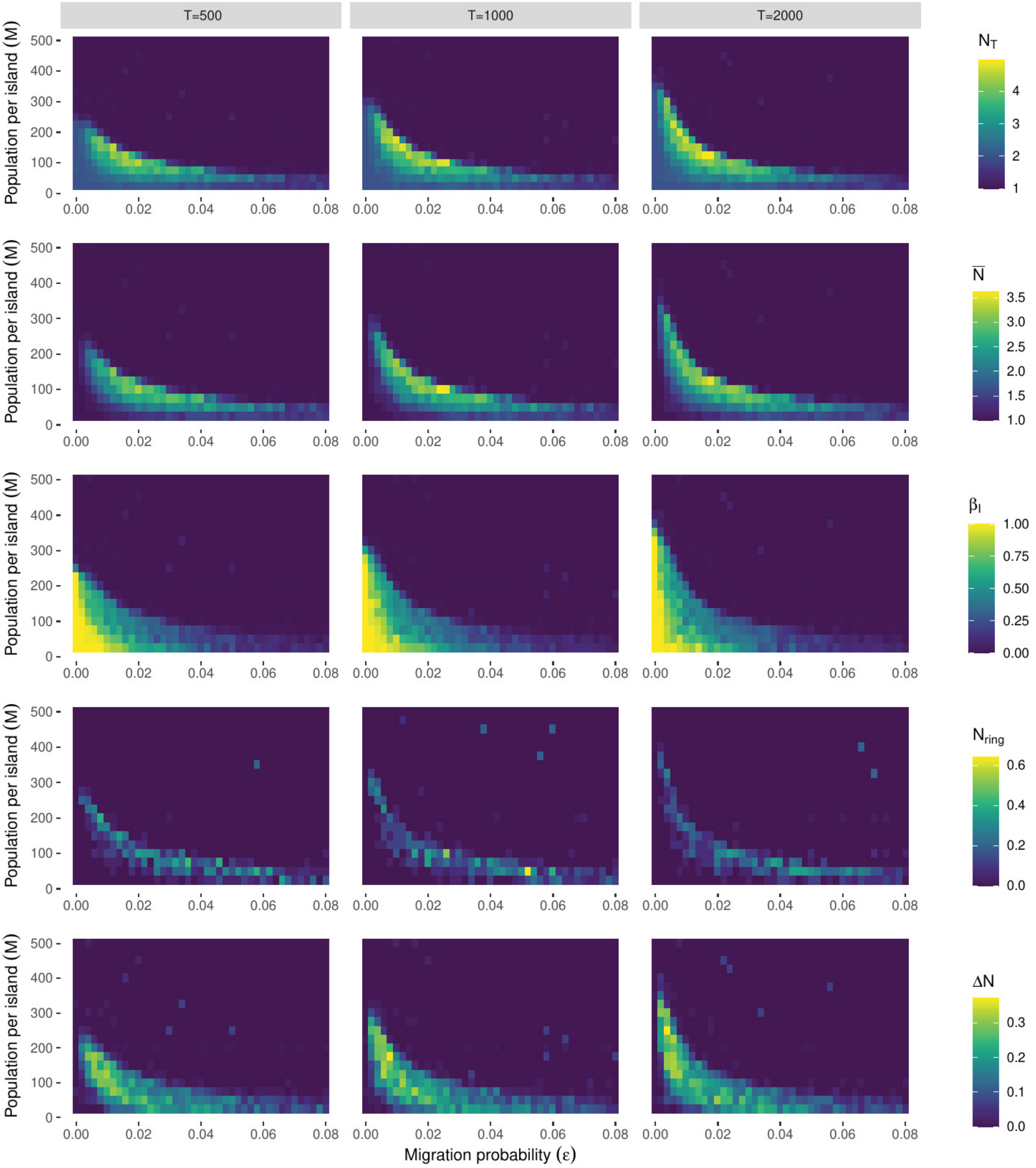

Figure S2. Diversity patterns of the two-island system as a function of population size (*M*) and migration probability (ε) for *B* = 1000 at *T* = 500 (left column), 1000 (middle) and 2000 (right column) generations.

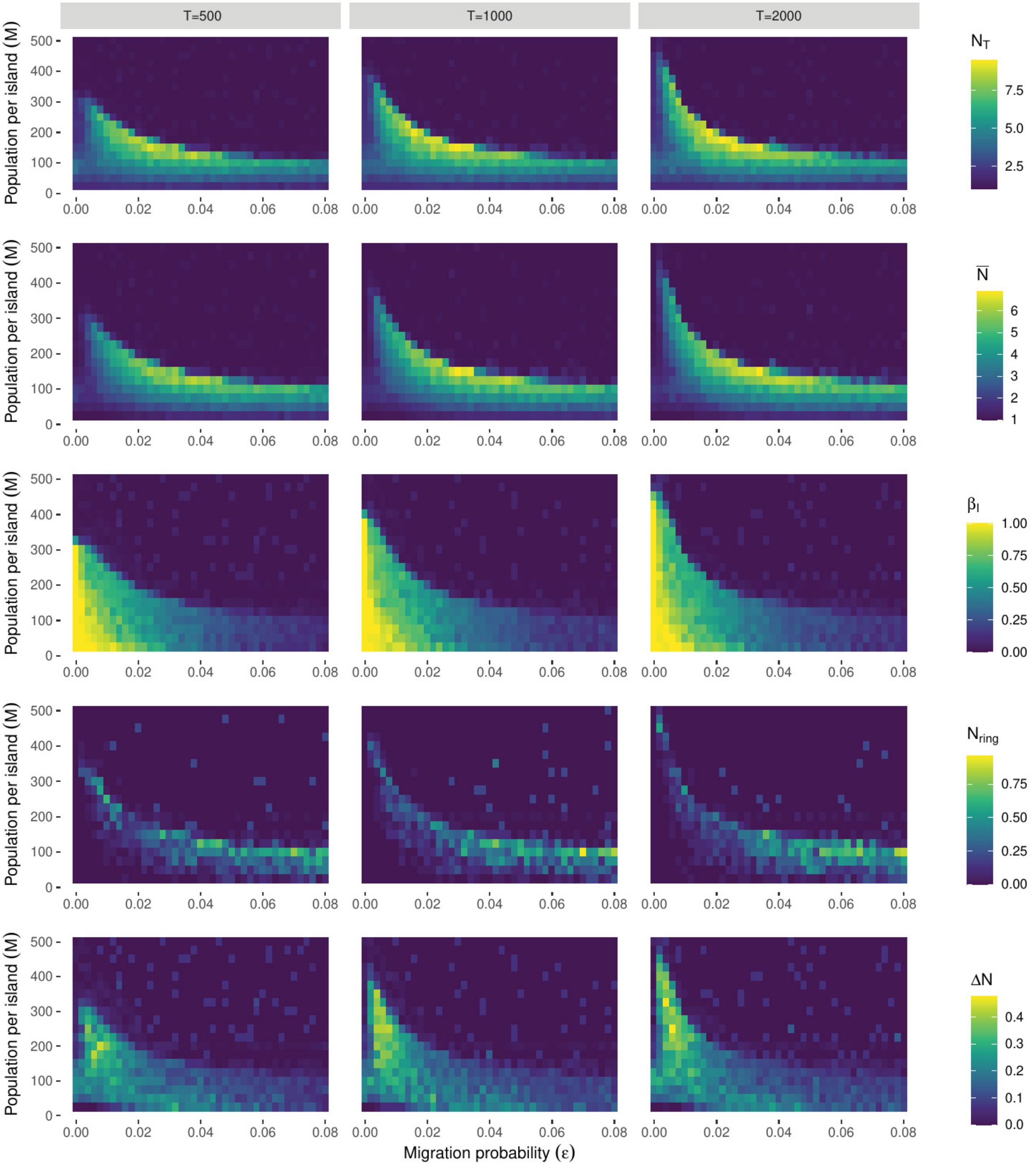

Figure S3. Diversity patterns of the two-island system as a function of population size (*M*) and migration probability (ε) for *B* = 2000 at *T* = 500 (left column), 1000 (middle) and 2000 (right column) generations.

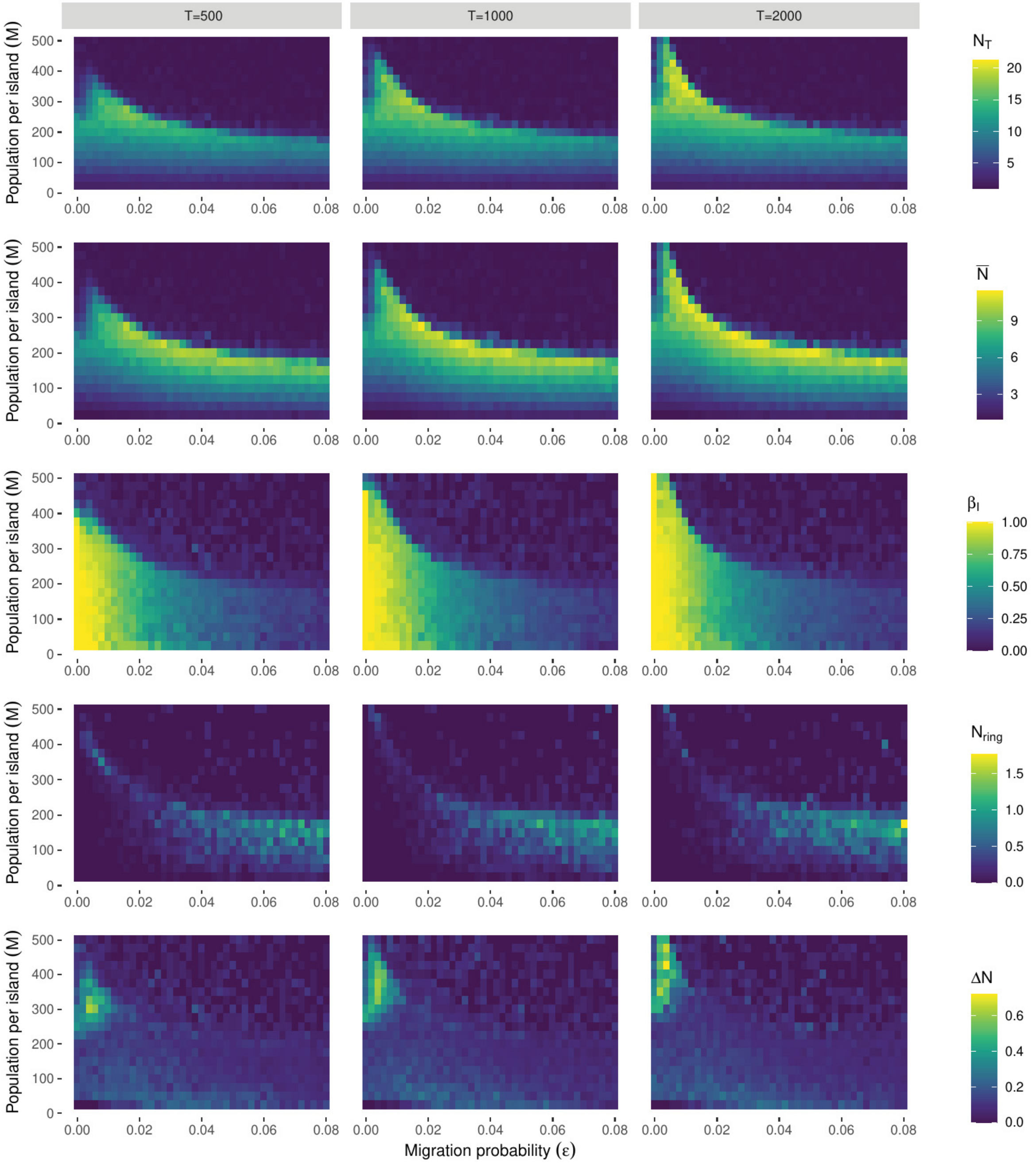

Figure S4. Diversity patterns of the two-island system as a function of population size (*M*) and migration probability (ε) for *B* = 3000 at *T* = 500 (left column), 1000 (middle) and 2000 (right column) generations.

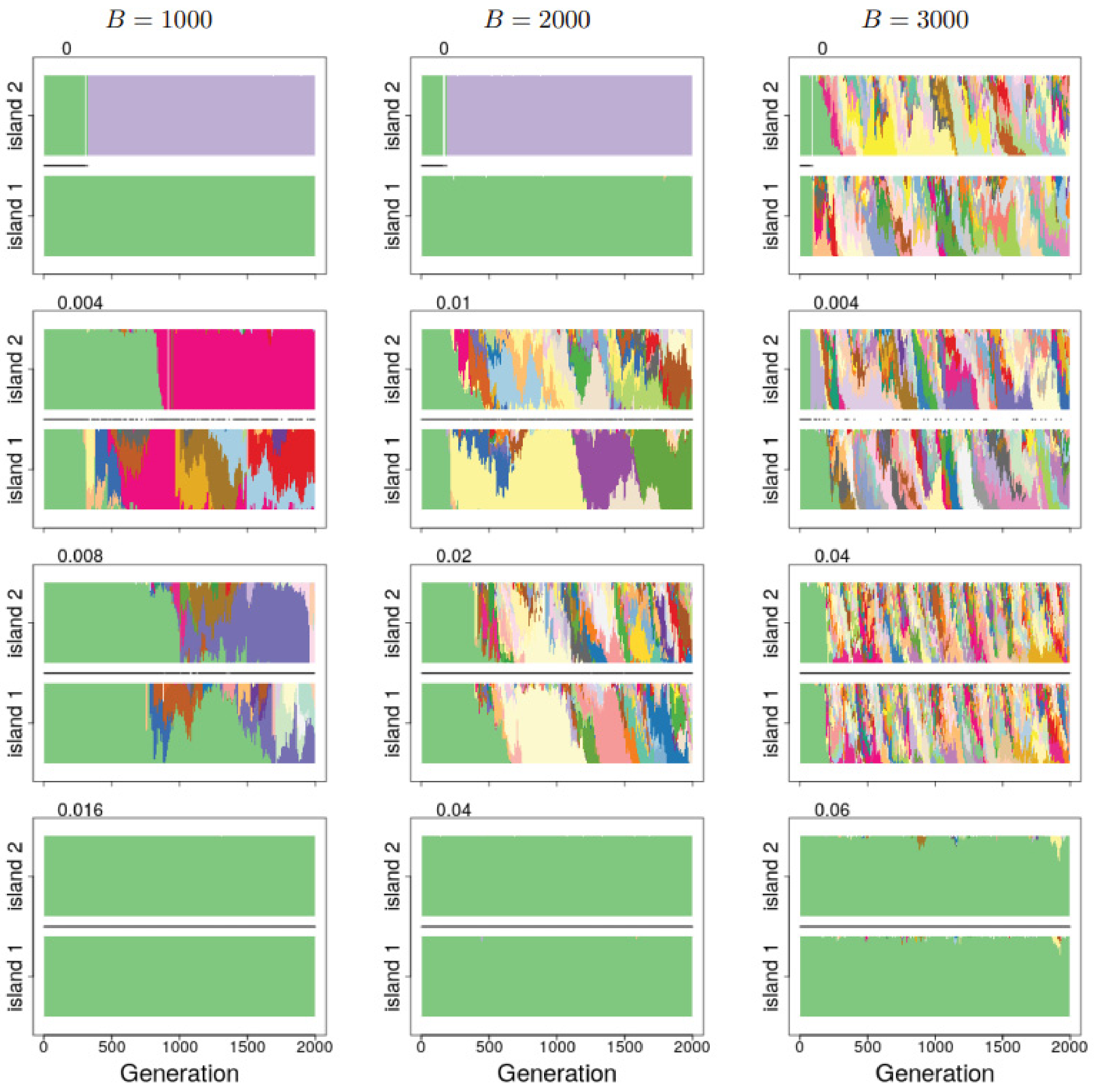

Figure S5. Distribution of species per island over time for different migration probabilities (indicated in each panel) and fixed population size M = 200, for B = 1000 (left column), 2000 (middle) and 3000 (left column). Each panel has two horizontal bars corresponding to each island. The colors identify species, and their vertical amplitude represents the species abundance. The horizontal black line between the bars indicates the intervals when the islands shared at least one common species.

C. Number of exclusive species

Figure S6 depicts the number of exclusive (endemic) species in the insular system for varied genome sizes, complimentary to Figures 3 and 4 of the main text. The number of exclusive species in each island can be calculated as follows: calling K_i the number of endemic species to the island *i* and *c* the number of common species, then $N_1 = K_1 + c$, $N_2 = K_2 + c$, and $N_T = K_1 + K_2 + c$. Then $c = N_1 + N_2 - N_T$, and K_1 and K_2 are trivially calculated. The beta diversity index is given by the ratio $(K_1 + K_2)/N_T$.

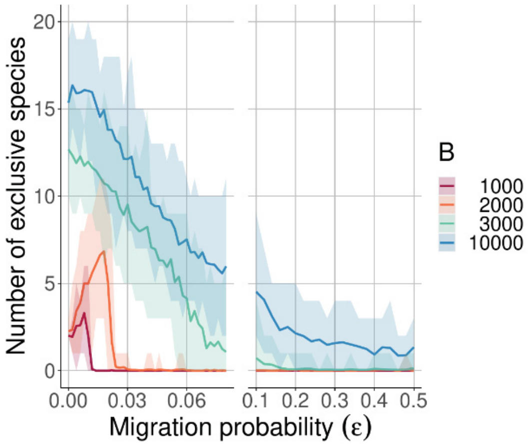

Figure S6. Number of exclusive species in the system, $K_1 + K_2$.

D. Null test of asymmetry

The asymmetry in species richness, calculated by the absolute value of the difference between the number of species in each island, $|N_1 - N_2|$, is equivalent to the modulus of the difference between the number of exclusive (endemic) species, $|K_1 - K_2|$. To verify if the asymmetry observed in our simulations was significant, we compared it to a null model where the exclusive species were randomly distributed between the islands with equal probability. We run the null model for each simulation output, using the number of exclusive species from the simulation. In each case, we ensured that at least one species inhabited each island: if the islands shared at least one species, $K_1 + K_2$ species were randomly distributed between the islands, otherwise only $K_1 + K_2 - 2$ species were distributed, since one species is placed at each island at the start. To compare the different genome sizes, we adopted the asymmetry normalized by the total number of species, ΔN (Eq. (1) in the main text). Figure S7 shows that the simulations differed from the random distribution when the migration probability was low (ε < 0.03). For small genomes (*B* = 1000 and 2000), the asymmetry was higher than expected by chance, while for large genomes (*B* = 3000 and 10000), it was lower than the expectation at random. The higher asymmetry for small genomes suggests that speciation by founding populations was probably the main speciation mechanism associated: random imbalances in N_1 and N_2 were enhanced because migrants leaving the island with lower richness were more likely to be genetically compatible and to found a new species in the arrival island. On the other hand, the number of species was higher for larger genomes, decreasing the fluctuations in species richness and the likelihood of founding populations. The divergence between the simulations and the null model is better observed in Figure S8, which compares the difference $N_1 - N_2$ (here is not the absolute value) for 1000 realizations with ε = 0.01 and two values of genome size, *B* = 2000 (left) and 3000 (right).

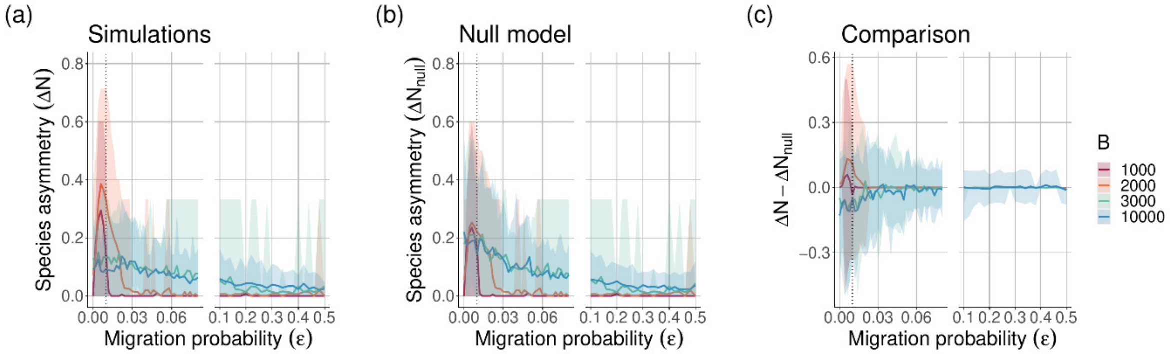

Figure S7. Asymmetry in species richness in the insular system (Δ*N*) for finite genomes. The solid lines represent the average value of all simulations, and the shadowed areas show a confidence interval of 90%. (a) Results from our simulations (similar to the plot in the manuscript (Fig. 3c) considering only finite genomes and more data – some averages were calculated over 1000 repetitions). (b) Species asymmetry expected by the null model, where species are randomly distributed over the islands. (c) Comparison between the obtained from simulation and null model ($\Delta N - \Delta N_{null}$) reveals that asymmetry is more expected than by chance (positive values) for low migration probability and small genomes, *B* = 1000 and 2000. The dashed vertical line highlight ε = 0.01 (same as Fig. S8).

The distribution of N_1 - N_2 when *B* = 2000 has a plateau for $|N_1 - N_2| \leq 3$ (blue bars), revealing that perfect symmetry ($N_1 - N_2 = 0$) is not more likely within this range, in opposite to what is expected by chance (red bars). On the other hand, the distribution of N_1 - N_2 for B = 3000 (right, blue bars) is narrower than expected by chance (red bars), then perfect symmetry is more likely to occur.

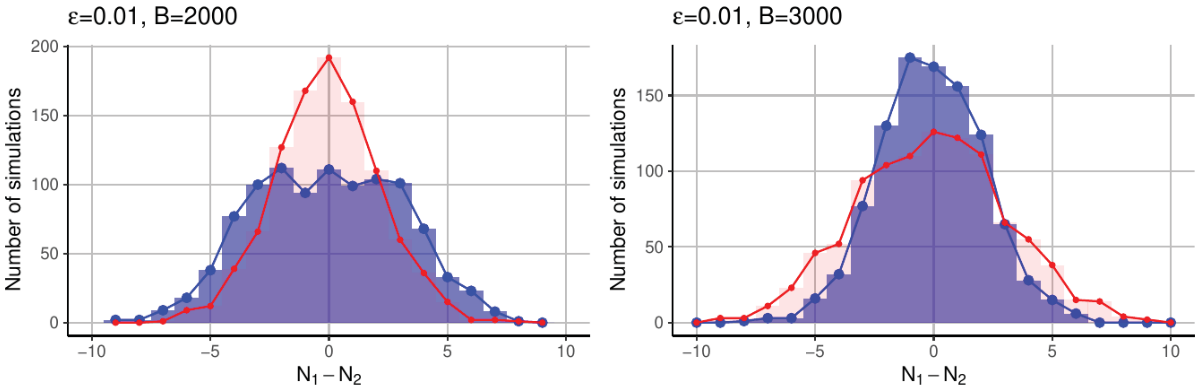

Figure S8. Histograms of the difference between the islands species richness, N_1 - N_2, obtained from the simulations (blue) and the null model (red) for 1000 replications when the migration probability is ε = 0.01. For B = 2000 (left), the asymmetry is higher than expected by chance, while for B = 3000 (right) the asymmetry is lower than expected by chance.

E. Link to the videos:

https://www.dropbox.com/sh/cehfwm4yqg1m7mr/AABq-p-1JX3G2qSwWdA7Zy9Ha?dl=0

REFERENCES

Agnarsson Ingi, Cheng Ren-Chung and Kuntner Matjaž 2014. A Multi-Clade Test Supports the Intermediate Dispersal Model of Biogeography. PLOS ONE 9:e86780.

Ashby Ben, Shaw Allison K. and Kokko Hanna 2020. An inordinate fondness for species with intermediate dispersal abilities. Oikos 129:311–319.

Baggio Rafael A, Stoiev Sérgio B, Spach Henry L and Boeger Walter A 2017. Opportunity and taxon pulse: the central influence of coastal geomorphology on genetic diversification and endemism of strict estuarine species. Journal of Biogeography 44:1626–1639.

Barraclough Timothy G and Vogler Alfried P 2000. Detecting the Geographical Pattern of Speciation from Species-Level Phylogenies. The American Naturalist 155:419–434.

Barton N H and Charlesworth B 1984. Genetic revolutions, founder effects, and speciation. Annual Review of Ecology and Systematics 15:133–164.

Bolnick Daniel I. 2004. Waiting for sympatric speciation. Evolution 58:895–899.

Bolnick Daniel I and Fitzpatrick Benjamin M 2007. Sympatric speciation: models and empirical evidence. Annual Review of Ecology, Evolution, and Systematics 38:459–487.

Caetano R. A., Sanchéz Sergio, Costa Carolina L.N. and De Aguiar Marcus Aloizio Martinez 2020. Sympatric speciation based on pure assortative mating. Journal of Physics A: Mathematical and Theoretical 53:155601.

Chaine Alexis S and Clobert Jean 2012. Dispersal. *In* Behavioural responses to a changing world. Oxford University Press.

Claramunt Santiago, Derryberry Elizabeth P., J. V. Remsen Jr, Brumfield Robb T., Remsen Jr V. and Brumfield Robb T. 2012. High dispersal ability inhibits speciation in a continental radiation of passerine birds. Proceedings of the Royal Society B: Biological Sciences 279:1567–1574.

Cooper Elizabeth A. and Uy J. Albert C. 2017. Genomic evidence for convergent evolution of a key trait underlying divergence in island birds. Molecular Ecology 26:3760–3774.

Costa Carolina L N, Lemos-Costa Paula, Marquitti Flavia M D, Fernandes Lucas D, Ramos Marlon F, Schneider David M, Martins Ayana B and de Aguiar Marcus A M 2018. Signatures of Microevolutionary Processes in Phylogenetic Patterns. Systematic Biology 68:131–144.

Cowie Robert H. and Holland Brenden S. 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. Journal of Biogeography 33:193–198.

Coyne Jerry A. and Orr H. Allen 2004. Speciation. Sinauer Associates, Inc., 1 edition.

de Aguiar Marcus A M 2017. Speciation in the Derrida-Higgs model with finite genomes and spatial populations. Journal of Physics A: Mathematical and Theoretical 50:085602.

de Aguiar M A M, Baranger M., Baptestini E. M., Kaufman L. and Bar-Yam Y. 2009. Global patterns of speciation and diversity. Nature 460:384–387.

Dieckmann Ulf and Doebeli Michael 1999. On the origin of species by sympatric speciation. Nature 400:354–357.

Everson Kathryn M., McLaughlin Jessica F., Cato Iris A., Evans Maryanne M., Gastaldi Angela R., Mills Kendall K., Shink Katie G., Wilbur Sara M. and Winker K. 2019. Speciation, gene flow, and seasonal migration in Catharus thrushes (Aves:Turdidae). Molecular Phylogenetics and Evolution 139:106564.

Fitzpatrick BM, Fordyce JA and Gavrilets S 2009. Pattern, process and geographic modes of speciation. Journal of Evolutionary Biology 22:2342–2347.

Garant DANY, Forde Samantha E and Hendry Andrew P 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. Functional Ecology 21:434–443.

Gascuel Fanny, Laroche Fabien, Bonnet-Lebrun Anne Sophie and Rodrigues Ana S.L. 2016. The effects of archipelago spatial structure on island diversity and endemism: predictions from a spatially-structured neutral model. Evolution 70:2657–2666.

Gavrilets Sergey 2000. Waiting time to parapatric speciation. Proceedings of the Royal Society of London. Series B: Biological Sciences 267:2483–2492.

Gavrilets Sergey 2003. Perspective: models of speciation: what have we learned in 40 years? Evolution 57:2197–2215.

Gavrilets Sergey 2006. The Maynard Smith model of sympatric speciation. Journal of Theoretical Biology 239:172–182.

Gavrilets Sergey and Hastings Alan 1996. Founder effect speciation: a theoretical reassessment. The American Naturalist 147:466–491.

Gavrilets S, Li H and Vose M D 1998. Rapid parapatric speciation on holey adaptive landscapes. Proceedings of the Royal Society B: Biological Sciences 265:1483–1489.

Gavrilets Sergey, Li Hai and Vose Michael D. 2000. Patterns of parapatric speciation. Evolution 54:1126– 1134.

Gyllenhaal Ethan F., Mapel Xena M., Naikatini Alivereti, Moyle Robert G. and Andersen Michael J. 2020. A test of island biogeographic theory applied to estimates of gene flow in a Fijian bird is largely consistent with neutral expectations. Molecular Ecology 29:4059–4073.

Hagen Melanie, Kissling W Daniel, Rasmussen Claus, De Aguiar Marcus AM, Brown Lee E, Carstensen Daniel W, Alves-Dos-Santos Isabel, Dupont Yoko L, Edwards Francois K, Genini Julieta et al. 2012. Biodiversity, species interactions and ecological networks in a fragmented world. Advances in Ecological Research 46:89–210.

Halas Dominik, Zamparo David and Brooks Daniel R 2005. A historical biogeographical protocol for studying biotic diversification by taxon pulses. Journal of Biogeography 32:249–260.

Hamilton Terrell H. and Rubinoff Ira 1963. Isolation, Endemism, and Multiplication of Species in the Darwin Finches. Evolution 17:388.

Hey Jody 2006. Recent advances in assessing gene flow between diverging populations and species. Current Opinion in Genetics & Development 16:592–596.

Hey Jody 2010. Isolation with migration models for more than two populations. Molecular Biology and Evolution 27:905–920.

Higgs P. G. and Derrida B. 1991. Stochastic models for species formation in evolving populations. Journal of Physics A: Mathematical and General 24:L985–L991.

Linck Ethan and Battey C. J. 2019. On the relative ease of speciation with periodic gene flow. bioRxiv p. 758664.

Manthey Joseph D., Oliveros Carl H., Andersen Michael J., Filardi Christopher E. and Moyle Robert G. 2020. Gene flow and rapid differentiation characterize a rapid insular radiation in the southwest Pacific (Aves: Zosterops). Evolution 74:1788–1803.

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

Martins Ayana B., de Aguiar Marcus A. M. and Bar-Yam Yaneer 2013. Evolution and stability of ring species. Proceedings of the National Academy of Sciences 110:5080–5084.

Mayr Ernst 1963. Animal Species and Evolution. Belknap of Harvard University Press. Mills L. Scott and Allendorf Fred W. 1996. The One-Migrant-per-Generation Rule in Conservation and Management. Conservation Biology 10:1509–1518.

Nosil Patrik 2008. Speciation with gene flow could be common. Molecular Ecology 17:2103–2106.

Pinheiro Fábio, Cozzolino Salvatore, Draper David, de Barros Fábio, Félix Leonardo P, Fay Michael F and Palma-Silva Clarisse 2014. Rock outcrop orchids reveal the genetic connectivity and diversity of inselbergs of northeastern Brazil. BMC Evolutionary Biology 14:1–16.

Slatkin Montgomery 1987. Gene flow and the geographic structure of natural populations. Science 236:787–792.

Smadja Carole M. and Butlin Roger K. 2011. A framework for comparing processes of speciation in the presence of gene flow. Molecular Ecology 20:5123–5140.

Smith J Maynard 1966. Sympatric speciation. The American Naturalist 100:637–650.

Spurgin Lewis G., Illera Juan Carlos, Jorgensen Tove H., Dawson Deborah A. and Richardson David S. 2014. Genetic and phenotypic divergence in an island bird: Isolation by distance, by colonization or by adaptation? Molecular Ecology 23:1028–1039.

Templeton Alan R 1980. The theory of speciation via the founder principle. Genetics 94:1011–1038. Templeton Alan R. 2008. The reality and importance of founder speciation in evolution. BioEssays 30:470–479.

Turbek Sheela P., Scordato Elizabeth S.C. and Safran Rebecca J. 2018. The Role of Seasonal Migration in Population Divergence and Reproductive Isolation. Trends in Ecology & Evolution 33:164–175.

von Rönn Jan A.C., Shafer Aaron B.A. and Wolf Jochen B.W. 2016. Disruptive selection without genome-wide evolution across a migratory divide. Molecular Ecology 25:2529–2541.

Winker Kevin 2000. Migration and speciation. Nature 404:36–36.

Winker Kevin and Pruett Christin L. 2006. Seasonal Migration, Speciation, and Morphological Convergence in the Genus Catharus (Turdidae). The Auk 123:1052–1068.

Yamaguchi Ryo and Iwasa Yoh 2013. First passage time to allopatric speciation. Interface Focus 3:20130026.

Yamaguchi Ryo and Iwasa Yoh 2016. Smallness of the number of incompatibility loci can facilitate parapatric speciation. Journal of Theoretical Biology 405:36–45.

Yamaguchi Ryo and Iwasa Yoh 2017a. Parapatric speciation in three islands: dynamics of geographical configuration of allele sharing. Royal Society Open Science 4:160819.

Yamaguchi Ryo and Iwasa Yoh 2017b. A tipping point in parapatric speciation. Journal of Theoretical Biology 421:81–92.

Yamaguchi Ryo, Iwasa Yoh and Tachiki Yuuya 2021. Recurrent speciation rates on islands decline with species number. Proceedings of the Royal Society B: Biological Sciences 288:20210255.

CAPÍTULO II

O papel das barreiras intermitentes em um modelo de especiação em ilhas
(The role of an intermittent barrier in a islands speciation model[2])

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[2] Artigo formatado para submissão à revista *Journal of Evolutionary Biology*.

ABSTRACT

Generally, geographic barriers prevent migration between populations, increasing the probability of speciation by allopatry. Nevertheless, barriers created by seawater can retreat when sea level drops to the point of connecting islands across the seabed, allowing contact between previously isolated populations. The cyclic fluctuation can promote taxon pulses, which are reflected in the species richness of the islands. Here we investigate how intermittent barriers, produced by sea-level fluctuations, affect species richness in a two-island system. We used a neutral evolutionary model based on individuals and performed simulations with real sea-level data over the past 800 thousand years assuming that individuals can only migrate form on island to the other in absence of seawater barrier. We investigated the speciation events for different seabed depths and migration rate. Under shallow seabed, the isolation periods are short, and speciation occurs only if migration is small. For deeper seabed the periods of isolation increase, and speciation can also happen by allopatry. We identified combinations of migration rate and isolation time where taxon pulses are responsible for increasing species richness on the islands and others that are not. The model discussed here allows insights into species evolutionary history and help understand why species respond differently to oscillatory barriers.

Keywords: sea-level fluctuation, gene flow, geographical isolation, speciation, taxon pulse

INTRODUCTION

The traditional understanding of speciation is based on the idea of geographic isolation, in which a population is divided by a barrier that interrupts gene flow (Coyne and Orr 2004). The separated populations accumulate independent genetic changes that eventually result in distinct species, a process known as allopatric speciation (Fitzpatrick et al 2009; Albert et al 2017). Empirical examples of allopatry show the close link between geographical barriers and diversification rate for many species, including island endemics (Turelli et al 2001). However, barriers are not always permanent, and might oscillate or even disappear before the process of speciation is completed. An important example is the change in sea level due to temperature changes during the Pleistocene. During the Last Glacial Maximum (LGM), for instance, the sea level dropped approximately to 120m below the present level and connected exposed seabeds (Bird et al 2005).

The cyclic formation and breakdown of geographical barriers promote successive events of expansion and isolation of populations. This is an ideal scenario for taxon pulse occurrence (Erwin 1979; 1981; Schweizer et al 2010; Brooks et al 2019). Pulses are triggered by large-scale environmental changes, including global climate change. The taxon pulse model was originally proposed to explain carabid distribution patterns (Erwin 1979; 1981; 1985). However, other systems can be explored in the context of the taxon pulse hypothesis, which has as its general patterns one vicariance event and one biotic expansion event after the original barrier breach. Episodes of vicariance, which produce stable and ecologically isolated populations, alternate with episodes of biotic expansion, during which members of the population living in adjacent geographic areas have the opportunity to contact each other (Hoberg and Brooks 2008; Brooks 2019). During the Pleistocene, for example, sea level fluctuated, affecting the species around the world (Hewitt 2000). There are numerous empirical studies that associate the glacial and interglacial cycles of the Pleistocene with the diversification of different animal and plant groups (Guo et al 2015; Tschá et al 2017; You et al 2010; Song et al 2009; Zhang et al 2008). The cavy *Cavia intermedia* is an endemic rodent to the Moleques do Sul Island, in southern Brazil. The species evolved from individuals of the *C. magna* that were isolated around 8,000 years ago with the rise in sea level (approximately above 32 m) at the end of the Last Glacial Maximum (Cherem et al 1999; 2004). In South-East Asia, fluctuating sea level periodically converted mountains into geographically isolated islands, which facilitated allopatric speciation of plants, and connected regions previously isolated by exposed seabeds, which promoted migration of their populations (Guo et al 2015). These previous empirical studies showed that all observed species were subjected to intermittent barriers due to global climatic oscillations. But despite having gone through the same events, the diversification rate is not the same for all of them because species with larger genomes tend to evolve faster than others (Princepe et al 2022), we hypothesized that the duration of isolation and connection cycles can profoundly impact the emergence of new species.

Here we propose a two-island neutral model to study the conditions that favor speciation in a scenario of sea-level oscillations, where events of isolation and reconnections occur cyclically. The model is based on our previous study (Princepe et al 2022) where individuals inhabit two spatial sites (islands) with equal carrying capacity and can migrate between them according to a constant rate. In the present work, we use this study to calibrate our model and tune the parameters so as to avoid sympatric speciation. This guarantees that when the sites are completely isolated, i.e., no migration, the population splits in exactly two species, one in each island. On the other hand, for large and constant migration rates, populations are well connected and evolution leads to a single species occupying both islands. Here we use the sea-level data of the past 800 thousand years, assuming that the two islands become isolated when the sea level rises above a threshold. On the other hand, when the sea level is below this threshold, the islands become connected and individuals can migrate with a constant probability. We investigate the effects of seabed depths and migration rate on the diversity patterns of the system. We also considered hypothetical periodic sea level oscillations to better understand the dynamics. We showed that speciation can be sensitive to these parameters and discuss our results in the light of empirical examples and theories that support our model predictions.

MATERIALS AND METHODS

The model

We propose a model to evaluate the effects of intermittent barriers on the species richness of populations inhabiting two islands. We use individual based simulations inspired by the model studied by Princepe et al (2022): the individuals are distributed in two islands with the same carrying capacity and can migrate from one to another when the barrier separating them is lifted. Mating occurs only between individuals in the same island and is restricted by a minimal genetic similarity. The genetic information of the population evolves due to recombination and mutation of their genomes and speciation events are inferred from the breakdown of gene flow. Unlike the original study (Princepe et al 2022), here we do not assume constant migration rate between islands, but cyclic phases of isolation and connection, that follow the historical (Spratt and Lisiecki 2016) or hypothetical sea-level fluctuation.

Following Princepe et al (2022), each individual is described by its biallelic genome, a chain of B loci where each locus can assume the alleles 0 or 1. Individuals are hermaphroditic and reproduction is sexual. The carrying capacity in each island, M, (hereafter called population size) remains constant throughout the simulation, with small fluctuations allowed during the migration step. The dynamic begins with genetically identical individuals equally distributed in two islands and follows the steps:

M*igration*: when the islands are connected, each individual can migrate from one island to another, with a probability ε, every iteration. Therefore, the population size in each island may fluctuate after migration, but the total in the two islands does not change.

Reproduction: after migration, individuals can reproduce with others in the same island. The first parent ($P1$) is chosen randomly, then the second parent ($P2$) is selected, also randomly, among the other individuals in the island. To mate, the genetic distance between the selected individuals must be less or equal the maximum (Hamming distance) of G loci. If the pair is incompatible, another $P2$ is randomly selected until this condition is satisfied. If, after M attempts, no matching individual is found, $P1$ is discarded, and a random individual (with replacement) is selected as $P1$. The offspring's genome is formed by the recombination of their parents, gene by gene, with equal probability followed by a mutation probability μ per *locus*. The generations do not overlap, i.e., in each island, *M* offsprings are born and replace the previous population. Thus, fluctuations in population size that may have occurred after migration are compensated, and the total population restores to *M* in each island.

Defining Species: A species is defined by the group of individuals that enable genetic flow regardless the island they inhabit, not only by direct genetic compatibility with others but also through intermediary individuals. The genetic distance between any pair of individuals belonging to different species is always larger than the threshold *G*, assuring reproductive isolation.

Intermittent barriers determined by sea level fluctuation

To investigate the effects of intermittent barriers on speciation, we used the sea level data from Spratt and Lisiecki (2016). This study, based on ocean sediment core data, is a compilation of several publications on sea-level reconstruction and covers the last 800 thousand years (Figure. 1). Considering that the depth of the seabed varies according to the local geomorphological features and, therefore, there are different heights capable of promoting the isolation of populations, we simulated several seabed depths. If the seabed is -25m, for example, it means that populations remain isolated until this value and are connected when the sea-level is below it, when migration becomes possible.

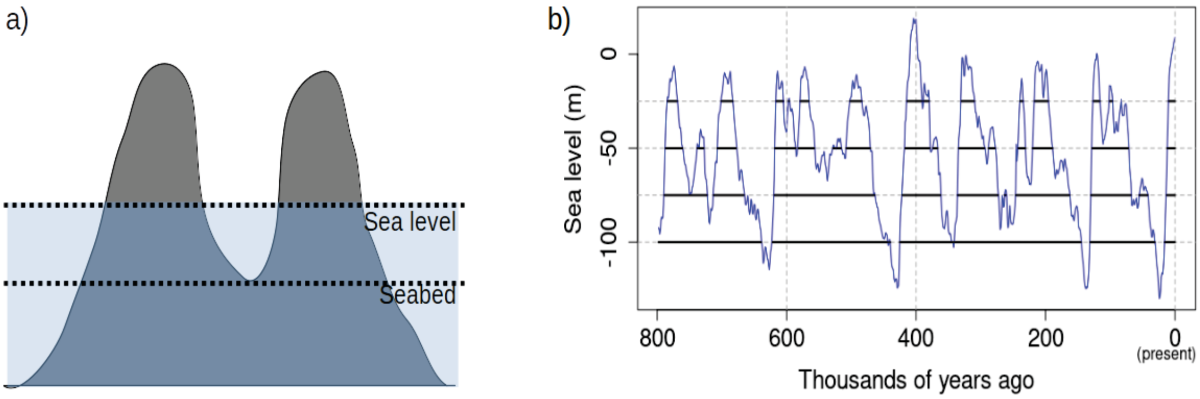

Figure 1. Model's elements. (a) The model simulates a scenario of two islands where individuals can migrate from one island to another when the sea level is above the seabed. (b) Sea level reconstruction of the last 800 thousand years (blue line) by Spratt and Lisiecki (2016). Horizontal lines highlight different seabed depths: it is solid when the sea level is above the seabed, promoting isolation, and it is dashed when migration is allowed.

Intermittent barriers in periodic sea level fluctuations:

To better evaluate the effect of cyclic barriers in speciation, we also considered a simplified version of the oscillations, assuming they are periodic with equal periods of isolation and connection (P). At the start of the simulation the islands are kept isolated for P years and, after that, they are connected for another P years, and so on, until the end of the simulation. As before, the migration occurs only in the connection period, with a probability ε per individual.

Parameters and data analysis

Based on Princepe et al (2022), we fixed the following parameters throughout the simulations: genome size (B = 2,000 loci), maximum genetic distance for mating ($G = 0.05B$), population size per island (M = 200) and mutation rate (μ = 0.001 per locus). These parameters guarantee that, in absence of migration, the model results in the formation of two species (one in each island), in agreement with strict allopatric speciation. Three parameters were varied: (i) *migration probability* (ε), defined as the probability of an individual migrating from one island to another when they are connected. We varied the migration probability between 0 and 0.4 at steps of 0.02; (ii) *seabed* (h), measured in relation to the present sea level. The connection between island occur only when the sea-level is below the seabed (Fig 1a). For this parameter, we studied values between -10 m and -100 m at steps of -5 m. Finally, (iii) period (P) for the periodic cycles simulations, defined as time populations are isolated or connected in each cycle, was varied between -10 and -100 m at steps of -5 m.

To analyze the last 800 thousand years of sea-level fluctuation we converted this time length into 2,000 iterations of the model, otherwise the computational cost would be too high. Then, 400 years is equivalent to one iteration of the model and the mutation rate fixed 0.001 corresponds to $2{,}5\text{x}10^{-6}$ per year. For each set of parameters, 50 repetitions were performed.

RESULTS

Seabed depths lead to long isolation periods and, therefore, to fewer oscillation cycles. An island whose seabed is -100 m, for instance, would go through only 5 oscillation cycles in which the isolation phases last approximately 200 thousand years. On the other hand, an island with seabed at -25 m would go through 12 oscillation cycles of approximately 10,000 years.

The first thing we are interested in is how species evolution depends on migration rate (ε) and on seabed depth (*h*). Figure 2 shows the species richness at three different times: (a) 600,000 years ago, (b) 400,000 years ago and (c) at the present as a function of ε and *h*. Except low values of migration rate (ε = 0.02) the presence of cyclic barriers is essential to promote speciation: low values of *h* results in the absence or rare speciation events (the darker areas on the right in Fig. 2), but as *h* increases, the time in isolation increases and speciation becomes more likely to occur. The higher species richness was observed when migration rates were intermediary values (0.02 < ε < 0.1). The seabed depth that most favors speciation varies over time: For 600,000 years ago, the maximum occurred around *h* = -85 m, whereas for 400,000 years ago, it was concentrated at about *h* = -50 m. At present time, on the other hand, the peaks were about *h* = -80 m (Fig. 2).

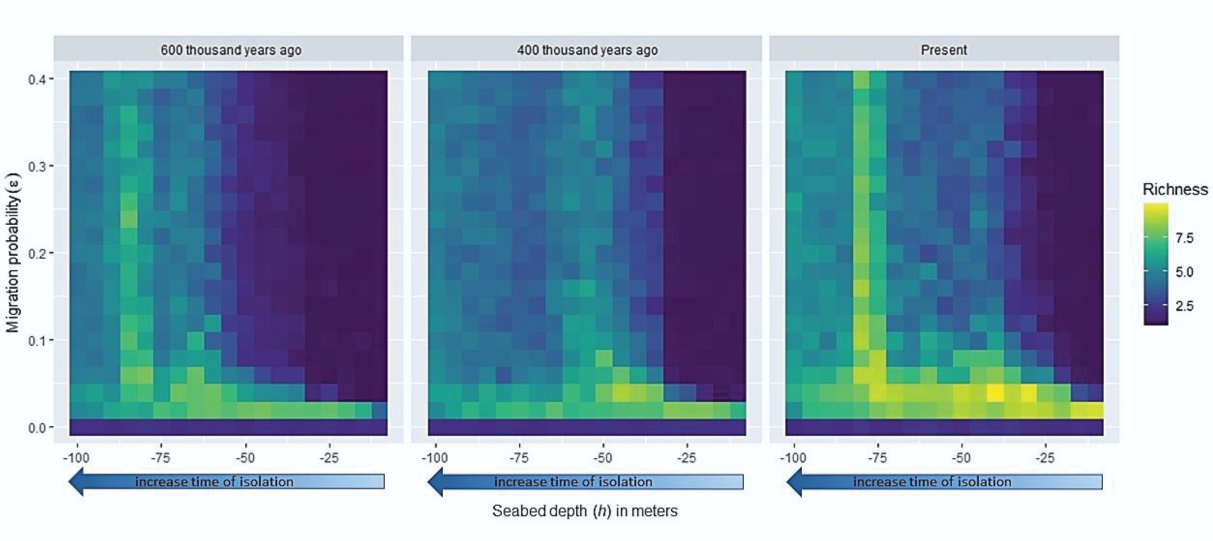

Figure 2. Species richness to different migration probability and seabed depths for different times. Each plot shows the species richness for different times over simulation. Lower migration probability (ε < 0.1) is responsible for increasing the number of species.

Figure 3 shows the temporal variation of species richness for different seabed depth. It helps to explain the displacement of the richness peak over time shown in Figure 2. In the absence of barrier, speciation is really rare, regardless the migration rate (see the figures in the first row of Fig. 3). For shallow seabed (*h* = -25), there are several cycles with short-term isolation and long-term connection. These short times in isolation are not enough to promote speciation under high migration (ε = 0.4), but it is enough under low migration rate (ε = 0.04) (compare the figures in the second row of Fig. 3). It is important to note that, although the time in isolation seems to be irrelevant, it was crucial to promote speciation when ε = 0.04. When the connection pattern is reversed (*h* = -100), that is, cycles with long-term isolation, and short-term connection, migration has a secondary effect on speciation. During the time the islands are connected, species from one island can colonize the other, and the subsequent isolation favors new speciation events for high migration, a typical pattern of taxon pulse theory. However, extinction events occur after the pulse, reducing the diversity back to one species per island after a few iterations (Fig. 3, *h* = -100, ε = 0.4). Under low migration rate this pattern is not so clear (Fig. 3, *h* = -100, ε = 0.04).

Cycles with intermediate isolation/connection duration are the ones with the highest species richness (Fig. 3, *h* = -50 and *h* = -75): the duration of the isolation phase must be long enough to promote speciation but not so long for allowing extinction.

Periodic cycles

The results for periodic cycles reinforce that lower migrations favor speciation (see species richness for ε = 0.04 and 0.4 in Fig. 4a). Nevertheless, the effect of the length of cycles on speciation is not so obvious, as some periods favor speciation while others do not. Interestingly, the periods that favor speciation at low migration (ε = 0.04) are opposite to the periods that favor speciation in high migration (ε = 0.4) (Fig. 4a). In Figure 4b (3), we found a pattern that is contrary to that expected for the taxon pulse, in which speciation events occur during the connection phases and not during the isolation phases.

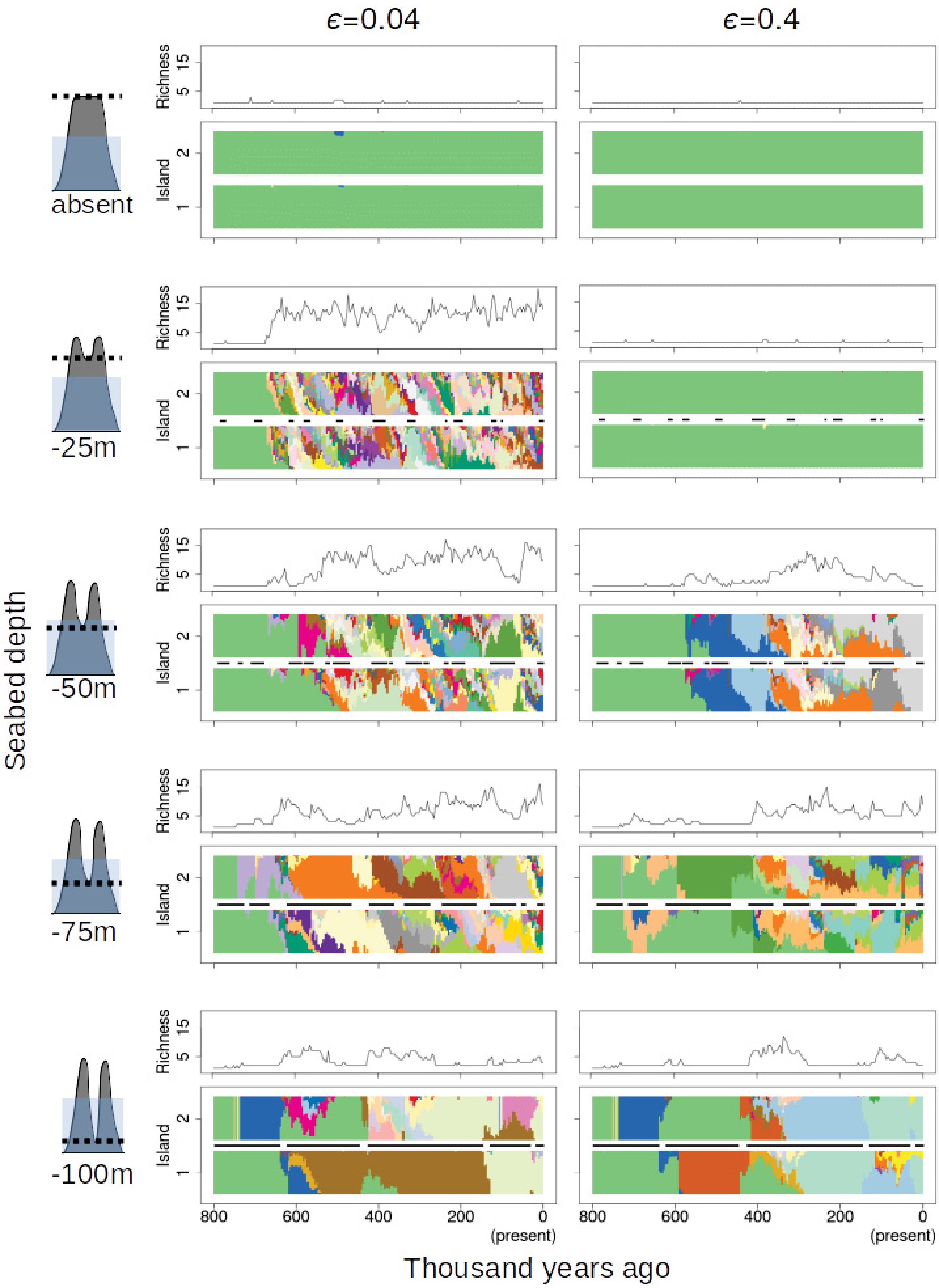

Figure 3. Population evolution on each island over 800 thousand years for different seabed depth and migration probability (indicated in the panel). At the top of each figure, the species richness throughout the simulation is highlighted. At the bottom the species are represented by different colors within each island and the vertical amplitude of the colors is proportional to the species' abundance. The black horizontal lines between the islands indicate the isolation time. The figures in the first row consider the absence of barrier with a constant migration rate ε.

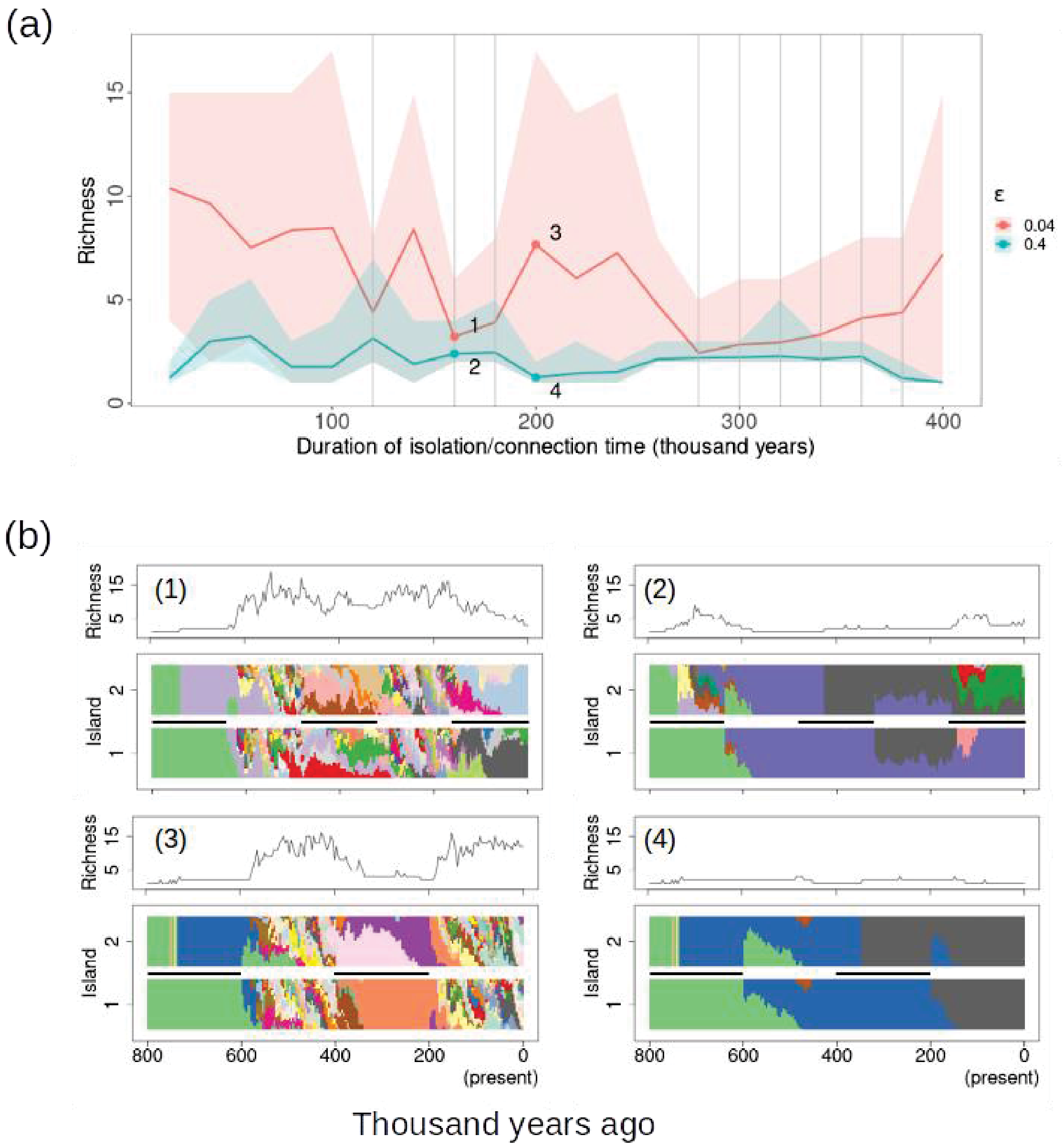

Figure 4. In (a), species richness for different isolation/connection times and migration probability (ε). The solid lines represent the average value of all simulations and the shadowed areas show a confidence interval of 90%. In (b), each figure (1, 2, 3 and 4) refers to the evolution of populations at specific points, indicated in (a).

DISCUSSION

Here we have shown that both the duration cycles of connection/isolation between islands and the intensity of migration promoted by the islands' connections affected species richness. Seabed depth controlled the duration of the isolation and connection phases of the cycles. This had implications for speciation. Additionally, the results of the simulations in which we varied the migration intensity revealed differences in the patterns of species richness between the populations studied. Populations subjected to lower migration probability (when comparing $\varepsilon = 0.04$ to $\varepsilon = 0.4$) showed greater species richness.

Here, intermittent barriers accelerate the speciation process due to the generated isolation. When the duration of the isolation phases of a cycle was short (seabed depth -25 m), the speciation was favored exclusively by low migration rate (see Fig. 3c). Under this situation, few individuals migrated and a short time of isolation was enough for speciation because of the accumulated genetic differences (Smadja and Butlin 2011; Cowie and Holland 2006). Additionally, speciation was leveraged/stimulated even with the maintenance of gene flow by founder mechanisms (Barton and Charlesworth 1984; Templeton 1980; Gavrilets and Hastings 1996; Templeton 2008), similarly to continuous migrations of low intensity (Princepe et al 2022). The opposite (high migration) led to the homogenization of populations and, consequently, little or no speciation. Indeed, as Ziwen et al (2019) have pointed out, gene flow during speciation would not necessarily prevent speciation, as long as migration is not so high as to homogenize populations.

Our theoretical results — that different patterns of diversification for different seabed depth and migration intensity — agree with previous empirical studies. According to Erwin's theory (1979; 1981; 1985), the taxon pulse, isolation phases during high sea level would provide opportunities for allopatric diversification, while the connection phases, at low sea level, would provide opportunities for population expansion (migration events). We observed these dynamics in some events (see Fig.3 fifth row for $\varepsilon = 0.04$), where, just after the third isolation period, the speciation increased. However, the long period in isolation favored extinction. The theory of island biogeography proposes that small populations are more vulnerable to extinction (MacArthur and Wilson 1967). Therefore, populations recently formed by the taxon pulse can go extinct, reducing species richness to one in each island if the isolation time is excessively long. Alternatively, the diversity decreases because the model's parameters do not allow sympatric speciation, and the maintenance of the species depends on non-interrupted population reproduction, which happens by chance. Therefore, the longer the time in isolation, the higher is the chance that the number of species in each island is reduced to one.

We also observed the opposite dynamics expected by the taxon pulse: isolation disfavoring speciation followed by migration favoring it. In Figure 4b (1), the first isolation event imposed allopatric speciation, resulting in two species. Then, a few individuals (due to the low migration rate) from each species colonize the other island during the connection. As the smaller the population size, the shorter the time for speciation, these two original species fastly evolve into four species, even in the absence of isolation. Surprisingly, these constant few migrants can create more than four species during the connection phase. The migration of few individuals led to rapid speciation by founder effect (Barton and Charlesworth 1984; Templeton 2008). Here there appears to be a sequence of founder events occurring, mediated by the combination of long-term connection and low migration rate. It is important to highlight that in the absence of a previous isolation event, those speciation would never occur. When the new isolation period occurred, the founder effect ceased, and only extinctions occurred.

Although our model is designed for islands, it can be used in different scenarios. In coastal regions, for example, wider continental shelves allow longer connection time between estuarine rivers at low sea level, this implies greater probability of freshwater species migration, while narrow continental shelves remain longer in geographic isolation during high sea level and, therefore, reduced migration opportunity for freshwater species. According to Baggio et al (2017) and Tscha et al (2017) the geomorphology of the continental shelves influenced the genetic diversification of estuarine species along the Brazilian coast. They reported greater diversity and higher rates of endemism in fish in northeastern Brazil (narrow continental shelf) compared to southern Brazil (wide continental shelf).

Three important lessons can be drawn from this work. First, intermittent barriers promoted by isolation and connection cycles, potentiated speciation events. Second, low-intensity migrations during connection phases are responsible for introducing genetic novelties and accelerating the speciation process. Third, although the model has limitations due to its simplifications in relation to the parameters used, such as population size, mutation rate, migration probability, it has the potential to explain the mechanisms behind the biological diversity of both two-island and other systems with similar scenarios that present cyclic isolation and connection events.

REFERENCES

Albert, J. S., Schoolmaster, D. R., Tagliacollo, V., & Duke-Sylvester, S. M. (2017). Barrier displacement on a neutral landscape: Toward a theory of continental biogeography. *Systematic Biology*, 66(2), 167–182.

Baggio, R. A., Stoiev, S. B., Spach, H. L., & Boeger, W. A. (2017). Opportunity and taxon pulse: the central influence of coastal geomorphology on genetic diversification and endemism of strict estuarine species. *Journal of Biogeography*, 44(7), 1626–1639.

Barton, N. H. & Charlesworth, B. (1984). Genetic revolutions, founder effects, and speciation. *Annual Review of Ecology and Systematics*, 15, 133–164.

Bird, M. I., Taylor, D. & Hunt, C. (2005). Paleoenvironments of insular Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? *Quaternary Science Reviews*, 24, 2228–2242.

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

Cherem, J. J., Olimpio, J. & Ximenez, A. (1999). Descrição de uma nova espécie do gênero *Cavia Pallas*, 1766 (Mammalia - Caviidae) das Ilhas dos Moleques do Sul, Santa Catarina, Sul do Brasil. *Biotemas*, 12(1), 95–117.

Cherem, J. J., Simões-Lopes, P. C., Althoff, S. & Graipel, M. E. (2004). Lista dos mamíferos do estado de Santa Catarina, sul do Brasil. *Mastozoología Neotropical*, 11(2), 151–184.

Costa, C. L. N., Lemos-Costa, P., Marquitti, F. M. D., Fernandes, L. D., Ramos, M. F., Schneider, D. M., Martins, A. B., & de Aguiar, M. A. M. (2019). Signatures of Microevolutionary Processes in Phylogenetic Patterns. *Systematic Biology*, 68(1),131–144.

Costa, C. L. N., Schneider, D. M., Ramos, M. F., & de Aguiar, M. A. M. (2018). Constructing phylogenetic trees in individual based models. *Physica A: Statistical Mechanics and its Applications*, 510, 1–14.

Cowie, R. H. & Holland, B. S. (2006). Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography* (33), 193–198.

Coyne J. A. & Orr H. A. (2004). *Speciation*. Sunderland, MA: Sinauer Assoc. 545 pp.

de Aguiar, M. A M, Baranger, M., Baptestini, E. M., Kaufman, L., & Bar-Yam, Y. (2009). Global patterns of speciation and diversity. *Nature*, 460(7253), 384–387.

Erwin, T. L. (1979). Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In T. L. Erwin, G. E. Ball, & D. R. Whitehead (Eds.), *Carabid beetles: their evolution, natural history, and classification* (pp. 539–592). Dr W. Junk Publishers.

Erwin, T. L. (1981). Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. In G. Nelson & D. E. Rosen (Eds.), *Vicariance Biogeography: a critique* (pp. 159–196). New York, Columbia University Press.

Erwin, T. L. (1985). The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In *Taxonomy, phylogeny and zoogeography of beetles and ants* (Issue 1).

Fitzpatrick, B. M., Fordyce, J. A., & Gavrilets, S. (2009). Pattern, process and geographic modes of speciation. *Journal of Evolutionary Biology*, 22(11), 2342–2347.

Gavrilets, S. (2003). Perspective: Models of speciation - What have we learned in 40 years? *Evolution*, 57(10), 2197–2215.

Gavrilets, S. (2014). Models of speciation: Where are we now? *Journal of Heredity*, 105(S1), 743–755.

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

Gavrilets, S., Li, H., & Vose, M. D. (2000). Patterns of Parapatric Speciation. *Evolution*, 54(4), 1126–1134.

Guo, Y. Y., Luo, Y. B., Liu, Z. J., & Wang, X. Q. (2015). Reticulate evolution and sea-level fluctuations together drove species diversification of slipper orchids (Paphiopedilum) in South-East Asia. *Molecular Ecology*, 24(11), 2838–2855.

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907–913.

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.

MacArthur, R. H. & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Princepe, D., Czarnobai, S., Pradella, T. M., Caetano, R. A., Marquitti, F. M. D., de Aguiar, M. A. M., and Araujo, S. B. L. 2022. “Diversity patterns and speciation processes in a two-island system with continuous migration”. *Evolution* (*In Press*)

Schweizer, M., Seehausen, O., Güntert, M. & Hertwig, S. T. (2010). The evolutionary diversification of parrots supports a taxon pulse model with multiple trans-oceanic dispersal events and local radiations. *Molecular Phylogenetics and Evolution 54*, 984–994.

Song, G., Qu, Y., Yin, Z., Li, S., Liu, N. & Lei, F. (2009). Phylogeography of the *Alcippe morrisonia* (Aves: Timaliidae): Long population history beyond late Pleistocene glaciations. *BMC Evolutionary Biology*, 9(1), 1–11.

Spratt, R. M. & Lisiecki, L. E. (2016). A Late Pleistocene sea level stack, *Climate of the Past*, 12, 1079–1092.

Smadja, C. M. & Butlin, R. K. (2011). A framework for comparing processes of speciation in the presence of gene flow. *Molecular Ecology*, 20, 5123–5140.

Templeton, A. R. (2008). The reality and importance of founder speciation in evolution. *BioEssays*, 30, 470–479.

Tschá, M. K., Baggio, R. A., Marteleto, F. M., Abilhoa, V., Bachmann, L. & Boeger, W. A. (2017). Sea-level variations have influenced the demographic history of estuarine and freshwater fishes of the coastal plain of Paraná, Brazil. *Journal of Fish Biology*, 90(3), 968–979.

Turelli, M., Barton, N. H., & Coyne, J. A. (2001). Theory of Speciation. *Trends in Ecology & Evolution*, 16(7), 330–343.

You, Y., Sun, K., Xu, L., Wang, L., Jiang, T., Liu, S., Lu, G., Berquist, S. W. & Feng, J. (2010). Pleistocene glacial cycle effects on the phylogeography of the Chinese endemic bat species, *Myotis davidii*. *BMC Evolutionary Biology*, 10, 208.

Zhang, H., Yan, J., Zhang, G. & Zhou, K. (2008). Phylogeography and demographic history of Chinese black-spotted frog populations (Pelophylax nigromaculata): Evidence for independent refugia expansion and secondary contact. *BMC Evolutionary Biology*, 8(1), 1–16.

Ziwen, H., Xinnian, L., Ming, Y., Xinfeng, W., Cairong, Z., Norman, C. D., Chung-I, W. & Suhua, S. (2019). Speciation with gene flow via cycles of isolation and migration: insights from multiple mangrove taxa, *National Science Review*, 6(2), 275–288.

CONSIDERAÇÕES FINAIS

Investigamos os processos pelos quais a migração leva à especiação. No Capítulo I, consideramos um modelo com migração contínua e observamos dois modos de especiação induzidos pela migração: (I) especiação por populações fundadoras e (II) especiação simpátrica induzida pela migração. O primeiro modo, ocorreu quando os migrantes que chegavam a uma ilha não conseguiam se reproduzir com a população residente por serem de uma espécie diferente e, quando conseguiam acumular ao longo de várias gerações e estabelecer uma população, fundam uma nova espécie, sendo o modo dominante para baixas probabilidades de migração. O segundo modo parece ocorrer com mais frequência sob probabilidades de migração ligeiramente maiores. Aqui as ilhas apresentavam espécies comuns, então os migrantes podiam se reproduzir com a população residente, e suas novidades genéticas incorporadas promoveram a especiação. No Capítulo II, consideramos um modelo com migração intermitente, seguindo as flutuações do nível do mar e vimos que os eventos cíclicos de isolamento e conexão aumentaram substancialmente os eventos de especiação. A intensidade da migração foi importante na determinação do tempo de isolamento necessário para haver especiação. Aqui também foi observado pulsos de diversificação condizentes com a teoria de pulso de táxon. Contudo, este trabalho fornece subsídios para ampliar o entendimento do papel da migração na especiação e na diversidade biológica.

REFERÊNCIAS BIBLIOGRÁFICAS

Albert, J. S., Schoolmaster, D. R., Tagliacollo, V., & Duke-Sylvester, S. M. (2017). Barrier displacement on a neutral landscape: Toward a theory of continental biogeography. *Systematic Biology*, *66*(2), 167–182. https://doi.org/10.1093/sysbio/syw080

Baggio, Rafael A., Stoiev, S. B., Spach, H. L., & Boeger, W. A. (2017). Opportunity and taxon pulse: the central influence of coastal geomorphology on genetic diversification and endemism of strict estuarine species. *Journal of Biogeography*, *44*(7), 1626–1639. https://doi.org/10.1111/jbi.12934

Baggio, R. A. (2016). *Desvendando a história antiga e recente de peixes neotropicais usando marcadores moleculares*. 129. https://doi.org/10.13140/RG.2.2.10627.91686

Baptestini, E. M., de Aguiar, M. A. M., & Bar-Yam, Y. (2013). Conditions for neutral speciation via isolation by distance. *Journal of Theoretical Biology*, *335*, 51–56. https://doi.org/10.1016/J.JTBI.2013.06.011

Bird MI, Taylor D, Hunt C. (2005). Palaeoenvironments of insu- lar Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? Quaternary Science Reviews, 24, 2228– 2242.

Bolnick, D. I., & Fitzpatrick, B. M. (2007). Sympatric Speciation: Models and Empirical Evidence. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 459–487. https://doi.org/10.1017/S1743921310002723

Costa, C. L. N., Lemos-Costa, P., Marquitti, F. M. D., Fernandes, L. D., Ramos, M. F., Schneider, D. M., Martins, A. B., & de Aguiar, M. A. M. (2018). Signatures of Microevolutionary Processes in Phylogenetic Patterns. *Systematic Biology*, *June*, 1–14. https://doi.org/10.1093/sysbio/syy049

Costa, C. L. N., Schneider, D. M., Ramos, M. F., & de Aguiar, M. A. M. (2017). *Constructing phylogenetic trees in individual based models*. http://arxiv.org/abs/1709.04416

Coyne J. A., Orr H. A. (2004). Speciation. Sunderland, MA: Sinauer Assoc. 545 pp.

Darwin C. (1859). The Origin of Species. John Murray, London

de Aguiar, M. A M, Baranger, M., Baptestini, E. M., Kaufman, L., & Bar-Yam, Y. (2009). Global patterns of speciation and diversity. *Nature*, *460*(7253), 384–387. https://doi.org/10.1038/nature08168

de Aguiar, Marcus A.M. (2017). Speciation in the Derrida-Higgs model with finite genomes and spatial populations. *Journal of Physics A: Mathematical and Theoretical*, *50*(8). https://doi.org/10.1088/1751-8121/aa5701

Erwin, T. L. (1979). Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In T. L. Erwin, G. E. Ball, & D. R. Whitehead (Eds.), *Carabid beetles: their evolution, natural history, and classification* (pp. 539–592). Dr W. Junk Publishers.

Erwin, T. L. (1981). Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. In G. Nelson & D. E. Rosen (Eds.), *Vicariance Biogeography: a critique* (pp. 159–196). New York, Columbia University Press.

Erwin, T. L. (1985). The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In *Taxonomy, phylogeny and zoogeography of beetles and ants* (Issue 1). https://doi.org/10.2165/11207260-000000000-00000

Fitzpatrick, B. M., Fordyce, J. A., & Gavrilets, S. (2009). Pattern, process and geographic modes of speciation. *Journal of Evolutionary Biology*, *22*(11), 2342–2347. https://doi.org/10.1111/j.1420-9101.2009.01833.x

Gavrilets, S. (2003). Perspective: Models of speciation - What have we learned in 40 years? *Evolution*, *57*(10), 2197–2215. https://doi.org/10.1111/j.0014-3820.2003.tb00233.x

Gavrilets, S. (2014). Models of speciation: Where are we now? *Journal of Heredity*, *105*(S1), 743–755. https://doi.org/10.1093/jhered/esu045

Gavrilets, S., Li, H., & Vose, M. D. (2000). Patterns of {Parapatric} {Speciation}. *Evolution*, *54*(4), 1126–1134. http://www.jstor.org.ezproxy.lib.uh.edu/stable/2640611

Guo, Y. Y., Luo, Y. B., Liu, Z. J., & Wang, X. Q. (2015). Reticulate evolution and sea-level fluctuations together drove species diversification of slipper orchids (Paphiopedilum) in South-East Asia. *Molecular Ecology*, *24*(11), 2838–2855. https://doi.org/10.1111/mec.13189

Higgs, P. G., & Derrida, B. (1991). Stochastic models for species formation in evolving populations. *Journal of Physics A: Mathematical and General*, *24*(17). https://doi.org/10.1088/0305-4470/24/17/005

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. https://doi.org/10.1111/j.1365-2699.2008.01951.x

Song, G., Qu, Y., Yin, Z., Li, S., Liu, N., & Lei, F. (2009). Phylogeography of the Alcippe morrisonia (Aves: Timaliidae): Long population history beyond late Pleistocene glaciations. *BMC Evolutionary Biology*, *9*(1), 1–11. https://doi.org/10.1186/1471-2148-9-143

Tschá, M. K., Baggio, R. A., Marteleto, F. M., Abilhoa, V., Bachmann, L., & Boeger, W. A. (2017). Sea-level variations have influenced the demographic history of estuarine and freshwater fishes of the coastal plain of Paraná, Brazil. *Journal of Fish Biology*, *90*(3), 968–979. https://doi.org/10.1111/jfb.13211

Turelli, M., Barton, N. H., & Coyne, J. A. (2001). Theory of Speciation. *Trends in Ecology & Evolution*, *16*(7), 330–343. http://tree.trends.com0169

You, Y., Sun, K., Xu, L., Wang, L., Jiang, T., Liu, S., Lu, G., Berquist, S. W., & Feng, J. (2010). Pleistocene glacial cycle effects on the phylogeography of the Chinese endemic bat species, Myotis davidii. *BMC Evolutionary Biology*, *10*(1). https://doi.org/10.1186/1471-2148-10-208

Zhang, H., Yan, J., Zhang, G., & Zhou, K. (2008). Phylogeography and demographic history of Chinese black-spotted frog populations (Pelophylax nigromaculata): Evidence for independent refugia expansion and secondary contact. *BMC Evolutionary Biology*, *8*(1), 1–16. https://doi.org/10.1186/1471-2148-8-21