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INSTITUTO DE CIÊNCIAS BIOLÓGICAS
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Jesús Nazareno Pinto Ledezma

**A ORIGEM E A ESTRUTURAÇÃO DAS ASSEMBLEIAS DE AVES DA
INFRAORDEM FURNARIIDES AO LONGO DO TEMPO E DO ESPAÇO: O
PAPEL DOS PROCESSOS HISTÓRICOS**

Orientador: Prof. Dr. José Alexandre F. Diniz-Filho

Co-orientador: Prof. Dr. Fabricio Villalobos

Goiânia

Junho 2017

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PAPEL DOS PROCESSOS HISTÓRICOS**

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Orientador: Prof. Dr. José Alexandre F. Diniz-Filho

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Goiânia

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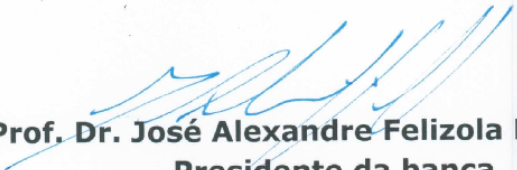


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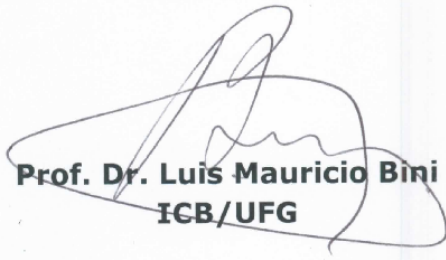
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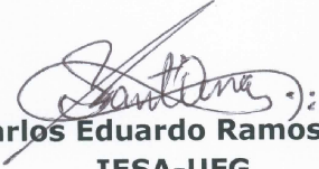
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Esta tesis está dedicada a mi madre Ángela Ledezma Vda. De Pinto, ¡la mujer más fuerte que conozco!

Dedico esta tese à minha mãe Ángela Ledezma Vda. De Pinto, a mulher mais forte que conheço!

“Nothing in biology makes sense except in the light of evolution”

Theodosius Dobzhansky

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RESUMO

Um dos principais desafios em biologia é entender os processos que dão origem e mantêm a diversidade de espécies, e que, por sua vez, determinam os padrões observados da diversidade biológica em diferentes escalas espaciais e temporais. Nesta tese, exploramos os processos históricos que geram a diversidade de espécies e a montagem de assembleias locais no infraorder dos Furnariides, a maior radiação continental endêmica de aves. De maneira geral se usaram dados de distribuição das espécies, de assembleias locais, historia de vida (e.g., preferência de habitat) e filogenias moleculares. Se demonstra que os Furnariides principalmente diversificaram no período Terciário, período no qual América do Sul foi uma ilha continente. Além disso, estão estreitamente relacionadas com o habitat que elas ocupam, sendo que os habitats de floresta representam o habitat ancestral deste clado. O padrão de riqueza de espécies de Furnariides segue o mesmo padrão de riqueza de aves em geral, com uma maior concentração de espécies em latitudes menores e em habitats de floresta. Embora a concentração de espécies seja maior em estas regiões, as regiões de latitudes maiores e de habitats abertos, apresentaram taxas de especiação, extinção e dispersão mais rápidas, sugerindo que os habitats abertos representam areias efetivas de diversificação no Neotrópico e são importantes para o mantimento da diversidade de espécies em habitats de floresta. Finalmente, a estrutura filogenética das assembleias dos Furnariides é influenciada pela preferência de habitat, além disso, a montagem de assembleias locais depende do efeito combinado das taxas diferenciadas de colonização e extinção local, assim como a conservação de nicho e da filtragem ambiental.

Palavras-chave: Aves passeriformes, Diversificação, Estrutura filogenética, Hipóteses filogenéticas, Habitats, Neotrópico, Processos macroevolutivos.

ABSTRACT

One of the major challenges in biology is to understand the processes that originate and maintain of species diversity, and that in turn, determinate the observed patterns of biological diversity at different spatial and temporal scales. Here, we explore the historical processes that generate the species diversity and the assembly of local assemblages of Furnariides, the largest bird continental endemic radiation. In general, we used data of geographic distribution, local assemblages, life history (e.g., habitat preference) and molecular phylogenies. Furnariides diversified mainly during the Tertiary period, period in which South America was an island continent. Also, they are tightly related with the habitat that they occupy, where, the forest habitats represent the ancestral habitat for this clade. The Furnariides species richness pattern follows the same species richness pattern of birds in general, with a higher concentration of species at low latitudes and in forest habitats. Although the concentration of species is higher in these regions, the regions at higher latitudes and of open habitats, present rapid rates of speciation, extinction and colonization, suggesting that these habitats represent an effective arena for diversification in the Neotropics, and that are important for the maintenance of species diversity in forest habitats. Finally, the phylogenetic structure of assemblages of Furnariides, is influenced for the habitat preferences, and that the assembly of local assemblages is determined by the combined effect of historical colonisation and local extinction, as well as, the niche conservatism and environmental filtering.

Keywords: Aves Passeriformes, Diversification, Phylogenetic structure, Phylogenetic hypotheses, Neotropics, Macroevolutionary processes.

RESUMEN

Uno de los principales desafíos en biología es entender los procesos que originan y mantienen la diversidad de especies y que a su vez determinan los patrones de observados de diversidad biológica en diferentes escalas espaciales y temporales. En esta tesis, exploramos los procesos históricos que general la diversidad de especies y el montaje de ensamblajes locales del infraorden Furnariides, la mayor radiación continental endémica de aves. Para esto, se usaron datos de distribución de especies, ensamblajes locales, historia de vida (e.g., preferencia de hábitat) y filogenias moleculares. Se muestra que los Furnariides diversification durante el periodo Terciario, en cual America del Sur era una isla continente. También se indica que las especies de este clado están estrechamente relacionadas con el hábitat que ellas ocupan, donde los hábitats de bosque representan su hábitat ancestral. El patrón de riqueza de especies, sigue el patrón de riqueza de aves en general, con una mayor concentración de especies en latitudes menores y en hábitats de bosque. Aunque la concentración de especies de Furnariides es mayor en hábitats de bosque, las regiones de latitudes mayores y de hábitats abiertos presentan tasas mas rápidas de especiación, extinción y dispersión, lo que sugiere que los hábitats abiertos son arenas efectivas para la diversificación en el Neotrópico y que son importantes para el mantenimiento de la diversidad de especies en hábitats de bosque. Por ultimo, la estructura filogenética de ensamblajes locales de Furnariides es influenciada por la preferencia de hábitat, además de que el montaje de las ensamblajes locales depende del efecto combinado de tasas diferenciales de colonización y extinción local, así como la conservación de nicho y de filtros ambientales.

Keywords: Aves Passeriformes, Diversificación, Estructura filogenética, Hipótesis filogenéticas, Hábitats, Neotrópico, Procesos macroevolutivos.

INTRODUÇÃO GERAL

Um dos principais desafios em biologia é entender os processos que dão origem e mantêm a diversidade de espécies, e que, por sua vez, determinam os padrões observados da diversidade biológica em diferentes escalas espaciais e temporais (e.g., especialmente o gradiente latitudinal de diversidade [LDG]) (Gaston, 2000). Embora estes padrões tenham sido explorados com maior frequência nos últimos anos, principalmente devido a disponibilidade de acesso a informações espaciais (e.g., áreas de distribuição, pontos de ocorrência) e evolutivas (i.e., hipóteses filogenéticas datadas), adicionado ao desenvolvimento de novos métodos analíticos, os aspectos ecológicos e evolutivos que dão origem a estes padrões ainda são extensivamente discutidos, principalmente por ainda não haver uma explicação geral satisfatória (Willig et al., 2003; Mittelbach et al., 2007; Condamine et al., 2012; Jasson et al., 2013; Brown, 2014; Fine, 2015; Schutler, 2016; Jablonski et al., 2017). No entanto, os processos macroevolutivos de especiação (formação de novas espécies) e extinção (desaparecimento de espécies) em diferentes regiões, além de dispersão entre regiões (Figura 1, ver também: Ricklefs, 2004; Goldberg et al., 2005; Jablonski et al., 2017) são processos determinantes na formação dos padrões atualmente observados (Ricklefs, 2004; Wiens, 2011). Além do mais, é importante ressaltar que eventos geológicos e climáticos podem afetar as dinâmicas destes processos macroevolutivos ao longo do tempo (Goldberg & Lande, 2007; Condamine et al., 2013), e consequentemente estruturar o padrão de riqueza e co-ocorrência de espécies em diferentes escalas espaciais (Goldberg et al., 2005; 2011; Mittelbach & Schemske, 2015; Pigot & Etienne, 2015). Os balanços entre esses diferentes processos e o modo com que eles afetam a estrutura espacial da diversidade em diferentes escalas, entretanto, ainda estão em discussão.

Diferentes explicações para os determinantes que geram e mantêm a diversidade de espécies vem sendo propostas, sendo que essas explicações podem ser agrupadas, em geral, em bióticas (intrínsecas) e abióticas (extrínsecas) (Benton, 2009). Os determinantes bióticos estão relacionados principalmente à interação entre espécies, dependendo principalmente da disponibilidade de habitats e recursos (MacArthur & MacArthur, 1961), enquanto que os determinantes abióticos geralmente estão relacionados às variáveis físicas e ambientais (Hawkins et al., 2003) e suas mudanças ao longo do tempo (Benton, 2009; Condamine et al., 2013; Clavel & Morlon, 2017). Baseado nestes determinantes, diferentes hipóteses têm sido propostas para explicar os padrões de riqueza de espécies em grandes escalas, embora algumas dessas hipóteses tenham se unificado nos últimos anos (Fine, 2015). No entanto, as hipóteses podem ser principalmente classificadas em (1) ecológicas, (2) macroevolutivas e (3) históricas (ver Pianka, 1966 e Fine, 2015 para uma revisão extensa das hipóteses).

Entre as hipóteses que consideram os processos macroevolutivos (hipóteses macroevolutivas), as mais importantes são: a hipótese de conservação tropical do nicho (Wiens & Donoghue, 2004, TNC), a hipótese de fora dos trópicos (Jablonski et al., 2006, OTT), a hipótese de taxas de diversificação (Mittelbach et al., 2007, DRH), e a hipótese dependente da diversidade (Rabosky, 2013, DDH). Estas hipóteses principalmente se diferenciam em como as taxas da especiação (λ), extinção (μ) e dispersão (d) variam entre regiões (e.g., tropical versus temperado) ou habitats (e.g., floresta versus savana) (Figura 1). Por exemplo, a TNC, sugere taxas iguais entre regiões, e que o padrão de riqueza de espécies é resultado da maioria dos clados terem origem em áreas tropicais e ocuparem estas regiões por mais tempo, permitindo assim a acumulação de maior número espécies nos trópicos (Wiens & Donoghue, 2004). A OTT, por outro lado, sugere taxas variáveis nos processos macroevolutivos, aonde,

embora os clados tenham origem tropical (semelhante a TNC), a dispersão é mais frequente de regiões tropicais para regiões temperadas do que o contrário (Jablonski et al., 2006). A DRH, também indica taxas variáveis, sugerindo que a diversificação (especiação menos extinção) nos trópicos é maior do que em regiões temperadas, resultando em um maior número de espécies em áreas tropicais (Mittelbach et al., 2007). Finalmente, a DDH sugere que as taxas de especiação e extinção podem variar ao longo da história evolutiva dos clados em função da diversidade de espécies, afetando o padrão atual de riqueza de espécies (Rabosky, 2013).

Como os processos que determinam a riqueza de espécies, e consequentemente a co-ocorrência entre elas, mudam com a escala (Mittelbach & Schemske, 2015), por exemplo, atuando ao nível de assembleia, as interações bióticas (e.g., competição) e os filtros ambientais geralmente são invocados para explicar a montagem dessas assembleias, seja inibindo ou promovendo a co-ocorrência entre espécies estreitamente relacionadas (Webb et al., 2002; Ndirebe *et al.*, 2013). No entanto, a co-ocorrência de espécies em uma assembleia, também pode ser determinada por processos históricos (Figura 1), posto que, a co-ocorrência depende (1) do tempo em que as espécies ocupam uma região ou habitat (Wiens, 2011) e (2) da expansão geográfica das espécies dentro de um clado de volta à simpatria (Pigot & Tobias, 2015). No entanto, o tempo para alcançar simpatria secundária depende de quão fortes são as interações entre espécies-irmãs (Pigot & Tobias, 2013; Pigot & Etienne, 2015). Neste sentido, a montagem das assembleias ao longo do tempo pode surgir como resultado de processos históricos de especiação, extinção local e dispersão (Mittelbach & Schemske, 2015; Pigot & Etienne, 2015).

Embora hajam diferentes hipóteses e explicações invocadas para explicar os padrões de riqueza de espécies e de montagem das assembleias, o estudo dos processos macroevolutivos, que finalmente geram estes padrões, é essencial para melhorar nosso entendimento sobre a origem e manutenção da diversidade biológica frente as mudanças climáticas e a destruição de habitats em todo o mundo.

Um modelo geral dos processos macroevolutivos

Dentre os processos macroevolutivos, é a especiação que origina novas espécies, (principalmente por especiação por alopatria, Phillimore et al., 2008), enquanto que a extinção e a dispersão são os processos determinantes para que as espécies ocorram em uma determinada região ou assembleia (Goldberg et al., 2005; Pigot & Etienne, 2015). A Figura (1) exemplifica como a dinâmica dos processos macroevolutivos geram o padrão observado de riqueza de espécies. Por exemplo, duas regiões ou habitats (região florestal = RF e região aberta = RO) apresentam um padrão de riqueza de espécies em um tempo (t), que é determinada pelas taxas de especiação (λ_F e λ_O) e extinção em cada região (μ_F e μ_O), e pelas taxas de dispersão entre regiões (d_F e d_O). Neste modelo, as taxas de especiação, extinção e dispersão são constantes ao longo do tempo e entre linhagens, e estão ligadas a cada região de maneira independente (Goldberg et al., 2011). Embora este esboço represente melhor a dinâmica dos processos macroevolutivos em grandes escalas, pode ser aplicado em escalas menores, como assembleias locais. Por exemplo, assumindo dinâmicas de expansão e contração das áreas de distribuição das espécies (Goldberg et al., 2011; Pigot & Etienne, 2015), as assembleias locais podem evoluir ao longo do tempo por especiação por alopatria, colonização e extinção local, onde as espécies em um tempo (t) podem ser adicionadas numa assembleia através da expansão de sua área de ocorrência (colonização) ou serem

removidas da assembleia por meio da contração de sua área de ocorrência (extinção local) (Pigot & Etienne, 2015).

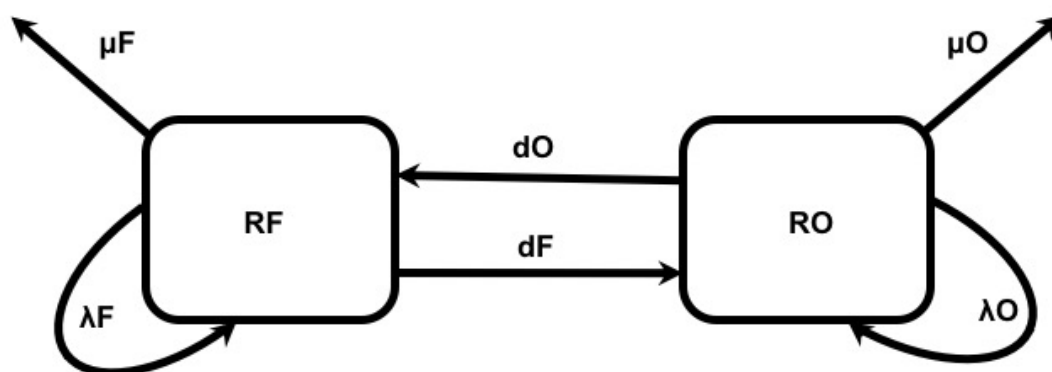


Figure 1. Esquema teórico que representa a dinâmica temporal e espacial da riqueza de espécies em diferentes habitats (se aplicar a diferentes áreas e/ou regiões geográficas). Neste caso, exemplifica que a riqueza de espécies em habitats de floresta (RF) e habitats abertos (RO) dependem das taxas de especiação (λ), extinção (μ) em cada habitat e da dispersão (d) entre habitats (adaptado de Goldberg et al., 2005; Jablonski et al., 2017).

O grupo de estudo

O Neotrópico, com mais de 3700 espécies de aves (um terço das espécies de aves conhecidas), é o reino zoogeográfico mais diversificado em espécies (Stotz et al., 1996). Do total de espécies que ocorrem no Neotrópico, cerca de 33% correspondem apenas a aves Suboscines-Passeriformes (Chesser, 2004). Este clado é considerado como a maior radiação continental endêmica (Ricklefs, 2002, Claramunt, 2010) e compreende a dois subclados, os infraordens dos Tyrannides (~502 espécies) e os Furnariides (~652 espécies) (Moyle et al., 2009). Este último, compreende sete famílias (Tamnophilidae [antbirds], Melanopareidae [crescentchests], Conopophagidae [gnateaters], Grallariidae [antpittas], Rhinocryptidae [tapaculos], Formicariidae [antthrushes], e Furnariidae [ovenbirds e allies]), das quais as famílias Furnariidae (~290 espécies) e

Thamnophilidae (229 espécies) estão entre as famílias com maior número de espécies no Hemisfério Ocidental. Os Furnariides, estão distribuídos em quase todos os habitats e micro-habitats do Neotrópico, embora sejam mais diversos e abundantes em habitats florestais (Stotz et al., 1996; Del Hoyo et al., 2003) e apresentem uma diversidade excepcional de adaptações morfológicas (Del Hoyo et al., 2003) especialmente em termos de tamanho corporal e forma do bico e cauda (Del Hoyo et al., 2003; Claramunt, 2010). A alta diversidade de espécies, sua origem endêmica e restrita ao Neotrópico e o fácil acesso a informação espacial e temporal, faz dos Furnariides um clado importante para o estudo dos processos macroevolutivos em diferentes escalas.

Apresentação da tese

Nesta tese exploramos como os processos macroevolutivos influenciam o padrão observado de riqueza de espécies e a montagem das assembleias locais (Figura 1) de aves no Neotrópico. Especificamente, a tese está dividida em três capítulos, cada um estruturado como um artigo científico. Em geral, para desenvolver a tese usamos dados publicados e disponíveis de relações evolutivas (filogenias), e dados espaciais (áreas de distribuição), ao nível de espécie e de assembleias locais de aves (Furnariides na Argentina e Bolívia), principalmente baseados em trabalho de campo e revisão de literatura. Adicionalmente, utilizamos diferentes enfoques e métodos filogenéticos comparativos que nos permitiram testar diferentes hipóteses macroevolutivas de maneira simultânea.

No primeiro capítulo, fez-se uma revisão da história evolutiva da avifauna Neotropical, usando dados do clado dos Furnariides (Suboscines, Passeriformes), um clado endêmico do Neotrópico, relacionando sua história evolutiva com os diferentes eventos geológicos, climáticos e biogeográficos que aconteceram no Neotrópico desde a

origem do clado. Mostramos que existem incongruências no tempo de origem dos Furnariides, embora a maior parte das evidências indiquem que o clado teve origem durante o período Terciário, tempo no qual a América do Sul era uma ilha-continente, e que sua história evolutiva é complexa devido a sua origem primitiva e seus altos níveis de riqueza de espécies nos diferentes habitats do Neotrópico. Finalmente, indicamos direções futuras que permitirão melhorar nosso conhecimento sobre a história evolutiva da avifauna neotropical.

No capítulo segundo examinamos as diferenças em riqueza de espécies em habitats de floresta e habitats abertos para testar três hipóteses macroevolutivas (diversification rate [DRH], out of the tropics [OTT] e tropical niche conservatism [TNC]) e analisar os papéis dos processos evolutivos como geradores do gradiente de riqueza de espécies. Mostramos que a maior parte da riqueza de espécies de Furnariides é encontrada em habitats de floresta, embora, as taxas de especiação, extinção e dispersão sejam maiores em habitats abertos. Indicamos também que a estrutura filogenética do gradiente de riqueza de espécies mostra um forte padrão espacial, onde espécies que divergiram mais cedo estão concentradas em habitats florestais e são as que determinam o gradiente de riqueza de espécies de Furnariides. Destacamos a dispersão e a extinção como os processos macroevolutivos que determinam as diferenças de riqueza de espécies entre habitats, neste caso, através da adição e extirpação de espécies de habitats abertos nas florestas. Finalmente, sugerimos a importância dos habitats abertos como áreas de diversificação para a avifauna neotropical os quais são chave para a manutenção da diversidade de aves em habitats de floresta.

No capítulo terceiro, investigamos a estrutura filogenética de assembleias locais de Furnariides no sul de América do Sul e analisamos as diferenças na riqueza de espécies entre habitats (aqui usamos a categorização de habitats do capítulo segundo). Avaliamos especificamente como os processos históricos (i.e., colonização e extinção local) determinam a montagem das assembleias locais e como a co-ocorrência de espécies dentro das assembleias está relacionada com suas taxas de diversificação e idade das espécies dentro das assembleias. Mostramos que a montagem das assembleias é governada pelo efeito combinado dos eventos históricos de colonização e extinção, assim como pela conservação de nicho e filtragem ambiental. Mostramos também, que assembleias sub-dispersas estão localizadas em habitats abertos, e assembleias não estruturadas em habitats de florestais, indicando que a preferência de habitat tem influência na estrutura filogenética das assembleias de Furnariides.

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Capítulo 1

The evolutionary history of the Neotropical Avifauna: a review based on phylogenies

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Furnariides evolutionary history

Review article

The evolutionary history of the Neotropical Avifauna: a review based on phylogenies

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ABSTRACT

We present a review about the evolutionary history of the Neotropical avifauna with focus on the largest continental endemic radiation, the Furnariides clade. We search and summarize all available phylogenetic information that includes the clade, since the publication of the phylogeny of Sibley & Ahlquist in 1990, and related this information with the major biogeographical events that happened in the Neotropics. Although there are incongruences in the estimated origin of the clade, the evidence suggest that Furnariides evolved mainly during the Tertiary period and that the lineage accumulation through time is not constant. Also, we propose future directions that can help to better understand the evolutionary history of the Neotropical avifauna based on phylogenetic information.

Keywords: Birds, Neotropics, divergence times, phylogenetic information

Historia evolutiva de la avifauna Neotropical: una revisión filogenética

RESUMEN

Presentamos una revisión sobre la historia evolutiva de la avifauna Neotropical con énfasis en el clado de los Furnariides, la mayor radiación continental endémica. Se buscó y resumió toda la información filogenética que incluye el clado de estudio, desde la publicación de la filogenia de Sibley & Ahlquist en 1990, para después relacionar esta información con los eventos biogeográficos que ocurrieron en el Neotrópico. Encontramos que hay incongruencias en el origen estimado del clado, pero la evidencia sugiere que los Furnariides evolucionaron principalmente durante el periodo Terciario y que la acumulación de linajes no fue constante a lo largo del tiempo. Finalmente

presentamos algunas direcciones futuras que nos ayudaran a entender mejor la historia evolutiva de la avifauna Neotropical en base a información filogenética.

Palabras clave: Aves, Neotrópico, tiempos de divergencia, información filogenética

INTRODUCTION

All species are related through descent from a common ancestor, which defines their evolutionary relationships. Darwin in his *Origin of Species* (Darwin 1859) illustrated the first representation of such evolutionary relationships among species in the form of a phylogenetic tree (PT). Since then, PTs have been widely used to understand the relationships among organisms or to understand how a family of related molecular sequences has been derived during evolution, helping us organizing our knowledge of life and its evolutionary history (Baum & Smith, 2013). Furthermore, PTs became the basis for the field of comparative biology and are now essential for investigating the tempo and mode of diversification, trait evolution, among other biological phenomena (Cooper et al., 2016).

Since genetic sequence-based data became widely available at early 80's (e.g., through online databases such as GenBank), reconstruction and use of PTs has steadily increased in popularity. For birds, for example, the number of publications that contain the term "avian phylogenetic reconstruction" escalated rapidly since the publication of the 'Bird Tapestry' by Sibley & Ahlquist in 1990 (Figure 1). First attempts to reconstruct avian PTs were aimed at determining phylogenetic relationships to improve taxonomic classification and estimating the genealogical relationships among bird species (Sibley, 1970; Cracraft, 1981). The main results of such studies demonstrated the monophyletic relationship among higher taxa (e.g., among families of oscine-passerines), although they did not completely resolve the monophyletic relationships among suboscines (Cracraft, 1981; Payesvsky, 2014). However, recent advances in avian phylogenetics and phylogenomics supports the monophyletic relationships among all passerine species (Chesser, 2004; Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015). Moving beyond such first attempts, nowadays most bird PTs are mainly

reconstructed to respond different ecological and evolutionary questions (e.g., How did birds evolve? Where and when did birds originate?), estimating divergence times and to infer evolutionary relationships at different taxonomic levels, especially at lower taxa level, such as, at species level (e.g., Derryberry et al., 2011; Jetz et al., 2012; Burleigh et al., 2015).

The Neotropics is the world's zoogeographical realm with more bird species, harboring around 3700 species (Stotz et al., 1996). Among these species, the New World suboscines (c. 1200 species) account for above 10% of the global avifauna and more than 30% of the Neotropical bird diversity (Chesser, 2004; Tobias et al., 2012). The New World suboscines includes two monophyletic subclades: the Tyrannides (502 species) and the Furnariides (651 species) (Renssen et al., 2017), both of which are mostly endemic to the Neotropics (~98%) and the latter one belonging to the largest continental endemic radiation (Ricklefs, 2002; Claramunt, 2010). Although the suboscines are mainly a New World clade, the infraorder Eurylaimides (52 species) is restricted to the Old World (Chesser, 2004; Moyle et al., 2006) with only one representative in the New World, the Sapayoa (*Sapayoa aenigma* [Eurylaimidae]) (Fjeldså, 2003).

Despite the Neotropical avifauna being the best-known vertebrate taxon in terms of scientific knowledge (e.g., taxonomy, ecology), little is known about their evolutionary history (but see, Brumfield, 2012; Fjeldså, 2012). The knowledge of such evolutionary history can help describe and explain diversity patterns under a temporal perspective. This can be achieved by applying a phylogenetic framework to study such patterns (Brumfield, 2012). In this review, we describe the evolutionary history of the Neotropical avifauna using the infraorder Furnariides as a model group. We focus on the clade of Furnariides, because i) this clade represents a natural evolutionary group

being clearly monophyletic (Hackett et al., 2008) and ii) its species are widely distributed along the Neotropics and its better adapted to their environmental conditions than species that arrived later in the evolutionary history (Ricklefs, 2002). These properties make the Furnariides clade an ideal model to explain the evolutionary history of birds in the Neotropics. We began our description by first exploring the ‘Bird Tapestry’ and then the sequence-based phylogenies. Finally, we relate the evolutionary history of the Neotropical avifauna to the major geological and biogeographical events that occurred in the region during the Cenozoic.

THE FURNARIIDES

Within the New World suboscines, the infraorder Furnariides (antbirds, crescentchesters, gnateaters, antpittas, tapaculos, antthrushes, and ovenbirds and allies) (Moyle et al., 2009) comprises 51% of suboscine species and 11% of all Passeriformes species (Claramunt, 2010; Remsen et al., 2017). This clade present highest levels of ecomorphological adaptations and ecological diversity, and is distributed in nearly all terrestrial habitats within the Neotropics (Stotz et al., 1996; Del Hoyo et al., 2003; Claramunt, 2010). Moreover, Furnariides species are associated with the distribution of major habitat types (Stotz et al., 1996; Pinto-Ledezma et al., 2016), where highest concentration of Furnariides species is found in the Amazonia and the Atlantic Forest ecoregions, and some peaks in the north-east Cerrado and the tropical Andes region. Conversely, lowest concentration can be found mainly in open vegetation types such as Andean and Patagonia deserts and the Llanos of Venezuela and Colombia in northern South America (Pinto-Ledezma et al., 2016). It is suggested that the Furnariides adaptation to a wide variety of habitats is the result of the clade diversifying mostly in forest habitats while still having some species that independently colonized and

diversified within open habitats (Fjeldså et al., 2005). However, recent evidence suggests that speciation and extinction rates are higher in open habitats, when compared with forest ones (Pinto-Ledezma et al., 201).

EVOLUTIONARY HISTORY OF THE NEOTROPICAL AVIFAUNA

The DNA-DNA hybridization phylogeny

A significant progress in the reconstruction of the avian evolutionary history happened in 1990, when Sibley and Ahlquist published their book “Phylogeny and Classification of Birds: A Study in Molecular Evolution” based on DNA-DNA hybridization (Sibley & Ahlquist, 1990). These authors had already published avian phylogenies but only for specific groups, including suboscines (Sibley & Ahlquist, 1985; 1986; Sibley et al., 1988). In their 1990 book, Sibley and Ahlquist presented the most inclusive account of the evolutionary history of birds, detailing all known (at that time) avian orders and families (Cracraft, 1992).

The goals of this study were to reconstruct a phylogeny of living birds and the derivation of a new taxonomic classification based on this phylogeny (Sibley & Ahlquist, 1990). The method for tree reconstruction was based on clustering techniques (i.e., UPGMA), assuming a molecular clock (Sibley & Ahlquist, 1990) in which rates of molecular evolution are equal among taxa (Zuckerkandl & Pauling, 1965). Then, the ΔT_{50H} composite measure was used to estimate the divergence rates between taxa, where each ΔT value expresses degrees of genomic divergence ($\Delta T_{50H} 1.0 = 4.5$ Ma) relative to time (Sibley & Ahlquist, 1990). Despite this great effort, their phylogeny was severely criticized mainly because of their use of the ΔT_{50H} composite measure as a proxy for absolute time and dubious correspondence with the genetic divergence between species (Cracraft, 1992; Mooers & Coltrane, 1994), which generated lack of

support in some groups such as ratites and birds of prey (Gill & Sheldon, 1991; Mindell, 1992), and the inappropriate use of the tree reconstruction method (Mindell, 1992; Harshman, 1994).

The main results based on such DNA-DNA hybridization phylogeny at least for the suboscine birds, suggested that Passeriformes and Non-passeriformes diverged at ΔT_{50H} 21.6, whereas, Passeri and Tyranni diverged at ΔT_{50H} 19.7. These results are congruent with a previous study of the same authors in 1985, which reconstructed the phylogenetic relationship among suboscine birds using the same DNA-DNA hybridization technique and morphological characters (Sibley & Ahlquist, 1985). In this study, the authors estimated the divergence between Old World suboscines (Eurylaimides) and New World suboscines (Tyranni) of ΔT_{50H} 15.8 (ca. 71.1 Ma) after the separation of South America and Africa, during the Late Mesozoic and Early Cenozoic, whereas within New World suboscines (Tyrannides and Furnariides) divergence between Tyrannides and Furnariides was estimated at ΔT_{50H} 13.8 (ca. 62.1 Ma) (Sibley & Ahlquist, 1985), during the Late Paleocene thermal maximum (Zachos et al., 2008) that also coincides with the origin and diversification of angiosperms (Beerling & Woodward, 2001).

The DNA sequence based phylogenies

After the publication of the phylogenetic hypothesis of Sibley and Ahlquist (hereafter SA phylogeny), several phylogenetic hypotheses (Figure 1a-b) for different bird groups have been reconstructed based on DNA sequence data. Some of these phylogenies include the Suboscines – Furnariides clade or are specific for this group (Appendix 1). These more recent phylogenetic hypotheses are generally congruent with the monophyly of Passeriformes (oscines and suboscines) (Barker et al., 2004; Ericson et

al., 2006; Hackett et al., 2008), although some incongruences in the tree topology have been found, causing misplacement of higher taxa (e.g., families) (Barker et al., 2002; 2004). Consequently, much effort has been placed trying to solve higher levels of phylogenetic relationships within Passeriformes (Irestedt et al., 2001; 2002; Barker et al., 2002; 2004; Chesser, 2004) and to reveal their extensive evolutionary history and biogeographic patterns (Derryberry et al., 2011; Claramunt & Cracraft, 2015).

Higher-level phylogenies

Higher-level (e.g. families, orders) phylogenies of passerine birds based on DNA sequence data (Irestedt et al., 2001; 2002; Barker et al., 2002; 2004) and inferred by different methods of phylogenetic reconstruction (e.g., Maximum Likelihood or Bayesian; see also Appendix 1), revealed new insights about the phylogenetic relationships and evolutionary history of Passeriformes. For example: i) the family Acanthisittidae is placed as a sister group of all passerine birds (Irestedt et al., 2001; 2002; Ericson et al., 2002), ii) oscines and suboscines form distinct monophyletic groups (Barker et al., 2004; Chesser, 2004) and iii) the most speciose families of suboscines such as Tyrannidae (tyrant fly-catchers) and Furnariidae (ovenbirds), represent monophyletic families (Chesser, 2004; Moyle et al., 2009).

Also, using Penalized Likelihood (PL) as a calibration method, Barker et al. (2004) suggested that oscines and suboscines diverged between 77-76 Ma (85-90 Ma, in the SA phylogeny), whereas the divergence between the New World and the Old World suboscines occurred around 67 Ma and the separation between Tyrannides and Furnariides at 61 ± 2.8 Ma, which is congruent with the divergence date of 62.1 Ma proposed in the SA phylogeny for these two clades (Sibley & Ahlquist, 1990). All of these studies indicate that all passerines had a Gondwanan origin (Irestedt et al., 2002;

Barker et al., 2002; 2004; Ericson et al., 2002), suggesting that the New World suboscines colonized South America before the opening of the Drake Passage and started to diversify near the Cretaceous-Tertiary boundary (Ericson et al., 2002; Barker et al., 2004), gradually colonizing new areas as environmental conditions changed (Irestedt et al., 2002; Ricklefs, 2002; Fjeldså, 2005).

Additionally, more recent studies of higher-level avian phylogenies using large concatenated datasets of different molecular DNA (nuclear and mitochondrial) and inferred by Maximum Likelihood and Bayesian methods (Ericson et al., 2006; Ohlson et al., 2013), indicated a sister relationship between Passeriformes, Psittaciformes and the family Falconidae and confirmed the division of oscines and suboscines as different monophyletic groups (Ericson et al., 2006). Taken together, these findings suggest an early diversification of Neoaves at the Late Cretaceous, with multiple adaptations according to changes in the environment (Fjeldså, 2005; Ericson et al., 2006). Also, they indicate that Furnariidae and Tyrannidae diverged around 55.5 Ma (Paleocene-Eocene transition), coinciding with the Paleocene-Eocene thermal maximum caused by the highest methane emissions in the Earth's history (Zachos et al., 2008).

Some of these, as well as other, studies have also suggested that Furnariidae started to diversify at ca. 44 Ma (Figure 2) during the Middle Eocene (Ohlson et al., 2013), when the climate was warm to temperate (Barreda & Palazzesi, 2010) and continued to do so over environmental changes especially during the Late Oligocene (ca. 26-24 Ma) (Derryberry et al., 2011; Fjeldså, 2012). Later in time, particularly at the climatic optimum during the Middle Miocene (ca. 16-12 Ma), the most speciose subclades (e.g., *Thamnophilinae*, *Synallaxinae*) began its radiations (Ericson et al., 2006; Hackett et al., 2008; Ohlson et al., 2013), which coincided with the major uplift of the Andes Mountain (Burnham & Graham, 1999; Hoorn et al., 2010) and the

posterior formation of the South American Arid Diagonal and the expansion of C4 grasses at the Late Miocene (Zachos et al., 2008; Le Roux, 2012) (Figure 2).

Although these studies have suggested that the New World suboscines are an old radiation (ca. 62 Ma, Ricklefs, 2002), a recent study (Claramunt & Cracraft, 2015) using a combination of DNA sequences and 130 fossil birds challenged this assertion. Reconstructing a new time-tree for Neornithes under a Bayesian framework, Claramunt & Cracraft (2015) suggested a recent origin of the New World suboscines with a divergence time estimation between Furnariides and Tyrannides at the Middle Eocene (ca. 44 Ma). Moreover, these authors also suggested that the Furnariides started to diversify at the end of the Eocene around ~36-37 Ma, when the climate was temperate to cold (Barreda & Palazzesi, 2010) just before of the Oligocene glaciation (Zachos et al., 2008; DeConto & Pollard, 2003). Accordingly, such diversification events as proposed by Claramunt & Cracraft (2015) are ~10 Ma most recent than the estimations of other studies of higher-level phylogenies (e.g., Ericson et al., Ohlson et al., 2013). Aside from the potential temporal discrepancy among studies, what is clear from all of them is that the diversification dynamics of extant birds is linked to the paleogeographic and climatic history of the Earth (Claramunt & Cracraft, 2015, see also Figure 2).

The species-level phylogenies

Within Furnariides, the only nearly complete species-level phylogeny (97% of taxon sampling) was reconstructed for the family Furnariidae (Derryberry et al., 2011). Nevertheless, there are other incomplete species-level phylogenies (Appendix 1) that have been reconstructed for particular families such as Thamnophilidae (Irestedt et al., 2004; Brumfield et al., 2007; Isler et al., 2014), Furnariidae (Fjeldså, 2005), Rhinocryptidae (Mata et al., 2009), Conopophagidae (Batalha-Filho et al., 2014), and

the subfamily Dendrocolaptinae (Rocha et al., 2015). Using both nuclear and mitochondrial DNA sequences and a Bayesian joint estimation of topology and divergence times (Appendix 1), Derryberry and colleagues (2011) reconstructed the sister relationships among all furnariid species and the between separate monophyletic relationships of the subfamilies Furnariinae (Tribes Synallaxini, Philydorini and Furnariini), Dendrocolaptinae and Sclerurinae. This phylogeny proposed that the diversification rate of Furnariids has been nearly constant for over 30 Ma with a more recent decrease in such rate around 1.7 Ma during the Pleistocene (Derryberry et al., 2011). Furthermore, they reported evidence for two increments in the diversification rate during the Furnariidae evolutionary history. The first of these increments occurred at 23 Ma in the Late Oligocene, when the climate was warm and humid (Zachos et al., 2008; Barreda & Palazzesi, 2010). The second diversification rate increment occurred at 3.5 Ma, mainly caused by a rapid speciation of the genera *Cranioleuca* (Tribe Synallaxini) (Derryberry et al., 2011) that occurred when the South American climatic pattern was established in the Late Pliocene (Simpson, 1983).

Large-scale phylogenies

Reconstructing large-scale phylogenetic trees – those comprising entire classes or higher taxonomic ranks – is still a major challenge in evolutionary biology (Smith et al., 2009). Still, about 20 years later of the publication of the SA phylogeny, large-scale and well-resolved phylogenies for the world's birds have already been reconstructed using different approaches such as supertree (Jönsson & Fjeldså, 2006), supermatrix (Burleigh et al., 2015) and modified supermatrix (Jetz et al., 2012) techniques (Appendix 1).

Particularly for suboscines and more specifically for Furnariides, most large-scale phylogenies have suggested that monophyly between suboscine species and that the diversification rates in this clade is relatively rapid (Jetz et al., 2012; Burleigh et al., 2015). For example, Jetz et al. (2012; hereafter JEA) reconstructed the first species-level megatree for extant birds, with the aim of studying and mapping the evolutionary history and diversification of all bird species. They used a concatenated DNA sequence data for 6663 bird species (67% of taxon sampling, see also Appendix 1) and placed missing species (33%) using taxonomic priors, under a Bayesian framework (See supplementary material in Jetz et al. 2012 for a detailed information of tree reconstruction). Notice that the JEA megatree was later updated according to the fossil calibrations suggested by Mayr (2013; see <http://birdtree.org/methods/> for details).

The JEA results suggested an increment in the avian diversification rate since the Early Eocene that lasted for about 45 million years (50 to 5 Ma), although the rates were not constant among bird clades (Jetz et al., 2012; Figure 2). JEA analyses also found that regions such as northern North America and Asia, as well as southern South America, present the highest diversification rates among geographic regions. Such spatial patterning is congruent with inferences derived from the higher-level phylogenies reviewed above, supporting the important role of geography and past climate dynamics influencing the patterns of extant bird diversity. Particularly for the Furnariides clade, JEA confirmed the strong contribution to the current bird richness gradient (Jetz et al., 2012; see also Figure 2) and reported that this clade presented one of the highest mean rates of lineage diversification among bird clades, only after the gulls (Laridae) and babblers (Timaliidae).

More recently, Burleigh and colleagues (2015) estimated the largest avian phylogeny using supermatrix technique. This phylogeny considered 6714 species (49

orders, 233 families and 1926 genera) and was reconstructed using 22 nuclear and seven mitochondrial loci under a Maximum Likelihood approach (Burleigh et al., 2015; see also Appendix 1). Regarding to the suboscines clade, this supermatrix phylogeny is congruent with the highest-level phylogeny of Hackett et al. (2008). For example, their results indicate a bootstrap support (BS) of 99% for the monophyletic relationship between New World suboscines (Furnariidae and Tyrannidae) and relatively low support at the family level (e.g., monophyly between Furnariidae and Formicariidae present a BS of 68%). These later findings reveal the lack of support for different nodes in the phylogeny. An issue that may only be resolved with a more comprehensive taxon sampling, particularly within problematic clades (e.g., Formicariidae, Rhinocryptidae) (Heath et al., 2008; Burleigh et al., 2015) and by using more genes or fragments of genes information, as those used in phylogenomics.

The Genome based phylogenies

Since the publication of the SA phylogeny, the reconstruction of birds evolutionary history using genome data represents the greatest advance in avian biology and evolution (Pennisi, 2014). The first attempt to reveal the avian evolutionary history using genome data was the study of Hackett et al., (2008). This study clearly supported the monophyly among Passerine birds (BS of 100%) and confirmed the monophyly among New World suboscines (BS of 100%). Interestingly, the Hackett et al. (2008) study included Parrots (Psittaciformes) and Falcons (Falconidae) as sister monophyletic groups of the Passeriformes (BS of 77% and 73% respectively) (Hackett et al., 2008). More recently, the Avian Phylogenomics Project reconstructed the first highly resolved genome-scale phylogenomic tree for the early branches in the tree of life of modern birds (Jarvis et al., 2014). The Jarvis et al. (2014) phylogeny also confirmed the

monophyly among Passeriformes and its sister relationships with parrots and falcons (in congruence with Hackett et al., 2008). However, the most surprising result from this phylogeny is that it suggested a more recent origin for all extant Neoaves (Jarvis et al., 2014), with the origin of the entire order Passeriformes being ca. 39 Ma at the end of the Eocene and the divergence between Oscines and Suboscines ca. 32 Ma at the Early Oligocene. These particular findings conflict with all previous phylogenetic studies that have used nuclear and mitochondrial DNA (e.g., Irestedt et al., 2001; 2002; Barker et al., 2002; 2004; Ohlson et al., 2013), implying that the New World suboscines represent a relatively recent group (e.g., 30 Ma instead of 50 Ma).

Surpassing the tremendous effort of Jarvis et al. (2014), a more recent work by Prum et al. (2015) presented the most comprehensive and accurate avian tree of life to date using genome data. Contrary to Jarvis et al. (2014), this recent study suggested an earlier origin of Passeriformes around ca. 50 Ma and a divergence time between Oscines and Suboscines at ca. 47 Ma during the Middle Eocene. Furthermore, regarding the New World suboscines, it proposed a split between Furnariides and Tyrannides at ca. 38 Ma, with the former clade starting to diversify at ca. 30 Ma during Early Oligocene, when the climate was humid and temperate with extensive ice sheets on East Antarctica (Barreda & Palazzesi, 2010). Although the use of genome data for reconstructing the evolutionary history of birds has certainly improved our knowledge about higher-level relationships in the avian tree of life (Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015), these genome-based phylogenies still fail to resolve the deepest relationships among bird clades. This is especially true for the Neoaves radiation, which presents a hard polytomy that could be the result of eight simultaneous cladogenetic events during the Cretaceous-Paleogene (K-Pg) boundary, as argued by Suh (2016).

CONCLUDING REMARKS

Here we have presented a review of the evolutionary history of the Neotropical avifauna, using Furnariides clade as model group, and relate their history with some of the major climatic and geological events that shape the current pattern of species distribution in the Neotropics. In summary, although there are some incongruences in the estimated divergence time of Furnariides using different data and methods to reconstruct their evolutionary history, all available evidence (see above and Appendix 1) suggests that the Furnariides evolved mainly in the Cenozoic period (Figure 2) when South America was an island continent (splendid isolation; Ricklefs, 2002) and its evolutionary history is complex due its relative antiquity and highest levels of diversity among different habitats in the Neotropics.

The reconstruction of the avian evolutionary history has advanced during the last 30 years (Figure 1) and is now largely resolved at the deepest lineage relationships. However, much work remains to be done to try to reconstruct fully resolve and complete species-level phylogenies (Moyle et al., 2009; Pyron, 2015; Jarvis, 2016; Suh, 2016). Such endeavor will help to fully understand avian evolutionary history by identifying the relevant historical processes driving avian diversity, past and present, and reconciling conflicting divergence times among lineages. For Neotropical birds, few clades are represented by fully resolved species-level phylogenies (e.g., Furnariidae, Derryberry et al., 2011; Emberizoidea, Barker et al., 2015; ~97% and ~95% of taxon sampling respectively). These clades, however, represent only a fraction of the avian diversity and evolutionary history. Although resolving complete PTs is problematic (e.g., because of the lack of data and computational demands, among others), further steps towards understanding avian evolutionary history is to increase the

amount of taxon sampling in underrepresented clades (Philippe & Roure, 2011) in conjunction with methodological advancements and the inclusion of fossil data (Heath et al., 2014; Foster, 2016). Such steps will allow the simultaneous evaluation of extant and fossil species, thus linking the resulting PTs with the geological and climatic history of the Earth (e.g., Claramunt & Cracraft, 2015). Furthermore, recent advancements in phylogenomics also represent an exciting avenue to reveal the evolutionary history of birds, the richest terrestrial vertebrate group (Jarvis, 2016).

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APPENDIX

Appendix 1. Phylogenies reconstructed for birds that include Furnariides - Suboscines birds. It shown the bird group, the objective of tree reconstruction, the taxonomic level and the number of taxa used to infer each phylogenetic tree. Also indicate the authors and the year of publication. The complete reference for each study used here is indicated at the end of the table.

To see the appendix for this chapter, please go to appendices section at the page 130.

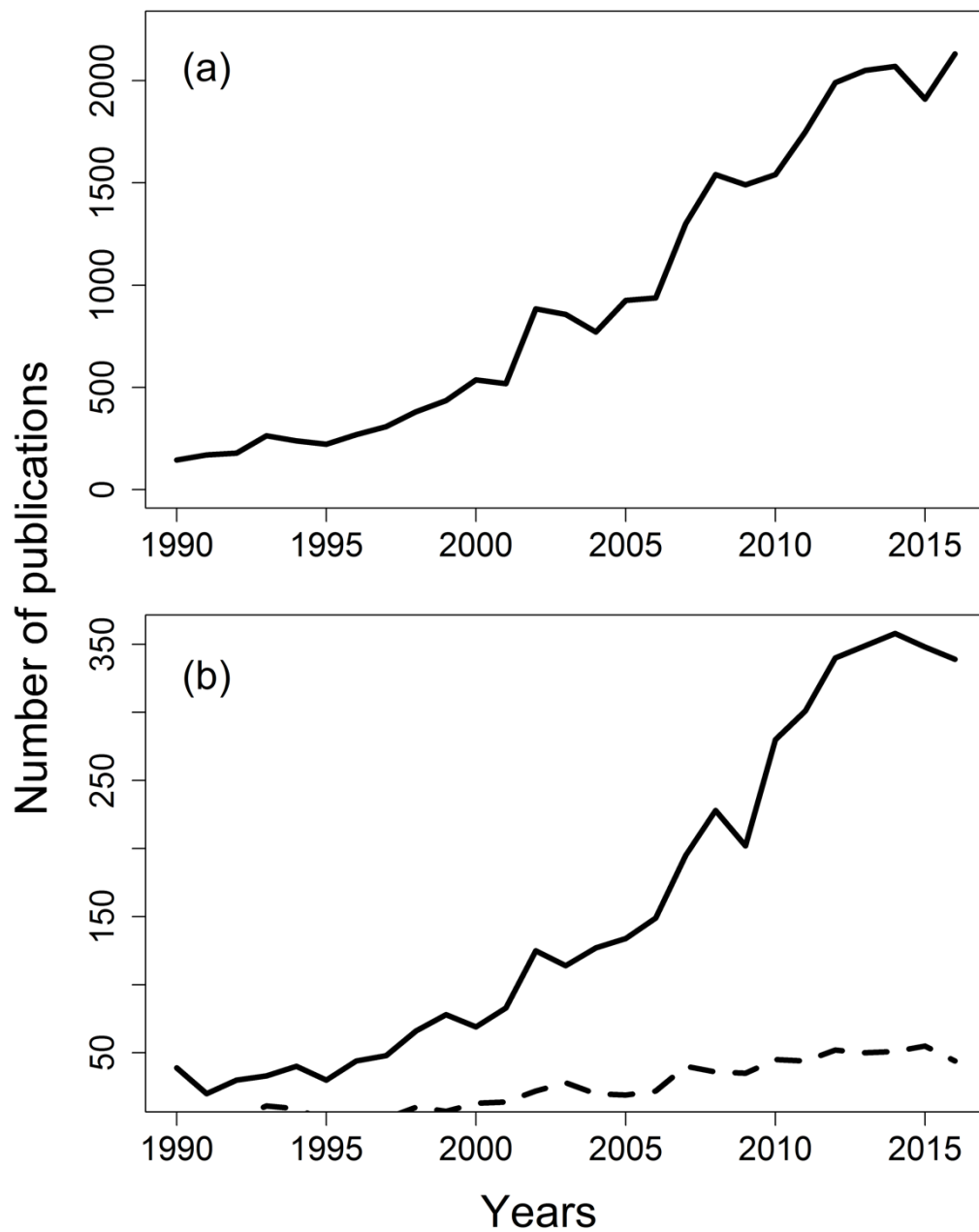


Figure 1. Number of publications containing the phrase a) avian phylogenetic reconstruction, b) passeriformes phylogenetic reconstruction (solid line) and suboscines phylogenetic reconstruction (dashed line), published from 1990 to 2016 (Google Scholar search 10 January 2017).

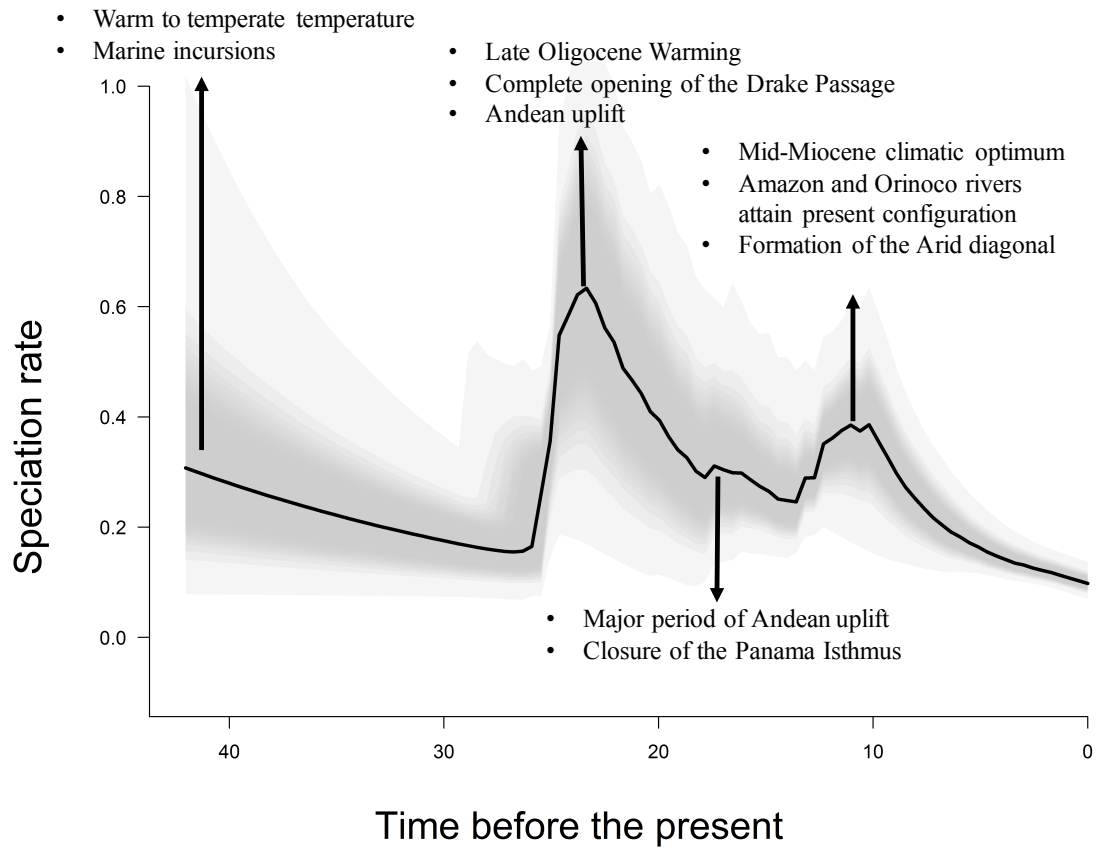


Figure 2. Speciation rate through time for Furnariides clade. The maximum peaks of speciation (solid line) match with the major climatic and geological events occurred during the Cenozoic. The speciation rate through time was estimated using the software BAMM (Bayesian Analysis of Macroevolutionary Mixtures) on a Furnariides Maximum Clade Credibility (MCC) tree of the JAE phylogenetic hypothesis.

Capítulo 2

The geographical diversification of Furnariides: the role of forest versus open habitats in driving the species richness gradients

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Original article

The geographic diversification of Furnariides: the role of forest versus open habitats in driving species richness gradients

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ABSTRACT

Aim Explaining species richness gradients in space and time requires understanding the evolutionary processes that ultimately alter the number of species. Here we examine species richness differences between primary habitats (forest versus open) for Furnariides birds, a Neotropical endemic bird clade, to test three major historical hypotheses – diversification rate, out of the tropics and tropical niche conservatism – and assess the role of evolutionary processes in driving the Furnariides species richness gradient.

Location Neotropics.

Methods We used phylogenetic and spatial data to test the historical hypotheses. First, we used GeoSSE and Bayesian Analysis of Macroevolutionary Mixture models to evaluate differential diversification and dispersal rates between habitats. Second, we quantify the root distance of each species and examined the phylogenetic structure of the richness gradient and the correlation between total species richness and the richness of early-diverged and recently originated species.

Results Furnariides species richness is higher in forest than in open habitats. However, we found higher speciation, extinction, and dispersal rates in open when compared to forest habitats, resulting in a higher diversification rate in open habitats and higher dispersal rate out of open habitats than into them. The phylogenetic structure of the richness gradient showed strong spatial pattern, with early diverged species richness peaking in forest habitats and driving the overall Furnariides gradient.

Main conclusions The Furnariides species richness gradient results from the joint effect of differential rates of macroevolutionary processes. Our findings highlight dispersal and extinction as dominant forces driving richness differences between habitats, through the addition and extirpation of species from open to forest habitats. Differences in

species richness between habitats support niche conservatism of forest habitat preferences of Furnariides species. We suggest that open habitats are effective evolutionary arenas and a key to the maintenance of bird diversity in forest habitats over evolutionary time.

Keywords: diversification rate, diversity gradients, Furnariides, Neotropics, niche conservatism, passerine birds

INTRODUCTION

Geographical gradients in species richness are one of the most conspicuous biological patterns (Hillebrand, 2004), yet the relative magnitude of distinct evolutionary and ecological processes behind these gradients at different spatial and temporal scales is still under discussion (Mittelbach *et al.*, 2007; Jansson *et al.*, 2013). Ultimately, geographical gradients in species richness in a clade are determined by the balance between the macroevolutionary processes of speciation, extinction in different regions and the dispersal among these regions (Ricklefs, 2004), as well as physical (i.e., geologic and climatic) events over long periods of time (Goldberg & Lande, 2007). Thus, historical and phylogenetic perspectives are crucial for testing alternative hypotheses about the processes driving species richness gradients (Jansson *et al.*, 2013).

Recently, at least three main evolutionary hypotheses were supported as explanations for the one of the major patterns in species richness, the latitudinal diversity gradient (LDG). First, the tropical niche conservatism hypothesis (TNC) suggests that most clades had a tropical origin and occupied tropical regions for longer time span, with only few of these clades being able to colonize and diversify in temperate regions, resulting in a higher accumulation of species in the tropics (Wiens & Donoghue, 2004). Similarly, the out of the tropics (OTT) hypothesis also assumes a tropical origin of most clades but with more frequent dispersal of these clades towards temperate regions (Jablonski *et al.*, 2006). Finally, the diversification rate hypothesis (DRH) advocates higher net diversification rates (speciation minus extinction) in the tropics, and thus more species, than in temperate regions (Mittelbach *et al.*, 2007). However, rates of speciation and extinction can also vary through time affecting the observed LDG (Rabosky, 2013). One explanation for such temporal variation in these

rates is that species diversification can decline over time as a function of species diversity (diversity-dependent hypothesis, DDH), which could be interpreted as a progressive niche filling process through time (Rabosky, 2013).

Although species richness gradients are most evident across latitude and between broad regions (e.g., tropical versus temperate), these gradients can also be observed within particular regions or across smaller areas (within- and between-habitat; MacArthur, 1965). For example, within the species-rich tropical regions, the Neotropics exhibit extreme richness gradients across major habitats (MacArthur, 1969), with species numbers increasing from dry and seasonal regions towards warm and wet regions (Fischer, 1960). Evolutionary hypotheses can also be applied to explain diversity gradients at smaller spatial scales focusing on the distribution of particular groups (Goldberg *et al.*, 2011; Cardillo & Pratt, 2013). For instance, one could expect higher diversity of a particular clade in regions/habitats where it originated according to niche conservatism.

In the Neotropics, the long isolation of South America from North America promoted the diversification of many plant and faunal lineages (Ricklefs, 2002). During this period of isolation, the South American part of the Neotropical region underwent a variety of changes owing to geologic and climatic episodes that continuously changed the landscape (e.g., Andean uplift, sea level fluctuations, forest expansion-retraction) and species distributions (Nores, 1992; Veblen *et al.*, 2007). Indeed, all these historical events participated in shaping the current diversity gradient observed throughout the Neotropics and thus could be explained by the processes discussed above (Ricklefs, 2002).

The avian species richness in the Neotropics, with more than 3,700 species (one third of all bird species), makes the Neotropics the most species-rich zoogeographical realm (Klopfer & MacArthur, 1960; Stotz *et al.*, 1996). Of these bird species, ~1,200 species are taxonomically classified as New World suboscines (Remsen *et al.*, 2015), which account for more than 30% of the Neotropical avifauna (Chesser, 2004) and includes two major subclades: the Tyrannides (502 species) and Furnariides (651 species) (Remsen *et al.*, 2015), the last one belonging to a large continental endemic radiation (Ricklefs, 2002; Claramunt, 2010).

The Furnariides, in particular, are considered as a predominant component of the avifauna in nearly all terrestrial habitats within the Neotropics, from drier and cold deserts to tropical rainforests (Stotz *et al.*, 1996; Del Hoyo *et al.*, 2003). This suboscine clade dates back at least to the early Eocene, around 55 Ma (Cracraft & Barker, 2009) with a suggested origin in forested areas of southern South America (Irestedt *et al.*, 2002; 2009; Cracraft & Barker, 2009). Furnariides have diversified throughout forest and open habitats, with most species inhabiting forests and other species having colonized open habitats independently (Del Hoyo *et al.*, 2003; Fjeldså *et al.*, 2005). Further adaptation to open habitats has been suggested as a result of environmental aridification allowing the invasion, and in-situ speciation, in non-forest habitats (Fjeldså *et al.*, 2005; Irestedt *et al.*, 2009). The spatially and temporally changing landscape of the Neotropics along with the ecological and evolutionary patterns of the Neotropical suboscine avifauna represents an ideal scenario for the study of avian diversification and biogeography (Ricklefs, 2002).

In this paper we examine the Furnariides' species richness differences between habitats (i.e., forest versus open) across the Neotropics to assess the relative roles of

evolutionary processes in shaping the current species richness gradient. More specifically, we test different, although not mutually exclusive, biogeographical hypotheses posed to explain the species richness gradient of Furnariides using both comparative (cross-species) and geographical assemblage approaches. First, we test the diversification rate hypothesis (DRH) using different methods to estimate speciation and extinction rates for each habitat type, as well as dispersal rates between these habitats to consider an out of the forest (OTF) hypothesis, in analogy with OTT. Under DRH, we expect higher net diversification rates in forest than open habitats underlying the higher species richness in the former habitat. A similar result but with differential dispersal from forest to open habitats would support our OTF hypothesis. In addition, we evaluate if diversification rates vary through time according to the number of species in each habitat (DDH). Under DDH, forest habitats would sustain higher diversity compared to open habitats owing to the higher carrying capacity of the former relative to the latter habitat. In both cases, the presence of diversity-dependent regulation species richness is expected to present slowdowns in the rates of diversification (Rabosky, 2013). Finally, we test an analogue hypothesis to TNC in the form of a forest niche conservatism (FNC) by evaluating the phylogenetic structure of the Furnariides richness gradient, following Hawkins *et al.* (2006; 2007; 2012). Under FNC, phylogenetic structure between habitats should differ with the species-rich forest habitat being dominated by early diverged species (i.e., originated and confined to the ancestral habitat) and the species-poor open habitat dominated by recently originated species (i.e., more recently originated species able to colonize other habitats), resulting in strong spatial congruence between early-diverged and the overall pattern for all Furnariides (Hawkins *et al.*, 2007; 2012).

MATERIALS AND METHODS

Furnariides species richness gradient

To describe the species richness pattern of Furnariides across the Neotropics and evaluate its phylogenetic structure (see below), we obtained distributional data for all Furnariides species (652) expressed in range maps (i.e., extent of occurrence) from Ridgely *et al.*, (2012). From these data, we only considered the breeding ranges of species, excluding any migratory or seasonal ranges. Then, we rasterized the bird distributional data into a grid of 0.5° x 0.5° resolution, resulting in a total of 7,171 cells. Species richness was calculated as the number of species ranges overlapping each cell.

Phylogenetic data

We obtained phylogenetic hypotheses for the Furnariides species from the mega phylogeny of Jetz *et al.*, (2012) by extracting our 652 studied species from this phylogeny. Owing to uncertainty in species relationships, we obtained 1,000 trees randomly sampled from the Bayesian pseudo-posterior distribution of stage-two, time-calibrated bird phylogenies based on the Hackett backbone (available at <http://birdtree.org>; cf Jetz *et al.*, 2012 for details). Our main analyses were performed on the 1,000 trees (except for those indicated in the main text) to consider phylogenetic uncertainty and because these phylogenies were explicitly designed to be used as a pseudo-posterior distribution of trees (Jetz *et al.*, 2012).

Diversification analyses

To test the hypothesis of differential diversification between habitats, we used two approaches, the geographic state speciation and extinction, GeoSSE, model (Goldberg *et al.*, 2011) implemented in the ‘diversitree’ R package (Fitzjohn, 2012) and the Bayesian analysis of macroevolutionary mixtures, using BAMM v2.3 (Rabosky, 2014).

The GeoSSE approach

The GeoSSE model (Goldberg *et al.*, 2011) is an extension of the binary state speciation and extinction model (BiSSE), proposed by Maddison *et al.* (2007), and considers species' occurrence within geographic regions as character states. According our species habitat categorization (see Appendix S1 in Supporting Information) and under GeoSSE model, we fitted 16 diversification scenarios (Table S2.1) partitioned into two model subsets (Rolland *et al.*, 2014): *a*) eight scenarios in which all parameters are free to vary and *b*) eight scenarios with constrained between-habitat speciation ($\lambda_{\text{forest} - \text{open}} = 0$) while the other parameters vary freely. These analyses were performed on the set of 1,000 trees (see above). We compared all 16 scenarios using a maximum likelihood (ML) approach and selected the best-fitting scenario using the Akaike information criterion (i.e., that with lower AIC and $\Delta\text{AIC} < 2$; Burnham & Anderson, 2002).

Recent studies have claim that SSE models can have inflated Type I error rates (Rabosky & Goldberg, 2015). Thus, to evaluate this potential problem we used a parametric bootstrap approach to simulate no direct effect of the geographic character on the estimated rates. See appendix S1 in Supporting Information for additional details on the GeoSSE model and simulations implemented in this study.

The BAMM approach

The Bayesian Analysis of Macroevolutionary Mixture (BAMM) analysis uses reversible-jump Markov chain Monte Carlo (RJMCMC) to estimate complex patterns of speciation, extinction and trait evolution on phylogenetic trees through time (see Rabosky, 2014 for a detailed description of BAMM). Moreover, BAMM can automatically find rate shifts that explain the diversification dynamics of a clade,

allowing the detection of diversification rate shifts (Rabosky, 2014). Here, we focused on the estimation of speciation and extinction rates. Before running BAMM, we estimated speciation and extinction priors using the R package ‘BAMMtools’ (Rabosky *et al.*, 2014), setting a value of 1.0 for the exponential hyperprior that governs the number of shifts along the tree. We performed two separate runs of BAMM, each one with 100 million of generations, discarding 10% of each run as burn-ins. We assessed the convergence of the results using the R package ‘coda’ (Plummer *et al.*, 2006) and to interpreted and summarized the results of BAMM using *BAMMtools*.

To compare the speciation and extinction rates between habitats, we partitioned the data into subclades according to our habitat categorization (see Appendix S1) using the “subtreeBAMM” function. To extract the time-weighted mean evolutionary rates for each subclade, we used the “getCladeRates” function, both in ‘BAMMtools’. As happens in the GeoSSE analyses, we calculated the net diversification rate from the MCMC samples from each subclade and assessed the variation of speciation and extinction rates between habitats. Given that the GeoSSE model also includes estimation of dispersal rates between character states (habitats in this case) and as complementary analysis of BAMM, we performed an analysis of range shifts through time (see Antonelli *et al.*, 2015 for details) to evaluate if dispersal from one habitat to the other was greater than vice versa (i.e., dispersal rates). We did this analysis using a Python script available on the package ‘SpeciesGeoCoder’ (Töpel *et al.*, 2014).

Diversity-dependent diversification

To assess the presence of diversity-dependent regulation on the Furnariides diversification between habitats, we applied a maximum likelihood (ML) approach following the framework of Etienne *et al.*, (2012) that also accounts for incomplete sampling. First, we partitioned the original phylogenetic data into two subclades

according to our habitat categorization (see species habitat categorization in Appendix S1) and then applied the ML approach on the partitioned data. We fitted four scenarios of diversity-dependence, two of which assuming constant rates (Yule and Birth-Death) and two assuming linear diversity-dependence (with extinction: DDL+E and without extinction: DDL-E), and selected the best-fitting scenario using AIC (Burnham & Anderson, 2002). The four scenarios were fitted using the R package ‘DDD’ (Etienne *et al.*, 2012) and run over a random sample of 100 trees owing to computational demands.

Phylogenetic structure of the Furnariides richness gradient

To explore the phylogenetic structure of the Furnariides species richness gradient in a simple assemblage approach, we used the mean root distance (MRD) of species occurring within each grid-cell (Kerr & Currie, 1999). MRD measures the evolutionary derivedness of species within an assemblage (Kerr & Currie, 1999) and can be used to determine whether a local fauna is constituted primarily by early-diverged or by recently-originated species (Hawkins *et al.*, 2012).

We first computed the root distance (RD) of each species for each of the 1,000 trees using the “distRoot” function in the R package ‘adephylo’ (Jombart *et al.*, 2010) and averaged these species’ RD values over the whole set of trees. We used the 35% and 65% percentiles to rank the 652 species as “early-diverged” and “recently-originated” species, respectively (Hawkins *et al.*, 2012), yielding a balanced number of early-diverged (283) and recently-originated (236) species. Then, we separately obtained and mapped the number of total, early-diverged, and recently-originated species occurring within each cell, as well as the mean root distance (MRD) of all species per cell.

Finally, we correlated the total species richness with both early-diverged and recently-originated species to quantify the similarity of the spatial patterns between these groups, using the Clifford's method to obtain effective degrees of freedom for Pearson's correlative coefficient and thus account for spatial autocorrelation, using 25 distance classes in the "modified.ttest" function in the R package 'SpatialPack' (Osorio & Vallejos, 2014).

RESULTS

Furnariides species richness gradient

Following the overall gradient of bird species richness in the Neotropics, Furnariides species exhibited a strong richness gradient that is associated with the distribution of the two primary habitat types (Fig. 1), as previously suggested for the group (Stotz *et al.*, 1996). Indeed, the highest concentration of Furnariides species was found in forest habitats of eastern (e.g., Atlantic Forest) and northern (e.g., Amazonia) South America. For instance, forested regions like the western Amazonian lowlands harboured as much as 165 Furnariides species. Conversely, open habitats showed lower richness of Furnariides species with open vegetation regions such as the dry diagonal of South America (e.g., Caatinga, Cerrado, and Chaco biomes) harbouring up to 90 species (Fig. 1b).

Habitat diversification rates

GeoSSE approach

Out of the 16 diversification scenarios tested, the model with seven parameters (i.e., all parameters being free to vary) possess the best fit across the majority of phylogenetic trees (86% of the trees presents $\Delta AIC < 2$), with mean $AIC = 4610.62 (\pm 192.22)$ (Table

S2.1). This diversification scenario indicated higher speciation, extinction and dispersal rates in open than in forest habitats (Figs. 2, S2.1). Thus, higher net diversification rates for open rather than forest habitats were also supported (Fig. 2e-f). In addition, the best-fit scenario indicated shifts in habitat occupancy, with open habitat species experiencing range expansion, whereas species from forest habitats experienced range contractions (see Appendix S2 and Fig. S2.2). According to our simulations, however, our GeoSSE procedures seemed to have low power in detecting differences between the observed and simulated datasets ($P = 0.104$; Fig. S2.3). Nevertheless, the application of alternative methods supported our GeoSSE findings, as pointed out below.

The BAMM approach

BAMM analysis confirmed the results of higher net diversification rate for open habitats than forest habitats ($rO - rF = 0.084 \pm 0.015$ lineages $\times$ Myr⁻¹; $rF = 0.099 \pm 0.007$ lineages $\times$ Myr⁻¹ and $rO = 0.182 \pm 0.012$ lineages $\times$ Myr⁻¹, respectively; Fig. 2). Range-shift through time analysis also indicated more dispersal events (DE) from open to forest habitats ($DE = 25,214 \pm 8,152$) than the reverse ($DE = 10,067 \pm 3,681$). Moreover, there was evidence that the relative dispersal events were higher from forest to open habitats at the beginning of the Furnariides history, but then the opposite pattern (dispersal from open to forest habitats) increased steadily from around 30Ma, surpassing the forest-to-open dispersal around 16 Ma and keeping that pace until the present (Fig S2.5).

Diversity-dependent diversification

Finally, evaluating the effect of diversity-dependence regulation on diversification rates, the best-fitted scenarios for forest habitats (birth-death) and open habitats (Yule)

indicated no evidence of slowdowns in the diversification rates within these habitats as a function of their species richness (Fig. S2.6).

Phylogenetic structure of Furnariides richness gradient

The phylogenetic structure of the Furnariides richness gradient also showed a strong spatial pattern (Fig. 3a). For instance, low MRD values were observed in species-rich regions corresponding to forest habitats (Fig. 3b), whereas high MRD values appeared in species-poor regions characterized by open habitats (Fig. 3c). Indeed, this observation was supported by the richness gradients of both early-diverged and recently-originated species, with the former species concentrating in forest habitats (e.g., northern Amazonia) whereas the latter species richness peaked in open habitats (e.g., the Pampas region of Argentina and Uruguay). Accordingly, there was a strong and higher association between early-diverged and total species richness ($r = 0.973$, $P < 0.01$) than between recently-originated and total species richness ($r = 0.774$, $P < 0.01$), as previously found (e.g., Hawkins *et al.*, 2006).

DISCUSSION

Furnariides diversification in the Neotropics

To explain species richness gradients, it is necessary to understand the processes that ultimately change the number of species within regions (Ricklefs, 2004). Here we identified the macroevolutionary processes that shape the geographical gradients in species richness of Furnariides within the Neotropics using distinct approaches that revealed coherent results. Furnariides birds exhibited a strong species richness gradient from the species-rich forests to the species-poor open habitats, conforming to the overall pattern of bird species richness across the Neotropics (Stotz *et al.*, 1996). Despite such

higher Furnariides richness in forest compared to open habitats, our results pointed towards higher diversification rates in open habitats as well as higher dispersal rates from these habitats to the forest ones. In addition, we found support for the phylogenetic conservatism of forest habitat preferences in Furnariides, with early diverged-species driving the overall richness gradient and concentrating in this habitat (Fig. 3). Our findings reveal a significant habitat effect on the geographical gradients of Neotropical species richness, at least for the Furnariides-suboscines birds.

Macroevolutionary processes and habitat changes in Neotropics and Furnariidae diversification

Bird species respond in different ways to climatic and vegetation changes that affect the structure and composition of communities at different spatiotemporal scales (Nores, 1992; Ricklefs, 2006). Such differential response results from the persistence of bird species being influenced by the capacity of habitats to provide a set of favourable conditions (e.g., potential sources of food, nesting and refuge areas; MacArthur & MacArthur, 1961). For instance, decreasing habitat availability and unfavourable conditions can produce rapid changes in the communities through increasing extinction and limiting ecological opportunities for speciation (Ricklefs, 2006). Here, we found different macroevolutionary rates for Furnariides species in distinct Neotropical habitats that may be related to habitat availability and changing conditions through time.

According to the diversification rate hypothesis, we expected net diversification rates to be higher in the species-rich forest habitat than in open habitats.

Complementarily, our “out of the forest” hypothesis also predicted diversification along with dispersal rates to be higher in forest than in open habitats. Contrary to these expectations, we found that all macroevolutionary rates (speciation, extinction, dispersal, and net diversification) were higher in open habitats rather than forest habitats

(Figs. 2; S2.1). Moreover, we found no slowdowns of diversification rates through time in both habitats (Fig. S2.6), suggesting constant diversification of Furnariides within habitats and thus rejecting diversity-dependent regulation. At first glance, this could be considered surprising owing to the low Furnariides species richness in open habitats, in comparison with forest habitats (Fig. 1b). However, previous studies have found similar results with higher speciation, extinction, and diversification rates in species-poor regions compared to species-rich ones, such as the temperate versus tropical regions (Weir & Schluter, 2007; Pyron, 2014). Consequently, these findings do not necessarily imply higher accumulation of species within a region exhibiting higher macroevolutionary rates. For instance, such higher species accumulation within a region could simply result from lineages having occupied that region for longer time without necessarily requiring high net diversification rates (Stephens & Wiens, 2003). This time-for-speciation effect (Stephens & Wiens, 2003) could, in turn, be promoted by the region's climatic and geological stability (Jansson, 2003).

Although we did not explicitly test for the time-for-speciation effect, ancestral character reconstruction indicated that forest habitats represent the ancestral habitat for Furnariides (see Appendix S2 and Fig. S2.7). Furnariides originated in forest habitats during the Eocene (around 55 Ma) and consequently have had more time to accumulate species in this habitat at constant low speciation and extinction rates. Accordingly, previous studies on avian diversification that mainly considered members of the Furnariides infraorder, found support for low, constant diversification rates with some increments during the late Oligocene and mid Miocene periods (Claramunt, 2010; Deryberry *et al.*, 2011; Fjeldså, 2012). At these time periods, the climate was characterized by warm and humid conditions (Frakes *et al.*, 1992; Beerling & Woodward, 2001) with Neotropical forest habitats being more stable and widely

distributed across the region, spanning down to ~40°S of latitude with elements of broad-leaved evergreen forests in southern South America (Romero, 1986; Burnham & Graham, 1999; Beerling & Woodward, 2001; see also Appendix S3). Also, these time periods were characterized by the complete opening of the Drake passage (late Oligocene) and the major period of Andean uplift and the closure of the Panama Isthmus (mid Miocene) (Zachos *et al.*, 2001; Hoorn *et al.*, 2010).

In contrast with the relative stability of forest habitats, open habitats within the Neotropics have experienced greater climatic variability through time and are less stable over geological time (Burnham & Graham, 1999; Beerling & Woodward, 2001). More specifically, significant geological and climatic changes during the late Oligocene and mid Miocene caused a reduction of open habitats in South America (Burnham & Graham, 1999), which then expanded during the late Miocene and early Pliocene when grassy savannahs and fire-adapted vegetation expanded into central and southern South America (Zachos *et al.*, 2001; Edwards *et al.*, 2010; Le Roux, 2012). These major geological and climatic changes could have certainly influenced the observed higher macroevolutionary rates in open habitats compared to those in forest habitats. In fact, two major shifts in clade diversity of suboscine birds have been suggested during the above-mentioned geological periods. For example, a suboscine diversity increment occurred during the late Oligocene (around 26-24 Ma) (Derryberry *et al.*, 2011; Fjeldså, 2012). In addition, a second suboscine diversity increment occurred during the mid Miocene (around 16-14 Ma) (Fjeldså, 2012), which coincided with the major uplift of the Andes (Burnham & Graham, 1999; Hoorn *et al.*, 2010) and the posterior formation of the South America Arid Diagonal and the expansion of C₄ grasses in the late Miocene (Zachos *et al.*, 2001; Le Roux, 2012; Edwards *et al.*, 2010). Finally, a diversification increment within the family Furnariidae was also suggested during the

late Pliocene (around 3.5 Ma), followed by a decrease of diversification during the Pleistocene (Deryberry *et al.*, 2011).

Dispersal and shifts in habitat occupancy

In addition to higher speciation, extinction, and diversification rates in open habitats compared to forest habitats, our findings suggest higher dispersal rates out of open habitats and into forest habitats (Figs. S2.1a, S2.5). Such differences in dispersal rates between open and forest habitats may have also been influenced by the geological and climatic changes mentioned before (see also Appendix S3). For example, according to the model of alternating episodes of suitable climate corridors (i.e., wet or dry), species can disperse to different regions or become isolated within particular regions (Vrba, 1992; Simões *et al.*, 2016). These changes may have favoured species with strong dispersal abilities, which are more capable of following favourable conditions (Smith *et al.*, 2014) or cause the extinction of populations that became isolated (Simões *et al.*, 2016). Accordingly, we found that open habitat species tended to expand their ranges and disperse into forest habitats (Figs. S2.1a, S2.2a, S2.5). Although open habitat species expanded their ranges into forest habitats, thus colonizing this habitat via dispersal, they also suffered higher extinction within open habitats (Fig. 2c-d).

Moreover, habitat specialization on, or range contraction to, particular habitats were the only rates lower for open habitats than for forest habitats (Fig. S2.2b), limiting the generation of open habitat specialists. Altogether, these rates differences ultimately favoured a higher accumulation of species within forest habitats over time.

Phylogenetic structure of Furnariides richness gradient

The geographical gradient in species richness of Furnariides across the Neotropics showed a strong phylogenetic structure supporting our predictions on forest niche

conservatism. Higher richness of early-diverged species concentrated on forest habitats whereas recently-originated species did so in open habitats, implying that the former species remained and accumulated in their ancestral niche conditions (forests). According to Ericson *et al.*, (2002) and Claramunt & Cracraft, (2015), the ancestor of New World suboscines reached South America before the opening of the Drake Passage, which separated this continent from Antarctica (around 40 Ma), and started to diversify during the late Eocene (Claramunt & Cracraft, 2015). At this period of time southern South American vegetation was characterized by tropical-temperate forests (Frakes *et al.*, 1992; Beerling & Woodward, 2001; Le Roux, 2012). In agreement with these conditions and the origin of the Furnariides (around 42-50 Ma; Claramunt, 2010; Jetz *et al.*, 2012; Ohlson *et al.*, 2013), the reconstructed ancestral niche conditions of New World suboscines favoured forest habitats (Fig. S2.7). Following this scenario and under inherited habitat preferences among suboscine Furnariides (i.e., niche conservatism), we found support for our prediction that early-diverged species remained confined and accumulated in forest habitats, defining the overall gradient for all Furnariides as evidenced by the strong spatial congruence between patterns of both species groups (Fig. 3).

Our findings of phylogenetic structure in the Furnariides richness gradient are generally concordant with the observed continental and global bird richness patterns (Hawkins *et al.*, 2006; 2007). In these groups, early diverged species richness peaks in regions that correspond with their ancestral niche conditions (Fig. 3b), whereas highest numbers of recently originated species are present in regions with different conditions. This patterning results in a strong spatial structure of root distances (Hawkins *et al.*, 2012). MRD values of Furnariides assemblages varied according to the richness gradient, with higher MRD values in species-poor regions and lower MRD values in

species-rich regions (Fig. 3). Moreover, it is important to highlight that phylogenetic structure of the Furnariides richness gradient suggests an early diversification of forest habitat species and a more recent diversification of open habitat species that correspond with our findings of macroevolutionary rates. In addition, the presence of early-diverged Furnariides species in species-rich forest habitats adds support to the time-for-speciation effect as a potential driver of the Furnariides richness pattern, revealing a longer occupation of forest habitats as suggested by our reconstruction of their ancestral niche.

Concluding remarks

Our findings indicate that the Furnariides species richness gradient across the Neotropics results from the joint effect of differential macroevolutionary rates between forest and open habitats and niche conservatism of forest habitat preferences. Hence, despite lower macroevolutionary rates in forest habitats in comparison with open habitats, higher species richness in forest persists as a consequence of the balance among those rates. Indeed, dispersal and extinction seem to be more important than speciation rates in driving richness differences between habitats by jointly influencing range shifts and thus changes in habitat occupancy. Finally, we suggest that the spatiotemporal heterogeneity of open habitats over time has made them an effective arena for diversification of the Neotropical bird fauna and a key habitat for the maintenance of bird diversity in forest habitats.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Expanded materials and methods.

Appendix S2 Expanded results.

Appendix S3 Climatic, geologic and vegetational history of South America during the Cenozoic.

To see the supporting information for this chapter, please go to appendices section at the page 142.

BIOSKETCH

Jesús N. Pinto-Ledezma is a doctoral student in ecology and evolution at the Universidade Federal de Goiás (UFG), Brazil. He is an ornithologist interested in macroecology, macroevolution and community phylogenetics, with special emphasis on the analysis of patterns in the Neotropical biota. The authors are members of the Theoretical Ecology and Synthesis lab at the UFG and work together on linking macroecological and macroevolutionary theory to understand diversity patterns across different taxa and spatial scales.

Author contributions: J.N.P.L., J.A.F.D.F. and F.V. conceived the idea; analyses were conducted by J.N.P.L., L.M.S. and F.V.; J.N.P.L. and F.V. led the writing and all authors contributed throughout the whole process.

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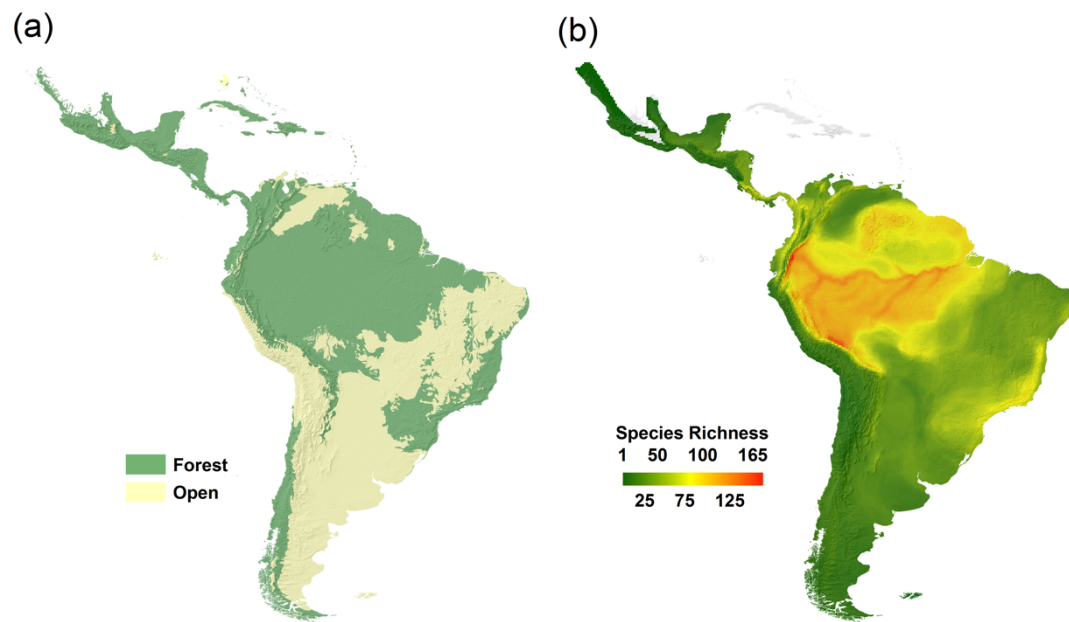


Figure 1. Neotropical geographical patterns of (a) primary habitats – forest and open – and (b) species richness (alpha diversity per grid-cell) of Furnariides birds.

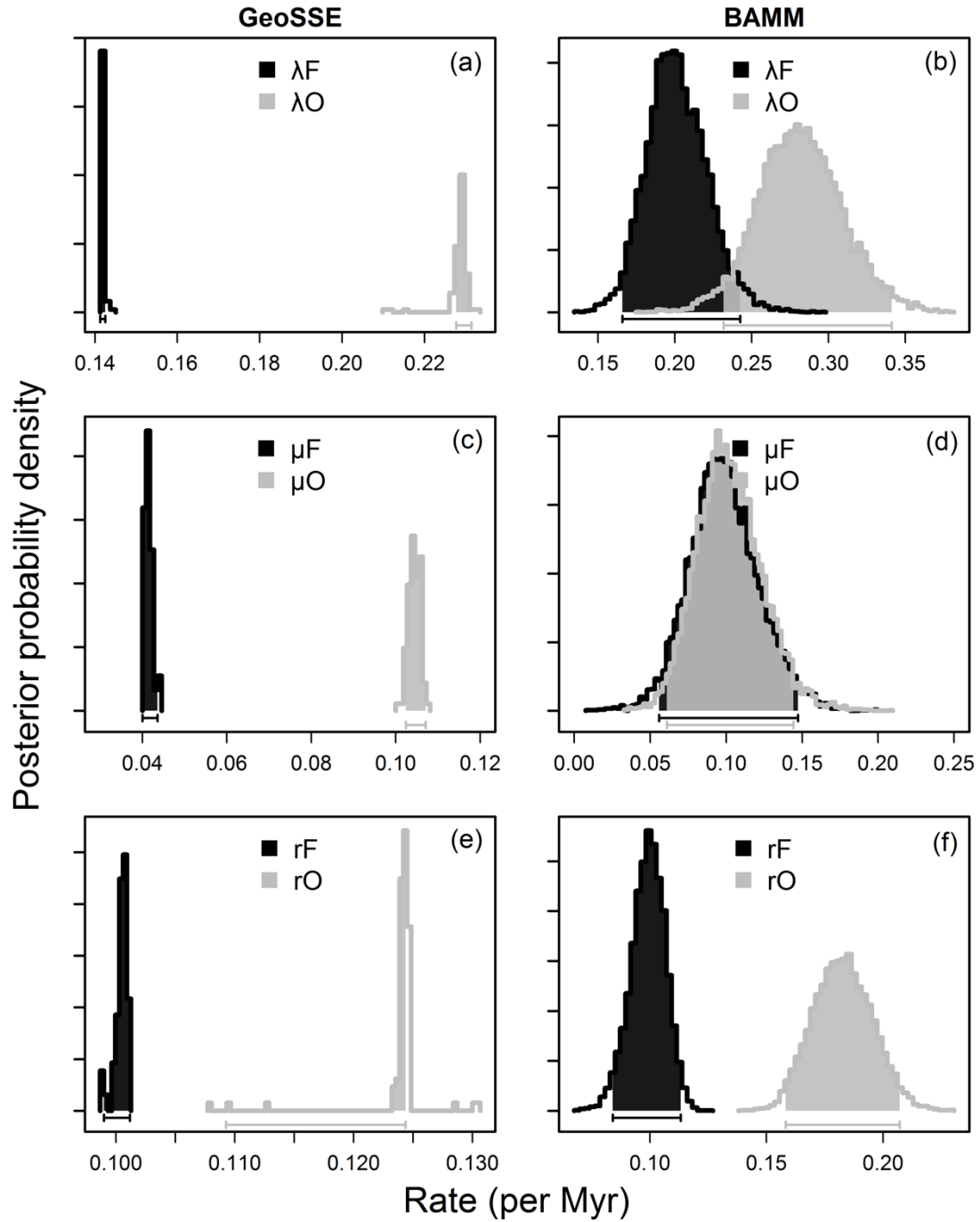


Figure 2. Speciation, extinction and diversification rates, based on GeoSSE and BAMM approaches. Posterior probability distributions of (a-b) speciation, (c-d) extinction and (e-f) diversification rates of Furnariides in forest habitats (black) and open habitats (grey).

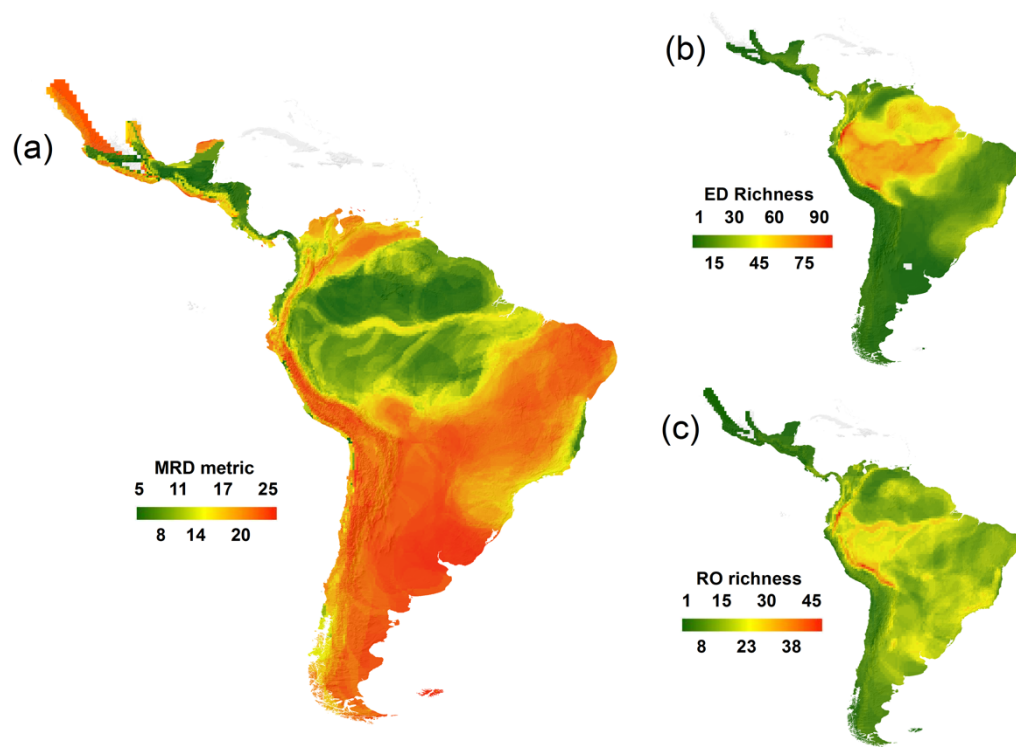


Figure 3. Geographical pattern of (a) mean root distance for Furnariides birds in the Neotropics and species richness (alpha diversity per grid-cell) for (b) early-diverged (ED) and (c) recently-originated (RO) species.

Capítulo 3

Drivers of phylogenetic assemblage structure of the Furnariides, a widespread clade of lowland Neotropical birds

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Drivers of phylogenetic assemblage structure of the Furnariides, a widespread clade of lowland Neotropical birds

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ABSTRACT

The number of species that co-occur in local assemblages is shaped by several mechanisms at different spatial and temporal scales. Here focussing in historical explanations, we examine the phylogenetic structure of local assemblages of the Furnariides (Aves: Passeriformes) clade and assess the influence of diversification rates on the assembly and species co-occurrence within those assemblages. Using 120 local assemblages distributed in the territories of Bolivia and Argentina and a nearly complete phylogeny for the clade, we analysed the phylogenetic structure of co-occurring species under a novel model (Damocles) that accounts for the evolutionary dynamics. Also, we quantified diversification rates (DRA) within each assemblage and examined how diversification determine the levels of species co-occurrence. We found that Furnariides assemblages were phylogenetically clustered or lack a clear pattern phylogenetic structure. Open habitats assemblages mainly showed phylogenetic clustering whereas forest habitats assemblages were dominated by a lack of phylogenetic structure. Further, range shifts were more frequently in assemblages with low species co-occurrence, whereas assemblages with high species co-occurrence presented less frequent range expansions and contractions. Through the incorporation of a dynamic assembly model through time, our results suggest that the historical events of colonisation and local extinction are important drivers structuring Furnariides assemblages and that their phylogenetic structure as well as species co-occurrence patterns are also influenced by habitat preferences of these birds.

INTRODUCTION

The structure of biotic assemblages represents the balance of local as well as broad-scale ecological and historical processes, which ultimately determine regional species diversity (Ricklefs 1987; Mittelbach and Schemske 2015). At the local spatial scale, biotic interactions (e.g., competition, facilitation) promote coexistence or exclusion of species (Webb et al. 2002; Mittelbach and Schemske 2015), allowing or not the persistence of new species arrived from neighbouring local assemblages (Herzog and Kessler 2006; Cornell and Harrison 2014). At broad spatial scales, speciation, extinction and dispersal processes determine the species pool from which local assemblages are sampled (Brown and Maurer 1987; Mittelbach and Schemske 2015). Although the processes that govern the structure of local assemblages varies with scale, the age and size of the regions as well as ecological limits can also play important roles in determining the structure of these local assemblages (Ricklefs 2007; Cornell and Harrison 2014; Fine 2015).

The field of community phylogenetics, which integrates ecological and evolutionary perspectives to explore the mechanisms governing community assembly, has offered specific predictions on species coexistence and its phylogenetic structure depending on the mechanisms involved (Webb et al. 2002; Cavender-Bares et al. 2009). Traditionally, two main processes have been invoked to predict community assembly: species interactions, particularly competition, and environmental filtering (Ndirebe et al. 2013). For instance, if local assemblages are formed by more closely (clustered pattern) or distantly (overdispersed pattern) related species than expected by chance, this may imply that environmental filtering or species interactions, respectively, determine the co-occurrence of species within local assemblages (Webb et al. 2002; Ndirebe et al. 2013). But, despite these simplistic predictions, both mechanisms can produce

alternative outcomes and thus must be considered as not mutually exclusive mechanisms (Cavender-Bares et al. 2009; Mayfield & Levine 2010; Gerold et al. 2015).

Also, the tendency of species to retain their ancestral niches (the “phylogenetic niche conservatism” hypothesis, PNC), has been invoked as potential explanation for the assembly of communities (Webb et al. 2002; Miller et al. 2013; Ndirebe et al. 2013). Under PNC, species colonisation and adaptation to new niches over time are infrequent and thus most species accumulate within their region of origin where they maintain their ancestral niche preferences (Wiens and Graham 2005; Peterson 2011), which consequently structures local assemblages over time (Qian et al. 2013; Miller et al. 2013). Accordingly, local assemblages tend to increase in clustering away from their ancestral conditions (Miller et al. 2013), so local assemblages are composed mostly by closely related species that exhibit high niche similarity (Webb et al. 2002; Ndirebe et al. 2013). Although PNC allows an integrative ecological and evolutionary explanation for community assembly over long periods of time (Wiens and Graham 2005), geological and environmental events also influence assembly of local assemblages through their effect on species ranges (Goldberg and Lande 2007; Pigot and Tobias 2015). For example, range shifts through time (i.e., range expansions and range contractions events) influence rates of speciation, colonisation and extinction (Gaston 2003; Pigot et al. 2010; Goldberg et al. 2011), thus also influencing assemblage structure. Indeed, range expansions can add species to assemblages through speciation and colonisation events (Pigot et al. 2010; Goldberg et al. 2011) whereas range contraction increases the chance of extinction of isolated populations and thus the removal of species from local assemblages (Gaston 2003; Goldberg et al. 2011).

Recently, novel methods that go beyond the traditional competition vs filtering inferences of community phylogenetics have become available so that more complex

balances of both ecological and historical processes at local and regional scales can be considered when studying assemblage structure (Mittelbach and Schemske 2015). Also, there is a need for correcting potential statistical issues on traditional community phylogenetic methods such as those based on simple randomization techniques. For instance, these methods may erroneously predict phylogenetic structure (e.g. overdispersion is commonly predicted) or fail to reject the null model, increasing the chance of erroneously rejecting the null hypothesis of random assembly (see Burbrink et al. 2015; Pigot and Etienne 2015). A consequence of such failure may lead to the conclusion that local assemblages are a result of biogeographical processes (Webb et al. 2002), even when these are not explicitly considered (Pigot and Etienne 2015). Therefore, a next step in modelling community phylogenetics should include the explicit consideration of historical mechanisms that underlie phylogenetic structure, allowing to better understand how local assemblages are structured over time (Ndirebe et al. 2013; Pigot and Etienne 2015; Warren et al. 2014). A recently developed model claims promise in this direction by accounting for the processes of speciation, colonisation and local extinction (DAMOCLES - Dynamic Assembly Model of Colonisation, Local Extinction and Speciation; Pigot and Etienne 2015) by incorporating the dynamic assembly of local assemblages through time for a particular clade, where the composition and diversity of assemblages changes as species diversify (Pigot and Etienne 2015).

The infraorder Furnariides (antbirds, crescentchesters, gnateaters, antpittas, tapaculos, antthrushes and ovenbirds) is a monophyletic clade endemic to the Neotropics that belongs to the largest continental bird radiation, the New World suboscines (Ricklefs 2002; Moyle et al. 2009; Claramunt 2010). Furnariides comprises 51% of the suboscines and nearly 11% of all Passerine species (Claramunt 2010;

Remsen *et al.*, 2016), and are distributed in all major habitats of South America, from drier deserts in southern South America to tropical rainforests to the north (Del Hoyo *et al.* 2003; Moyle *et al.* 2009), although this radiation is richer and abundant in forest habitats (Stotz *et al.* 1996; Pinto-Ledezma *et al.* 2017). It has been suggested that Furnariides originated in forested areas in southern South America during the Eocene, around 40-50 Ma (Irestedt *et al.* 2002; Cracraft and Barker 2009; Ohlson *et al.* 2013; Pinto-Ledezma *et al.* 2017), and some species independently colonized other habitats (Fjeldså *et al.* 2005), including open habitats at low and high elevations (Stotz *et al.* 1996; Del Hoyo *et al.* 2003). During most of the Eocene, South America was an “island continent” (Ricklefs 2002) and was characterized mainly by tropical forest vegetation (Fine and Ree 2006). This would have facilitated the accumulation of Furnariides species within these forest habitats (Claramunt and Cracraft 2015; Pinto-Ledezma *et al.* 2017) and consequently influenced the species richness and the assembly of Furnariides assemblages (Pinto-Ledezma *et al.* 2017). Hence, the Furnariides’ continental endemism and long evolutionary history primarily within South American forested habitats (Ricklefs 2002; Fjeldså 2012; Pinto-Ledezma *et al.* 2017) make this clade an ideal system to evaluate the effect of historical processes on patterns of phylogenetic assemblage structure within habitats.

A plethora of studies have explored the phylogenetic structure of bird assemblages (e.g., Gómez *et al.* 2010; Graham *et al.* 2009; Miller *et al.* 2013), including those focusing on the influence of environmental gradients (Graham *et al.* 2009; Parra *et al.* 2011; Miller *et al.* 2013; Lessard *et al.* 2016), the effect of traits (Gómez *et al.* 2010; Barnagaud *et al.* 2014; Lessard *et al.* 2016; Miller *et al.*, 2017), as well as the role of biotic interactions and environmental filtering and the effect of spatial scale on phylogenetic structure (Gómez *et al.* 2010; González-Caro *et al.* 2012; Sobral and

Cianciaruso 2015; Yan et al. 2016). However, very few studies have focused on historical explanations for community assembly (see Parra et al. 2010; Graham et al. 2012; importantly these two studies focused on the Hummingbirds).

Here, we aim to examine the phylogenetic structure of Furnariides assemblages in southern South America (Argentina and Bolivia) under a historical framework by explicitly considering evolutionary processes (i.e., historical colonisation and local extinction rates). Under this framework, we evaluate differences in species richness (i.e., species that co-occur within assemblages) between habitats (i.e., forest versus open). To do so, we first estimate the within assemblage colonisation and local extinction rates using DAMOCLES (Pigot and Etienne 2015) and then examine how co-occurring species within assemblages are related to their rates of diversification and age (Wiens, 2011). In particular, we ask the following questions: (1) Is there a typical pattern of rates of colonisation and local extinction that underlie community assembly of Furnariides? (2) How does the phylogenetic structure of co-occurring species differ between habitats? (3) Do rates of assemblage colonisation and local extinction vary between habitats? and (4) Is the variation in rates of diversification and species ages within assemblages related to species co-occurrence?

Following evidence for PNC in Furnariides, with most extant species remaining in their ancestral habitats (i.e., forest) and range expansion as well as adaptation to novel environments (i.e., open habitats) being rare (Pinto-Ledezma et al. 2017), we expect differential phylogenetic structure of co-occurring Furnariides species among habitats. For instance, species-rich assemblages mainly found in forest habitats (hereafter ‘FA’) should present phylogenetic overdispersion, whereas species-poor assemblages located in open habitats (hereafter ‘OA’) should exhibit phylogenetic clustering (Qian et al. 2013; Barnagaud et al. 2014). Additionally, we expect a

differential effect of the rates of colonisation and local extinction underlying community assembly; hence, rapid rates of colonisation and local extinction should lead to phylogenetic overdispersion in FA and clustering in OA (Cornell and Harrison 2014; Eiserhardt et al. 2015; Emerson and Gillespie 2008; Li et al. 2015; Weigelt et al. 2015). Conversely, slow rates of colonisation and local extinction should lead to phylogenetic clustering in FA and phylogenetic overdispersion in OA (Cardillo 2011; Cornell and Harrison 2014; Li et al. 2015; Razafindratsima et al. 2013). Finally, because co-occurrence of species in a specific region or habitat is affected by 1) the length of time that those species have occupied that region or habitat, 2) rates of diversification (Wiens 2011), and 3) the geographic expansion of species within a clade to attain secondary sympatry (Pigot and Tobias 2015), we expect differential levels of species co-occurrence between habitats, where FA (i.e., high co-occurrence) should present low rates of diversification, whereas OA (i.e., low co-occurrence) should present high rates of diversification (Wiens 2011).

MATERIALS AND METHODS

Species assemblage data and habitat categorizations

Using field surveys and bibliographic sources, we compiled information for a total of 120 local assemblages of Furnariides bird species in Argentina and Bolivia (Fig. 1), spanning a latitudinal extent of $\sim 45^\circ$. Most of the assemblages ($N = 80$) were collected by the first three authors from early 1990 to 2014. Data collection was generally conducted from October to January, which corresponds to the wet season in the study region. Surveys were conducted using 10 x 50 binoculars, along trails and roads, traveling through as many habitats at each locality as possible. Each locality was visited

on different occasions for a period of three to seven days. Each trail or road was surveyed both in the morning (before dawn [06:00 to 11:00]) and in the afternoon (until dusk [16:00 to 19:00]), and data collected included presence and absence as well as relative abundance of birds seen or heard, and the habitat and stratum they were in, according Parker et al. (1996).

To evaluate phylogenetic structure between habitats, we used the habitat categorization of Pinto-Ledezma et al. (2017) that defined forest and open habitats following the primary habitats of the Neotropics according to the terrestrial ecoregions of Olson et al. (2001). We categorized each assemblage as belonging to one habitat type (i.e., forest or open) within the study area (Fig. 1) considering the species habitat preferences as proposed by Stotz et al. (1996), which is specifically tailored for Neotropical birds. Following this habitat characterization, 66 assemblages were defined as belonging to forest (55%) and 54 to open habitats (45%).

Phylogenetic data

We simultaneously estimated topology and divergence times of Furnariides in a Bayesian framework using BEAST v2.2 (Bouckaert et al. 2014) and nine genes, four mitochondrial (CyTB, CO2, ND2, ND3) and five nuclear (BF5, BF7, ODC, RAG1, RAG2) obtained from GeneBank (Table S1). Before the BEAST analyses, we estimated the optimal combination of partition schemes among genes and substitution models using PartitionFinder v1.1 (Lanfear et al. 2012). We selected the optimal partition scheme using the corrected Akaike Information Criterion (AICc) and found that the model GTR+ Γ +I was the best for almost all partitions. Tree topology and divergence times were estimated under an uncorrelated lognormal relaxed clock model and a Yule speciation process as a tree prior. No restrictions were placed in the topology to account

for uncertainty in the topology estimation (Derryberry et al. 2011; Ohlson et al. 2013). Because fossil data are scarce for birds, especially for small passerines such as furnariids (see Claramunt and Rinderknecht 2005), we used as calibration point the split between Tyrannoidea and the Furnarioidea, which yielded a divergence date of 61 ± 2.8 Ma (Barker et al. 2004; see also Derryberry et al. 2011; Ohlson et al. 2013). This calibration point was set as a normal distribution, which allowed for bi-directional uncertainty (Derryberry et al. 2011; Ohlson et al. 2013). BEAST analyses were run in the CIPRES science gateway (CSG; Miller et al. 2011) with a chain length of 300×10^6 generations sampled every 10,000 generations. Using Tracer v1.6 (Rambaut et al. 2014), we assessed the effective sample size (ESS) for all parameters.

Phylogenetic assemblage structure

To investigate the phylogenetic structure of Furnariides assemblages, we used the Dynamic Assembly Model of Colonisation, Local Extinction and Speciation model (DAMOCLES; Pigot and Etienne 2015). In DAMOCLES, species are assigned to one of two geographical states (i.e., locally present = 1 or locally absent = 0) (Pigot and Etienne 2015). Under DAMOCLES, local assemblages evolve over time by speciation (λ), colonization (γ) and local extinction (μ), where species at any time (t) can exist in one of the two geographic states (Pigot and Etienne 2015). Additionally, a transition from state 0 to state 1 implies that a species is added to a local community via colonisation (range expansion), and a transition from 1 to 0 implies that a species became locally extinct (range contraction) (Pigot and Etienne 2015).

Using DAMOCLES, we estimated colonisation and extinction rates for each local assemblage and quantified the phylogenetic structure of Furnariides assemblages using the Mean Phylogenetic Distance (MPD) and Mean Nearest Taxon Distance

(MNTD) indices (Webb et al. 2002). We summarized the results using standardized effect sizes (*SESMetric*), which compares the value of an assemblage to the mean expected values under an Equal Rate null model, correcting for their standard deviation. *SESMetric* values greater than 0 indicate increase in phylogenetic clustering and values less than 0 increase in phylogenetic overdispersion (as in; Webb et al. 2002; Pigot and Etienne 2015).

Within-assemblage diversification

To explore how diversification rate determines the co-occurrence of species within assemblages we first estimated the overall diversification rate using a species-level approach (DR; *sensu* Jetz et al. 2012; see also Kennedy et al. 2014, 2016). DR represents the number of diversification events that occurred in a lineage leading to a species from the root of the phylogeny, weighted by the relative timing of these events (Jetz et al. 2012). Using these estimates, we calculated the diversification rate within each assemblage (DRA) by averaging the species DRs by the number of species that co-occur in each assemblage. As a complementary analysis to DRA, we estimated the average age (AA) within each assemblage by averaging the species ages (i.e., terminal branch lengths) by the number of species that co-occur within the assemblage. For instance, assemblages with low DRA values should be composed of early-diverged species, whereas assemblages with high DRA values should be made up of recently-originated species (Kennedy et al. 2016). As pointed out by Freckleton et al. (2008) for ultrametric trees, DRA values could be also approximated by considering the species root distances (i.e. mean root distance), a procedure widely used to evaluate evolutionary patterns of niche conservatism in macroecology (Hawkins et al., 2005, 2006; Pinto-Ledezma et al. 2017). DRA and AA values were obtained using a sample of 100 trees from the posterior distribution to account for phylogenetic uncertainty. Both

DRA and AA estimates were highly correlated ($r = -0.80$; $p < 0.001$), thus we only report results for DRA.

RESULTS

Furnariides' phylogenetic and assemblage data

Our phylogenetic hypothesis included 592 species of the 651 known species of Furnariides for South America (91% of taxon sampling; Remsen *et al.*, 2016). All the ESS values were > 300 for all parameters, which resulted in a well-resolved and supported phylogeny. Importantly, all species listed in our assemblages' dataset were present in our phylogenetic hypothesis (Fig. S1).

Our assemblage dataset ($N = 120$) included 289 Furnariides species (Table S2), which represent 120 species of Furnariides out of the total 133 species found in Argentina and 231 species out of the total 235 species found in Bolivia. In general, species richness within our assemblage dataset follows the overall gradient of bird richness in the Neotropics (Fig. 2a), with species-rich assemblages (max = 74 species) located primarily in forest habitats of the Amazonian lowlands (e.g. Madidi National Park, Bolivia) and species-poor assemblages (max = 5 species) located in forest habitats of Patagonia (e.g. Tierra del Fuego National Park, Argentina).

Within-assemblage colonisation and local extinction

In general, Furnariides assemblages in South America were driven by slow rates of colonisation ($\gamma = 0.00277$ [0.0018 : 0.3163, values represent 95% CI] to 4.412 [3.677 : 4.971] per lineage per million years), whereas local extinction varied from very slow rates ($\mu = 0.029$ [0.056 : 6.742] per lineage per million years) to extremely rapid

extinction rates ($\mu = 63.114$ [47.198:89.518] per lineage per million years). Both local extinction and colonisation rates were highly correlated ($r = 0.957$; $p < 0.001$), indicating that assemblages that present slow or rapid rates of colonization also present slow or rapid rates of extinction (Fig. 3). The correlation between colonisation (γ) and local extinction (μ) rates was also high when analysed separately by habitat ($r = 0.949$, $p < 0.001$; $r = 0.969$, $p < 0.001$; FA and OA respectively; Fig. 3). In addition, when comparing within habitats, there were differences in the rates local extinction (mean $\mu_{FA} = 9.979$, mean $\mu_{OA} = 34.842$, $t = -5.241$, $p < 0.001$) and colonisation (mean $\gamma_{FA} = 0.437$, mean $\gamma_{OA} = 1.169$, $t = -3.784$, $p < 0.001$), where OA was characterized by faster rates of local extinction and colonisation than FA.

Phylogenetic structure of Furnariides assemblages

The two metrics analysed in the DAMOCLES model (i.e., MPD and MNTD) were highly correlated with one another ($r = 0.743$; $p < 0.001$). Most assemblages presented positive *SES-MPD* and *SES-MNTD* (93% and 80% respectively) values, suggesting that the dominant pattern of phylogenetic structure of Furnariides is clustering (Table S2). Interestingly, only 37% and 17% for *SES-MPD* and *SES-MNTD*, respectively, were different from expected by the DAMOCLES model (Fig. 4), with none of these significantly structured assemblages showing phylogenetic overdispersion (i.e. all were phylogenetically clustered). Additionally, both metrics were significantly different between habitats ($t = -4.7445$, $df = 71.473$, $p < 0.0001$ for *SES-MPD* and $t = -7.1706$, $df = 113.49$, $p < 0.0001$ for *SES-MNTD*), suggesting that assemblages in open habitats are more clustered than assemblages in forest habitats (Figs. 1; 2b-c; 4). Indeed, most of the assemblages that were different from the DAMOCLES model are located in open habitats (29 for *SES-MPD* and 17 for *SES-MNTD*, Fig 4b; e-f) and only 15 for *SES-MPD* and 3 for *SES-MNTD* in forest habitats (Fig. 4a; c-d).

Furnariides' diversification within assemblages

The diversification rate within assemblages (DRA) showed that diversification rates of Furnariides assemblages vary from low to high diversification (mean = 0.144; sd = 0.029; min = 0.091; max = 0.222). When comparing between habitats, a low DRA (mean = 0.132; sd = 0.0295) was observed in assemblages located in forest habitats (FA), whereas high DRA values (mean = 0.157; sd = 0.024) were found in assemblages within open habitats (OA) ($t = -5.061$; $p < 0.001$; Fig. 2d).

DISCUSSION

The number of species that co-occur in local assemblages is shaped by several mechanisms at different spatial and temporal scales (Ricklefs 1987; Cavender-Bares et al. 2009). Here, using the largest continental endemic clade of birds (Furnariides - Passeriformes) as a study system and applying a novel dynamic null model (DAMOCLES; Pigot and Etienne 2015), we identified that local assemblages across southern South America (Bolivia and Argentina) present differential patterns of phylogenetic structure (Fig. 4; Table S2), where a lack of phylogenetic structure is the dominant pattern (63% and 83% of the assemblages, for MPD and MNTD respectively).

Interestingly, co-occurrence in species-rich assemblages mainly located in forest habitats (FA) did not differ from the DAMOCLES null expectation (i.e., present phylogenetic unstructured pattern) (Fig. 4a-b; Pigot and Etienne 2015), which imply that species co-occurrence in FA is determined by slow rates of speciation, colonisation and local extinction (Figs. 2d; 3). Conversely, co-occurrence in species-poor assemblages located in open habitats (OA) did differ from the DAMOCLES expectation

(Fig. 4e-f), with closely related species tending to co-occur within these assemblages (clustered pattern) and the co-occurrence pattern in these assemblages being driven by rapid rates of speciation, colonisation and local extinction (Fig. 2a and 2d). We also found a tendency for OA assemblages to be formed by recently-originated species whereas FA assemblages were mainly composed by early-diverged species (Fig. 2d), suggesting that species-rich assemblages have had more time to accumulate species compared with species-poor assemblages. Overall, our results highlight that historical mechanisms are important drivers structuring the local assemblages of Neotropical birds, at least of the infraorder Furnariides. In addition, our study confirms the importance of explicitly considering historical mechanisms into the analysis of assemblage phylogenetic structure to reveal how assemblages are structured over time (Warren et al. 2014; Pigot and Etienne 2015).

Phylogenetic structure of Furnariides assemblages

Our results show differential levels of phylogenetic structure in Furnariides local assemblages between forest and open habitats (Figs. 1, 4). In a broad sense, our results are congruent with those of Barnagaud et al. (2014), who found that in most of their cases assemblage phylogenetic structure for habitat preferences does not differ from the null model expectation (Barnagaud et al. 2014; Fig. 5). But it is important to highlight that in our analyses assemblages located in open habitats tend to be more clustered than in forest habitats (Figs. 1, 2b-c). This differential pattern between habitats could be explained by different, non-mutually exclusive mechanisms. For example, phylogenetic niche conservatism (PNC) predicts an increase in phylogenetic clustering away from the ancestral niche conditions of a clade (Graham and Wiens 2005; Miller et al. 2013). Accordingly, our results show a change from unstructured phylogenetic pattern in forest habitats, which also represent the ancestral habitat for Furnariides (Pinto-Ledezma et al.

2017), to clustered phylogenetic structure in open habitats (Fig. 1). Other possibility for this change in the phylogenetic structure, could be explained by the rapid diversification rates of lineages that colonised new habitats (Hortal et al. 2011; Parra et al. 2011). This might be also the case for assemblages located in open habitats, which also present rapid rates of diversification and are formed mostly by recently-derived species (Fig. 2b-d). Interestingly, the colonisation of open-like habitats by Furnariides and their posterior diversification within these habitats is relatively new and coincide with the formation of the Arid diagonal and the expansions of C4 grasses during the Miocene (Pinto-Ledezma et al. 2017).

An intriguing result is that about 80% of Furnariides local assemblages in forest habitats present an unstructured pattern of phylogenetic structure. This finding contrast with that of other studies of birds in tropical lowland areas in South America. For instance, some studies have found a pattern of phylogenetic overdispersion (e.g., Graham et al. 2009 [hummingbirds]) or clustering (e.g., Gómez et al. 2010 [antbirds]) in forest local assemblages. In both studies, the authors diverge in their conclusions about that competitive interactions can play an important role in structuring local assemblages. However, our result is concordant with that of Pigot and Etienne (2015), who indicated a lack of phylogenetic structure in birds (ovenbirds and hummingbirds) and primates (New World primates) assemblages at the Manu reserve in Perú (Pigot and Etienne 2015). A potential explanation for such lack of phylogenetic structure, including our result for forest assemblages, could simply be because traditional randomization methods used in other studies erroneously reject the null model of random assembly (Burbrink et al. 2015; Pigot and Etienne 2015). Thus, it might be worth to explore this assumption in more clades and at different spatial scales.

Our finding of a lack of phylogenetic structure in forest habitat assemblages could be explained by considering the dynamics of historical mechanisms that are independent of species traits (Webb et al. 2002; Pigot and Etienne 2015). Indeed, local assemblages evolve over time with species being added or removed dynamically from such assemblages (Pigot and Etienne 2015). In this context, recent studies suggest that depending on the velocity of the rates of historical mechanisms, local assemblages will present differential patterns of phylogenetic structure (Cardillo 2011; Razafindratsima et al. 2013; Li et al. 2015; Yan et al. 2016). For example, rapid rates of speciation coupled with slow colonisation and extinction rates can lead to clustered assemblages (Cardillo 2011). Conversely, rapid colonisation and extinction rates can result in overdispersed assemblages (Li et al. 2015; Yan et al. 2016). Our results indicate that Furnariides assemblages in forest habitats are characterised by slow rates of speciation, colonisation and local extinction (Figs. 2d; 3), suggesting that assemblages located in tropical forests are assembled through slow rates of historical mechanisms over time.

Finally, biotic interactions can be important in structuring local bird assemblages (Pigot and Tobias 2013; Miller et al. 2015), for example by excluding species from local assemblages through competitive exclusion (Cornell and Lawton 1992; HilleRisLambers et al. 2012) or by limiting range overlap between recently-diverged species (Pigot and Tobias 2013). Despite strict territoriality and the high levels of interspecific aggression within the Furnariides (Del Hoyo et al. 2003), divergent phenotypes allow coexistence of sister lineages (Del Hoyo et al. 2003; Pigot and Tobias 2013). In fact, within the Furnariides, thamnophilid species are exceptionally divergent in terms of body size and furnariid species in bill and tail shape (Del Hoyo et al. 2003; Claramunt 2010). Such phenotypic divergences among species can potentially enable the exploitation of resources at different foraging strata (Stotz et al. 1996), reducing the

competition over time and consequently allowing the co-occurrence of sister lineages of Furnariides. Indeed, recent evidence indicates that sister lineages with divergent phenotypes attain secondary sympatry faster than those with similar phenotypes (Pigot and Etienne 2013) and that this phenotypic divergence in coexisting furnariid species accumulates over time or through differences acquired in allopatry (Tobias et al. 2014).

Evolutionary mechanisms drive community assembly of co-occurring species of Furnariides

As new species arise from speciation through allopatry, the formation of local assemblages composed by phylogenetically related species depends on the time of those species to expand their geographic ranges allowing secondary sympatry (Pigot and Etienne 2015). Our results show that the degree of co-occurrence in Furnariides assemblages (Fig. 2a) depend on the divergence time of species composing each assemblage. For instance, FA are mostly composed by early-diverged species and OA by recently-originated species (Fig 4d). Indeed, differences in assemblage diversification rates (DRA) suggest that assemblages that are composed by early-diverged species have had more time to attain secondary sympatry, thus allowing the accumulation of more species within FA (Pigot and Etienne 2015; Pigot et al. 2016). Moreover, a previous study of ours (Pinto-Ledezma et al. 2017) showed that recently-originated species co-occur mainly in open habitats, whereas a high co-occurrence of early-diverged species was more typical in forest habitats, suggesting that early-diverged species remained and accumulated in forest habitats, most likely related to the stable environmental conditions of this habitat (Pinto-Ledezma et al. 2017).

In addition, the success to achieve secondary sympatry also depends on the capacity of species to colonise and adapt within local assemblages (Goldberg and Lande

2007; Kraft et al. 2015). Indeed, new species that arise from speciation are added to local assemblages through historical colonisation events (Pigot et al. 2010; Goldberg et al. 2011) or removed by local extinction events (Goldberg et al. 2011; Pigot and Etienne 2015). Considering the historical events of colonisation (range expansion) and local extinction (range contraction) (Fig. 3), we found that phylogenetic structure of co-occurring Furnariides in local assemblages is governed by slow (in FA) and rapid (in OA) rates of colonisation and local extinction (Fig. 3). These findings indicate that the degree of co-occurrence in Furnariides assemblages decreases as rapid colonization and local extinction rates increase. Interestingly, although species co-occurrence of Furnariides decrease as rates of historical mechanisms increase or vice versa, we also show that assemblages with low co-occurrence tend to be formed by closely related species (i.e., increase in phylogenetic clustering; Fig. 2b-c) and by recently-originated species (Fig. 4d) and that assemblages with high co-occurrence are composed by both, closely and distantly related species (i.e., phylogenetic unstructured assemblages) and by early-diverged species (Fig. 4).

Although different mechanisms that promote or constraint species co-occurrence among assemblages have been invoked (Cavender-Bares et al. 2009; Pigot and Tobias 2013), it seems that low co-occurrence in OA can be a result of the similarity in the environmental tolerances that its species share (Cavender-Bares et al. 2009; Miller et al. 2013), suggesting that environment is playing an important role in filtering the species that do not tolerate stressful environments (see Fig. 2; Graham et al. 2009; Graham et al. 2012; Miller et al. 2013) through rapid rates of local extinction (Fig. 3) despite their rapid rates of speciation and colonisation over time when compared with those assemblages in forest habitats (Figs. 3, 2d). In fact, Furnariides species experienced more events of range contractions in open habitats since early Miocene (around 20 Ma)

(Pinto-Ledezma et al. 2017), thus indicating that assemblages located in open habitats experienced rapid extinction rates as Furnariides species became exposed to highly dry and cold environments. In addition, various closely related and recently-originated species that co-occur in OA are distributed and restricted to open-like habitats (e.g., *Geossita antarctica*, *G. rufipennis*, *Cinclodes fuscus*, *C. patagonicus*, *Limnortyx rectirostris*, *Cranioleuca sulphurifera*) of the Great Chaco, Pampas, Espinal and Patagonia ecoregions, that are characterized by their high climatic seasonality and aridity and low species diversity.

Contrary to OA, FA that present the highest levels of co-occurrence could result simply from the accumulation of species in the habitat where Furnariides originated and radiation from (Pinto-Ledezma et al. 2017). Indeed, forest habitats represent the ancestral habitats for Furnariides (Pinto-Ledezma et al. 2017) and have been environmentally stable during most of the Cenozoic (Beerling and Woodward 2001). This environmental stability over time is likely a factor that allow the accumulation of species and also one that reduce the potential local extinction Furnariides in FA. For example, the slowest rates of species origination coupled with slowest rates of range expansions that we report for the assemblages of forest habitats may reflect that species accumulation in this habitats is slow but constant, which could also be constrained by biotic interactions during species range expansions (Pigot and Tobias 2013). Also, another possibility is that complexity observed in forest habitats facilitates the coexistence of ecologically similar bird species (MacArthur 1964; Pigot et al. 2016), suggesting that high co-occurrence of Furnariides species in FA is also facilitated by the high complexity and food resources that these kind of habitat offers to these bird species (MacArthur and MacArthur 1961; Smith et al. 2014).

Concluding remarks

To the best of our knowledge, this is the first study to directly investigate how the historical mechanisms drive the phylogenetic structure of local avian assemblages. Our results show that the phylogenetic structure in Furnariides assemblages are governed by the combined effect of differential rates of historical mechanisms (speciation, colonisation and extinction) as well as by habitat preferences. In sum, our results reported here do not exclude the potential effect of other mechanisms (e.g., environmental filtering or strong negative species interactions) of community assembly and species co-occurrence, but provides an alternative approach to understand the roles of evolutionary mechanisms in explaining the differences in species co-occurrence among local assemblages.

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SUPPORTING INFORMATION

Appendix S1 Plot of the Furnariides MCC-tree used in this study.

Appendix S2 Table with all mitochondrial and nuclear loci sampled from GenBank used for phylogenetic inference.

Appendix S3 Table summary of all assemblages used in this study showing coordinates, country, habitat types, richness, extinction and colonisation estimations, phylogenetic assemblage structure statistics, within-assemblage diversification statistics, environmental variables.

Appendix S4 R code for run DAMOCLES.

To see the supporting information for this chapter, please go to appendices section at the page 162.

BIOSKETCH

Jesús N. Pinto-Ledezma is a doctoral student in ecology and evolution at the Universidade Federal de Goiás (UFG), Brazil. He is an ornithologist interested in macroecology, macroevolution and community phylogenetics, with special emphasis on the analysis of patterns in the Neotropical biota.

Author contributions: J.N.P.L., J.A.F.D.-F. and F.V. conceived the idea; J.N.P.L., A.E.J. and V.R.C. collected the data; analyses were conducted by J.N.P.L. and F.V.; J.N.P.L., F.V. and J.A.F.D.-F. led the writing and all authors contributed throughout the whole process.

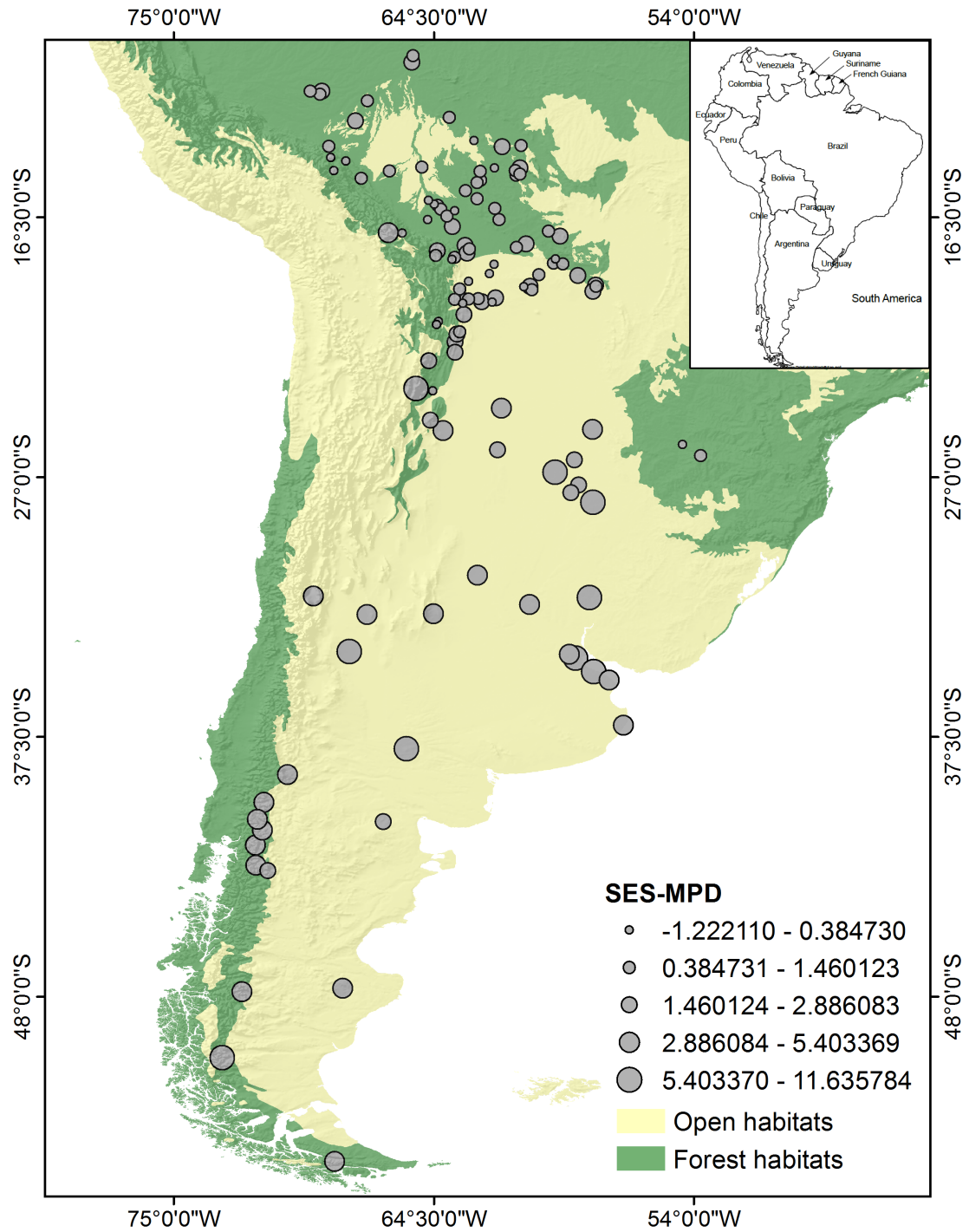


Figure 1. Map of southern South America showing the distribution of the major habitats (i.e., forest and open habitats) and the location of the 120 assemblages analysed in this study. The size of the circles is proportional to the SES-MPD in each assemblage.

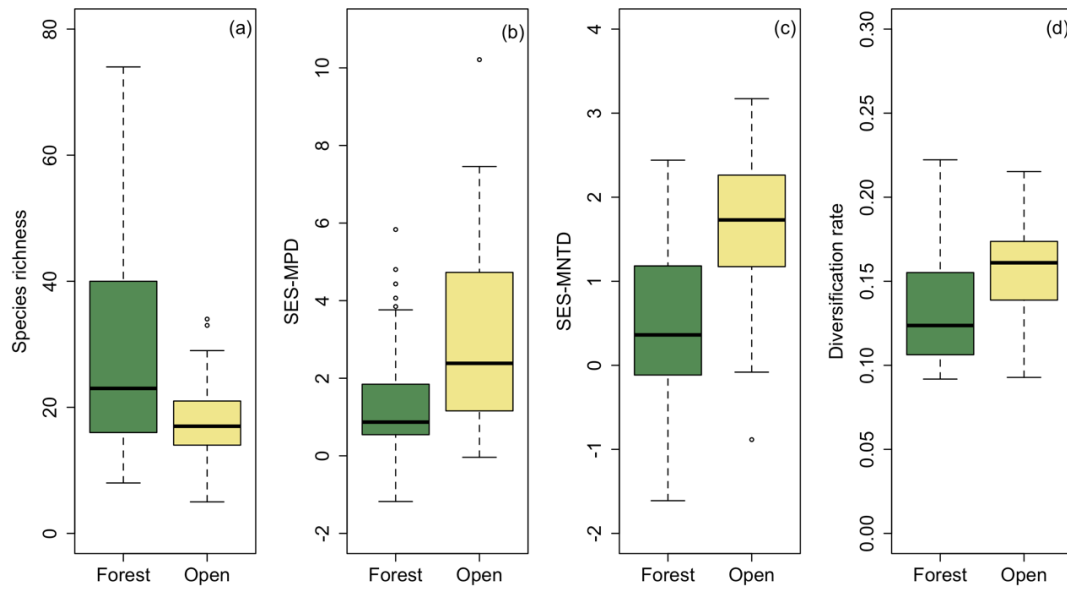


Figure 2. Differences in species richness (SR), phylogenetic structure (SES-MPD and SES-MNTD), and diversification rate (DRA). The box plots show the differences of SR, SES-MPD and SES-MNTD and DRA in Furnariides assemblages comparing forest versus open habitats

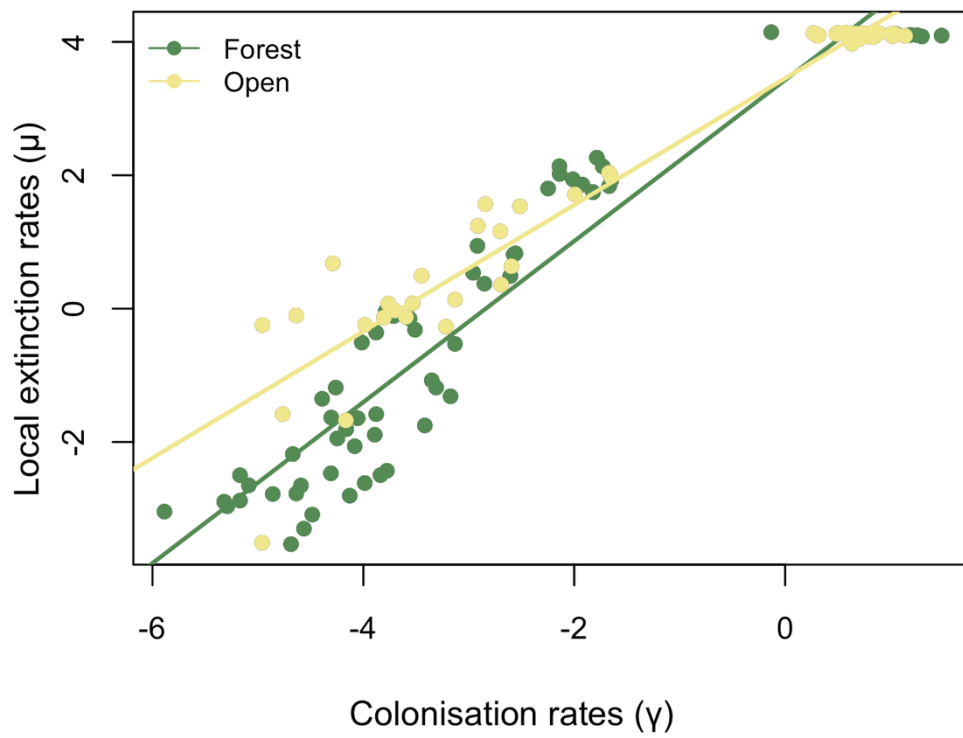


Figure 3. Relationship between colonisation (γ) rates and extinction rates (μ). The plot shows this relationship in forest habitat assemblages (FA), and open habitat assemblages (OA). Note that the values of colonisation and extinction were log transformed for plotting.

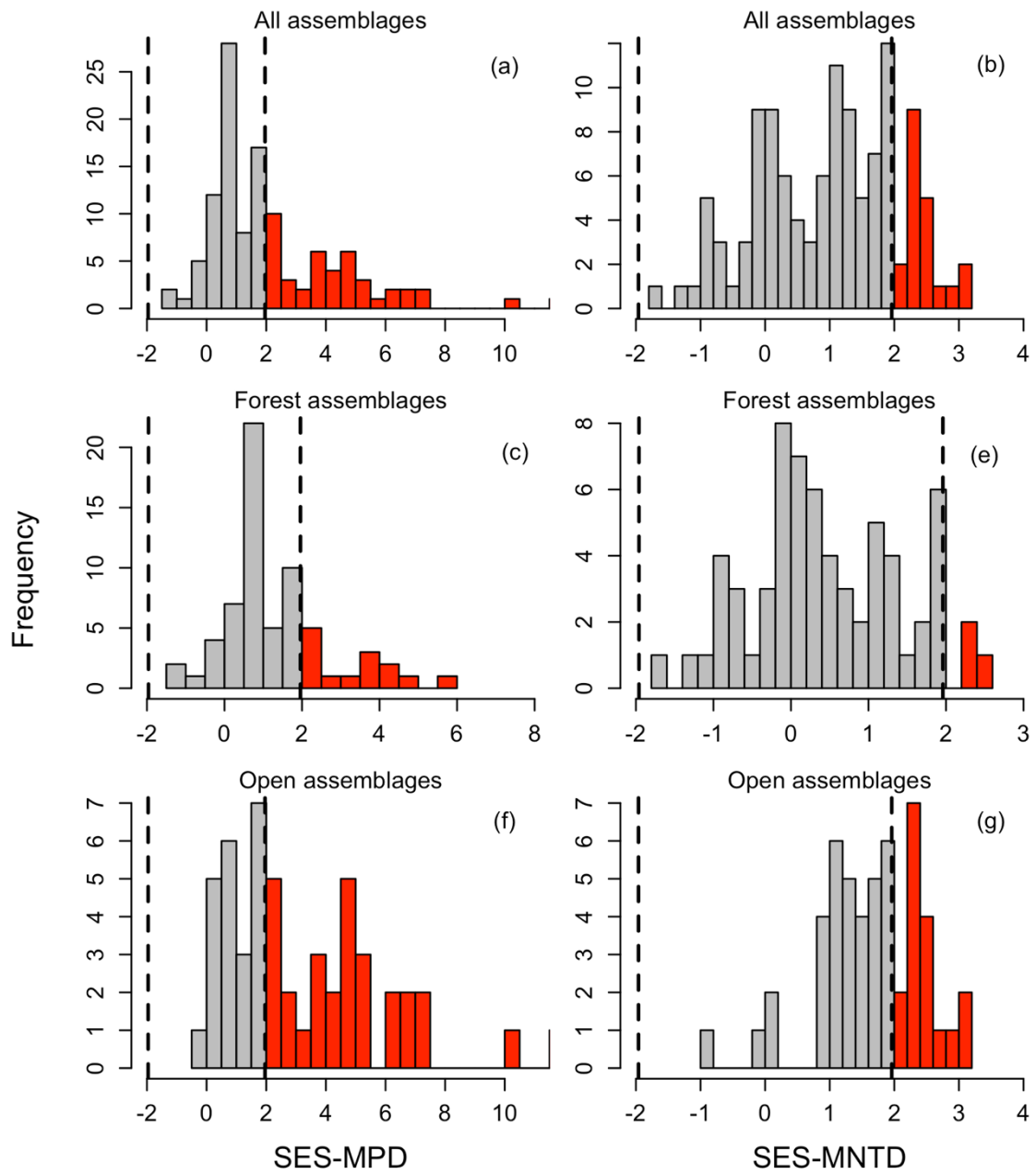


Figure 4. Probability of clustering under the DAMOCLES model. The histograms show the frequency distribution of SES-MPD and SES-MNTD (red interval values below -1.96 or above 1.96) of a-b) all assemblages, c-d) forest habitat assemblages (FA), and e-f) open habitat assemblages (OA). The dotted vertical lines in all figures represent the cut-off of -1.96 and 1.96.

CONCLUSÃO GERAL

Os avanços recentes em reconstrução de filogenias e métodos filogenéticos comparativos, que possibilitaram a integração de informações históricas, geográficas e biológicas das espécies em um contexto macroevolutivo, novos caminhos foram abertos para o estudo da origem e estruturação das assembleias biológicas. Nesta tese, através do uso de filogenias e destes novos métodos, exploramos como os processos macroevolutivos de especiação, extinção e dispersão determinam a riqueza de espécies e a estruturação das assembleias de aves no Neotrópico, mais especificamente, no clado dos Furnariídes. Há indícios que a grande diversidade de espécies no clado dos Furnariídes tem origem no período Terciário e está relacionada às variações ambientais que aconteceram na América do Sul (Capítulo 1). Encontramos que a riqueza de espécies de Furnariídes está profundamente relacionada com a preferência de habitat, onde indica-se que espécies que divergiram mais cedo permaneceram nas condições de seu nicho ancestral (habitats de floresta) e tiveram mais tempo para se acumular em estes habitats. Além disso, através do uso de diferentes métodos, mostramos que os processos macroevolutivos de especiação, extinção e dispersão acontecem com maior frequência em habitats abertos comparados com os habitats de floresta. Isto nos permite concluir que o gradiente de riqueza de espécies ao longo do Neotrópico é resultado do efeito combinado dos processos macroevolutivos e da conservação do nicho, e que os habitats abertos representam áreas efetivas para a diversificação de aves no Neotrópico (Capítulo 2). Também, ao estudar assembleias locais de Furnariídes (Capítulo 3), observamos que a montagem filogenética das assembleias é determinada principalmente pelos processos macroevolutivos em detrimento dos processos tradicionalmente invocados (i.e., filtragem ambiental e interações bióticas). Além disso, mostramos que a preferência de habitat também tem influência sobre a montagem das assembleias locais, por exemplo, assembleias localizadas em habitats abertos tendem a estar

compostas de espécies estreitamente relacionadas. Finalmente, embora nosso estudo esteja focado num clado particular, as conclusões apresentadas podem se expandir para toda a avifauna Neotropical, isto porque o clado dos Furnariides é considerado como um componente importante da avifauna em quase todos os habitats que ocorrem no Neotrópico.

Apêndices

Apêndice Capítulo 1

The evolutionary history of the Neotropical avifauna: a review based on phylogenies

Jesús N. Pinto-Ledezma, José Alexandre F. Diniz-Filho, and Fabricio Villalobos

APPENDIX

The evolutionary history of the Neotropical avifauna: a review based on phylogenies

Jesús N. Pinto-Ledezma, José Alexandre F. Diniz-Filho, and Fabricio Villalobos

Appendix S1. Phylogenies reconstructed for birds that include Furnariides - Suboscines birds. It shown the bird group, the objective of tree reconstruction, the taxonomic level and the number of taxa used to infer each phylogenetic tree. Also indicate the authors and the year of publication. The complete reference for each study used here is indicated at the end of the table.

Group	Objective	Level	N taxa	Data	Alignment method	Model of evolution	Method of reconstruction	Calibration method	Author's	Year
New World Suboscine	To reconstruct the phylogeny and taxonomic classification of New World suboscine birds	Family, Genera		DNA-DNA hybrid		-	Distance - Cluster	$\Delta T50H$ statistic as absolute time	Sibley, Ch.G. and Ahlquist, J.E.	1985

World's birds	To present the phylogenetic classification of the living birds of the world based on the results of DNA-DNA hybridization studies	Order, family		DNA-DNA hybrid		-	Distance - Cluster	ΔT_{50H} statistic as absolute time	Sibley, Ch.G. and Ahlquist, J.E.	1990
New World Suboscine	Outline the phylogenetic relationships among the major lineages of suboscine birds To provide a robust phylogeny for the major groups of tracheophone birds and thereby create a framework for more detailed evolutionary and biogeographic analyses	Family	50	Nuclear RAG-1, c-myc	Multiple alignment by eye	-	MP and ML	-	Irestedt, M. et al.	2001
New World Suboscine	To test the monophyletic relationships between passerine birds and highlight the biogeographic implications of the reconstructed tree	Family, subfamily	32	Nuclear RAG-1, c-myc and Mitochondrial cyt-b	Multiple alignment by eye	GTR+ Γ	MP and ML	-	Irestedt, M. et al.	2002
Passerine	To reconstruct the phylogeny and study the diversification of the passerine birds	Family	34	Nuclear genes RAG-1, c-mos		GTR+I+ Γ	MP and ML	-	Barker, F.K. et al.	2002
Passerine		Family		Nuclear RAG-1, RAG-2	Multiple alignment by hand	GTR+I+ Γ	MP, ML and Bayesian	NPRS and PL at the root of the tree	Barker, F.K. et al.	2004

Thamnophilidae	To test the potential incongruences between the use of mitochondrial and nuclear genes and to explore how substitution models affect this incongruence	Species	51	Mitochondrial cyt-b and Nuclear myoglobin-2 and G3PDH	Multiple alignment by hand	GTR+I+Γ	Bayesian	-	Irestedt, M. et al.	2004
New World Suboscine	To reconstruct the phylogeny for New World birds to test the monophyly between suboscines and taxonomic relationships of traditional and non-traditional groups	Species, genera	53	Nuclear β-fibrinogen and Mitochondrial ND3, COII	Multiple alignment ClustalX and correction by hand	HKY85+Γ (nuclear) GTR+I+Γ (mitochondrial) GTR+I+Γ (combined)	MP and ML	-	Chesser, R.T.	2004
Furnariidae	To define the deep branching pattern of the ovenbird-woodcreeper radiation	Species	33+3	Nuclear myoglobin-2, G3PDH and Mitochondrial cyt-b	Multiple alignment by hand	GTR+Γ (myoglobin-2) HKY+Γ (G3PDH) GTR+I+Γ (mitochondrial)	Bayesian	-	Fjeldsa, J. et al.	2005
Neoaves	To reconstruct the higher level molecular for Neoaves and estimate the divergence times	Family, Genera	87+2	Nuclear c-myc, RAG-1, myoglobin-2, β-fibrinogen, and ornithine decarboxylase (ODC) intron 6-7	Multiple alignment by hand	GTR+I+Γ (c-myc, RAG-1, β-fibrinogen, ODC) GTR+Γ (myoglobin-2)	Bayesian	Fossils and molecular calibration using 23 point calibrations using PL. Constraint the root of the tree at 100 Myr	Ericson, P.G.P et al.	2006

Thamnophilidae	To reconstruct the phylogeny of Thamnophilidae to gain insights into its evolution and biogeography	Species	70	Nuclear β -fibrinogen and Mitochondrial ND2, ND3, cyt-b	Multiple alignment by hand	HKY+ Γ (β -fibrinogen) GTR+I+ Γ (ND2, ND3, cyt-b)	ML and Bayesian	Molecular clock calibration (1.6% of divergence with one million of evolution)	Brumfield, R.T.	2007
World's birds	To reconstruct the avian phylogenetic relationships and reveal their evolutionary history	Family, Genera	169+2	Phylogenomic	Multiple alignment ClustalX and correction by hand	GTR+I+ Γ	MP, ML and Bayesian	Calibration at the root of the tree. Two crocodilian species as outgroups	Hackett, Sh.J. et al.	2008
Furnariidae	To study the relationship between major shifts in nest construction and habitat preference with climatic and ecological history of South America	Species	105+17	Nuclear G3PDH, myoglobin-2, β -fibrinogen, ODC and Mitochondrial cyt-b	Multiple alignment and correction by hand	GTR+I+ Γ	ML and Bayesian	Relaxed clock with calibration point at the root of the tree	Irestedt, M. et al.	2009
Rhinocryptidae	To explore the phylogenetic relationships among all eastern Scytalopus and Eleoscytalopus species, using mitochondrial and nuclear markers	Genera	87	Nuclear G3PDH and Mitochondrial ND2, ND5, cyt-b	Multiple alignment and correction by hand	HKY+I+ Γ	MP, ML and Bayesian	Lineage substitution rate of 0.008 per site/million years	Mata, H. et al.	2009
Furnariides	To reconstruct a comprehensive phylogenetic hypothesis for Furnariides	Genus		Nuclear RAG-1, RAG-2		GTR+I+ Γ	MP, ML and Bayesian	-	Moyle, R.G. et al.	2009

Furnariidae	To reconstruct the phylogeny of the family Furnariidae to test hypotheses of lineage diversification and morphological evolution	Species	285	Nuclear RAG-1, RAG-2, β -fibrinogen and Mitochondrial ND2, ND3, COII	Multiple alignment manually	16 data block under GTR+ Γ and GTR+I+ Γ , the best model was GTR+I+ Γ and fully partitioned	Bayesian	Priors on the divergence times of the tMRCA	Derryberry, E.P. et al.,	2011
World's birds	To reconstruct the avian phylogenetic relationships to investigate patterns of speciation through their evolutionary history	Species	6670	Nuclear MUSK, myoglobin-2, ODC, TGF-beta 2, RHO, TPM1, GAPDH, ZENK, RAG-1&2, c-myc and Mitochondrial cyt-b, COI, ND2, ND3	Multiple alignment MAFFT and correction by hand	13 different models based on partition schemes	Bayesian	Topological and fossil constraints using secondary information at 10 nodes (uncorrelated lognormal relaxed clock)	Jetz, W. et al.,	2012
New World Suboscine	To explore the effects of increased data on the topology of the New World suboscines	Genera, species	209	Nuclear G3P, mioglobin-2, ODC, RAG-1 RAG-2		GTR+I+ Γ	ML and Bayesian	Molecular clock with point calibration of 85-65 Myr	Ohlson, J.L. et al.	2013

Passerine	To provide an update time-scale for the evolution of the major passerine clades and to present the age estimates for major groups of passerines	Family	55	Nuclear MOS, c-myc, myoglobin-2, RAG-1 RAG-2, GAPDH		GTR+Γ	Bayesian	Molecular relaxed clock with different calibration points	Ericson, P.G.P et al.	2014
Thamnophilidae	To reconstruct a comprehensive phylogenetic hypothesis for the genus Myrmeciza (Thamnophilidae)	Species	57	Nuclear β-fibrinogen, RAG-1, RAG-2 and Mitochondrial ND2, ND3, cyt-b	Multiple alignment MAFFT	GTR+Γ	ML and Bayesian	-	Isler, M.L. et al.	2014
Conopophagidae	To infer phylogenetic relationships, divergence time and biogeography of the family Conopophagidae	Species	45	Nuclear TGFB2, G3PDH and Mitochondrial ND2, ND3, cyt-b	Multiple alignment ClustalW and correction by hand	GTR+I+Γ (ND3 and ND2), HKY+I+Γ (cytb), GTR+I (G3PDH) HKY+I (TGFB2)	ML and Bayesian	Secondary calibration of the root (molecular relaxed uncorrelated clock)	Batalha-Filho, H.	2014
World's birds	To combine data from extant and fossil taxa, to reconstruct the avian phylogeny	Species	6326	1036 source trees		-	MPR supertree	-	Davies, K.E. and Page, R.D.M.	2014
Dendrocolaptinae	To corroborate the subspecies definitions based on plumage taxonomy and mtDNA variation and evaluate the extent of spatial and	Species	58	Nuclear β-fibrinogen and Mitochondrial ND2, cyt-b	Multiple alignment ClustalW and correction by hand	-	ML and Bayesian	Priors on the divergence times of the tMRCA	Rocha, T.C. et al.	2015

temporal
diversification

World's birds	To estimate the avian phylogeny based on a large molecular dataset	Species	6714	Nuclear and Mitochondrial	MAFFT and MUSCLE and corrections by hand	GTRCAT	ML supermatrix	-	Burleigh et al.	2015
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Apêndices Capítulo 2

**The geographic diversification of Furnariides: the role of forest versus open
habitats in driving species richness gradients**

Jesús N. Pinto-Ledezma, Lorena Mendes Simon, José Alexandre F. Diniz-Filho, and
Fabricio Villalobos

SUPPORTING INFORMATION

The geographic diversification of Furnariides: the role of forest versus open habitats in driving species richness gradients

Jesús N. Pinto-Ledezma, Lorena Mendes Simon, José Alexandre F. Diniz-Filho, and
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Appendix S1. Expanded Materials and Methods

Species habitat categorization

To categorize all Furnariides species as belonging to one (or more) habitat types within the Neotropics, we first defined the primary habitats within this region based on the terrestrial ecoregions of the world (Olson *et al.*, 2001). This categorization was then reclassified (see below) according to the habitat classification system of Stotz *et al.*, (1996), which is specifically tailored for Neotropical birds. This habitat classification system includes 41 principal habitats for birds in South America grouped into three primary habitat types: forest, scrubs/grasslands/savannahs, and aquatic habitats (for more detailed information see Stotz *et al.*, 1996). Based on this information, we classify the Neotropical region into two primary habitat types: forest and open vegetation (including scrubs, grasslands, and savannahs) (Fig. 1a).

Following the habitat classification and based on the information about species' habitat preferences provided in Stotz *et al.*, (1996), we categorized species as belonging to either one or both primary habitats: forest and open vegetation. In the few instances where habitat information for a species was lacking, habitat membership was

determined from the literature (mainly del Hoyo *et al.*, 2003 [volume 8]) and field observations (JNPL personal observations). The 652 Furnariides species were defined as members of: forest (67.79%), open vegetation (13.19%) and forest-open vegetation (19.01%). Note that this species habitat categorization was solely based on species locality data (e.g., Stotz *et al.*, 1996) to assure a local-scale and ecologically informed categorization and avoid potential overestimation of species' habitat preferences by using range maps (Tobias *et al.*, 2014).

Diversification analysis

GeoSSE approach

The GeoSSE model is an extension of the Binary State Speciation and Extinction model (BiSSE, Maddison *et al.*, 2007) that considers species' occurrence within geographical regions as character states. In GeoSSE, species are categorized as belonging to either one of two regions (e.g., forest or open habitats) or simultaneously to both regions (e.g., occurring in both forest and open habitats). In GeoSSE, transitions between states (e.g., forest to open) are parameterized in terms of range expansion through dispersal and range contraction by local extirpation (Goldberg *et al.*, 2011). In our case comparing the two types of habitat, it allowed us to evaluate potential shifts in habitat occupancy. The GeoSSE model estimates are obtained under a Maximum Likelihood approach that generates parameters for speciation (λ_{forest} and λ_{open}), extinction (μ_{forest} and μ_{open}), and dispersal (d_{forest} and d_{open}) rates for each habitat. In addition, it includes a third separate parameter for the between-habitat speciation ($\lambda_{\text{forest-open}}$), which assumes that a widespread species (i.e., occupying both habitats) may undergo speciation between-habitats (Goldberg *et al.*, 2011).

As indicated in the main text, we fitted 16 scenarios under a maximum likelihood approach and select the best-fitted scenario using Akaike Information Criterion (i.e., that with lower AIC and $\Delta AIC < 2$; Burnham & Anderson, 2002). To assess the confidence around parameters estimates of the best-fitted scenario, we ran a Bayesian Markov Chain Monte Carlo (MCMC) analysis over the 1,000 trees. We used the parameter estimates from the selected scenario to start the chain and applied an exponential prior $1/(2r)$ (Fitzjohn, 2012). We applied a burn-in of 1,000 generations and ran 20,000 generations of chain. We used the MCMC samples to calculate the net diversification rate ($r = \lambda - \mu$) for each character state (forest vs. open) and to assess the variation of speciation, extinction, and dispersal between character states.

Additionally, to the estimations of speciation, extinction and diversification rates, we calculated historical habitat shifts as net range expansion ($d - \mu$) and habitat specialization as net range contraction ($\mu - \lambda$) (Goldberg et al., 2011). Under net range expansion, species have broad opportunity to enter and adapt to alternative habitats (Goldberg et al., 2011). Positive net range expansion occurs when the balance between dispersal and extinction rates is greater than 0 (i.e., $dF - \mu O > 0$ or $dO - \mu F > 0$). Conversely, habitat specialization or range contraction occurs via local extirpation (μ) and/or local speciation (λ), which can explain the production of range-limited species (i.e., endemic species). Positive values of net range contraction are interpreted as anagenetic specialization and occur under local extirpation. That is, when the extinction of one habitat is higher than the speciation of another habitat (i.e., $\mu F - \lambda O > 0$ or $\mu O - \lambda F > 0$). Conversely, negative values of net range contraction indicate cladogenetic specialization, which occurs when the local speciation of one habitat exceed the extinction of the another habitat (i.e., $\mu F - \lambda O < 0$ or $\mu O - \lambda F < 0$) (Goldberg et al., 2011).

GeoSSE simulations

As pointed out in the main text (see GeoSSE approach in the methods section), we evaluate the potential problem that SSE models under a parametric bootstrap approach. To do this, we first, simulated 100 datasets of neutral characters (applying the “sim.history” function in the *phytools* package; Revell, 2012; see also Appendix S1) along a set of empirical phylogenies (100 trees to reduce computation time), using the estimated ancestral value at the root of each tree reconstructed with the “make.simmap” function of *phytools* (Revell, 2012). Then we applied a similar procedure than with the original data by applying the GeoSSE model to the simulated dataset. Given that the best-fitted GeoSSE scenario to the observed data was that with all parameters varying freely (scenario 1 in Table S2.1; see below), we compared its fit to the scenario where all parameters are constrained (scenario 9 in Table S2.1). Using the 1000 trees, we compared the fit of both of these scenarios to the observed data and calculated the log-likelihood difference (ΔLL), along with their mean and standard deviations (see Fig. S2.3). Following this procedure, we fitted the same two scenarios (1 and 9 scenarios in Table S2.1) to the simulated dataset and calculated the corresponding ΔLL between these. Finally, we calculated the *P*-value as the proportion of simulated ΔLL that were as extreme as the observed mean ΔLL (Feldman *et al.*, 2016). As the simulations assumed no direct effect of the geographic character on the relative estimations of speciation, extinction and dispersal, a *P*-value below 0.05 indicate that the performance of the model was good and can be interpreted as significant support for the hypothesis that habitat type affects the macroevolutionary rates of Furnariides (Rabosky & Goldberg, 2015; Feldman *et al.*, 2016).

BAMM approach

To run BAMM we generated two maximum clade credibility trees (hereafter MCC) from the 1,000 trees (described in the main text) using Tree Annotator (included in BEAST v2.1.2; Bourkaert *et al.*, 2014). The first MCC includes all species as described in Jetz *et al.*, (2012) and we call this tree as fullTree. Due that the insertion of missing species (i.e., species without genetic information) using taxonomic constraints can bias the macroevolutionary inferences (Rabosky, 2015), we pruned all species without genetic information (32.36% in Furnariides clade) and generated the second MCC, that we call nonzeroTree.

As described in the main text we performed two separate runs of BAMM of 100 million of generations and discarded 10% of each run as burn-in. We applied the same procedure for both MCC, the fullTree and the nonzeroTree, obtaining four separate runs. In the main text we describe the results based on the fullTree. The conclusions based on the results of the nonzeroTree not differ from the fullTree, although the estimated values of the rates of speciation, extinction and diversification varies slightly (Fig. S2.4).

Ancestral habitat estimation

We estimate the ancestral character states (i.e., ancestral habitat) for Furnariides using two complementary methods. First, we use the ancestral character estimation (ace) using the function “ace” in the R package *ape* (Paradis *et al.*, 2004). Second, we used stochastic character mapping (Simmap, Huelsenbeck *et al.*, 2003), which randomly map possible character histories on phylogenetic trees under a continuous-time discrete-state Markov chain (Huelsenbeck *et al.*, 2003). We simulated 100 stochastic maps on each tree obtaining a total of 100,000 stochastic character maps, using the function “make.simmap” in the R package *phytools* (Revell, 2012).

Appendix S2. Expanded Results

Diversification analysis

GeoSSE approach

In the table S2.1 we present the comparison of 16 scenarios considered for the Furnariides using the 1,000 trees from posterior distribution. The scenarios are listed according to the partitions indicated in the main text.

As indicated in the main text, our best fitted diversification scenario (model with seven parameters, scenario 1 in table S2.1) indicated a higher speciation rate for open habitats than for forest habitats (Fig. 2) within the Neotropics, ($\lambda_O - \lambda_F = 0.084 \pm 0.045$ lineages Myr⁻¹; Fig. S2.1b). This scenario also considered between-habitat speciation ($\lambda_{FO} = 0.042$ lineages Myr⁻¹). In addition, this best-fitting scenario indicated higher extinction (Fig. 2c) and dispersal rates (Fig. S2.1a) for open habitats than for forest habitats ($\mu_O - \mu_F = 0.067 \pm 0.049$ lineages x Myr⁻¹ and $d_O - d_F = 0.290 \pm 0.111$ lineages x Myr⁻¹, respectively). Net diversification rates were also higher for open habitats than for forest habitats, indicating a faster (1.171 times) net diversification rate in open habitats compared to that for forest habitats (Forest = 0.099 ± 0.006 lineages x Myr⁻¹ and Open = 0.116 ± 0.010 lineages x Myr⁻¹, respectively; Fig. 2e).

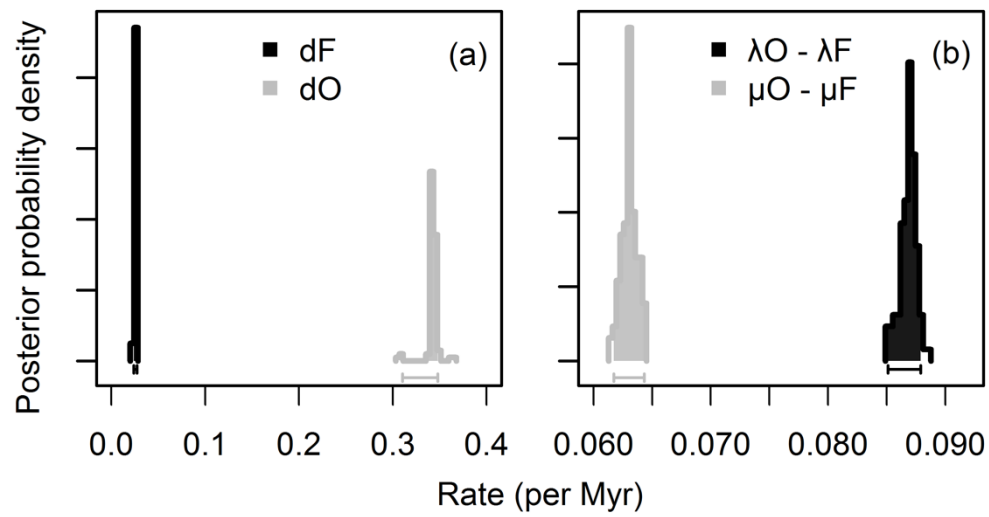


Figure S2.1. Posterior probability distributions based on the GeoSSE approach. Rates of (a) dispersal of Furnariides in forest habitats (black) and open habitats (gray), and (b) differences in speciation and extinction rates between habitats.

1 **Table S2.1.** The first column shows the 16 evaluated scenarios of diversification of Furnariides between habitats in the Neotropics, where F =

2 forest, O = open, and FO = forest-open. The values of separate speciation (λ), extinction (μ), and dispersal (d) are reported as Mean $\pm$ sd for each

3 scenario over the 1,000 phylogenies. The best scenario (marked as gray) was selected based on the lowest AIC.

Scenarios	λ_{Forest}		λ_{Open}		$\lambda_{\text{Forest-Open}}$		μ_{Forest}		μ_{Open}		d_{Forest}		d_{Open}		lnLik		AIC	
	Mean $\pm$ sd		Mean $\pm$ sd		Mean $\pm$ sd		Mean $\pm$ sd		Mean $\pm$ sd		Mean $\pm$ sd		Mean $\pm$ sd		Mean $\pm$ sd		Mean $\pm$ sd	
Full scenario	0.139	0.020	0.223	0.065	0.041	0.020	0.040	0.025	0.107	0.075	0.021	0.004	0.311	0.114	-2298.311	96.112	4610.623	192.224
($\lambda_{\text{FO}} \sim 0$)	0.140	0.020	0.260	0.067	NA	NA	0.052	0.025	0.168	0.069	0.024	0.004	0.321	0.109	-2302.757	96.524	4617.513	193.048
($\mu_{\text{F}} \sim \mu_{\text{O}}, \lambda_{\text{FO}} \sim 0$)	0.166	0.026	0.209	0.046	NA	NA	0.083	0.044	NA	NA	0.016	0.004	0.373	0.160	-2308.394	95.556	4626.787	191.112
($d_{\text{F}} \sim d_{\text{O}}, \lambda_{\text{FO}} \sim 0$)	0.145	0.020	0.262	0.079	NA	NA	0.004	0.007	0.271	0.108	0.083	0.023	NA	NA	-2327.961	93.073	4665.922	186.145
($\lambda_{\text{F}} \sim \lambda_{\text{O}}, \lambda_{\text{FO}} \sim 0$)	0.174	0.030	NA	NA	NA	NA	0.069	0.037	0.075	0.026	0.019	0.004	0.315	0.129	-2311.481	94.359	4632.962	188.719
($\mu_{\text{F}} \sim \mu_{\text{O}}, d_{\text{F}} \sim d_{\text{O}}, \lambda_{\text{FO}} \sim 0$)	0.175	0.028	0.137	0.022	NA	NA	0.043	0.015	NA	NA	0.045	0.007	NA	NA	-2361.791	91.024	4731.582	182.049
($\lambda_{\text{F}} \sim \lambda_{\text{O}}, d_{\text{F}} \sim d_{\text{O}}, \lambda_{\text{FO}} \sim 0$)	0.162	0.025	NA	NA	NA	NA	0.013	0.012	0.180	0.051	0.073	0.016	NA	NA	-2335.320	91.906	4678.639	183.812
($\lambda_{\text{F}} \sim \lambda_{\text{O}}, \mu_{\text{F}} \sim \mu_{\text{O}}, \lambda_{\text{FO}} \sim 0$)	0.174	0.029	NA	NA	NA	NA	0.071	0.031	NA	NA	0.019	0.003	0.318	0.114	-2311.700	94.393	4631.400	188.787
($\lambda_{\text{F}} \sim \lambda_{\text{O}}, \mu_{\text{F}} \sim \mu_{\text{O}}, d_{\text{F}} \sim d_{\text{O}}, \lambda_{\text{FO}} \sim 0$)	0.165	0.025	NA	NA	NA	NA	0.035	0.010	NA	NA	0.043	0.006	NA	NA	-2363.507	91.074	4733.014	182.149
($d_{\text{F}} \sim d_{\text{O}}$)	0.145	0.020	0.242	0.078	0.017	0.012	0.002	0.006	0.246	0.106	0.080	0.022	NA	NA	-2326.096	92.861	4664.193	185.722
($\lambda_{\text{F}} \sim \lambda_{\text{O}}$)	0.158	0.026	NA	NA	0.055	0.026	0.041	0.027	0.023	0.023	0.017	0.003	0.296	0.112	-2303.419	94.295	4618.839	188.591
($\mu_{\text{F}} \sim \mu_{\text{O}}$)	0.149	0.022	0.189	0.041	0.056	0.027	0.044	0.033	NA	NA	0.017	0.003	0.320	0.138	-2300.528	95.354	4613.057	190.708
($\mu_{\text{F}} \sim \mu_{\text{O}}, d_{\text{F}} \sim d_{\text{O}}$)	0.153	0.022	0.136	0.026	0.039	0.012	0.005	0.007	NA	NA	0.041	0.006	NA	NA	-2351.315	90.593	4712.630	181.187
($\lambda_{\text{F}} \sim \lambda_{\text{O}}, d_{\text{F}} \sim d_{\text{O}}$)	0.156	0.024	NA	NA	0.027	0.012	0.004	0.009	0.157	0.044	0.069	0.014	NA	NA	-2330.954	91.727	4671.908	183.453
($\lambda_{\text{F}} \sim \lambda_{\text{O}}, \mu_{\text{F}} \sim \mu_{\text{O}}$)	0.158	0.026	NA	NA	0.048	0.020	0.038	0.025	NA	NA	0.019	0.003	0.284	0.103	-2303.863	94.150	4617.727	188.301
($\lambda_{\text{F}} \sim \lambda_{\text{O}}, \mu_{\text{F}} \sim \mu_{\text{O}}, d_{\text{F}} \sim d_{\text{O}}$)	0.150	0.022	NA	NA	0.040	0.012	0.004	0.005	NA	NA	0.041	0.006	NA	NA	-2352.075	90.793	4712.150	181.586

Considering the rates of range expansion and contraction, the best-fitting model indicated shifts in habitat occupancy with open habitat species experiencing range expansion ($dO - \mu F = 0.270 \pm 0.140$ lineages x Myr⁻¹; Fig. S2.2a), whereas species from forest habitats experienced range contraction ($dF - \mu O = -0.086 \pm 0.071$ lineages x Myr⁻¹; Fig. S2.2a). This pattern of shifting habitat occupancy over time is corroborated by a more rapid dispersal (14.826 times) out of open habitats than into them. Additionally, we found that habitat specialization in open habitats was a result of anagenetic specialization ($\mu F - \lambda O = -0.183 \pm -0.039$ lineages x Myr⁻¹; Fig. S2.2b), whereas habitat specialization for forest habitats resulted from cladogenetic specialization ($\mu O - \lambda F = -0.032 \pm 0.055$ lineages x Myr⁻¹; Fig. S2.2b).

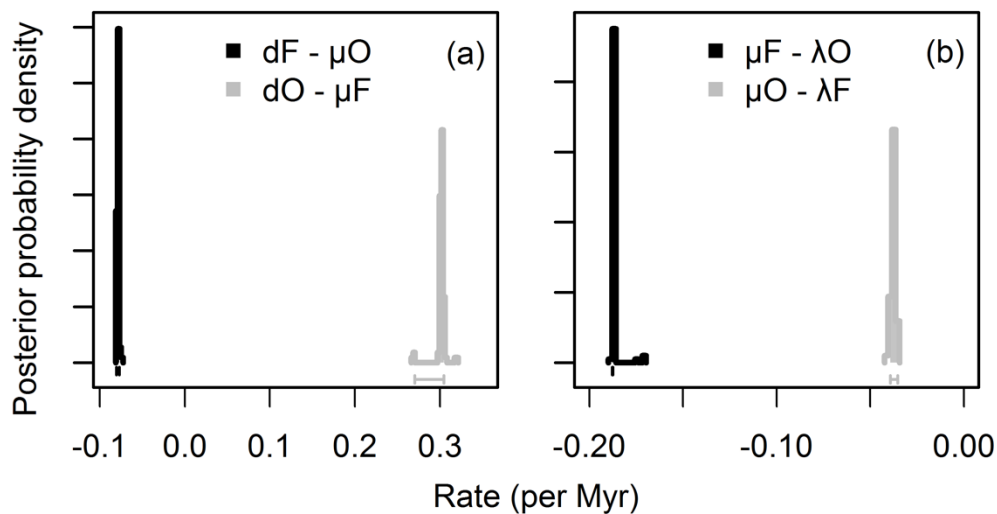


Figure S2.2. Shifts in habitat occupancy, based on the GeoSSE approach. Posterior probability distributions of shifts in habitat occupancy described by (a) range expansion/contraction and (b) habitat specialization.

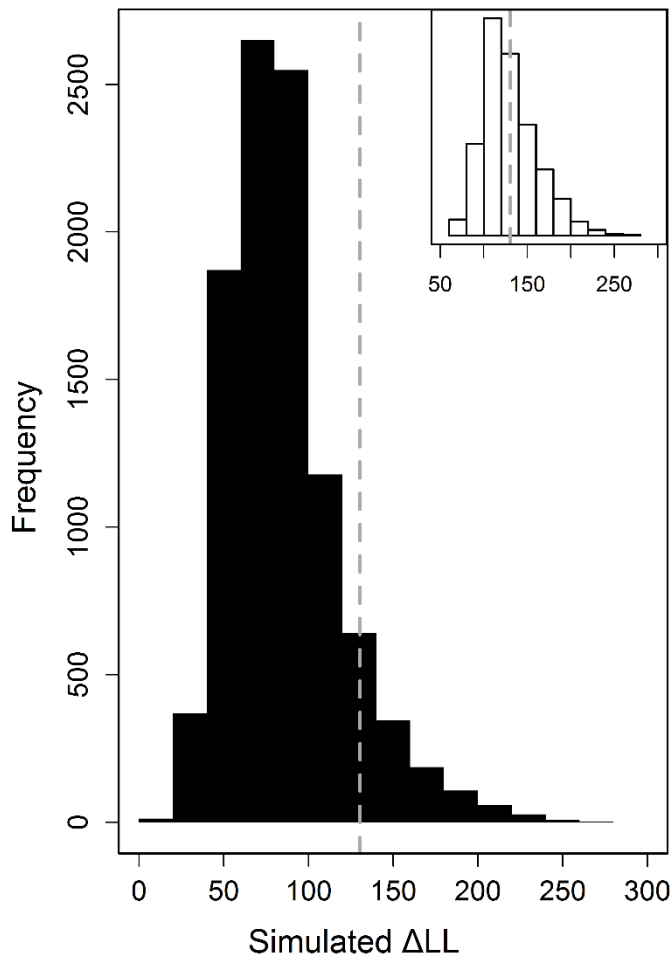


Figure S2.3. Simulation based GeoSSE for Furnariides clade. It shows the distribution of the log-likelihood difference (ΔLL) between the best-fitted scenario and the null scenario for 10,000 simulations. The grey dotted-line indicate the mean ΔLL based on the 1,000 empirical phylogenies, whose distribution is shown in the inset histogram.

BAMM Approach

BAMM analysis also indicate higher speciation rate for open habitats than for forest habitats, using the two MCCtrees (fullTree: $\lambda O - \lambda F = 0.080 \pm 0.007$ lineages x Myr-1 and nonzeroTree: $\lambda O - \lambda F = 0.031 \pm 0.007$ lineages Myr-1, respectively). Extinction rates also were higher in open

habitats compared with forest habitats (fullTree: $\mu_O - \mu_F = 0.003 \pm 0.001$ lineages x Myr-1 and (nonzeroTree: $\mu_O - \mu_F = 0.002 \pm 0.001$ lineages x Myr-1, respectively), although, contrasting with the GeoSSE analysis, the estimate extinction rates varies slightly between habitats (Fig. 2d). Net diversification rates also was higher for open habitats (fullTree = 0.183 ± 0.012 lineages x Myr-1 and nonzeroTree = 0.200 ± 0.019 lineages x Myr-1, respectively; Fig. S2.4) than for forest habitats (fullTree = 0.099 ± 0.007 lineages x Myr-1 and nonzeroTree = 0.167 ± 0.012 lineages x Myr-1, respectively; Fig. S2.4).

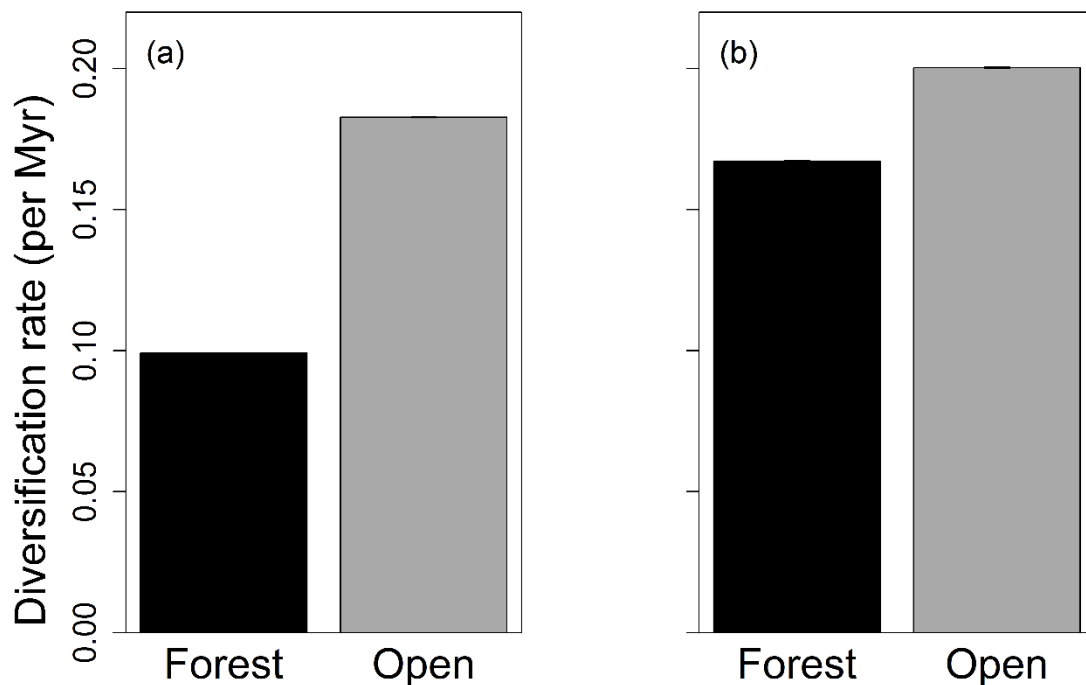


Figure S2.4. Rates of diversification based on the BAMM analysis. The barplot shows the mean diversification rates for forest habitats and open habitats (a) mean diversification rates for the fullTree and (b) mean diversification rates for the nonzeroTree.

Range shifts through time

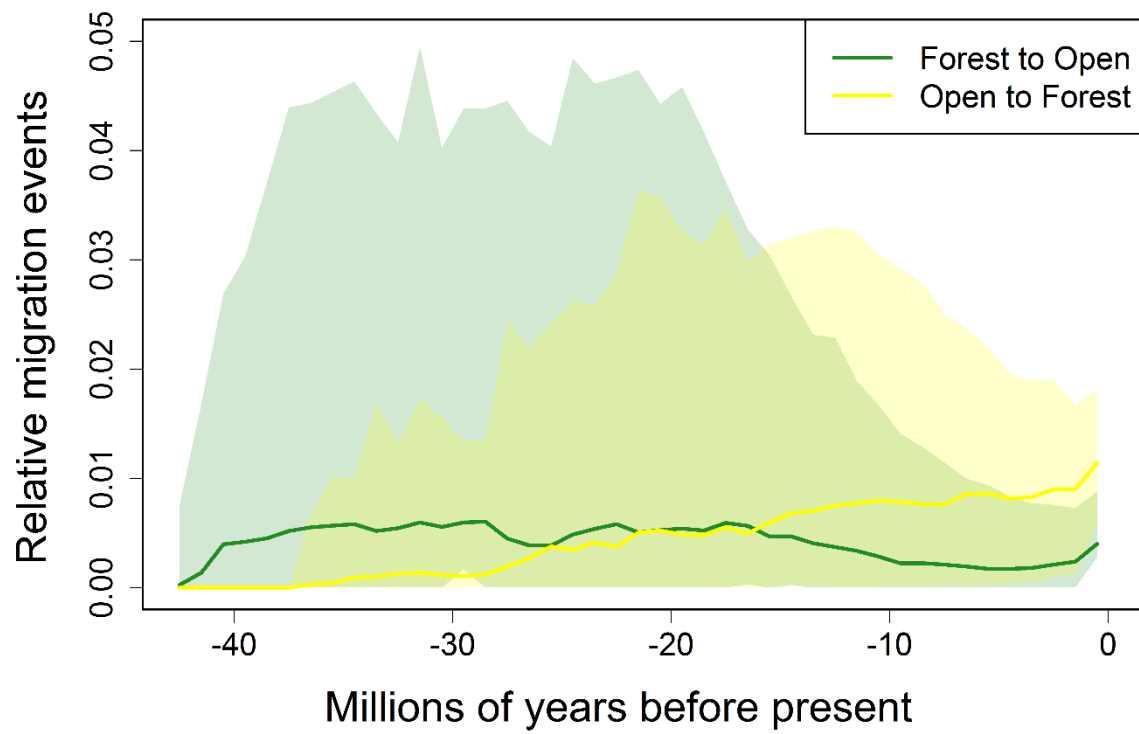


Figure S2.5. Range shifts through time for Furnariides clade. Show the relative number of range shifts events (i.e. range expansions) through time (see Antonelli *et al.*, 2015 for details).

Diversity-dependent regulation

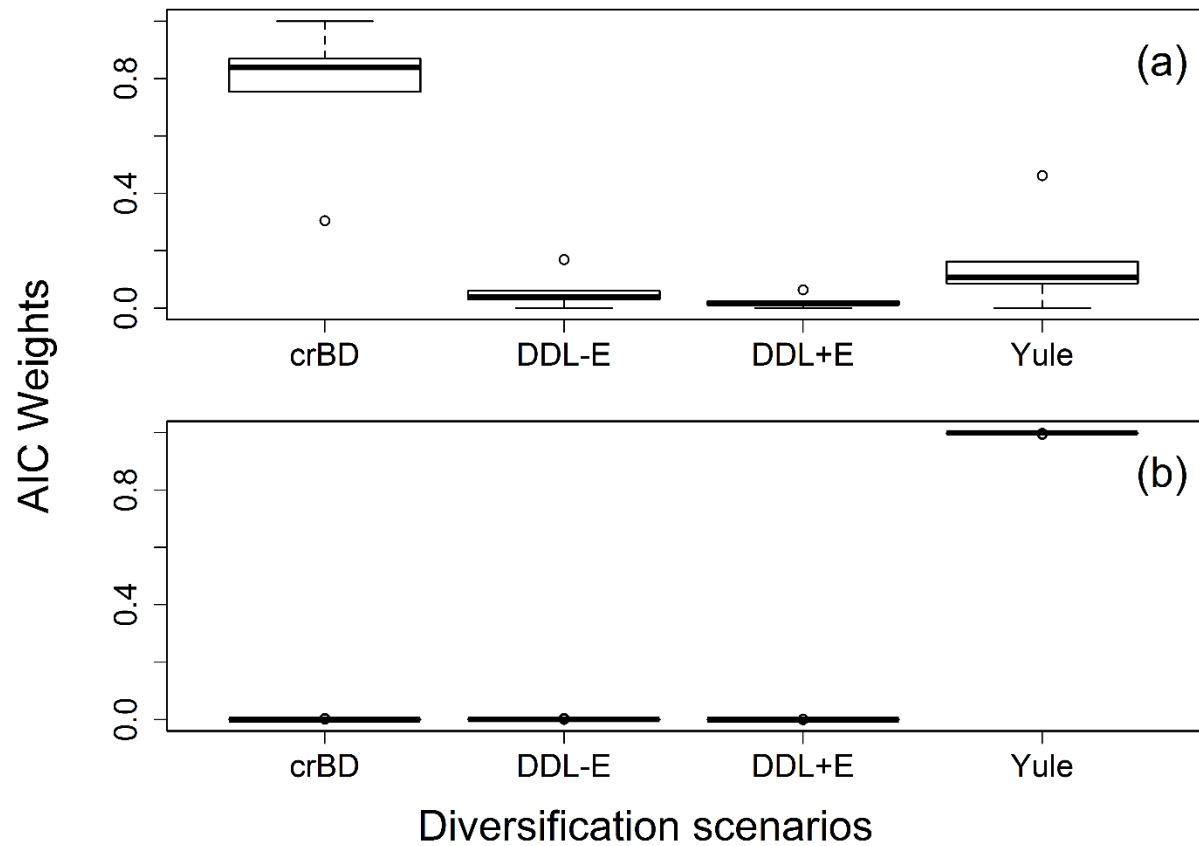


Figure S2.6. Summary of diversification analysis through time under the diversity-dependent hypothesis. Boxplots represent the distribution of AIC weights (w_i) values for 100 trees under the four scenarios of diversity-dependent hypotheses (a) Furnariides diversification on forest habitats and (b) Furnariides diversification on open habitats. crBD = constant rate birth-death, DDL-E = diversity-dependent model without extinction, DDL+E = diversity-dependent model with extinction, Yule = Pure birth.

Ancestral habitat estimation

The ace analysis indicated a higher marginal ancestral states for forest habitats ($0,793 \pm 0,217$), whereas the marginal ancestral states for open and forest-open habitats are lower ($0,130 \pm 0,167$; $0,076 \pm 0,081$ respectively). Simmap analysis suggest that forest habitat was present in the

common ancestor of Furnariides in 80,3%. Both analysis suggest that forest habitats represent the ancestral habitat for Furnariides (Fig. S2.7).

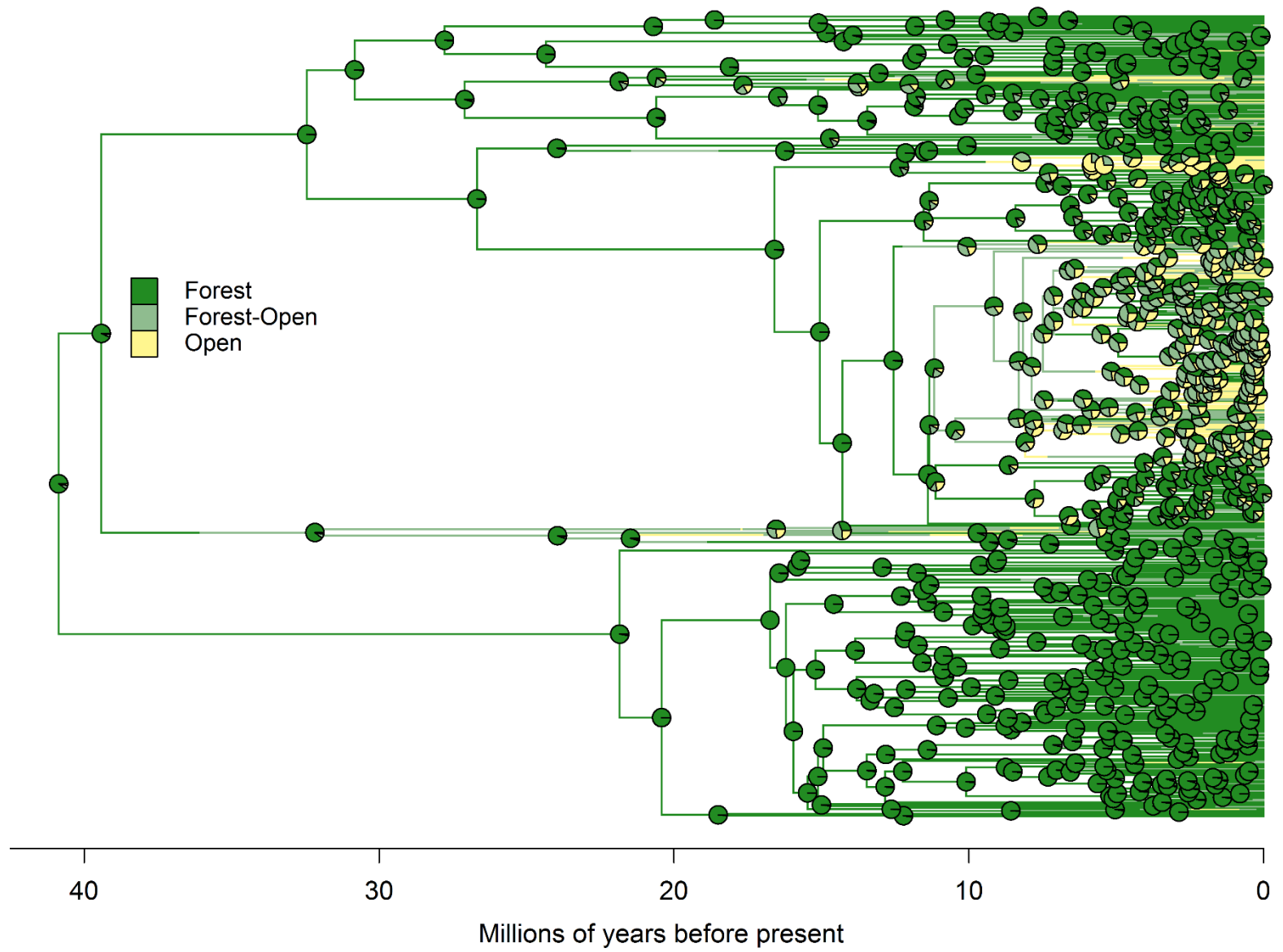


Figure S2.7. A random time-calibrated phylogeny of Furnariides clade (from Jetz *et al.*, 2012) showing the ancestral reconstructions of habitats using stochastic character mapping. The branch colours depict the posterior probability of the character mapped along the tree. The node colours summarize the total set of stochastic maps.

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Appendix S3. Climatic, geological and vegetational history of South America during the Cenozoic.

Due to the size of the table, this can be found in the next link:

https://drive.google.com/open?id=0Bx5_Spbv4O84dWVlRWo0R2FtRk0

Apêndices Capítulo 3

Drivers of phylogenetic assemblage structure of the Furnariides, a widespread clade of lowland Neotropical birds

Jesús N. Pinto-Ledezma, Alex E. Jahn, Victor R. Cueto, Fabricio Villalobos, and José

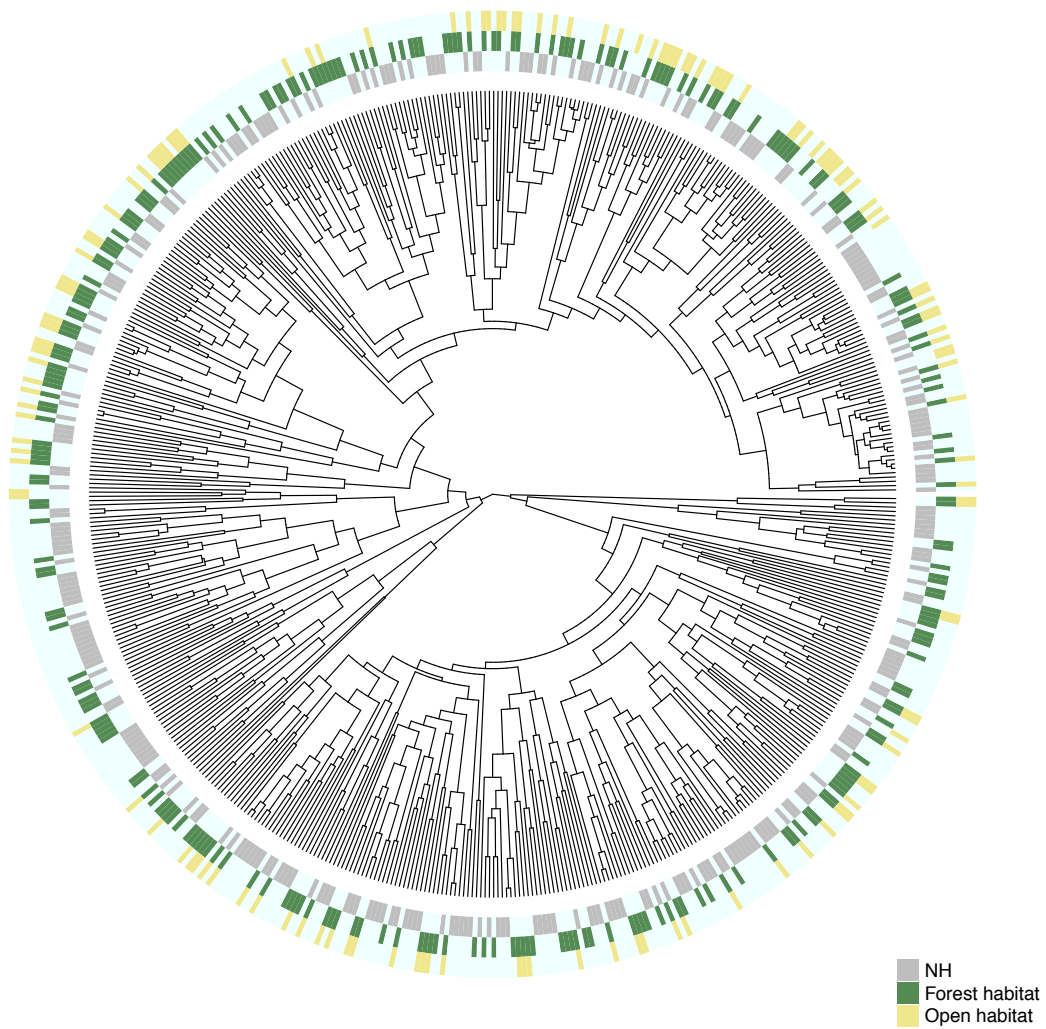
Alexandre F. Diniz-Filho

SUPPORTING INFORMATION

**Drivers of phylogenetic assemblage structure of the Furnariides, a widespread
clade of lowland Neotropical birds**

Jesús N. Pinto-Ledezma, Alex E. Jahn, Victor R. Cueto, Fabricio Villalobos, and José
Alexandre F. Diniz-Filho

Appendix S1. Plot of the Furnariides MCC-tree used in this study. It shows the
distribution of the species in our assemblage datasets according to the primary habitats.
NH = species not presented in our assemblage datasets.



Appendix S2. List of all mitochondrial and nuclear loci obtained from GenBank used for phylogenetic inference.

Taxon	Total length	No of charsets	BF5	BF7	COII	CYTB	ND2	ND3	ODC	RAG1	RAG2
<i>Acrobatornis fonsecai</i>	5416 bp	4	-	-	-	-	1042	350	-	2872	1152
<i>Acropternis orthonyx</i>	4572 bp	3	-	-	-	-	-	-	548	2872	1152
<i>Anabacerthia amaurotis</i>	2983 bp	4	-	862	729	-	1042	350	-	-	-
<i>Anabacerthia striaticollis</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Anabacerthia variegaticeps</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Anabazenops dorsalis</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Anabazenops fuscus</i>	6872 bp	6	-	862	594	-	1042	350	-	2872	1152
<i>Ancistrops strigilatus</i>	7950 bp	7	-	862	671	1001	1042	350	-	2872	1152
<i>Anumbius annumbi</i>	9145 bp	9	566	862	690	1001	1042	350	610	2872	1152
<i>Aphrastura masafuerae</i>	647 bp	1	-	-	647	-	-	-	-	-	-
<i>Aphrastura spinicauda</i>	9149 bp	9	566	862	694	1001	1042	350	610	2872	1152
<i>Asthenes anthoides</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Asthenes baeri</i>	6972 bp	6	-	862	694	-	1042	350	-	2872	1152
<i>Asthenes cactorum</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Asthenes dorbignyi</i>	3466 bp	6	566	320	694	926	-	350	610	-	-
<i>Asthenes flammulata</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Asthenes hudsoni</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Asthenes humicola</i>	3255 bp	4	-	862	-	1001	1042	350	-	-	-
<i>Asthenes humilis</i>	6278 bp	5	-	862	-	-	1042	350	-	2872	1152
<i>Asthenes luizae</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Asthenes maculicauda</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Asthenes modesta</i>	5124 bp	7	566	862	693	1001	1042	350	610	-	-
<i>Asthenes ottonis</i>	4430 bp	6	566	862	-	1001	1041	350	610	-	-
<i>Asthenes patagonica</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Asthenes pudibunda</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Asthenes punensis</i>	1001 bp	1	-	-	-	1001	-	-	-	-	-
<i>Asthenes pyrrholeuca</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Asthenes sclateri</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Asthenes steinbachi</i>	2946 bp	4	-	862	694	-	1040	350	-	-	-

<i>Asthenes urubambensis</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Asthenes vilcabambae</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Asthenes virgata</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Asthenes wyatti</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Automolus infuscatus</i>	5855 bp	5	-	862	729	-	1042	350	-	2872	-
<i>Automolus lammi</i>	1007 bp	2	-	657	-	-	-	350	-	-	-
<i>Automolus leucophthalmus</i>	4775 bp	6	566	862	694	1001	1042	-	610	-	-
<i>Automolus melanopezus</i>	3037 bp	4	-	862	-	-	1042	350	-	783	-
<i>Automolus ochrolaemus</i>	4805 bp	6	-	860	747	1042	1042	350	-	764	-
<i>Automolus paraensis</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Automolus roraimae</i>	6930 bp	6	-	862	652	-	1042	350	-	2872	1152
<i>Automolus rubiginosus</i>	6983 bp	6	-	862	652	1095	-	350	-	2872	1152
<i>Automolus rufipectus</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Automolus rufipileatus</i>	6930 bp	6	-	862	652	-	1042	350	-	2872	1152
<i>Batara cinerea</i>	7013 bp	6	549	-	-	1047	1042	351	-	2872	1152
<i>Berlepschia rikeri</i>	9104 bp	9	566	862	649	1001	1042	350	610	2872	1152
<i>Campylorhamphus falcularius</i>	3265 bp	4	-	862	-	1011	1042	350	-	-	-
<i>Campylorhamphus procurvoides</i>	3284 bp	4	-	862	-	1033	1042	347	-	-	-
<i>Campylorhamphus pucherani</i>	6261 bp	5	-	862	-	-	1042	350	-	2871	1136
<i>Campylorhamphus pusillus</i>	3872 bp	5	-	862	-	1008	1042	350	610	-	-
<i>Campylorhamphus trochilirostris</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Cercomacra brasiliana</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Cercomacra carbonaria</i>	3642 bp	5	550	-	652	1047	1042	351	-	-	-
<i>Cercomacra cinerascens</i>	3658 bp	5	566	-	652	1047	1042	351	-	-	-
<i>Cercomacra ferdinandi</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Cercomacra laeta</i>	3676 bp	5	549	-	733	1001	1042	351	-	-	-
<i>Cercomacra manu</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Cercomacra melanaria</i>	4127 bp	6	550	-	253	1001	1042	351	-	930	-
<i>Cercomacra nigrescens</i>	3595 bp	5	549	-	652	1001	1042	351	-	-	-
<i>Cercomacra nigricans</i>	3040 bp	4	-	-	652	995	1042	351	-	-	-
<i>Cercomacra parkeri</i>	2965 bp	4	525	-	-	1047	1042	351	-	-	-
<i>Cercomacra serva</i>	3757 bp	5	549	-	-	1047	1042	351	-	768	-

<i>Cercomacra tyrannina</i>	7665 bp	7	549	-	652	1047	1042	351	-	2872	1152
<i>Certhiaxis cinnamomeus</i>	9199 bp	9	566	862	744	1001	1042	350	610	2872	1152
<i>Certhiaxis mustelinus</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Chamaeza campanisona</i>	3954 bp	5	-	862	652	1047	1042	351	-	-	-
<i>Chamaeza meruloides</i>	3909 bp	5	566	-	731	1001	-	-	681	930	-
<i>Chamaeza mollissima</i>	380 bp	1	-	-	-	380	-	-	-	-	-
<i>Chamaeza nobilis</i>	4024 bp	2	-	-	-	-	-	-	-	2872	1152
<i>Chamaeza ruficauda</i>	226 bp	1	-	-	226	-	-	-	-	-	-
<i>Chilia melanura</i>	8335 bp	8	566	862	-	964	1042	350	527	2872	1152
<i>Cichlocolaptes leucophrus</i>	6278 bp	5	-	862	-	-	1042	350	-	2872	1152
<i>Cinclodes albidiventris</i>	1207 bp	2	-	856	-	-	-	351	-	-	-
<i>Cinclodes albiventris</i>	1207 bp	2	-	856	-	-	-	351	-	-	-
<i>Cinclodes antarcticus</i>	351 bp	1	-	-	-	-	-	351	-	-	-
<i>Cinclodes aricomae</i>	4425 bp	6	566	856	-	1001	1042	350	610	-	-
<i>Cinclodes atacamensis</i>	5120 bp	7	566	856	694	1001	1042	351	610	-	-
<i>Cinclodes comechingonus</i>	2249 bp	3	-	856	-	-	1042	351	-	-	-
<i>Cinclodes excelsior</i>	2883 bp	4	-	856	634	-	1042	351	-	-	-
<i>Cinclodes fuscus</i>	5172 bp	7	566	862	740	1001	1042	351	610	-	-
<i>Cinclodes nigrofumosus</i>	5237 bp	4	-	862	-	-	-	351	-	2872	1152
<i>Cinclodes olrogi</i>	2249 bp	3	-	856	-	-	1042	351	-	-	-
<i>Cinclodes oustaleti</i>	3250 bp	4	-	856	-	1001	1042	351	-	-	-
<i>Cinclodes pabsti</i>	2248 bp	3	-	856	-	-	1042	350	-	-	-
<i>Cinclodes palliatus</i>	2249 bp	3	-	856	-	-	1042	351	-	-	-
<i>Cinclodes patagonicus</i>	2942 bp	4	-	856	694	-	1042	350	-	-	-
<i>Cinclodes taczanowskii</i>	2248 bp	3	-	856	-	-	1042	350	-	-	-
<i>Clibanornis dendrocolaptoides</i>	8308 bp	8	566	862	-	972	1041	350	527	2858	1132
<i>Conopophaga ardesiaca</i>	4367 bp	3	-	-	-	-	-	343	-	2872	1152
<i>Conopophaga aurita</i>	3265 bp	5	566	862	747	-	-	343	747	-	-
<i>Conopophaga castaneiceps</i>	343 bp	1	-	-	-	-	-	343	-	-	-
<i>Conopophaga cearae</i>	343 bp	1	-	-	-	-	-	343	-	-	-
<i>Conopophaga lineata</i>	3846 bp	5	-	862	702	1001	-	351	-	930	-
<i>Conopophaga melanogaster</i>	995 bp	2	-	-	652	-	-	343	-	-	-

<i>Conopophaga melanops</i>	1090 bp	2	-	-	747	-	-	343	-	-	-
<i>Conopophaga peruviana</i>	723 bp	2	-	-	-	380	-	343	-	-	-
<i>Conopophaga roberti</i>	1090 bp	2	-	-	747	-	-	343	-	-	-
<i>Coryphistera alaudina</i>	9149 bp	9	566	862	694	1001	1042	350	610	2872	1152
<i>Cranioleuca albicapilla</i>	3569 bp	5	566	-	-	1001	1042	350	610	-	-
<i>Cranioleuca albiceps</i>	1628 bp	3	-	-	-	236	1042	350	-	-	-
<i>Cranioleuca antisimensis</i>	1628 bp	3	-	-	-	236	1042	350	-	-	-
<i>Cranioleuca baroni</i>	2449 bp	3	-	-	-	1057	1042	350	-	-	-
<i>Cranioleuca curtata</i>	1628 bp	3	-	-	-	236	1042	350	-	-	-
<i>Cranioleuca demissa</i>	3142 bp	5	-	862	652	236	1042	350	-	-	-
<i>Cranioleuca erythrops</i>	6416 bp	5	-	-	-	1000	1042	350	-	2872	1152
<i>Cranioleuca gutturalis</i>	5416 bp	4	-	-	-	-	1042	350	-	2872	1152
<i>Cranioleuca hellmayri</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Cranioleuca henricae</i>	236 bp	1	-	-	-	236	-	-	-	-	-
<i>Cranioleuca marcapatae</i>	1628 bp	3	-	-	-	236	1042	350	-	-	-
<i>Cranioleuca muelleri</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Cranioleuca obscura</i>	1626 bp	3	-	-	-	234	1042	350	-	-	-
<i>Cranioleuca pallida</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Cranioleuca pyrrhophia</i>	5192 bp	7	566	-	693	1001	1042	350	610	930	-
<i>Cranioleuca semicincta</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Cranioleuca subcristata</i>	3301 bp	4	-	862	-	1047	1042	350	-	-	-
<i>Cranioleuca sulphurifera</i>	8221 bp	8	566	-	652	1001	1042	350	610	2848	1152
<i>Cranioleuca vulpecula</i>	1628 bp	3	-	-	-	236	1042	350	-	-	-
<i>Cranioleuca vulpina</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Cymbilaimus lineatus</i>	8082 bp	7	-	894	703	1047	1047	367	-	2872	1152
<i>Cymbilaimus sanctaemariae</i>	5417 bp	4	-	-	-	-	1042	351	-	2872	1152
<i>Deconychura longicauda</i>	5583 bp	7	566	862	-	1001	1042	350	610	-	1152
<i>Deconychura stictolaema</i>	6278 bp	5	-	862	-	-	1042	350	-	2872	1152
<i>Dendrocincla rufigula</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Dendrocincla anabatina</i>	3260 bp	4	-	862	-	1006	1042	350	-	-	-
<i>Dendrocincla fuliginosa</i>	5583 bp	7	566	862	-	1001	1042	350	610	-	1152
<i>Dendrocincla homochroa</i>	3240 bp	4	-	851	-	997	1042	350	-	-	-

<i>Dendrocincla merula</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Dendrocincla turdina</i>	1004 bp	1	-	-	-	1004	-	-	-	-	-
<i>Dendrocincla tyrannina</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Dendrocolaptes certhia</i>	4431 bp	6	566	850	-	1013	1042	350	610	-	-
<i>Dendrocolaptes concolor</i>	2242 bp	3	-	850	-	-	1042	350	-	-	-
<i>Dendrocolaptes hoffmannsi</i>	2242 bp	3	-	850	-	-	1042	350	-	-	-
<i>Dendrocolaptes picumnus</i>	3292 bp	4	-	850	-	1050	1042	350	-	-	-
<i>Dendrocolaptes platyrostris</i>	4419 bp	6	566	850	-	1001	1042	350	610	-	-
<i>Dendrocolaptes sanctithomae</i>	7287 bp	6	-	862	-	1009	1042	350	-	2872	1152
<i>Dichrozona cincta</i>	6967 bp	6	549	-	-	1001	1042	351	-	2872	1152
<i>Drymophila caudata</i>	1767 bp	3	-	-	-	374	1042	351	-	-	-
<i>Drymophila devillei</i>	4398 bp	3	-	-	-	374	-	-	-	2872	1152
<i>Drymophila ferruginea</i>	719 bp	1	-	-	719	-	-	-	-	-	-
<i>Drymophila genei</i>	7013 bp	6	549	-	-	1047	1042	351	-	2872	1152
<i>Drymophila hellmayri</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Drymophila klagesi</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Drymophila malura</i>	701 bp	1	-	-	701	-	-	-	-	-	-
<i>Drymophila ochropyga</i>	722 bp	1	-	-	722	-	-	-	-	-	-
<i>Drymophila rubricollis</i>	691 bp	1	-	-	691	-	-	-	-	-	-
<i>Drymophila squamata</i>	2626 bp	3	-	-	696	1000	-	-	-	930	-
<i>Drymophila striaticeps</i>	5417 bp	4	-	-	-	-	1042	351	-	2872	1152
<i>Drymornis bridgesii</i>	5583 bp	7	566	862	-	1001	1042	350	610	-	1152
<i>Dysithamnus mentalis</i>	8356 bp	8	549	-	733	1001	1042	351	656	2872	1152
<i>Dysithamnus plumbeus</i>	3407 bp	5	549	-	418	1047	1042	351	-	-	-
<i>Dysithamnus puncticeps</i>	1740 bp	2	-	-	-	1001	739	-	-	-	-
<i>Dysithamnus xanthopterus</i>	237 bp	1	-	-	237	-	-	-	-	-	-
<i>Eleoscytalopus indigoticus</i>	3401 bp	5	-	849	241	857	928	-	526	-	-
<i>Eleoscytalopus psychopompus</i>	2448 bp	3	-	862	-	869	717	-	-	-	-
<i>Epinecrophylla dentei</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Epinecrophylla erythrura</i>	3771 bp	5	550	-	-	1047	1042	351	-	781	-
<i>Epinecrophylla fjeldsaai</i>	2175 bp	3	-	-	-	-	1042	351	-	782	-
<i>Epinecrophylla fulviventris</i>	3596 bp	5	550	-	652	1001	1042	351	-	-	-

<i>Epinecrophylla gutturalis</i>	3642 bp	5	550	-	652	1047	1042	351	-	-	-
<i>Epinecrophylla haematonota</i>	7014 bp	6	550	-	-	1047	1042	351	-	2872	1152
<i>Epinecrophylla leucophthalma</i>	5967 bp	5	550	-	-	-	1042	351	-	2872	1152
<i>Epinecrophylla ornata</i>	3092 bp	4	-	-	652	1047	1042	351	-	-	-
<i>Epinecrophylla spodionota</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Eremobius phoenicurus</i>	9050 bp	9	566	862	694	984	1042	351	527	2872	1152
<i>Eugralla paradoxa</i>	5983 bp	5	-	729	-	-	704	-	526	2872	1152
<i>Formicarius analis</i>	2933 bp	4	-	-	733	380	1042	-	-	778	-
<i>Formicarius colma</i>	8072 bp	7	-	862	734	1049	1052	351	-	2872	1152
<i>Formicarius nigricapillus</i>	2612 bp	3	-	-	-	1001	-	-	681	930	-
<i>Formicarius rufipectus</i>	652 bp	1	-	-	652	-	-	-	-	-	-
<i>Formicivora grantsaui</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Formicivora grisea</i>	7044 bp	7	550	-	703	374	1042	351	-	2872	1152
<i>Formicivora iheringi</i>	5417 bp	4	-	-	-	-	1042	351	-	2872	1152
<i>Formicivora littoralis</i>	1391 bp	2	-	-	-	-	1042	349	-	-	-
<i>Formicivora melanogaster</i>	3703 bp	5	550	-	713	1047	1042	351	-	-	-
<i>Formicivora rufa</i>	7619 bp	7	550	-	651	1001	1042	351	-	2872	1152
<i>Formicivora serrana</i>	5835 bp	5	-	-	418	-	1042	351	-	2872	1152
<i>Frederickena fulva</i>	4024 bp	2	-	-	-	-	-	-	-	2872	1152
<i>Frederickena unduligera</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Frederickena viridis</i>	8060 bp	7	-	862	734	1047	1042	351	-	2872	1152
<i>Furnarius cristatus</i>	5189 bp	7	566	862	-	830	1042	350	609	930	-
<i>Furnarius figulus</i>	2900 bp	4	-	862	645	-	1042	351	-	-	-
<i>Furnarius leucopus</i>	5083 bp	7	566	862	652	1001	1042	350	610	-	-
<i>Furnarius minor</i>	2251 bp	3	-	862	-	-	1042	347	-	-	-
<i>Furnarius rufus</i>	8589 bp	8	566	862	694	1051	1042	350	-	2872	1152
<i>Furnarius torridus</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Geositta antarctica</i>	1710 bp	4	-	862	-	262	298	288	-	-	-
<i>Geositta crassirostris</i>	1710 bp	4	-	862	-	262	298	288	-	-	-
<i>Geositta cunicularia</i>	3209 bp	5	-	862	694	262	1041	350	-	-	-
<i>Geositta isabellina</i>	5797 bp	6	-	862	-	262	298	351	-	2872	1152
<i>Geositta maritima</i>	2516 bp	4	-	862	-	262	1042	350	-	-	-

<i>Geositta peruviana</i>	2454 bp	4	-	862	-	262	1042	288	-	-	-
<i>Geositta poeciloptera</i>	6540 bp	6	-	862	-	262	1042	350	-	2872	1152
<i>Geositta punensis</i>	3210 bp	5	-	862	694	262	1042	350	-	-	-
<i>Geositta rufipennis</i>	7303 bp	7	566	862	-	1001	1042	350	610	2872	-
<i>Geositta saxicolina</i>	2516 bp	4	-	862	-	262	1042	350	-	-	-
<i>Geositta tenuirostris</i>	5083 bp	7	566	862	652	1001	1042	350	610	-	-
<i>Glyphorhynchus spirurus</i>	9212 bp	9	566	850	719	1051	1042	350	610	2872	1152
<i>Grallaria albigula</i>	694 bp	1	-	-	694	-	-	-	-	-	-
<i>Grallaria andicolus</i>	4024 bp	2	-	-	-	-	-	-	-	2872	1152
<i>Grallaria blakei</i>	380 bp	1	-	-	-	380	-	-	-	-	-
<i>Grallaria dignissima</i>	1413 bp	2	-	-	-	358	1055	-	-	-	-
<i>Grallaria eludens</i>	4404 bp	3	-	-	-	380	-	-	-	2872	1152
<i>Grallaria guatemalensis</i>	2087 bp	3	-	-	652	380	1055	-	-	-	-
<i>Grallaria hypoleuca</i>	1435 bp	2	-	-	-	380	1055	-	-	-	-
<i>Grallaria nuchalis</i>	1432 bp	2	-	-	-	380	1052	-	-	-	-
<i>Grallaria ridgelyi</i>	1055 bp	1	-	-	-	-	1055	-	-	-	-
<i>Grallaria ruficapilla</i>	6672 bp	6	-	862	-	380	1055	351	-	2872	1152
<i>Grallaria rufula</i>	1435 bp	2	-	-	-	380	1055	-	-	-	-
<i>Grallaria squamigera</i>	7349 bp	6	565	-	-	1043	1055	-	681	2853	1152
<i>Grallaria varia</i>	2653 bp	4	566	-	652	380	1055	-	-	-	-
<i>Grallaria watkinsi</i>	1435 bp	2	-	-	-	380	1055	-	-	-	-
<i>Grallaricula flavirostris</i>	380 bp	1	-	-	-	380	-	-	-	-	-
<i>Grallaricula lineifrons</i>	1435 bp	2	-	-	-	380	1055	-	-	-	-
<i>Grallaricula nana</i>	5889 bp	5	-	862	652	-	-	351	-	2872	1152
<i>Gyalophylax hellmayri</i>	5657 bp	5	-	-	241	-	1042	350	-	2872	1152
<i>Gymnocichla nudiceps</i>	7618 bp	7	549	-	651	1001	1042	351	-	2872	1152
<i>Gymnopathys bicolor</i>	1943 bp	3	550	-	-	-	1042	351	-	-	-
<i>Gymnopathys leucaspis</i>	3917 bp	5	-	-	739	1001	1042	351	-	784	-
<i>Gymnopathys lunulatus</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Gymnopathys rufigula</i>	7761 bp	7	550	-	747	1047	1042	351	-	2872	1152
<i>Gymnopathys salvini</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Heliobletus contaminatus</i>	9150 bp	9	566	862	695	1001	1042	350	610	2872	1152

<i>Hellmayrea gularis</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Herpsilochmus atricapillus</i>	3661 bp	5	549	-	718	1001	1042	351	-	-	-
<i>Herpsilochmus axillaris</i>	7013 bp	6	549	-	-	1047	1042	351	-	2872	1152
<i>Herpsilochmus dorsimaculatus</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Herpsilochmus longirostris</i>	3224 bp	5	549	-	235	1047	1042	351	-	-	-
<i>Herpsilochmus motacilloides</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Herpsilochmus parkeri</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Herpsilochmus pileatus</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Herpsilochmus praedictus</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Herpsilochmus roraimae</i>	652 bp	1	-	-	652	-	-	-	-	-	-
<i>Herpsilochmus rufimarginatus</i>	3642 bp	5	550	-	652	1047	1042	351	-	-	-
<i>Herpsilochmus sellowi</i>	740 bp	1	-	-	740	-	-	-	-	-	-
<i>Herpsilochmus stictocephalus</i>	3641 bp	5	549	-	652	1047	1042	351	-	-	-
<i>Herpsilochmus sticturus</i>	6069 bp	5	-	-	652	-	1042	351	-	2872	1152
<i>Herpsilochmus stotzi</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Hylexetastes perrotii</i>	9157 bp	9	566	862	680	1023	1042	350	610	2872	1152
<i>Hylexetastes stresemanni</i>	2242 bp	3	-	850	-	-	1042	350	-	-	-
<i>Hylexetastes uniformis</i>	734 bp	1	-	-	734	-	-	-	-	-	-
<i>Hylocryptus erythrocephalus</i>	8373 bp	8	566	862	-	1001	1042	350	610	2807	1135
<i>Hylocryptus rectirostris</i>	2872 bp	4	-	862	618	-	1042	350	-	-	-
<i>Hyloctistes subulatus</i>	8102 bp	8	566	862	689	1001	-	350	610	2872	1152
<i>Hyloctistes virgatus</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Hylopezus berlepschi</i>	7666 bp	7	550	-	652	1047	1042	351	-	2872	1152
<i>Hylopezus fulviventr</i>	6667 bp	5	-	-	652	1001	1055	-	-	2872	1087
<i>Hylopezus macularius</i>	1005 bp	2	-	-	652	-	353	-	-	-	-
<i>Hylopezus nattereri</i>	281 bp	1	-	-	-	-	281	-	-	-	-
<i>Hylopezus ochroleucus</i>	3383 bp	4	-	857	731	866	929	-	-	-	-
<i>Hylophylax naevioides</i>	7013 bp	6	549	-	-	1047	1042	351	-	2872	1152
<i>Hylophylax naevius</i>	4435 bp	6	549	-	730	1001	1042	351	-	762	-
<i>Hylophylax punctulatus</i>	3691 bp	5	549	-	702	1047	1042	351	-	-	-
<i>Hypocnemis cantator</i>	7715 bp	7	550	-	747	1001	1042	351	-	2872	1152
<i>Hypocnemis flavescens</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-

<i>Hypocnemis hypoxantha</i>	2234 bp	4	-	-	736	374	-	351	-	773	-
<i>Hypocnemis ochrogyna</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Hypocnemis peruviana</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Hypocnemis rondoni</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Hypocnemis striata</i>	5066 bp	3	-	-	-	-	1042	-	-	2872	1152
<i>Hypocnemoides maculicauda</i>	7619 bp	7	549	-	652	1001	1042	351	-	2872	1152
<i>Hypocnemoides melanopogon</i>	652 bp	1	-	-	652	-	-	-	-	-	-
<i>Hypoedaleus guttatus</i>	6967 bp	6	549	-	-	1001	1042	351	-	2872	1152
<i>Lepidocolaptes affinis</i>	5072 bp	7	566	850	653	1001	1042	350	610	-	-
<i>Lepidocolaptes albolineatus</i>	3810 bp	5	-	850	570	998	1042	350	-	-	-
<i>Lepidocolaptes angustirostris</i>	6245 bp	8	566	850	653	1022	1042	350	610	-	1152
<i>Lepidocolaptes falcinellus</i>	2242 bp	3	-	850	-	-	1042	350	-	-	-
<i>Lepidocolaptes lacrymiger</i>	3914 bp	5	-	862	653	1007	1042	350	-	-	-
<i>Lepidocolaptes leucogaster</i>	3898 bp	5	-	850	653	1003	1042	350	-	-	-
<i>Lepidocolaptes souleyetii</i>	2858 bp	4	-	850	652	1006	-	350	-	-	-
<i>Lepidocolaptes squamatus</i>	836 bp	2	-	-	598	238	-	-	-	-	-
<i>Leptasthenura aegithaloides</i>	7882 bp	7	-	862	694	910	1042	350	-	2872	1152
<i>Leptasthenura andicola</i>	2888 bp	4	-	862	634	-	1042	350	-	-	-
<i>Leptasthenura fuliginiceps</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Leptasthenura pileata</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Leptasthenura platensis</i>	2947 bp	4	-	862	693	-	1042	350	-	-	-
<i>Leptasthenura setaria</i>	2791 bp	4	-	862	537	-	1042	350	-	-	-
<i>Leptasthenura striata</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Leptasthenura striolata</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Leptasthenura xenothorax</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Leptasthenura yanacensis</i>	4430 bp	6	566	862	-	1000	1042	350	610	-	-
<i>Limnortites rectirostris</i>	9107 bp	9	566	862	652	1001	1042	350	610	2872	1152
<i>Limnornis curvirostris</i>	9006 bp	9	566	766	652	1001	1042	350	610	2869	1150
<i>Liosceles thoracicus</i>	7550 bp	7	550	-	-	1047	1052	351	526	2872	1152
<i>Lochmias nematura</i>	9172 bp	9	566	862	717	1001	1041	351	610	2872	1152
<i>Mackenziaena leachii</i>	7665 bp	7	549	-	652	1047	1042	351	-	2872	1152
<i>Mackenziaena severa</i>	7153 bp	6	-	-	735	1001	1042	351	-	2872	1152

<i>Margarornis bellulus</i>	1875 bp	3	-	483	-	-	1042	350	-	-	-
<i>Margarornis rubiginosus</i>	7977 bp	7	-	862	652	1047	1042	350	-	2872	1152
<i>Margarornis squamiger</i>	7303 bp	7	566	862	-	1001	1042	350	610	2872	-
<i>Margarornis stellatus</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Megastictus margaritatus</i>	7710 bp	7	549	-	743	1001	1042	351	-	2872	1152
<i>Megaxenops parnaguae</i>	9187 bp	9	566	862	732	1001	1042	350	610	2872	1152
<i>Melanopareia elegans</i>	6279 bp	5	-	862	-	-	1042	351	-	2872	1152
<i>Melanopareia maranonica</i>	1285 bp	2	-	-	-	-	942	343	-	-	-
<i>Melanopareia maximiliani</i>	2603 bp	3	-	-	-	1001	-	-	673	929	-
<i>Melanopareia torquata</i>	7006 bp	6	-	862	727	-	1042	351	-	2872	1152
<i>Merulaxis ater</i>	3169 bp	4	-	854	-	855	913	-	547	-	-
<i>Metopothrix aurantiaca</i>	7493 bp	7	566	-	-	984	1042	350	527	2872	1152
<i>Microrhopias quixensis</i>	7612 bp	7	549	-	645	1001	1042	351	-	2872	1152
<i>Myornis senilis</i>	6641 bp	6	-	862	-	318	889	-	548	2872	1152
<i>Myrmeciza atrothorax</i>	7748 bp	7	549	-	735	1047	1042	351	-	2872	1152
<i>Myrmeciza berlepschi</i>	6418 bp	5	-	-	-	1001	1042	351	-	2872	1152
<i>Myrmeciza castanea</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Myrmeciza exsul</i>	3641 bp	5	549	-	652	1047	1042	351	-	-	-
<i>Myrmeciza ferruginea</i>	7106 bp	6	-	-	652	1047	1042	351	-	2872	1142
<i>Myrmeciza fortis</i>	3725 bp	5	549	-	-	1001	1042	351	-	782	-
<i>Myrmeciza goeldii</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Myrmeciza griseiceps</i>	1001 bp	1	-	-	-	1001	-	-	-	-	-
<i>Myrmeciza hemimelaena</i>	3618 bp	5	550	-	674	1001	1042	351	-	-	-
<i>Myrmeciza hypertyra</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Myrmeciza immaculata</i>	3641 bp	5	549	-	652	1047	1042	351	-	-	-
<i>Myrmeciza laemosticta</i>	3055 bp	4	-	-	652	1010	1042	351	-	-	-
<i>Myrmeciza longipes</i>	3603 bp	5	549	-	652	1009	1042	351	-	-	-
<i>Myrmeciza loricata</i>	1419 bp	2	-	-	418	1001	-	-	-	-	-
<i>Myrmeciza melanocephala</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Myrmeciza nigricauda</i>	2440 bp	3	-	-	-	1047	1042	351	-	-	-
<i>Myrmeciza pelzelni</i>	7014 bp	6	550	-	-	1047	1042	351	-	2872	1152
<i>Myrmeciza squamosa</i>	3697 bp	5	550	-	707	1047	1042	351	-	-	-

<i>Myrmoborus leucophrys</i>	6069 bp	5	-	-	652	-	1042	351	-	2872	1152
<i>Myrmoborus myotherinus</i>	4446 bp	6	549	-	747	1001	1042	351	-	756	-
<i>Myrmochanes hemileucus</i>	6967 bp	6	549	-	-	1001	1042	351	-	2872	1152
<i>Myrmorchilus strigilatus</i>	7705 bp	7	549	-	738	1001	1042	351	-	2872	1152
<i>Myrmornis torquata</i>	7725 bp	7	549	-	702	1047	1052	351	-	2872	1152
<i>Myrmothera campanisona</i>	2870 bp	4	-	-	652	380	1055	-	-	783	-
<i>Myrmothera simplex</i>	6269 bp	6	-	862	652	380	-	351	-	2872	1152
<i>Myrmotherula ambigua</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Myrmotherula assimilis</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Myrmotherula axillaris</i>	7725 bp	7	550	-	711	1047	1042	351	-	2872	1152
<i>Myrmotherula behni</i>	3596 bp	5	550	-	652	1001	1042	351	-	-	-
<i>Myrmotherula brachyura</i>	7116 bp	6	-	-	652	1047	1042	351	-	2872	1152
<i>Myrmotherula cherriei</i>	2925 bp	4	550	-	-	982	1042	351	-	-	-
<i>Myrmotherula grisea</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Myrmotherula gularis</i>	6118 bp	5	-	-	701	-	1042	351	-	2872	1152
<i>Myrmotherula guttata</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Myrmotherula haematonota</i>	2650 bp	4	-	860	737	-	702	351	-	-	-
<i>Myrmotherula hauxwelli</i>	7069 bp	7	549	-	739	374	1042	351	-	2872	1142
<i>Myrmotherula ignota</i>	2478 bp	3	-	-	-	1085	1042	351	-	-	-
<i>Myrmotherula iheringi</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Myrmotherula klagesi</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Myrmotherula leucophthalma</i>	1649 bp	3	-	-	702	377	570	-	-	-	-
<i>Myrmotherula longicauda</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Myrmotherula longipennis</i>	3846 bp	6	550	-	747	374	1042	351	-	782	-
<i>Myrmotherula menetriesii</i>	7715 bp	7	550	-	747	1001	1042	351	-	2872	1152
<i>Myrmotherula minor</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Myrmotherula multostriata</i>	2944 bp	4	550	-	-	1001	1042	351	-	-	-
<i>Myrmotherula obscura</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Myrmotherula pacifica</i>	2948 bp	4	550	-	-	1005	1042	351	-	-	-
<i>Myrmotherula schisticolor</i>	3603 bp	5	550	-	652	1008	1042	351	-	-	-
<i>Myrmotherula sclateri</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Myrmotherula snowi</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-

<i>Myrmotherula surinamensis</i>	7029 bp	6	-	-	652	960	1042	351	-	2872	1152
<i>Myrmotherula unicolor</i>	2112 bp	3	-	-	719	-	1042	351	-	-	-
<i>Myrmotherula urosticta</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Nasica longirostris</i>	9215 bp	9	566	862	733	1028	1042	350	610	2872	1152
<i>Neotantes niger</i>	7014 bp	6	550	-	-	1047	1042	351	-	2872	1152
<i>Oreophylax moreirae</i>	8442 bp	8	566	862	-	1001	1042	350	610	2872	1139
<i>Percnostola leucostigma</i>	2039 bp	3	-	-	652	-	1042	345	-	-	-
<i>Percnostola lophotes</i>	7013 bp	6	549	-	-	1047	1042	351	-	2872	1152
<i>Percnostola minor</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Percnostola rufifrons</i>	7665 bp	7	549	-	652	1047	1042	351	-	2872	1152
<i>Percnostola saturata</i>	1387 bp	2	-	-	-	-	1042	345	-	-	-
<i>Percnostola schistacea</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Phacellodomus dorsalis</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Phacellodomus erythrophthalmus</i>	2739 bp	4	566	-	645	1001	-	-	527	-	-
<i>Phacellodomus ferrugineigula</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Phacellodomus maculipectus</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Phacellodomus ruber</i>	5112 bp	7	566	862	681	1001	1042	350	610	-	-
<i>Phacellodomus rufifrons</i>	9149 bp	9	566	862	694	1001	1042	350	610	2872	1152
<i>Phacellodomus sibilatrix</i>	2904 bp	4	-	862	652	-	1040	350	-	-	-
<i>Phacellodomus striaticeps</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Phacellodomus striaticollis</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Phaenostictus mcleannani</i>	6967 bp	6	549	-	-	1001	1042	351	-	2872	1152
<i>Philydor atricapillus</i>	6090 bp	8	566	862	729	1001	1042	350	610	930	-
<i>Philydor dimidiatum</i>	2899 bp	4	-	862	645	-	1042	350	-	-	-
<i>Philydor erythrocerum</i>	7016 bp	6	-	862	747	-	1042	350	-	2872	1143
<i>Philydor erythropterus</i>	3031 bp	4	-	862	-	-	1039	350	-	780	-
<i>Philydor fuscipenne</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Philydor lichtensteini</i>	6935 bp	6	-	862	694	-	1042	350	-	2872	1115
<i>Philydor pyrrhodes</i>	6931 bp	6	-	862	652	-	1042	351	-	2872	1152
<i>Philydor ruficaudatum</i>	2955 bp	4	-	862	701	-	1042	350	-	-	-
<i>Philydor rufum</i>	2899 bp	4	-	862	645	-	1042	350	-	-	-
<i>Phlegopsis erythroptera</i>	4473 bp	6	549	-	746	1001	1042	351	-	784	-

<i>Phlegopsis nigromaculata</i>	7729 bp	7	549	-	716	1047	1042	351	-	2872	1152
<i>Phleocryptes melanops</i>	9053 bp	9	547	785	694	1001	1042	350	610	2872	1152
<i>Pithys albifrons</i>	8055 bp	7	-	862	729	1047	1042	351	-	2872	1152
<i>Pithys castaneus</i>	2990 bp	4	550	-	-	1047	1042	351	-	-	-
<i>Pittasoma michleri</i>	2601 bp	4	-	828	-	380	1042	351	-	-	-
<i>Pittasoma rufopileatum</i>	5688 bp	5	-	-	-	380	941	343	-	2872	1152
<i>Premnoplex brunnescens</i>	9107 bp	9	566	862	652	1001	1042	350	610	2872	1152
<i>Premnoplex tatei</i>	3301 bp	4	-	862	-	1047	1042	350	-	-	-
<i>Premnornis guttuligera</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Pseudocolaptes boissonneautii</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Pseudocolaptes johnsoni</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Pseudocolaptes lawrencii</i>	7276 bp	6	-	862	-	1015	1025	350	-	2872	1152
<i>Pseudoseisura gutturalis</i>	2948 bp	4	-	862	694	-	1042	350	-	-	-
<i>Pseudoseisura lophotes</i>	8563 bp	9	566	862	652	1001	1042	350	610	2871	609
<i>Pseudoseisura unirufa</i>	2879 bp	4	-	862	625	-	1042	350	-	-	-
<i>Psilorhamphus guttatus</i>	3786 bp	5	-	861	582	868	927	-	548	-	-
<i>Pterotochos castaneus</i>	4886 bp	3	-	862	-	-	-	-	-	2872	1152
<i>Pterotochos tarnii</i>	3173 bp	4	-	-	694	1001	-	-	548	930	-
<i>Pygarrhichas albogularis</i>	9149 bp	9	566	862	694	1001	1042	350	610	2872	1152
<i>Pygiptila stellaris</i>	7619 bp	7	549	-	652	1001	1042	351	-	2872	1152
<i>Pyriglena atra</i>	1017 bp	1	-	-	-	-	1017	-	-	-	-
<i>Pyriglena leuconota</i>	7698 bp	7	549	-	731	1001	1042	351	-	2872	1152
<i>Pyriglena leucoptera</i>	2965 bp	4	-	862	735	-	1017	351	-	-	-
<i>Rhegmatorhina berlepschi</i>	1328 bp	2	-	-	-	-	977	351	-	-	-
<i>Rhegmatorhina cristata</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-
<i>Rhegmatorhina gymnops</i>	7013 bp	6	549	-	-	1047	1042	351	-	2872	1152
<i>Rhegmatorhina hoffmannsi</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Rhegmatorhina melanosticta</i>	2943 bp	4	549	-	-	1001	1042	351	-	-	-
<i>Rhinocrypta lanceolata</i>	8464 bp	8	566	862	-	1001	1051	351	609	2872	1152
<i>Rhopornis ardesiacus</i>	418 bp	1	-	-	418	-	-	-	-	-	-
<i>Roraimia adusta</i>	9107 bp	9	566	862	652	1001	1042	350	610	2872	1152
<i>Sakesphorus bernardi</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-

<i>Sakesphorus canadensis</i>	4007 bp	5	-	894	652	1047	1047	367	-	-	-
<i>Sakesphorus cristatus</i>	1798 bp	3	-	-	418	-	1047	333	-	-	-
<i>Sakesphorus luctuosus</i>	8031 bp	7	-	894	652	1047	1047	367	-	2872	1152
<i>Sakesphorus melanonotus</i>	1414 bp	2	-	-	-	-	1047	367	-	-	-
<i>Sakesphorus melanothorax</i>	919 bp	2	-	-	-	-	598	321	-	-	-
<i>Scelorchilus rubecula</i>	6106 bp	5	-	862	694	-	-	-	526	2872	1152
<i>Schistocichla leucostigma</i>	6418 bp	5	-	-	-	1001	1042	351	-	2872	1152
<i>Schizoeaca coryi</i>	1386 bp	2	-	-	-	-	1042	344	-	-	-
<i>Schizoeaca fuliginosa</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Schizoeaca griseomurina</i>	1904 bp	2	-	862	-	-	1042	-	-	-	-
<i>Schizoeaca harterti</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Schizoeaca helleri</i>	6278 bp	5	-	862	-	-	1042	350	-	2872	1152
<i>Schizoeaca palpebralis</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Schizoeaca perijana</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Schoeniophylax phryganophilus</i>	8287 bp	8	566	-	694	1001	1042	350	610	2872	1152
<i>Sclateria naevia</i>	7619 bp	7	549	-	652	1001	1042	351	-	2872	1152
<i>Sclerurus albigularis</i>	2243 bp	3	-	851	-	-	1042	350	-	-	-
<i>Sclerurus caudacutus</i>	3649 bp	5	-	851	652	-	1042	350	-	754	-
<i>Sclerurus guatemalensis</i>	2906 bp	4	-	862	652	-	1042	350	-	-	-
<i>Sclerurus mexicanus</i>	8032 bp	8	566	862	729	1001	1042	350	610	2872	-
<i>Sclerurus rufigularis</i>	2956 bp	4	-	862	702	-	1042	350	-	-	-
<i>Sclerurus scansor</i>	5348 bp	7	566	851	-	1001	1042	350	608	930	-
<i>Scytalopus affinis</i>	1291 bp	2	-	-	-	255	1036	-	-	-	-
<i>Scytalopus argentifrons</i>	967 bp	2	-	-	652	315	-	-	-	-	-
<i>Scytalopus atratus</i>	315 bp	1	-	-	-	315	-	-	-	-	-
<i>Scytalopus canus</i>	2213 bp	3	-	862	-	315	1036	-	-	-	-
<i>Scytalopus caracae</i>	844 bp	1	-	-	-	-	844	-	-	-	-
<i>Scytalopus diamantinensis</i>	615 bp	1	-	-	-	-	615	-	-	-	-
<i>Scytalopus femoralis</i>	286 bp	1	-	-	-	286	-	-	-	-	-
<i>Scytalopus fuscus</i>	315 bp	1	-	-	-	315	-	-	-	-	-
<i>Scytalopus gettyae</i>	1042 bp	1	-	-	-	-	1042	-	-	-	-
<i>Scytalopus griseicollis</i>	1154 bp	2	-	-	-	310	844	-	-	-	-

<i>Scytalopus iraiensis</i>	2640 bp	3	-	846	-	863	931	-	-	-	-
<i>Scytalopus latebricola</i>	1128 bp	2	-	-	-	284	844	-	-	-	-
<i>Scytalopus latrans</i>	315 bp	1	-	-	-	315	-	-	-	-	-
<i>Scytalopus magellanicus</i>	8110 bp	7	553	862	693	926	1052	-	-	2872	1152
<i>Scytalopus meridanus</i>	844 bp	1	-	-	-	-	844	-	-	-	-
<i>Scytalopus micropterus</i>	315 bp	1	-	-	-	315	-	-	-	-	-
<i>Scytalopus nigricans</i>	844 bp	1	-	-	-	-	844	-	-	-	-
<i>Scytalopus novacapitalis</i>	2642 bp	3	-	847	-	865	930	-	-	-	-
<i>Scytalopus pachecoi</i>	2659 bp	3	-	862	-	867	930	-	-	-	-
<i>Scytalopus parvirostris</i>	1453 bp	2	-	-	-	-	905	-	548	-	-
<i>Scytalopus petrophilus</i>	247 bp	1	-	-	247	-	-	-	-	-	-
<i>Scytalopus schulenbergi</i>	318 bp	1	-	-	-	318	-	-	-	-	-
<i>Scytalopus speluncae</i>	1732 bp	3	-	-	253	-	931	-	548	-	-
<i>Scytalopus spillmanni</i>	2478 bp	3	-	-	-	1000	-	-	548	930	-
<i>Scytalopus stilesi</i>	931 bp	1	-	-	-	-	931	-	-	-	-
<i>Scytalopus superciliaris</i>	2593 bp	4	-	-	694	315	1036	-	548	-	-
<i>Scytalopus unicolor</i>	319 bp	1	-	-	-	319	-	-	-	-	-
<i>Scytalopus vicini</i>	2103 bp	3	-	862	-	310	931	-	-	-	-
<i>Scytalopus zimmeri</i>	862 bp	2	-	-	-	315	-	-	547	-	-
<i>Simoxenops striatus</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Simoxenops ucayalae</i>	9107 bp	9	566	862	652	1001	1042	350	610	2872	1152
<i>Siptornis striaticollis</i>	6417 bp	5	-	-	-	1001	1042	350	-	2872	1152
<i>Siptornopsis hypochondriaca</i>	7493 bp	7	566	-	-	984	1042	350	527	2872	1152
<i>Sittasomus griseicapillus</i>	4421 bp	6	566	851	-	1001	1042	351	610	-	-
<i>Skutchia borbae</i>	2544 bp	4	-	-	698	453	1042	351	-	-	-
<i>Spartonoica maluioides</i>	9049 bp	9	566	862	694	984	1042	350	527	2872	1152
<i>Stymphalornis acutirostris</i>	1391 bp	2	-	-	-	-	1040	351	-	-	-
<i>Stymphalornis paludicolus</i>	5417 bp	4	-	-	-	-	1042	351	-	2872	1152
<i>Sylviorthorhynchus desmursii</i>	8978 bp	9	566	862	694	913	1042	350	527	2872	1152
<i>Synallaxis albescens</i>	6521 bp	6	-	-	694	411	1042	350	-	2872	1152
<i>Synallaxis albigularis</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis albilora</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-

<i>Synallaxis azarae</i>	2086 bp	3	-	-	694	-	1042	350	-	-	-
<i>Synallaxis brachyura</i>	2043 bp	3	-	-	651	-	1042	350	-	-	-
<i>Synallaxis cabanisi</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis candei</i>	3301 bp	4	-	862	-	1047	1042	350	-	-	-
<i>Synallaxis castanea</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis cherriei</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis cinerascens</i>	2907 bp	4	-	862	652	-	1042	351	-	-	-
<i>Synallaxis cinerea</i>	645 bp	1	-	-	645	-	-	-	-	-	-
<i>Synallaxis cinnamomea</i>	3301 bp	4	-	862	-	1047	1042	350	-	-	-
<i>Synallaxis courseni</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis erythrothorax</i>	3569 bp	5	566	-	-	1001	1042	350	610	-	-
<i>Synallaxis frontalis</i>	2086 bp	3	-	-	694	-	1042	350	-	-	-
<i>Synallaxis gujanensis</i>	2121 bp	3	-	-	729	-	1042	350	-	-	-
<i>Synallaxis hypospodia</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis kollari</i>	2044 bp	3	-	-	652	-	1042	350	-	-	-
<i>Synallaxis macconnelli</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis maranonica</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis moesta</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis propinqua</i>	5384 bp	4	-	-	-	-	1042	350	-	2840	1152
<i>Synallaxis ruficapilla</i>	4882 bp	6	566	-	733	1001	1042	-	610	930	-
<i>Synallaxis rutilans</i>	2129 bp	3	-	-	737	-	1042	350	-	-	-
<i>Synallaxis scutata</i>	8339 bp	8	565	-	747	1001	1042	350	610	2872	1152
<i>Synallaxis spixi</i>	2914 bp	4	-	862	660	-	1042	350	-	-	-
<i>Synallaxis stictothorax</i>	5416 bp	4	-	-	-	-	1042	350	-	2872	1152
<i>Synallaxis subpudica</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis tithys</i>	1358 bp	2	-	-	-	-	1008	350	-	-	-
<i>Synallaxis unirufa</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Synallaxis zimmeri</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Syndactyla guttulata</i>	2251 bp	3	-	862	-	-	1039	350	-	-	-
<i>Syndactyla ruficollis</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Syndactyla rufosuperciliata</i>	9149 bp	9	566	862	694	1001	1042	350	610	2872	1152
<i>Syndactyla subalaris</i>	2878 bp	4	-	841	645	-	1042	350	-	-	-

<i>Taraba major</i>	7678 bp	7	549	-	711	1001	1042	351	-	2872	1152
<i>Teledromas fuscus</i>	4572 bp	3	-	-	-	-	-	-	548	2872	1152
<i>Terenura callinota</i>	3046 bp	4	-	-	652	1001	1042	351	-	-	-
<i>Terenura humeralis</i>	3563 bp	5	549	-	-	1001	1042	351	620	-	-
<i>Terenura maculata</i>	5417 bp	4	-	-	-	-	1042	351	-	2872	1152
<i>Terenura sharpei</i>	7326 bp	6	-	862	-	1047	1042	351	-	2872	1152
<i>Terenura spodioptila</i>	6069 bp	5	-	-	652	-	1042	351	-	2872	1152
<i>Thamnistes anabatinus</i>	6968 bp	6	550	-	-	1001	1042	351	-	2872	1152
<i>Thamnomanes ardesiacus</i>	7727 bp	7	549	-	714	1047	1042	351	-	2872	1152
<i>Thamnomanes caesius</i>	8116 bp	7	-	894	737	1047	1047	367	-	2872	1152
<i>Thamnomanes saturninus</i>	3724 bp	5	549	-	735	1047	1042	351	-	-	-
<i>Thamnomanes schistogynus</i>	2989 bp	4	549	-	-	1047	1042	351	-	-	-
<i>Thamnophilus aethiops</i>	4101 bp	5	-	894	746	1047	1047	367	-	-	-
<i>Thamnophilus amazonicus</i>	4636 bp	6	541	894	740	1047	1047	367	-	-	-
<i>Thamnophilus ambiguus</i>	1822 bp	2	-	-	-	839	983	-	-	-	-
<i>Thamnophilus aroyae</i>	3896 bp	5	541	894	-	1047	1047	367	-	-	-
<i>Thamnophilus atrinucha</i>	3850 bp	5	541	894	-	1001	1047	367	-	-	-
<i>Thamnophilus bridgesi</i>	4007 bp	5	-	894	652	1047	1047	367	-	-	-
<i>Thamnophilus caerulescens</i>	9262 bp	9	566	894	694	927	1047	367	743	2872	1152
<i>Thamnophilus capistratus</i>	239 bp	1	-	-	239	-	-	-	-	-	-
<i>Thamnophilus cryptoleucus</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thamnophilus divisorius</i>	1356 bp	2	-	-	-	-	1024	332	-	-	-
<i>Thamnophilus doliatus</i>	8090 bp	7	-	894	711	1047	1047	367	-	2872	1152
<i>Thamnophilus insignis</i>	4007 bp	5	-	894	652	1047	1047	367	-	-	-
<i>Thamnophilus multistriatus</i>	367 bp	1	-	-	-	-	-	367	-	-	-
<i>Thamnophilus murinus</i>	4783 bp	6	-	894	719	1047	1047	367	-	709	-
<i>Thamnophilus nigriceps</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thamnophilus nigrocinereus</i>	7948 bp	7	566	894	-	1047	1050	367	-	2872	1152
<i>Thamnophilus palliatus</i>	3608 bp	5	-	894	253	1047	1047	367	-	-	-
<i>Thamnophilus pelzelni</i>	2557 bp	3	-	-	735	839	983	-	-	-	-
<i>Thamnophilus praecox</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thamnophilus punctatus</i>	3773 bp	5	-	894	418	1047	1047	367	-	-	-

<i>Thamnophilus ruficapillus</i>	4049 bp	5	-	894	694	1047	1047	367	-	-	-
<i>Thamnophilus schistaceus</i>	4139 bp	5	-	894	-	1047	1047	367	-	784	-
<i>Thamnophilus stictocephalus</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thamnophilus sticturus</i>	1012 bp	1	-	-	-	1012	-	-	-	-	-
<i>Thamnophilus tenuipunctatus</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thamnophilus torquatus</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thamnophilus unicolor</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thamnophilus zarumae</i>	3355 bp	4	-	894	-	1047	1047	367	-	-	-
<i>Thripadectes flammulatus</i>	5359 bp	7	565	862	-	1001	1042	350	609	930	-
<i>Thripadectes holostictus</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Thripadectes ignobilis</i>	4431 bp	6	566	862	-	1001	1042	350	610	-	-
<i>Thripadectes melanorhynchus</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Thripadectes rufobrunneus</i>	6931 bp	6	-	862	652	-	1042	351	-	2872	1152
<i>Thripadectes scrutator</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Thripadectes virgaticeps</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Thripophaga berlepschi</i>	5413 bp	4	-	-	-	-	1042	350	-	2872	1149
<i>Thripophaga cherriei</i>	5380 bp	4	-	-	-	-	1042	350	-	2836	1152
<i>Thripophaga fusciceps</i>	5416 bp	4	-	-	-	-	1042	350	-	2872	1152
<i>Tityra semifasciata</i>	3402 bp	4	-	862	-	-	1037	351	-	-	1152
<i>Tyrannus melancholicus</i>	2255 bp	3	-	862	-	-	1042	351	-	-	-
<i>Tyrannus tyrannus</i>	1152 bp	1	-	-	-	-	-	-	-	-	1152
<i>Upucerthia albigula</i>	2254 bp	3	-	862	-	-	1042	350	-	-	-
<i>Upucerthia andaecola</i>	3875 bp	6	566	408	-	984	1042	351	524	-	-
<i>Upucerthia certhioides</i>	5023 bp	7	566	862	693	983	1042	350	527	-	-
<i>Upucerthia dumetaria</i>	9050 bp	9	566	862	694	984	1042	351	527	2872	1152
<i>Upucerthia harterti</i>	8454 bp	8	566	862	-	1001	1042	350	609	2872	1152
<i>Upucerthia jelskii</i>	5361 bp	7	566	862	-	1001	1042	350	610	930	-
<i>Upucerthia ruficaudus</i>	9049 bp	9	566	862	694	984	1042	350	527	2872	1152
<i>Upucerthia serrana</i>	8455 bp	8	566	862	-	1001	1042	350	610	2872	1152
<i>Upucerthia validirostris</i>	4982 bp	7	565	862	652	984	1042	350	527	-	-
<i>Willisornis poecilinotus</i>	7730 bp	7	550	-	716	1047	1042	351	-	2872	1152
<i>Willisornis vidua</i>	1393 bp	2	-	-	-	-	1042	351	-	-	-

<i>Xenerpestes minlosi</i>	1392 bp	2	-	-	-	-	1042	350	-	-	-
<i>Xenerpestes singularis</i>	6417 bp	5	-	-	-	1001	1042	350	-	2872	1152
<i>Xenops milleri</i>	9099 bp	9	566	862	644	1001	1042	350	610	2872	1152
<i>Xenops minutus</i>	9202 bp	9	566	862	747	1001	1042	350	610	2872	1152
<i>Xenops rutilans</i>	5127 bp	7	566	862	696	1001	1042	350	610	-	-
<i>Xenops tenuirostris</i>	2906 bp	4	-	862	652	-	1042	350	-	-	-
<i>Xenornis setifrons</i>	652 bp	1	-	-	652	-	-	-	-	-	-
<i>Xiphocolaptes albicollis</i>	2242 bp	3	-	850	-	-	1042	350	-	-	-
<i>Xiphocolaptes falcirostris</i>	2242 bp	3	-	850	-	-	1042	350	-	-	-
<i>Xiphocolaptes major</i>	5583 bp	7	566	862	-	1001	1042	350	610	-	1152
<i>Xiphocolaptes promeropirhynchus</i>	4450 bp	6	566	850	-	1032	1042	350	610	-	-
<i>Xiphorhynchus chunchotambo</i>	2241 bp	3	-	850	-	-	1041	350	-	-	-
<i>Xiphorhynchus elegans</i>	3249 bp	4	-	850	-	1007	1042	350	-	-	-
<i>Xiphorhynchus erythropygius</i>	4417 bp	6	566	850	-	1000	1042	349	610	-	-
<i>Xiphorhynchus eytoni</i>	2237 bp	3	-	850	-	-	1037	350	-	-	-
<i>Xiphorhynchus flavigaster</i>	7930 bp	7	-	850	652	1031	1035	349	-	2872	1141
<i>Xiphorhynchus fuscus</i>	8461 bp	8	566	862	-	1010	1039	350	610	2872	1152
<i>Xiphorhynchus guttatus</i>	4447 bp	6	566	850	-	1029	1042	350	610	-	-
<i>Xiphorhynchus kienerii</i>	2241 bp	3	-	850	-	-	1042	349	-	-	-
<i>Xiphorhynchus lachrymosus</i>	3267 bp	4	-	850	-	1025	1042	350	-	-	-
<i>Xiphorhynchus obsoletus</i>	4424 bp	6	566	850	-	1006	1042	350	610	-	-
<i>Xiphorhynchus ocellatus</i>	3805 bp	5	558	850	-	1010	1037	350	-	-	-
<i>Xiphorhynchus pardalotus</i>	3765 bp	5	565	843	-	966	1042	349	-	-	-
<i>Xiphorhynchus picus</i>	4423 bp	5	-	850	-	1029	1042	350	-	-	1152
<i>Xiphorhynchus spixii</i>	3809 bp	5	562	850	-	1007	1040	350	-	-	-
<i>Xiphorhynchus susurrans</i>	3254 bp	4	-	850	-	1030	1038	336	-	-	-
<i>Xiphorhynchus triangularis</i>	4419 bp	6	566	850	-	1001	1042	350	610	-	-

Appendix S3. Table summary of all assemblages used in this study showing coordinates, countries, habitat types, richness, extinction and colonisation estimations, phylogenetic structure statistics, within-assemblages diversification statistics, environmental variables.

Due to the size of the table, this can be found in the next link:

https://drive.google.com/open?id=0Bx5_Spbv4O84dFpDcnJVUE03Y2M

Appendix S4. R code for run DAMOCLES.

DAMOCLES MODEL

Jesus N. Pinto-Ledezma

Contents

Prepare the data for run DAMOCLES

```
library("doParallel")
library("DAMOCLES")
library("picante")

comms <- read.table("YOUR_ASSEMBLAGES_DATA", header = T, row.names = 1)

tree <- read.nexus("YOUR_PHYLOGENETIC_DATA")

matched2 <- match.phylo.comm(phy = tree, comm = t(comms))
```

General function to run DAMOCLES in parallel

```
DamBootsClus <- function(tree, comm, initparsopt, idparsopt, parsfix, idparsfix,
                        pars2, pchoice, runs, estimate_pars, conf.int){
  n.cores <- detectCores()-2
  cl <- makeCluster(getOption("cl.cores", n.cores))
  clusterExport(cl, "matched2")
  dat <- lapply(c(1:length(row.names(comm))),
               function(x) cbind(row.names(t(comm)),
                                as.matrix(as.numeric(comm[x,]))));
  out2 <- parallel::parLapply(cl = cl, X = dat,
                             function(x) DAMOCLES::DAMOCLES_bootstrap(phy = tree, pa = x, initparsopt,
                                                                           idparsopt, parsfix, idparsfix,
                                                                           pars2, pchoice, runs,
                                                                           estimate_pars, conf.int));

  stopCluster(cl)
  return(out2)
}
```

Appendix S5. Spatial correlograms for all estimations.

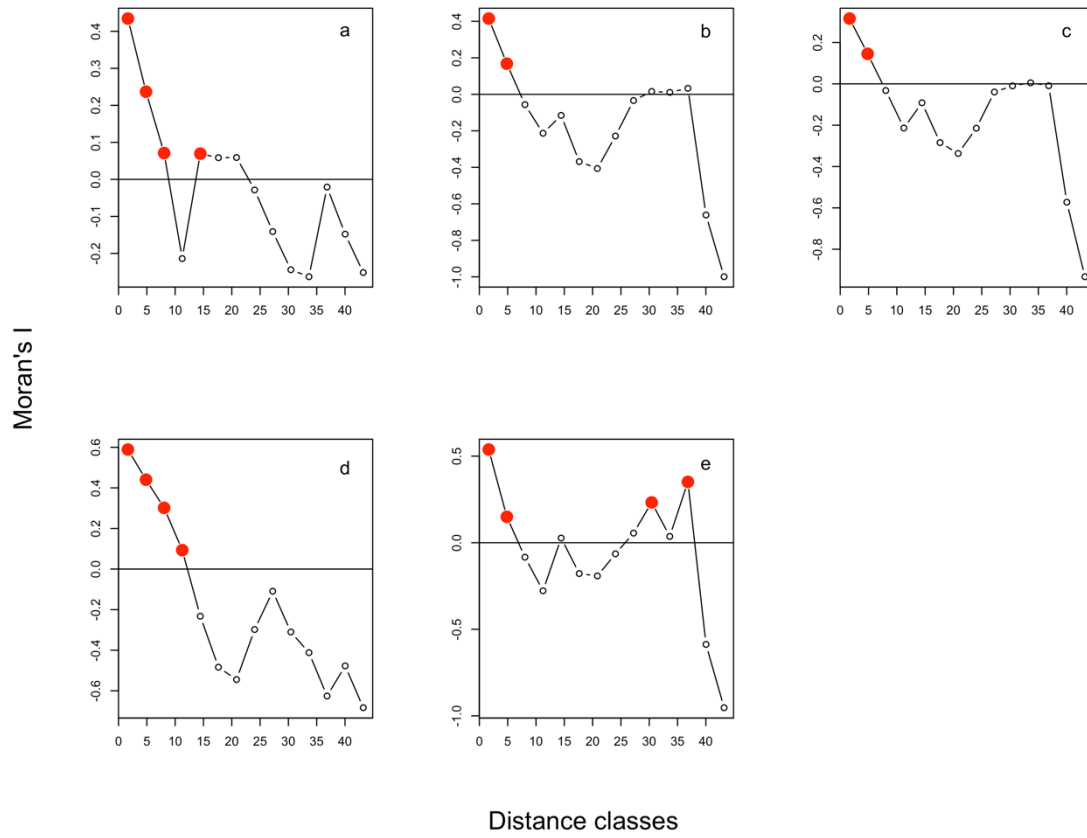


Figure S1. Spatial correlograms for (a) species richness, (b) local extinction, (c) colonization, (d) MPD and (e) DRA among local assemblages.