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A importância das interações bióticas e atributos na distribuição das espécies e estruturação das comunidades ecológicas

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MÁRCIA NEUNSCHWANDER KURTZ

A importância das interações bióticas e atributos na distribuição das espécies e estruturação das comunidades ecológicas

Tese apresentada ao programa de pós-graduação em Ecologia e Evolução do Departamento de Ecologia do Instituto de Ciências Biológicas da Universidade Federal de Goiás como parte das exigências para a obtenção do título de Doutora em Ecologia e Evolução.

Área de concentração: Ecologia e Evolução

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ATA DE DEFESA DE TESE

Ata Nº **103** da sessão de Defesa de Tese de **Márcia Neunschwander Kurtz** que confere o título de Doutora em **Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução.**

Aos **trinta dias do mês de novembro de dois mil e vinte (30/11/2020),** a partir das **08h00min**, por **webconferência, seguindo portaria CAPES no. 36 de 16 de março de 2020 e recomendação da UFG**, realizou-se a sessão pública de Defesa de Tese intitulada **"A importância das interações bióticas e atributos na distribuição das espécies e estruturação das comunidades ecológicas"**. Os trabalhos foram instalados pelo Orientador, **Prof. Dr. Marcus Vinicius Cianciaruso (Depto de Ecologia/UFG),** com a participação dos demais membros da Banca Examinadora: **Profa. Dra. Levi Carina Terribile (Depto. Ciências Biológicas/UFJ)**, membro titular interno**;** **Prof. Dr. Joaquin Hortal Munoz (Depto. de Ecologia/UFG),** membro titular interno; **Profa. Dra. Hélida Ferreira da Cunha (RENAC/UEG)**, membro titular externo**;** e **Dr. Lucas Lacerda Caldas Zanini Jardim (DTI PosDoc Depto. de Ecologia/UFG)**, membro titular externo. Durante a argüição os membros da banca **[não fizeram]** sugestão de alteração do título do trabalho **[(em caso de sugestão) conforme explicitado abaixo]**. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da tese, tendo sido a candidata **[aprovada]** pelos seus membros. Proclamados os resultados pelo **Prof. Dr. Marcus Vinicius Cianciaruso**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, ao(s) **trinta dias do mês de novembro de dois mil e vinte (30/11/2020).**

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SUMÁRIO

Resumo geral

As perturbações estruturais e climáticas criadas direta ou indiretamente pela atividade humana atuam profundamente sobre os organismos e são responsáveis pela crescente mudança na biodiversidade. Tais mudanças estão associadas a alterações relevantes na abundância relativa, extinção e habilidade invasiva das espécies. Nesse contexto de mudanças iminentes, é cada vez mais urgente a necessidade de descrever os padrões e entender os processos que regem a biodiversidade, a fim de predizer e mitigar as mudanças atuais e futuras. Uma forma de fazer isso é através dos modelos de distribuição de espécies, que são geralmente construídos apenas com preditores abióticos já que a importância das interações bióticas é considerada irrelevante em grandes escalas espaciais (hipótese do ruído Eltoniano). Para testar a hipótese do ruído Eltoniano, nós modelamos a distribuição de várias espécies de beija-flores distribuídas através do continente americano e avaliamos o efeito das interações bióticas no desempenho dos modelos e nas predições espaciais (**Capítulo 1**). Nós encontramos que a adição das interações bióticas teve pouco efeito sobre a performance dos modelos e a adequabilidade ambiental predita, mas alterou a distribuição geográfica estimada das espécies. Essa dissimilaridade espacial não melhorou o modelo, o que sugere que os modelos de distribuição de espécies podem ser sensíveis a inclusão de variáveis preditoras, especialmente em grandes extensões espaciais. Além disso, a fim de entender os processos que regem a montagem e manutenção das comunidades, investigamos o papel da partição de recursos para a coexistência das espécies. Para isso, avaliamos quais atributos associados a aquisição de recursos tróficos podem explicar a coexistência de espécies similares nas comunidades (**Capítulo 2**). Concluímos que comunidades com maior sobreposição de espécies são, na verdade, particionadas em fina escala, associadas ao comportamento de forrageio das espécies. Por fim, sabendo que informações sobre as espécies são essenciais para estudar a biodiversidade, propomos avaliar o tamanho e as relações causais associadas à lacuna Raunkiaerana de aves (**Capítulo 3**). Identificamos que a lacuna de conhecimento sobre os atributos investigados é maior principalmente para espécies de regiões tropicais e com pequena distribuição geográfica, mas também mostramos que a maior disponibilização e mobilização de dados pode ampliar significativamente nosso conhecimento atual.

Palavras-chave: Bases de dados, Completude de informação, Co-ocorrência de espécies, Diagrama BAM, Interações positivas, Sobreposição de nicho, Trochilidae.

General abstract

Structural and climatic disturbances created directly or indirectly by human activity have a profound effect on organisms and are responsible for the increasing changes in biodiversity. Such changes are associated with relevant modification in the relative abundance, extinction and invasive ability of the species. In this context of imminent changes, there is an increasingly urgent need to describe patterns and understand processes that govern biodiversity, in order to predict and mitigate current and future changes. One way of doing this is through species distribution models, which are generally built only with abiotic predictors since the importance of biotic interactions is considered irrelevant at large spatial scales (Eltonian noise hypothesis). To test the Eltonian noise hypothesis, we modeled the distribution of several species of hummingbirds distributed across the American continent and evaluated the effect of biotic interactions on model performance and spatial predictions (Chapter 1). We found that the addition of biotic interactions had little effect on model performance and predicted environmental suitability, but altered the estimated geographic distribution of the species. This spatial dissimilarity did not improve the model, what suggests that species distribution models might be sensitive to the inclusion of predictor variables, especially in large spatial extents. Moreover, in order to understand the processes that govern the assembly and maintenance of communities, we investigated the role of resource partition for species coexistence. Specifically, we evaluated which traits associated with the acquisition of trophic resources can explain the coexistence of similar species in the communities (Chapter 2). We conclude that communities with more overlapping species are, in fact, partitioned on a fine scale, associated with the species' foraging behavior. Finally, knowing that information about species are essential for biodiversity studies, we propose to assess the size and the sources of the Raunkiaeran shortfall of birds (Chapter 3). We show that the knowledge gap on the investigated traits is large mainly for small-ranged species from tropical regions, but we also show that data sharing and mobilization can significantly expand our current knowledge.

Key-words: BAM diagram, Data base, Information completeness, Niche overlap, Positive interactions, Species co-occurrence, Trochilidae.

Introdução geral

O ser humano tem causado impactos substanciais no planeta Terra, que resultaram no surgimento do antropoceno (Steffen *et al.* 2011). As transformações que estão ocorrendo na superfície terrestre, como por exemplo a perda e fragmentação de habitats devido ao uso da terra, e alteração da composição do solo e da atmosfera através da deposição de substâncias nitrogenadas e liberação de carbono (Lewis & Maslin 2015) são rápidas e persistentes. Tais perturbações estruturais e climáticas criadas direta ou indiretamente pela atividade humana atuam profundamente sobre os organismos nos ambientes afetados e são responsáveis pela crescente mudança na biodiversidade. Essas alterações na biodiversidade estão associadas a alterações drásticas na abundância relativa, extinção e habilidade invasiva das espécies (Hermoso *et al.* 2011; Pyron 2018), o que resulta na desestabilização das interações biológicas (Tylianakis *et al.* 2008). Todas essas alterações podem modificar os padrões e reduzir os processos ecológicos essenciais realizados pelas comunidades e ecossistemas, incluindo serviços necessários ao bem-estar humano (e.g. serviços ecossistêmicos, Knapp 2019). Nesse contexto de mudanças iminentes, é cada vez mais urgente a necessidade de descrever e entender, da melhor forma possível, os padrões e processos que regem a biodiversidade, além de identificar a lacuna de dados faltantes, para tentar predizer e mitigar as mudanças na biodiversidade que estão ocorrendo e que ocorrerão nas próximas décadas.

Biodiversidade não é um conceito simples, ela abrange múltiplos elementos da variabilidade biótica, como a diversidade taxonômica, genética, funcional e de interações (Maier 2012; Pereira *et al.* 2013). Essas diferentes formas de acessar a biodiversidade refletem diferentes objetivos que contribuem para entender melhor os padrões e processos como um todo, em escala local e global. Os estudos clássicos em ecologia frequentemente descrevem a biodiversidade em termos de identidade das espécies, enquanto os outros componentes da biodiversidade são geralmente subestimados (Díaz & Cabido 2001; van der

Plas 2019). O fato de a riqueza de espécies e medidas relacionadas serem mais populares está provavelmente associado a restrição de dados (Pereira *et al.* 2013; Schneider *et al.* 2019). Apesar da lacuna nos dados de biodiversidade ser bastante expressiva, especialmente em animais, diversos esforços têm sido realizados para compilação e ampliação dos conjuntos de dados disponíveis livremente (Wilman *et al.* 2014; Rodrigues *et al.* 2019; Gallagher *et al.* 2020; Ortega *et al.* 2020). Nesse sentido, a investigação de outros elementos associados a variabilidade biológica, como a pesquisa baseada em atributos funcionais e o uso de interações bióticas, vem ganhando bastante espaço na literatura (Heikkinen *et al.* 2007; Freitas & Mantovani 2018; Gherghel *et al.* 2018). Essas duas facetas da biodiversidade têm auxiliado na identificação de padrões e processos que moldam a distribuição das espécies e a associação entre as espécies nas comunidades, e portanto, são fundamentais para compreender melhor como as comunidades e os ecossistemas são estruturados, e como podem responder às mudanças globais atuais e futuras.

De modo geral, a distribuição das espécies no planeta pode ser determinada pela interação de três processos: barreiras físicas que limitam seu movimento (M), condições abióticas (A) adequadas aos seus requisitos fisiológicos e condições bióticas (B) formadas por interações favoráveis à sua ocorrência. Tais processos foram reunidos conceitualmente no diagrama BAM (Soberón 2007). Um ou mais desses componentes de tolerância das espécies são frequentemente combinados a dados de presença para, através de algoritmos correlativos (Urbina-Cardona *et al.* 2019), gerar modelos de distribuição que podem ser subsequentemente projetados para o espaço geográfico devido a “dualidade de Hutchinson” (Hutchinson 1957; Colwell & Rangel 2009; Peterson *et al.* 2011; Peterson & Soberón 2012).

Em geral é aceito que os processos associados ao diagrama BAM operam concomitantemente de forma hierarquia através das escalas espaciais. É esperado que as variáveis abióticas e aquelas associadas a dispersão dos organismos exerçam um papel dominante na distribuição das espécies em escalas regionais e continentais, enquanto as interações bióticas devem desempenhar um papel importante em escalas locais (Pearson & Dawson 2003; Peterson *et al.* 2011). Essa abordagem assume que as espécies ocorrem em todos os locais acessíveis e dentro da sua tolerância climática (Kearney & Porter 2009), e, consequentemente, essa distribuição será mais ampla que a área hipoteticamente ocupada pela espécie, i.e., aquela que leva em consideração as outras limitações à ocorrência das espécies (Soberón *et al.* 2017). A suposição de que o impacto relativo das interações bióticas pode se tornar insignificante ao considerar escalas espaciais maiores é conhecida como hipótese do ruído Eltoniano (Soberón 2007). Esse pressuposto, associado a baixa disponibilidade de dados de interações bióticas, tem levado a maioria dos estudos a concentrarem seus esforços nos efeitos das condições abióticas sobre a distribuição das espécies. Só recentemente o crescente número de evidências tem demostrado que as interações das espécies podem ser importantes em maiores escalas geográficas. Contudo, a maioria desses estudos são limitados a um pequeno conjunto de espécies (Araújo & Luoto 2007; Heikkinen *et al.* 2007; Atauchi *et al.* 2018; Palacio & Girini 2018; Raath *et al.* 2018), ou a uma área geográfica restrita (Meier *et al.* 2010; Pellissier *et al.* 2010; da Cunha *et al.* 2018; Kass *et al.* 2020). Além disso, ainda falta uma investigação da influência de preditores bióticos para além do desempenho do modelo, incluindo também análises espaciais associadas a mudanças nas projeções geográficas e estimativas das áreas de distribuição (Simões & Peterson 2018). Por isso, no **Capítulo 1** nós avaliamos a importância das interações bióticas para estimar a distribuição de várias espécies de beija-flores distribuídas sobre todo o continente americano usando tanto as medidas de desempenho dos modelos quanto análises de similaridade espacial.

O pressuposto hierárquico citado acima também representa um processo de filtragem ambiental que, consequentemente, seleciona em um local espécies que contém atributos funcionais mais similares que o esperado ao acaso (Petchey *et al.* 2007). Contudo, a teoria da competição assume que para as espécies coexistirem elas devem apresentar alguma limitação às suas similaridades, de modo que as comunidades sejam compostas por espécies com características complementares em pelo menos uma dimensão do nicho (Hutchinson 1961; MacArthur & Levins 1967). Assim, é esperado que a coexistência entre espécies troficamente similares seja impulsionada principalmente pela disponibilidade de recursos alimentares e/ou partição de nicho nas comunidades, como por exemplo diferenças morfológicas ou comportamentais. No entanto, estudos que inferem a partição de nicho têm evidências conflitantes (Gómez *et al.* 2010; Hidasi-Neto *et al.* 2012). Por isso, no **Capítulo 2** propomos o uso de informações ecológicas detalhadas, como as contidas em redes de interações ecológicas, para quantificar a sobreposição de nicho e atributos associados a partição do nicho trófico como preditores da coexistência de espécies similares nas comunidades, a fim de entender melhor os mecanismos associados a coexistência entre espécies semelhantes.

Ao realizar os dois estudos anteriores, observamos que tanto as informações de atributos quanto de interações bióticas enfrentam fortes restrições ou ausência de dados. Enquanto algumas medidas, como os registros de ocorrência das espécies, por exemplo, tornaram-se mais populares e acessíveis nos últimos anos, outras ainda permanecem pouco conhecidas. As principais lacunas existentes na área de biodiversidade foram catalogadas por Hortal *et al.* (2015), mas ainda são poucos os estudos que quantificam essas lacunas. Apesar do grande esforço dos pesquisadores em coletar e disponibilizar os mais variados dados relacionados à biodiversidade, ainda estamos longe de ter um conjunto de informações robusto (Cornwell *et al.* 2019). Nessa linha, uma das lacunas que tem sido pouco explorada é a Raunkiaerana. Até recentemente não tínhamos nenhuma noção da dimensão dessa lacuna. Apenas nos últimos anos é que alguns estudos iniciaram a tarefa de tentar quantificá-la e propor soluções para reduzí-la (Etard *et al.* 2020; Gallagher *et al.* 2020). Contudo, ainda não existem critérios bem estabelecidos sobre quais atributos são importantes de serem avaliados, principalmente para os grupos animais, e quais os fatores socioambientais associados a essa lacuna. Sabendo que a lacuna de conhecimento sobre os dados de atributos pode afetar o desenvolvimento dos estudos em biodiversidade, no **Capítulo 3** nós quantificamos a lacuna Raunkiaerana para aves. Especificamente, nós sintetizamos os atributos considerados ecologicamente relevantes de acordo com seu uso na literatura, avaliamos a completude de dados abertamente acessíveis para cada atributo, e mapeamos a completude média de cada região com base na distribuição das espécies. Com isso, avaliamos os fatores socioambientais que podem influenciar a existência de dados para aves e que podem, potencialmente, afetar também outros taxa.

Referências

Araújo, M.B. & Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.*, 16, 743–753.

Atauchi, P.J., Peterson, A.T. & Flanagan, J. (2018). Species distribution models for Peruvian plantcutter improve with consideration of biotic interactions. *J. Avian Biol.*, 49, 1–8.

Colwell, R.K. & Rangel, T.F. (2009). Hutchinson's duality: the once and future niche. *Proc. Natl. Acad. Sci.*, 106, 19651–19658.

Cornwell, W.K., Pearse, W.D., Dalrymple, R.L. & Zanne, A.E. (2019). What we (don't) know about global plant diversity. *Ecography*, 42, 1819–1831.

da Cunha, H.F., Ferreira, É.D., Tessarolo, G. & Nabout, J.C. (2018). Host plant distributions and climate interact to affect the predicted geographic distribution of a Neotropical termite. *Biotropica*, 50, 625–632.

Díaz, S. & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 645–655.

Etard, A., Morrill, S. & Newbold, T. (2020). Global gaps in trait data for terrestrial vertebrates. *Glob. Ecol. Biogeogr.*, (*In press*).

Freitas, J.R. & Mantovani, W. (2018). An overview of the applicability of functional diversity in biological conservation. *Brazilian J. Biol.*, 78, 517–524.

Gallagher, R.V., Falster, D.S., Maitner, B.S., Salguero-Gómez, R., Vandvik, V., Pearse, W.D., *et al.* (2020). Open Science principles for accelerating trait-based science across the Tree of Life. *Nat. Ecol. Evol.*, 4, 294–303.

Gherghel, I., Brischoux, F. & Papeş, M. (2018). Using biotic interactions in broad-scale estimates of species' distributions. *J. Biogeogr.*, 45, 2216–2225.

Gómez, J.P., Bravo, G.A., Brumfield, R.T., Tello, J.G. & Cadena, C.D. (2010). A phylogenetic approach to disentangling the role of competition and habitat filtering in community assembly of Neotropical forest birds. *J. Anim. Ecol.*, 79, 1181–1192.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G. & Körber, J.H. (2007). Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Glob. Ecol. Biogeogr.*, 16, 754–763.

Hermoso, V., Clavero, M., Blanco-Garrido, F. & Prenda, J. (2011). Invasive species and habitat degradation in Iberian streams: An analysis of their role in freshwater fish diversity loss. *Ecol. Appl.*, 21, 175–188.

Hidasi-Neto, J., Barlow, J. & Cianciaruso, M. V. (2012). Bird functional diversity and wildfires in the Amazon: the role of forest structure. *Anim. Conserv.*, 15, 407–415.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 46, 523–549.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.*, 22, 415–427.

Hutchinson, G.E. (1961). The paradox of the plankton. *Am. Nat.*, 95, 137–145.

Kass, J.M., Anderson, R.P., Espinosa-Lucas, A., Juárez-Jaimes, V., Martínez-Salas, E., Botello, F., *et al.* (2020). Biotic predictors with phenological information improve range estimates for migrating monarch butterflies in Mexico. *Ecography*, 43, 341–352.

Kearney, M. & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. Ecol. Lett., 12, 334–350.

Knapp, S. (2019). The Link Between Diversity, Ecosystem Functions, and Ecosystem Services. In: *Atlas of Ecosystem Services*. Springer International Publishing, Cham, pp. 13–15.

Lewis, S.L. & Maslin, M.A. (2015). Defining the Anthropocene. Nature, 519, 171–180.

MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nauralist*, 101, 377–384.

Maier, D.S. (2012). *What's so good about biodiversity? A call for better reasoning about nature's value*. The International Library of Environmental, Agricultural and Food Ethics. Springer Netherlands, Dordrecht; new York.

Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.C., Thuiller, W., Araújo, M.B., *et al.* (2010). Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, 33, 1038–1048.

Ortega, R., Fortuna, M.A. & Bascompte, J. (2020). The Web of Life: ecological networks database. Web of Life http://www.web-of-life.es.

Palacio, F.X. & Girini, J.M. (2018). Biotic interactions in species distribution models enhance model performance and shed light on natural history of rare birds: a case study using the straight-billed reedhaunter Limnoctites rectirostris. *J. Avian Biol.*, 49, e01743.

Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.*, 12, 361–371.

Pellissier, L., Anne Bråthen, K., Pottier, J., Randin, C.F., Vittoz, P., Dubuis, A., *et al.* (2010). Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography*, 33, 1004–1014.

Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., *et al.* (2013). Essential Biodiversity Variables. *Science*, 339, 277–278.

Petchey, O.L., Evans, K.L., Fishburn, I.S. & Gaston, K.J. (2007). Low functional diversity and no redundancy in British avian assemblages. *J. Anim. Ecol.*, 76, 977–985.

Peterson, A.T. & Soberón, J. (2012). Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right. *Nat. Conserv.*, 10, 102–107.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., *et al.* (2011). *Ecological Niches and Geographic Distributions*. Princeton University Press.

van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biol. Rev.*, 94, 1220-1245.

Pyron, R.A. (2018). Global amphibian declines have winners and losers. *Proc. Natl. Acad. Sci.*, 115, 3739–3741.

Raath, M.J., le Roux, P.C., Veldtman, R. & Greve, M. (2018). Incorporating biotic interactions in the distribution models of African wild silk moths (Gonometa species, Lasiocampidae) using different representations of modelled host tree distributions. *Austral Ecol.*, 43, 316–327.

Rodrigues, R.C., Hasui, É., Assis, J.C., Pena, J.C.C., Muylaert, R.L., Tonetti, V.R., *et al.* (2019). ATLANTIC BIRD TRAITS : a data set of bird morphological traits from the Atlantic forests of South America. *Ecology*, 100, e02647.

Schneider, F.D., Fichtmueller, D., Gossner, M.M., Güntsch, A., Jochum, M., König-Ries, B., *et al.* (2019). Towards an ecological trait-data standard. Methods Ecol. Evol., 10, 2006–2019.

Steffen, W., Grinevald, J., Crutzen, P. & McNeill, John. (2011). The Anthropocene: conceptual and historical perspectives. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.*, 369, 842–867.

Simões, M.V.P. & Peterson, A.T. (2018). Importance of biotic predictors in estimation of potential invasive areas: The example of the tortoise beetle Eurypedus nigrosignatus, in Hispaniola. *PeerJ*, 2018, e6052.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.*, 10, 1115–1123.

Soberón, J., Osorio-Olvera, L. & Peterson, T. (2017). Diferencias conceptuales entre modelación de nichos y modelación de áreas de distribución. *Rev. Mex. Biodivers.*, 88, 437–441.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 11, 1351–1363.

Urbina-Cardona, N., Blair, M.E., Londoño, M.C., Loyola, R., Velásquez-Tibatá, J. & Morales-Devia, H. (2019). Species Distribution Modeling in Latin America: A 25-Year Retrospective Review. *Trop. Conserv. Sci.*, 12, 1–19.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals. *Ecology*, 95, 2027–2027.

CAPÍTULO 1

Biotic interactions do not improve species distribution models for hummingbirds[1]

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Biotic interactions do not improve species distribution models for hummingbirds

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Abstract

Species distribution models (SDMs) are an important tool in ecology, biogeography and conservation planning. However, these models generally include only abiotic variables to access the environmental suitability and the potential distribution of the species in the geographic space. This occurs because the influence of biotic interactions in species distributions is assumed to decrease with the coarse resolution of the models (i.e. the Eltonian noise hypothesis). Although many studies have shown that the addition of biotic predictors can indeed increase the predictability of the models, these studies are generally limited in terms of number of species and spatial extent. In addition, these studies rarely evaluate the effect of biotic predictors on the spatial output of the models. In this study, we tested whether incorporating information about species interactions affects the quality and prediction of SDMs for 100 hummingbird species distributed throughout the New World. For each species, we generated two models: the first SDM was based only on climatic variables, while the second SDM included both the climatic variables and the environmental suitability of the main plant species visited by each hummingbird. Then, we compared the models' performance, spatial projection and geographic range estimation. Overall, we found that models purely abiotic and those combining biotic predictors showed similar performance values and indistinguishable projections of environmental suitability. Only the estimated geographic range of the species changed after including biotic predictors, especially for species occurring in large areas. However, this spatial dissimilarity did not improve the models, which can indicate a sensibility of SDMs to variables addition under large extents rather than a positive effect of biotic interactions. Thus, our study suggests that the inclusion of biotic interactions has little effect on the performance and spatial predictions of SDMs of hummingbirds. However, additional tests using different modelling techniques are still necessary to confirm the generality of these results.

Key-words: BAM diagram, Eltonian niche, Niche models, Positive interactions, Trochilidae.

Introduction

Species distribution models (SDMs) have become increasingly important to predict the impacts of anthropic threats and the current climate changes. In recent years, a number of SDM studies have been published focusing mostly on conservation planning and biological invasions (Guisan *et al.* 2013; Urbina-Cardona *et al.* 2019). These models are often built using correlative algorithms that combine points of occurrence and one or more predictor variable to define the niche space for a given species and subsequently project into the geographic space the regions that are suitable for its survival and population growth (Urbina-Cardona *et al.* 2019). The choice of the predictor variables should then represent those factors most likely affecting the species distribution.

In general, the distribution of the species depends on several factors that are currently represented in a simplified way by the "BAM diagram". The diagram is based on a theoretical framework that lists three main components (Biotic, Abiotic and Mobility) that causally determine the distribution area of a species. Biotic conditions (B) are based on the concept of Eltonian niche (Elton 1927), which deals with biological interactions between organisms. These interactions can be of several types, so that they can facilitate or inhibit the persistence of a species in a given environment. Abiotic conditions (A) are based on the concept of Grinnellian niche (sensu Soberón 2007), which are associated with environmental variables that limit species physiologically. Mobility (M), on the other hand, represents the restriction to species dispersion and it is linked to the species' ability to disperse in areas favorable to their existence (Soberón & Peterson 2005). Although biotic, abiotic and mobility components represent a set of complementary conditions that enable the survival and permanence of the species in certain places, most models are based only on the abiotic needs of the species and rarely include the role of mobility and, specially, biotic interactions (Peterson *et al.* 2011; Record *et al.* 2018). The non-consideration of biotic interaction in

SDM is endorsed by the Eltonian noise hypothesis, which state that at large-spatial scales abiotic variables and dispersion restrictions should have a greater influence on species distribution than biotic interactions (Sóberon & Nakamura 2009).

However, no organism exists in absolute isolation in nature and, therefore, its interactions with other organisms are inevitable and fundamental for its survival and for the functioning of the ecosystem. These ecological interactions can be defined as the effects that an organism has on another one and are differentiated by the type of relationship that the organisms maintain with each other. These relationships either facilitate or limit the presence of species in favorable abiotic environments (Araújo & Rozenfeld 2014). For example, species that provide trophic or reproductive requirements for other species, can affect population growth and consequently the presence of the dependent species, directly influencing their geographic distribution at different scales (Abrams 1983; Heikkinen *et al.* 2007; Araújo & Rozenfeld 2014; da Cunha *et al.* 2018; Gherghel *et al.* 2018). Therefore, when a given species depends, to some degree, on another to survive, it must necessarily occur within the geographic range of its biotic resources (Cohen 1977; da Cunha *et al.* 2018; Gherghel *et al.* 2018).

Studies that use and assess the influence of biotic variables on modeling performance over large spatial scales have increased considerably in the last years (Heikkinen *et al.* 2007; Araújo & Rozenfeld 2014; da Cunha *et al.* 2018; Kass *et al.* 2020 and others). So far, these studies have shown that the inclusion of biotic variables increases the performance of SDMs. However, the inclusion of biotic variables in SDMs has still being a challenge due to the insufficient data availability on geographical distribution and biotic interactions for most species (i.e. Wallacean and Eltonian shortfall, Hortal *et al.* 2015), besides the dynamic nature of interactions in the temporal and spatial scope (Sóberon & Nakamura 2009; Peterson *et al.* 2011). In this sense, most analyses have been limited to a small set of focal and interactors species (Araújo & Luoto 2007; Heikkinen *et al.* 2007; Gianini *et al.* 2013; Atauchi *et al.* 2018; Palacio & Girini 2018; Raath *et al.* 2018), or in a restricted geographical area such as one country or biome (Meier *et al.* 2010; Pellissier *et al.* 2010; da Cunha *et al.* 2018; Kass *et al.* 2020). Even for the few studies that evaluate a large number of species or species distributed over a wide geographic extent (Belmaker *et al.* 2015; Ilsøe *et al.* 2017), it is still lacking an investigation of the influence of biotic predictors beyond model performance, including also analyses of spatial changes in geographical projections and size/position of range estimates (Simões & Peterson 2018).

In this study, we assessed the importance of biotic interactions to estimate the distribution of hummingbird species on a large spatial scale. Hummingbirds have an obligatory relationship with nectar-producing plants, since 90% of their diet is based on nectar (Gass & Montgomerie 1981). In addition, they are considered highly specialized at the community level (Maglianesi *et al.* 2014). Since hummingbirds are a popular group, there are many studies on their distribution and ecology, so records of spatial occurrence and interactions records with nectar-producing plants are gradually becoming more available over time (Wolf 1970; Stiles 1985; Sazima *et al.* 1996; Rodríguez Flores 2009; Las-Casas *et al.* 2012; Tinoco *et al.* 2017). We compiled this data and constructed SDMs for the plants that interact with each hummingbird species and included them as biotic predictors for the construction bird’s distribution model, combining abiotic and biotic variables. Finally, we compared the performance and prediction of these SDMs with those generated in function of purely abiotic predictors.

Methods

To assess the influence of biotic interactions on the performance and prediction of SDMs, we built two types of models for each hummingbird species: a) Abiotic Model, it was generated in a standard way, using the occurrence of the hummimgbird species and climatic variables as predictors; b) Combined Model, it was similar to the Abiotic Model but here we also included the environmental suitability of the plants that interact with the hummingbird as predictors. To project the environmental suitability of the plants we generate for each species a standard SDM using climatic and soil variables as environmental predictors (Velazco *et al.* 2017). According to Anderson (2017), the method described above is the most appropriated for including biotic predictors in SDMs as long as the distribution of the interacting species (here, the plants) does not depend exclusively on the focal species (hummingbirds). Since even plant species commonly visited by hummingbirds, such as Bromeliaceae, can be pollinated by insects and other vertebrates, not depending then exclusively on one hummingbird species (Fumero-Cabán & Meléndez-Ackerman 2007; Scrok & Varassin 2011), we considered this method adequate to our purpose.

Interaction records

In order to identify the plants consumed by each hummingbird, we first compiled data on the trophic ecology of different hummingbird species from the literature and from databases of ecological interactions. Specifically, we searched for quantitative interaction networks in the Web of Science database from 1945 to January 2020 with the following combinations of keywords: (hummingbird AND pollination) OR (hummingbird AND interaction) OR Trochilidae. In addition, we included data from scientific articles, theses and dissertations obtained only through Google Scholar®, the CAPES thesis and dissertations catalog (catalogodeteses.capes.gov.br), Web of Life (www.web-of-life.es), and the Interaction Web Database (iwdb.nceas.ucsb.edu). We selected only quantitative interaction networks with a minimum sampling period of eight months, covering the main annual climatic variations, as we consider that these networks present a sufficient sampling effort to describe the species’ diet. Our search resulted in a total of 58 networks derived from 43 different sources. We then checked the taxonomic nomenclature of the species of hummingbirds and plants, respectively, in the HBW & BirdLife International (2019) and The Plant List (www.theplantlist.org). After correcting for synonyms, this initial dataset was composed by 2,060 unique interactions between 124 hummingbird and 637 plant species.

We assume that not all plants visited by a hummingbird species have a determining role in its distribution. That is, while the high consumption of a given plant should indicate a great dependence on this resource, sporadic consumption could reflect a resource independence, and including these sporadic interactions may not improve the distribution model (de Araújo *et al.* 2014). Therefore, we selected the most relevant plants in the diet of each hummingbird species based on the index proposed by de Araújo *et al.* (2014). According to this index, the most important plant species in the hummingbird's diet are the ones with high consumption over a broad area. So, we first calculated for each hummingbird species the proportion of visits to each plant recorded in each study. We then standardized this value so that the importance of each plant for a given hummingbird in each study varied from 0 to 1. Finally, we summed the standardized values of each plant across the interaction networks to find the most important plants for each hummingbird species. We selected for using as biotic variables, for each hummingbird species, plants with an importance value ≥ 0.9. This value was chosen to ensure that each hummingbird species would have at least one biotic predictor in the model (de Araújo *et al.* 2014). After this process our data set was reduced to 488 unique interactions and 257 plant species.

Occurrence records and data cleaning procedures

The occurrence data for all selected species of hummingbirds and plants were obtained from the Global Biodiversity Information Facility database (www.gbif.org). After retrieving the data, we eliminated records: without coordinates information, made by machine or unknown sources, repeated geographical coordinates and outside the American continent.

To avoid using records outside the native range of the species due to misidentification, taxonomic change, geographical errors or introduced/cultivated distribution, we checked manually if the filtered records lay inside the countries where the species are naturally distributed. We used country limits to validate species occurrence because that was the only information easily accessible to compare the available occurrence records with the native distribution of the plants. For hummingbirds, this procedure was conducted consulting the species distribution in the BirdLife International (www.birdlife.org/). For plants, we consulted the Plants of the world online (www.plantsoftheworldonline.org), PLANTS Database (plants.sc.egov.usda.gov/java) and Invasive Specie Compendium (www.cabi.org/isc); when necessary we also checked the "Flora del Conosur" (www.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm), "Flora do Brasil" (floradobrasil.jbrj.gov.br/) and "Catálogo de plantas y líquenes de Colombia" (catalogoplantasdecolombia.unal.edu.co). Any record classified as introduced or unclassified records with no evidence of natural distribution were removed and species of plants classified as exotic in the continent were completely excluded. Finally, we removed outliers by eliminating records >500 km from other records of the species using the "CoordinateCleaner" package (Zizka *et al.* 2019). We chose this distance because it performed best to our data in a previous visual examination. After this rigorous cleaning process, we selected only species occurring in 10 or more cells of our spatial grid in order to avoid biases caused by low number of occurrences (see Wisz *et al.* 2008). We also removed hummingbirds for which the total distribution of all interacting plants do not cover at least 90% of its occurrence records and disregarded interactions for which the plant species do not cover at least 25% of the focal species occurrence. We recognize that these overlap thresholds are arbitrary, but we considered that using hummingbirds for which the area occupied by the plants available cover only a small fraction of their occurrence records could bias our modelling results.

Therefore, our final data set was composed by 362 unique interactions between 100 hummingbirds and 202 plant species (Table S1), with a median of three and a maximum of 20 plant interaction per hummingbird species (see Fig. S1 in Supplementary Material for the distribution of the species).

Environmental variables

To characterize the climatic variation across the American continent, we used the CHELSA v1.2 database (Karger *et al.* 2017). This database provides 19 bioclimatic variables obtained from downscaling temperature and precipitation outputs from a global circulation model based on a statistical approach that includes the influence of local scale terrain features (topography, wind fields, etc.) and bias corrections using climatologic stations. Variables related to physical and chemical soil properties were obtained from the SoilGrids database (soilgrids.org/). SoilGrids provides nine variables for six different soil dephts, totalizing 54 layers. Both climatic and edaphic variables were obtained at very high resolution (CHELSA: 30 arc-seconds; SoilGrids: 7.5 arc-seconds) and upscaled to the average value at 0.1° (5 arc-minutes). For a complete list of the variables used, see Table S2 of the Supplementary Material.

To avoid multicollinearity among predictors variables and overfitting of SDMs, we reduced the dimensionality of the predictors through a principal component analysis (PCA). This procedure extracts the dominant patterns from a group of predictor variables and summarizes this information in new uncorrelated predictors, the principal components (PCs). For each species, we selected the PCs that captured 95% of the total variation found in the original variables (i.e. climate and climate plus plant's suitability for abiotic and combined models, respectively) to calibrate the species' distribution models. The number of predictors used for each hummingbird species varied from an average of 5.52 ± 0.66 (mean ± SD) in abiotic to 7.53 ± 2.15 in combined models (Supplementary Material Table S3).

Species modelling

To build the SDMs we used MaxEnt, a machine learning algorithm based on principles of maximum entropy that calculates the probability of presence of a species along the study background (Phillips *et al.* 2006). The definition of the geographical background (the extent of the study area) is a key point that can affect the performance and prediction of niche models (Acevedo *et al.* 2012). Therefore, we restricted the background region to areas that are potentially accessible for species. To do so, we first circumscribed the occurrence records of each species using a convex hull. Then, we selected the ecoregions (Olson *et al.* 2001) encompassed by this convex hull. Since both birds and plants show strong fidelity to ecoregions boundaries (Smith *et al.* 2018), our background represents a proxy for the species' historical dispersal area (see also Cooper & Soberón 2020). Then, a maximum of 10,000 background cells were randomly sampled from predictor layers.

To reduce the spatial autocorrelation between training and test records in each model, we used the 'block' method. This method partitions data into four bins based on the lines of latitude and longitude that divide occurrence localities as equally as possible in geographic (and environmental) space. Then, four models are run iteratively using three bins for training and the remaining one for testing. Metrics of model evaluation are then summarized across the 4 iterations (Muscarella *et al.* 2014). In addition, we optimized the models' performance by selecting among models with different combinations of features classes (Linear, Linear Quadratic, Hinge, Linear Quadratic Hinge, Linear Quadratic Hinge Product and, Linear Quadratic Hinge Product and Threshold) and regularization multiplier values (RM: 0.5, 1, 1.5, 2). The set of configurations that calibrated the ideal model was defined by the Akaike information criterion corrected for small sample sizes (AICc). The use of AICc for the comparison of SDMs represents a trade-off between the quality of the fit and the complexity of the model (Warren & Seifert 2011). In general, the optimized models are expected to be less overfitted and exhibit lower omission rates than MaxEnt default models (Muscarella *et al.* 2014). All the models were run using the "*dismo*" (Hijmans *et al.* 2017) and "*ENMeval*" (Muscarella *et al.* 2014) R packages.

Model evaluation

To test the importance of including plants used as a trophic resource in the modeling of hummingbird species, we selected two different metrics, widely used in the literature, that capture different aspects associated with performance of the SDMs to compare purely abiotic and combined models: Sensitivity and Specificity (Fielding & Bell 1997; Jiménez-Valverde 2014). Sensitivity and Specificity quantify, respectively, the errors of omission and commission, that is, the proportion of presence and absence records correctly classified (Jiménez-Valverde 2014). To calculate these threshold-based metrics, we converted continuous predictions into binary maps using a threshold that maximizes the sum of sensitivity and specificity for each model. This method has proven to be robust for use with both presence/absence and presence-only data (Liu *et al.* 2005; Liu *et al.* 2016).

Data analysis

The overall performance of purely abiotic and combined models was compared with the Wilcoxon matched-pairs test, using each hummingbird species as a sample. We used the Wilcoxon test because our data did not meet the assumptions necessary for the parametric analysis. We also assessed the best fit between the two models comparing their second-order Akaike information criterion (AICc; Burnham & Anderson 2002). To evaluate the possible changes in spatial predictions when biotic variables are included, we also calculated the spatial similarity in environmental suitability and geographic range projection between results from abiotic and combined models. The degree of similarity in environmental suitability was estimated using the Schoener's D index (Warren *et al.* 2008), which ranges from 0 (suitability completely divergent) to 1 (identical suitability) and has been widely used in species distribution modelling studies. Geographical range similarity was measured using the Jaccard index after converting the continuous suitability estimates to binary presence/absence maps by applying the maximum sensitivity plus specificity threshold, that is, area hypothetically occupied by species according to the models. Specifically, we compared for each species whether its set of grid cells occupied according to the abiotic model is similar to the set of grid cells that are occupied according to the combined model. We evaluated both the total dissimilarity and the fraction resulting from turnover and nestedness component using the "*betapart*" package (Baselga *et al.* 2018).

Finally, using a linear regression, we evaluated whether differences in environmental suitability and estimated geographical range between abiotic to combined models can be influenced by the geographic extent (number of grid cells within the area occupied by the species), number of records (number of grid cells comprising the species record) and number of interactions. In all regression models, the predictor variables were log-transformed to increase normality and a weighted regression using fitted values from the estimated variance as weights was adopted when we detected heteroscedasticity. All analyzes were conducted in the R programming environment version 3.6.0 (R Core Team 2019) using the packages cited above.

Results

Model performance

Metrics of SDM performance for each hummingbird species showed, on average, high values with little variation, regardless of whether the predictor was abiotic or combined (Table 1). Sensitivity and Specificity mean values were ≥ 0.83 (Table 1), indicating that both abiotic and combined models have adequate performance, correctly predicting most of the presence and absence of hummingbird species. The AICc criterion was lower for most models that included both abiotic and biotic predictors (73%) compared to those that included only abiotic predictors (27%, see Table S3 of the Supplementary Material).

Table 1. Average values of performance metrics of species distribution models for hummingbird species using abiotic and combined predictors. We also report the mean values, standard deviation and results of the Wilcoxon matched-pairs test between the two models.

	Abiotic model		Combined model				
	Mean	s.d.	Mean	s.d.	es	Wilcoxson	p-value
Se	0.87	0.1	0.88	0.08	0.01	1629	0.13
Sp	0.83	0.08	0.83	0.09	<0.01	2380	0.62

Sensitivity (Se) and Specificity (Sp), degrees of freedom (df), es (effect size).

Spatial predictions

Our spatial prediction comparisons revealed a high overlap between environmental suitability estimated by purely abiotic and combined models (median = 0.97; Figure 1 and Table S4 of the Supplementary Material). This high similarity did not change with the number of interactions of the hummingbird species ($R^2_{\text{interactions}} < 0.07$; $p > 0.05$), number of occurring cells ($R^2_{\text{occurrence}} = 0.01$; $p > 0.05$) or geographic extent ($R^2_{\text{geog.exten.}} = 0.01$; $p > 0.05$). On the other hand, the geographic range estimation after converting continuous projections to binary presence/absence maps showed only a moderate and variable similarity between the two models, with a median of 0.69 (Figure 1). Changes in geographic similarity were not affected by the number of interactions ($R^2_{\text{interations}} = 0.04$; $p > 0.05$) or number of occurring cells ($R^2_{\text{occurrence}} = 0.03$; $p > 0.05$), but it was influenced by geographic extent ($R^2_{\text{geog.exten.}} = 0.16$; $p < 0.01$). Overall, we found that the geographic similarity of the binary maps decreases with the increasing geographic extent (Figure 2). We also found that the contribution of turnover is greater than that of nestedness to the total geographic dissimilarity between the models ($t = 4.83$, $df = 198$, $p < 0.01$), and the number of cells designated as a potential presence did not vary between the models (paired t = -0.16, df = 99, p > 0.05). This predominance of the turnover component in the geographic dissimilarity of the two models indicates that there is a spatial shift in the binary maps of the hummingbird species instead of a reduction in the number of occupied cells when biotic variables are added to the models.

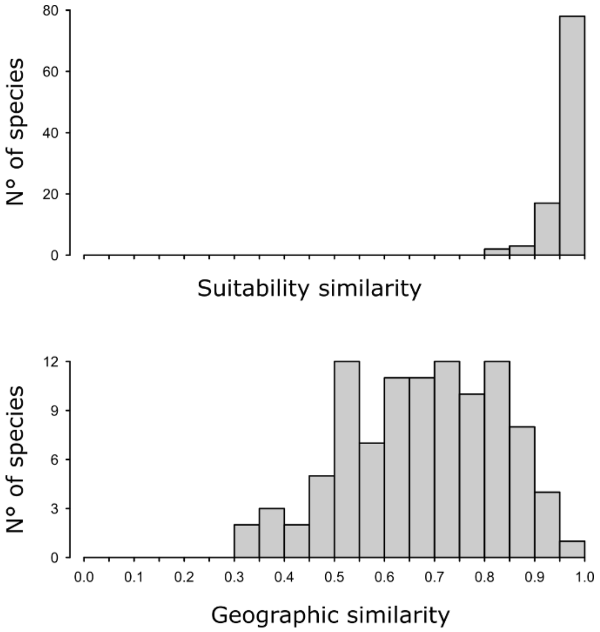

Figure 1. Histograms showing the distribution of similarity in environmental suitability (top) and binary geographic projection (bottom) between models including only abiotic and combined (abiotic + biotic) predictors. Environmental suitability similarity was calculated using Schoener's D index estimations, and geographic similarity was calculated using Jaccard similarity to compare the cells potentially occupied by the species after converting continuous projection into binary presence/absence maps.

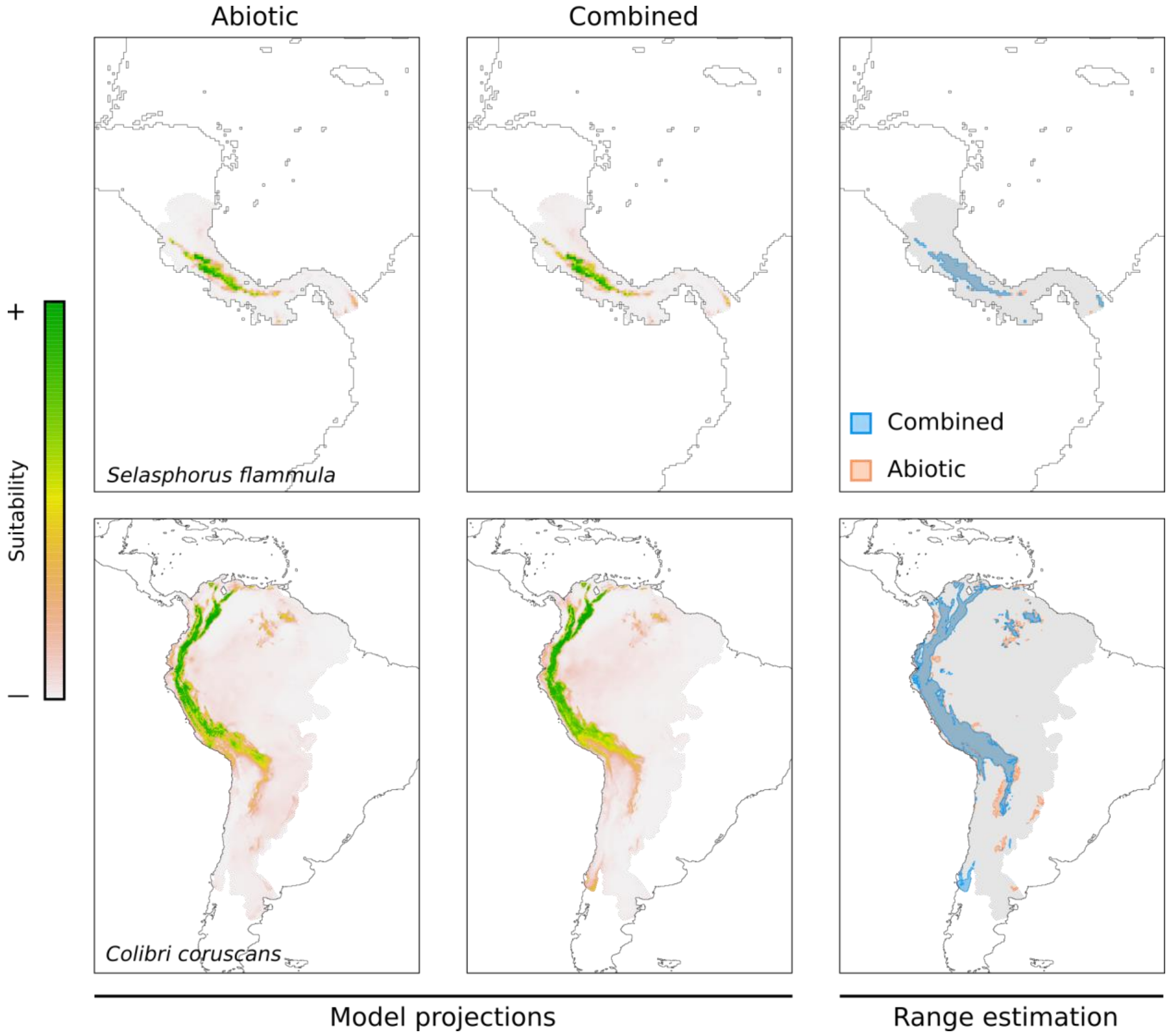

Figure 2. Example of the difference in model projection and range estimation for two hummingbird species with different geographical extent. Species distribution models were generated using only abiotic or the combined (abiotic + biotic) predictor variables and the estimated range were defined based on the maximum sensitivity plus specificity threshold.

Discussion

In this study, we evaluated the importance of including biotic interactions in SDMs (specifically MaxEnt), a step generally neglected in models at large geographic scales (Sóberon & Nakamura 2009). We found that the inclusion of biotic predictors improves model fit (AICc), but the accuracy of the model is not affected. Our results show that the addition of biotic interactions in SDMs can noticeably modify only the estimated range of the widely distributed species after binarizing model’s output to presence/absence maps. However, as we explain below, considering the overall results, this geographic dissimilarity seems to support rather than contradict the Eltonian noise hypothesis.

Generally, the inclusion of biotic predictors tends to increase the complexity of the models through greater overfitting and omission errors (false absences; Radosavljevic & Anderson 2014). However, we found that both the sensitivity and specificity values do not change significantly, indicating that the accuracy of the models is not altered by the inclusion of biotic interactions. Despite this result, most models still showed better fit (AICc). At first glance, this could indicate an influence of biotic interaction on large-scale geographic distributions, in line with the growing number of studies which show that different types of biotic interactions significantly improve SDMs predictions over a wide range of taxa (Heikinnen *et al.* 2007; Meier *et al.* 2010; Atauchi *et al.* 2018; Gherghel *et al.* 2018; Kass *et al.* 2020). However, we consider that the difference in projections between models that include combined predictors (i.e., abiotic and biotic) and those only abiotic is too small to contest the Eltonian noise hypothesis.

Most of the studies that assess the influence of biotic predictors have evaluated species that have a strong relationship with their interactors, being it trophic or related to reproductive dependence (Heikkinen *et al.* 2007; da Cunha *et al.* 2018; Gherghel *et al.* 2018; Palacio *et al.* 2018; Atauchi *et al.* 2018). For this reason, it has been suggested that the importance of biotic interactions for SDMs may be linked to the level of ecological dependence of the focal species (Araújo & Rozenfeld 2014). Although we have selected only the most relevant plant species to act as predictors of the occurrence of hummingbirds, these strong interactions are not necessarily exclusive and, as showed by our data, less frequent visits also occurred in other plants. In addition, it is not totally clear if the number of interactions of the local specialists would not increase at a regional scale (Gaston *et al.* 1997).

For these species, interactions can be too complex and dynamic to be accurately represented by a static model (Peterson *et al.* 2011; Anderson 2017). Therefore, the lack of exclusive relationships across scales may be the main reason why we did not find influence of biotic interactions on the hummingbirds' SDMs.

Although environmental suitability was highly similar between models using abiotic and combined predictors, our results revealed that the projected ranges were spatially variable. Generally, studies that do not support the Eltonian noise hypothesis also find some spatial changes resulting from a reduction in the size of the potential range (Cunha *et al.* 2018; Gherghel *et al.* 2018). The inclusion of biotic predictors reduces the overestimation of the geographic distribution generated based solely on abiotic predictors (da Cunha *et al.* 2018; Raath *et al.* 2018), and brings the projection closer to the realized distribution of the species (occupied area, *sensu* Soberón *et al.* 2017). This pattern is in line with the hierarchical niche structure proposed by Soberón (2007), which suggests that large-scale environmental conditions determine all the potentially suitable areas that meet the physiological requirements of a species (i.e. the Grinnellian niche), but biotic interactions are necessary to determine the subset of these areas that remain ecologically habitable (i.e. the Eltonian niche). However, we did not find a reduction in the size of the estimated range of the species as in previous studies. Conversely, the geographic dissimilarity identified here was associated mainly to turnover, indicating that there is some degree of spatial change in the location of the estimated geographic ranges after including biotic predictors.

The variability of the estimated range was not affected by the number of interactions or number of occurrence cells, but by the geographic extent of the area occupied by the species. According to visual inspections, this dissimilarity seems to be result from the spatial mismatch of the potentially occupied cells at the edges of the estimated ranges (i.e. noise, Figure. 2). The perception of this noise becomes more evident for species with large geographic extent, when the edge mismatch increases to consistent patches of spatial displacement. Considering that these outputs are not better in terms of sensitivity and specificity estimates than those generated by models using climate-only predictors, this result shows that adding interactions changed the projected distribution without necessarily improving it. Therefore, the spatial displacement found here does not seem robust to reject the Eltonian noise hypothesis. Instead, it seems indicate a higher sensibility of SDMs to model changes under large extents. Larger ranges generally encompass greater environmental heterogeneity, which could lead to higher uncertainty in the occurrence-environment relationship for wide compared to narrow-ranging species (McPherson & Jetz 2007). Other studies have already shown that the addition of predictor variables had only minor effects in the spatial output of range-restricted species (Bucklin *et al.* 2015), and that these species produce models with better performance than those widely distributed (McPherson & Jetz 2007; Tessarolo *et al.* 2014). Range projections of environmentally restricted species are also more spatially consistent even when comparing outputs from different algorithms, which tends to decrease as species become environmentally more generalist (Grenouillet *et al.* 2011). However, further studies are needed to investigate how sensible are the SDMs' outputs to the addition of predictor variables under different geographic extents.

In summary, our study shows that the inclusion of biotic interactions does not increase the performance and spatial predictions of SDMs for hummingbirds, at least not using the MaxEnt algorithm. Specifically, our study suggests that the scale at which biotic interactions remain important may depend on the exclusive dependence of the focal consuming species on their resource species, in addition to the type of interaction studied (Araújo & Rozenfeld 2014). Therefore, future studies should investigate how the changes in the interaction dependence (not only interaction strength) affect the performance and output of distribution models. We also highlight that projections of species with large geographic range tend to be more sensitive to the addition of predictor variables, though such effects are noticed only when continuous projections are converted to binary maps. Overall, the small influence of biotic variables detected in our study may be seen as the representation of the Eltonian noise. Therefore, although several studies have reported evidence contrary to the Eltonian noise hypothesis, our result indicates that the relevance of biotic interactions in SDMs is more nuanced than previously expected. However, additional tests using different methods to model the distribution of species are still necessary to confirm the generality of these results.

References

Abrams, P. (1983). The Theory of Limiting Similarity. *Annu. Rev. Ecol. Syst.*, 14, 359–376.

Acevedo, P., Jiménez-Valverde, A., Lobo, J.M. & Real, R. (2012). Delimiting the geographical background in species distribution modelling. *J. Biogeogr.*, 39, 1383–1390.

Anderson, R.P. (2017). When and how should biotic interactions be considered in models of species niches and distributions? J. Biogeogr., 44, 8–17.

Araújo, M.B. & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, 37, 406–415.

Atauchi, P.J., Peterson, A.T. & Flanagan, J. (2018). Species distribution models for Peruvian plantcutter improve with consideration of biotic interactions. *J. Avian Biol.*, 49, 1–8.

Baselga, A., Orme, D., Villeger, S., Bortoli, J. De & Leprieur, F. (2018). betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1. https://CRAN.R-project.org/package=betapart.

Belmaker, J., Zarnetske, P., Tuanmu, M.N., Zonneveld, S., Record, S., Strecker, A., *et al.* (2015). Empirical evidence for the scale dependence of biotic interactions. *Glob. Ecol. Biogeogr.*, 24, 750–761.

Bucklin, D.N., Basille, M., Benscoter, A.M., Brandt, L.A., Mazzotti, F.J., Romañach, S.S., *et al.* (2015). Comparing species distribution models constructed with different subsets of environmental predictors. *Divers. Distrib.*, 21, 23–35.

Burnham, K.P. & Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. In: Model Selection and Multimodel Inference. Springer New York, New York, NY, USA.

Cohen, J.E. (1977). Food webs and the dimensionality of trophic niche space. *Proc. Natl. Acad. Sci.*, 74, 4533–4536.

da Cunha, H.F., Ferreira, É.D., Tessarolo, G. & Nabout, J.C. (2018). Host plant distributions and climate interact to affect the predicted geographic distribution of a Neotropical termite. *Biotropica*, 50, 625–632.

de Araújo, C.B., Marcondes-Machado, L.O. & Costa, G.C. (2014). The importance of biotic interactions in species distribution models: a test of the Eltonian noise hypothesis using parrots. *J. Biogeogr.*, 41, 513–523.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., *et al.* (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011). A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.*, 17, 43–57.

Elton, C., 1927. Animal Ecology. Sedgwick and Jackson, London.

Fielding, A.H. & Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv. 24*, 24, 38–49.

Fumero-Cabán, J.J. & Meléndez-Ackerman, E.J. (2007). Relative pollination effectiveness of floral visitors of Pitcairnia angustifolia (Bromeliaceae). *Am. J. Bot.*, 94, 419–424.

Gass, C.L. & Montgomerie, R.D. (1981). Hummingbird foraging behaviour: decision-making and energy regulation. In: Foraging behaviour: Ecological, ethological and physiological approaches (eds. Kamil, A. & Sargent, T.). Garland STPM, New York, pp. 159–196.

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997). Interspecific Abundance-Range Size Relationships: An Appraisal of Mechanisms. *J. Anim. Ecol.*, 66, 579.

Gherghel, I., Brischoux, F. & Papeş, M. (2018). Using biotic interactions in broad-scale estimates of species' distributions. *J. Biogeogr.*, 45, 2216–2225.

Grenouillet, G., Buisson, L., Casajus, N. & Lek, S. (2011). Ensemble modelling of species distribution: The effects of geographical and environmental ranges. *Ecography*, 34, 9–17.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., *et al.* (2013). Predicting species distributions for conservation decisions. *Ecol. Lett.*, 16, 1424–1435.

HBW & BirdLife International (2019) Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 4. Available at:

http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v4_Dec19.zip.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G. & Körber, J.H. (2007). Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Glob. Ecol. Biogeogr.*, 16, 754–763.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2017). dismo: Species distribution modeling with R. v 1.1-4. Retrieved from http://cran.r-project.org/web/packages/dismo/index.html.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 46, 523–549.

Ilsøe, S.K., Kissling, W.D., Fjeldså, J., Sandel, B. & Svenning, J.C. (2017). Global variation in woodpecker species richness shaped by tree availability. *J. Biogeogr.*, 44, 1824–1835.

Janzen, D.H. (1980). *When is it Coevolution? Evolution.*

Jiménez-Valverde, A. (2014) Threshold-dependence as a desirable attribute for discrimination assessment: Implications for the evaluation of species distribution models. *Biodiversity and Conservation*, **23**, 369–385.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., *et al.* (2017). Climatologies at high resolution for the earth's land surface areas. *Sci. Data*, 4, 1–20.

Kass, J.M., Anderson, R.P., Espinosa-Lucas, A., Juárez-Jaimes, V., Martínez-Salas, E., Botello, F., *et al.* (2020). Biotic predictors with phenological information improve range estimates for migrating monarch butterflies in Mexico. *Ecography*., 43, 341–352.

Las-Casas, F.M.G., Azevedo Júnior, S.M. & Dias Filho, M.M. (2012). A comunidade de beija-flores (Aves: Trochilidae) e a assembleia de flores em uma área de Caatinga. *Brazilian J. Biol.*, 72, 51–58.

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28, 385–393.

Liu, C., Newell, G. & White, M. (2016). On the selection of thresholds for predicting species occurrence with presence-only data. *Ecol. Evol.*, 6, 337–348.

Lunau, K. (2004). Adaptive radiation and coevolution - Pollination biology case studies. *Org. Divers. Evol.*, 4, 207–224.

Maglianesi, M.A., BlüThgen, N., BöHning-Gaese, K. & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, 95, 3325–3334.

McPherson, J.M. & Jetz, W. (2007). Effects of species' ecology on the accuracy of distribution models. *Ecography,* 30, 135–151.

Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.C., Thuiller, W., Araújo, M.B., *et al.* (2010). Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, 33, 1038–1048.

Mouton, A.M., De Baets, B. & Goethals, P.L.M. (2010). Ecological relevance of performance criteria for species distribution models. *Ecol. Modell.*, 221, 1995–2002.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., *et al.* (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol. Evol.*, 5, 1198–1205.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., *et al.* (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. *Bioscience,* 51, 933–938.

Palacio, F.X. & Girini, J.M. (2018). Biotic interactions in species distribution models enhance model performance and shed light on natural history of rare birds: a case study using the straight-billed reedhaunter Limnoctites rectirostris. *J. Avian Biol.*, 49, e01743.

Pellissier, L., Anne Bråthen, K., Pottier, J., Randin, C.F., Vittoz, P., Dubuis, A., *et al.* (2010). Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography,* 33, 1004–1014.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., *et al.* (2011). *Ecological Niches and Geographic Distributions*. Princeton University Press.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.,* 190, 231–259.

R Core Time (2018). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org.

Raath, M.J., le Roux, P.C., Veldtman, R. & Greve, M. (2018). Incorporating biotic interactions in the distribution models of African wild silk moths (Gonometa species, Lasiocampidae) using different representations of modelled host tree distributions. *Austral Ecol.*, 43, 316–327.

Radosavljevic, A. & Anderson, R.P. (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *J. Biogeogr.*, 41, 629–643.

Record, S., Strecker, A., Tuanmu, M.N., Beaudrot, L., Zarnetske, P., Belmaker, J., *et al.* (2018). Does scale matter? A systematic review of incorporating biological realism when predicting changes in species distributions. *PLoS One*, 13, e0194650.

Rico-Guevara, A., Rubega, M.A., Hurme, K.J. & Dudley, R. (2019). Shifting Paradigms in the Mechanics of Nectar Extraction and Hummingbird Bill Morphology. *Integr. Org. Biol.*, 1, 1–15.

Rodríguez Flores, C.I. (2009). Dinámica de las estrategias de forrajeo por néctar en colibríes (Aves: Trochilidae) en la Reserva de la Biósfera Sierra de Manantlán (Jalisco, México). Universidad Nacional Autónoma de México.

Sazima, I., Buzato, S. & Sazima, M. (1996). An assemblage of hummingbird-pollinated flowers in a montane forest in southeastern Brazil. *Bot. Acta*, 109, 149–160.

Scrok, G.J. & Varassin, I.G. (2011). Reproductive biology and pollination of aechmea distichantha lem. (Bromeliaceae). *Acta Bot. Brasilica*, 25, 571–576.

Simões, M.V.P. & Peterson, A.T. (2018). Importance of biotic predictors in estimation of potential invasive areas: The example of the tortoise beetle Eurypedus nigrosignatus, in Hispaniola. *PeerJ*, 2018, e6052.

Smith, J.R., Hendershot, J.N., Nova, N. & Daily, G.C. (2020). The biogeography of ecoregions: Descriptive power across regions and taxa. *J. Biogeogr.*, 47, 1413–1426.

Sóberon, J. & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Proc. Natl. Acad. Sci.*, 106, 19644–19650.

Soberon, J. & Peterson, A.T. (2005). Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. *Biodivers. Informatics*, 2, 1–10.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.*, 10, 1115–1123.

Soberón, J., Osorio-Olvera, L. & Peterson, T. (2017). Diferencias conceptuales entre modelación de nichos y modelación de áreas de distribución. *Rev. Mex. Biodivers.*, 88, 437–441.

Stiles, F.G. (1985). Seasonal Patterns and Coevolution in the Hummingbird-Flower Community of a Costa Rican Subtropical Forest. *Ornithol. Monogr.*, 757–787.

Tessarolo, G., Rangel, T.F., Araújo, M.B. & Hortal, J. (2014). Uncertainty associated with survey design in species distribution models. Divers. Distrib., 20, 1258–1269.

Tinoco, B.A., Graham, C.H., Aguilar, J.M. & Schleuning, M. (2017). Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos*, 126, 52–60.

Urbina-Cardona, N., Blair, M.E., Londoño, M.C., Loyola, R., Velásquez-Tibatá, J. & Morales-Devia, H. (2019). Species Distribution Modeling in Latin America: A 25-Year Retrospective Review. *Trop. Conserv. Sci.*, 12, 1–19.

Velazco, S.J.E., Galvão, F., Villalobos, F. & De Marco, P. (2017). Using worldwide edaphic data to model plant species niches: An assessment at a continental extent. *PLoS One*, 12, e0186025.

Warren, D.L. & Seifert, S.N. (2011). Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecol. Appl.*, 21, 335–342.

Wogan, G.O.U. (2016). Life history traits and niche instability impact accuracy and temporal transferability for historically calibrated distribution models of North American birds. *PLoS One*, 11, e0151024.

Wolf, L.L. (1970). The Impact of Seasonal Flowering on the Biology of Some Tropical Hummingbirds. *Condor*, 72, 1–14.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., *et al.* (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods Ecol. Evol.*, 10, 744–751.

CAPÍTULO 2

Availability of resources shapes niche overlap in hummingbird communities

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[2] Kurtz, M.N., Almeida Neto, M, Cianciaruso, M.V. Availability of resources shapes niche overlap in hummingbird communities. *Manuscript in preparation.*

Availability of resources shapes niche overlap in hummingbird communities

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Abstract

The limiting similarity theory predicts that ecological communities should be formed by species with complementary traits in at least one niche dimension. However, studies using morphological traits to infer niche partitioning have conflicting evidences regarding the relationship between coexistence and species trait similarity. In this study, we used ecological information of hummingbird-plant ecological networks to quantify niche overlap. Then, we evaluated the effect of hummingbird morphological traits linked to resource acquisition and foraging behavior on the niche overlap. In addition, we quantified the availability and diversity of resources as control variables. We found a positive relationship between niche overlap and dominant behavior of species and a negative relationship with bill length variation and availability of resources. Thus, communities where species share more resources are those localized in less productive regions with morphologically less specialized species. Although this composition may intensify competition among species, it is offset by differences in the dynamics of foraging behavior. On the other hand, highly productive communities allows hummingbirds to optimize resource acquisition through less defensive behaviors and the selection of the resource based on their aptitude for consumption, reducing niche overlap. Thus, the niche partition through the foraging behavior justifies the coexistence of ecologically similar species, in communities with scarce resources. While communities with abundant resources do not seem to depend heavily on the partition of resources due to relaxation of competitive interactions.

Key-words: Net Primary Productivity (NPP), Mean Pairwise Distance (MPD), Wing Disc Loading (WDL), competitive ability, co-occurring species, dominant and subordinate behavior, theory of optimal foraging.

Introduction

A central goal in community ecology is to understand the main processes that control the assembly and maintenance of ecological communities (Hutchinson 1957; Hubbell 2001). Niche-based theories assume that communities are assembled by environmental filtering and by interspecific competition (Keddy 1992; Díaz *et al.* 1999; McGill *et al.* 2006). If environmental filtering is strong, then co-occurring species should be functionally more similar than expected by chance (Petchey *et al.* 2007). However, competition theory assumes that there is a limiting similarity among co-occurring species, so that communities should consist of species with complementary traits in at least one niche dimension (Hutchinson 1961; MacArthur & Levins 1967). For instance, the coexistence of species that compete for some limiting resource is expected to be facilitated if the competing species show some level of morphological dissimilarity (Chesson & Case 1986; Leibold 1998). Non-random dissimilarity in morphological traits within ecological communities have been interpreted as an indirect evidence of the importance of competition (Young *et al.* 2010, Abrahamczyk & Kessler 2015, Guterres *et al.* 2020). For vertebrates, such evidence arises through the analysis of different traits, such as head length in lizards, dental morphology in rodents, and bill size in birds (e.g., Huey 1974; Dayan & Simberloff 1994; Maglianesi *et al.* 2014, Sottas *et al.* 2020).

Food resources are one of the most relevant niche dimensions for the stable coexistence of species, because it is directly linked to the growth and reproduction of the organisms. A greater amount of energy can lead to higher availability of trophic resources, thus supporting a greater number of individuals and species, i.e. high niche overlap, due to the relaxation of the competition (Wright 1983; Evans *et al.* 2006; Pigot *et al.* 2016). On the other hand, a lower amount of energy will lead to greater competition for trophic resources, promoting morphological and behavioral divergences between species (Kelt & Brown 1999;

Maglianesi *et al.* 2015a,b; Lattanzio & Miles 2016), i.e. high partition of the trophic niche. The availability and diversity of food resources are especially important for trophically specialized guilds, such as hummingbirds, in which floral nectar usually comprise more than 85% of their diet (Gass & Montgomerie 1981). The combination of dietary specialization and high metabolic rates (Schuchmann 1999) makes constant access to food indispensable for hummingbirds. Thus, the segregation of the trophic niche can be particularly important for species coexistence in hummingbird communities. In general, a higher phenotypic specialization to feeding nectar is expected to facilitate the resource sharing among coexisting hummingbird species (Maglianesi *et al.* 2014).

The close morphological matching between traits of hummingbirds and plants is widely documented, especially the matching between bill and corolla length (Sazima *et al.* 1996; Walther & Brieschke 2001; Maglianesi *et al.* 2014). More specialized hummingbirds are generally slightly larger and have a longer and often curved bill (Feinsinger *et al.* 1982; Cotton 1998a; Maglianesi *et al.* 2014), feeding regularly on flowers that have a long corolla whose flowers store more nectar (Snow & Snow 1972; Cotton 1998a). On the other hand, species with a straight bill and medium to short length are generally smaller and can efficiently use small flowers (Snow & Snow 1972; Araujo & Sazima 2003; Dalsgaard *et al.* 2009). These species are adapted to use many plant species, being classified as less specialized (Snow & Snow 1972; Cotton 1998a; Walther & Brieschke 2001). The high degree of matching between the morphological characteristics of hummingbirds and consumed flowers is advantageous for the bird species as it increases the acquisition of nectar due to the fast and efficient ingestion, which contributes to increase their fitness (Temeles 1996; Dohzono *et al.* 2011; Maglianesi *et al.* 2014). This food segregation reduces interspecific competition in communities and facilitates resource allocation (Feinsinger & Colwell 1978; Lara 2006).

Behavioral differences in foraging activities also contribute to the species segregation in the trophic niche, increasing hummingbird coexistence (Lyon 1976; del Rio & Eguiarte 1987; Walther & Brieschke 2001; Ornelas *et al.* 2002; Lara *et al.* 2011). Hummingbird species usually adopt a dominant or a subordinate behavioral strategy during their foraging activities. Dominant species are territorial, i.e. their individuals defend a territory containing food resources against potential competitors (Feinsinger 1976; Feinsinger & Colwell 1978; Cotton 1998b), with more aggressive defense on areas with higher quality or quantity of nectar (Temeles *et al.* 2005; Justino *et al.* 2012). The subordinate species, in turn, explore their resources without exhibiting territorial behavior (Feinsinger & Colwell 1978; Rios *et al.* 2010; Tello-Ramos *et al.* 2015). Because the dominant species feed on resource-rich, the subordinate species are forced to explore areas less rich in nectar (Lara *et al.* 2009; Abrahamczyk & Kessler 2010).

Niche partitioning is widely used in the literature to explain the coexistence of species (Safi *et al.* 2011; Hidasi-Neto *et al.* 2012; Sobral *et al.* 2016), where competitive exclusion and limiting similarity should favor the coexistence of functionally different species, promoting the exploitation of different resources (Pianka 1974, Schoener 1974). However, some studies have shown that species richness may not necessarily be associated with an increase in trait dissimilarity and may even be associated with an increase in trait similarity (Gómez *et al.* 2010; Hidasi-Neto *et al.* 2012). In this sense, the use of interaction networks and functional traits of species can help us to better understand the coexistence of species. Here, we investigate how resource partitioning, a broad concept of resource acquisition that includes different dimensions of the niche, like consuming slightly different resources or consuming the same resource at different locations, interfere in the overlapping of the trophic niche of hummingbird communities. Based on networks of plant-hummingbird trophic interactions, we quantified niche overlapping and the mean and variation of morphological and behavioral traits of hummingbirds related to resource acquisition. We expect that communities with greater niche overlap will have competition attenuated by different ways of obtaining and foraging on the resources, especially in communities that have less resource availability. On the other hand, communities with high resource availability will have relaxed competition interactions and coexistence will be independent of bill morphological or foraging behavior.

Methods

Data collection

Our study units were flower-visiting networks composed of hummingbirds and plants. To gather hummingbird-plant networks, we performed a search on the ISI Web of Science with the following keywords: (hummingbird OR trochilidae) AND (communit* OR pollinat* OR interact* OR visit*). In addition, we compiled data from published scientific articles not included in the ISI Web of Science database, dissertation and theses using Google Scholar®, the CAPES thesis and dissertation catalog (https://catalogodeteses.capes.gov.br/catalogo-teses), the NCEAS Interaction Web Database (www.nceas.ucsb.edu/interactionweb) and Web of Life (www.web-of-life.es). Among the 92 plant-hummingbird networks we found in the literature, we selected 43 that meet the requirements mentioned below (details in Appendix A).

In order to minimize potential biases, some criteria were established for the inclusion of the networks in this study: i) only networks in which all species of hummingbird and plants visited by hummingbirds were potentially sampled in the same location, i.e. include legitimate (with pollination) and illegitimate (without pollination) visits. Studies that focused only on a particular group or species of hummingbirds or plants, or on a particular type of visit were excluded; ii) only networks with a minimum sampling period of six months and that contemplated the annual seasonal variation were included, in order to avoid the influence of the sampling effort and seasonal variations (Cotton 2007; Vizentin-Bugoni *et al.* 2016); and iii) only networks with little or no anthropic influence were selected to avoid potential biases on the results (Mason *et al.* 2011; Hidasi-Neto *et al.* 2012).

We evaluated the degree of niche overlap (NO) among hummingbird species in each network by using the Morisita-Horn index (Horn 1966), which measures the similarity in the pattern of interactions among the species of the same guild. Thus, communities with many specialist species will have a low value of niche overlap (NO ≅ 0, i.e., high resource partitioning), while communities with a predominance of generalists will have a higher value of niche overlap (NO ≅ 1, i.e., low resource partitioning).

For each community, we also compiled hummingbird trait data that reflect resource use and partitioning. The morphology of the bill varies widely among hummingbird species and is strongly related to the morphological characteristics of the flowers (Walther & Brieschke 2001; Maglianesi *et al.* 2014). Here, we used bill length (BL) as it can directly influences resource obtaining and the foraging efficiency (Dalsgaard *et al.* 2009; Temeles *et al.* 2009; Maglianesi *et al.* 2014). Additionally, we compiled body mass and wing length data to calculate the wing disc-loading index. Higher wing disc-loading index values promote greater speed and maneuverability that provide greater competitive ability, these characteristics are associated with the territorial dominance and, consequently, the resources dominance in hummingbird species (Feinsinger & Chaplin 1975; Feinsinger & Colwell 1978 (Table 1 and details in Appendix B). That is why in our study the wing disc loading (WDL) was considered a surrogate of defense behavior.

Table 1. Specifications of the traits used.

Traits	Definition	Unity
Bill length (BL)	Measure efferent to exposed culmen. Length from beginning of feathers to tip of beak.	cm
Wing disc loading (WDL)	Calculated by the formula WDL = $BM/\pi * (2.5 * WL/2)^2$, where BM is body mass (g), and WL is wing length (cm) (Feinsinger & Chaplin 1975). WL can be defined as wing chord and were measured as the distance from the carpus to the tip of the longest primary feather (Stiles & Altshuler 2004).	g/cm^2

For each community (i.e., plant-hummingbird network) we generated a Euclidean distance trait matrix to calculate the average dissimilarity between the trait's values of the species (mean pairwise distance), which was calculated separately for BL and WDL. These measure reflect niche differences among species independent of species richness (de Bello *et al.* 2016). In each community, the index was standardized by its maximum distance to vary between 0-1 ranges, from communities with functionally similar species (mean pairwise distance ≅ 0; low dissimilarity) to functionally unique species (mean pairwise distance ≅ 1; high dissimilarity). Communities with lower functional similarity among species indicate greater specialization and consequently greater resource partitioning. In addition to the mean pairwise distance, we also evaluate the average values of the BL and WDL across communities. The NO index was calculated with the "bipartite" package version 2.15 (Dormann *et al.* 2009) and the mean pairwise distance with the "melodic" function (de Bello *et al.* 2016).

The Net Primary Productivity (NPP) at each community was extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) data, MOD17A3 data set (Running *et al.* 2017). We averaged the daily estimates between the years 2000 and 2017 and extracted the NPP values of the cells where the studied communities were located using *raster* package (Hijmans & Etten 2019). High NPP values are associated with high energy availability. In tropical forests, reproductive structures (flowers and fruits) represent about 6-15% of total NPP and have small spatial variation (Malhi *et al.* 2011). Therefore, we assumed that NPP is positively associated with the number of available flowers and consequently the greater availability of nectar resources. In addition, we used the ratio between the species richness of hummingbirds and plants as an indicative of potential competition, where the higher values of the ratio reflect a higher number of species of hummingbirds visiting the same plants, that is, potentially sharing the same resources.

Data Analysis

To test if niche overlap could be explained by the predictor variables, we used a multiple linear regression analysis. To assess the extent of collinearity between the explanatory variables included in the model, we kept only variables with variation inflation factors (VIFs) < 5 (Zuur *et al.* 2010). Because our tests revealed collinearity between the mean value of BL and the mean pairwise distance of BL, we opted to remove mean BL from the model. Thus, the global model to explain variation in niche overlap was composed of mean pairwise distance of WDL, mean pairwise distance of BL, mean value of WDL, NPP and the ratio between hummingbird richness and plant richness. The last two variables were added as control variables, as they can affect network structure and consequently species coexistence. When necessary, the variables were transformed by $\log_{(x + 1)}$ to meet the normality assumption.

We used all possible combinations of predictive variables, and compared the models adjusted by maximum likelihood. Each model was ranked according to its value determined by Akaike's information criterion (AIC) corrected for small sample size (AICc: Second-order Akaike Information Criterion; Burnham & Anderson 2002) and the best model was selected

(Table S1). In addition, we measured the relative importance of each predictor variable with the method LMG, which calculates the r-squared contribution averaged over orderings among regressors. Finally, based on geographical coordinates of each locality, we also evaluated the existence of spatial autocorrelation in the model's residuals using the Moran's I index. Overall, no evidence of spatial autocorrelation was detected (Moran's I = -0.10, p-value = 0.47). All analyses were performed in the software R (R Development Core Team, 2019) with package "*MuMIn*" (Bartoń 2018), "*relaimpo*" (Grömping 2006), "*ape*" (Paradis & Schliep 2019) and "*fields*" (Nychka *et al.* 2017).

Results

Among the 43 analyzed flower-visiting networks (Fig. S1), the species richness of hummingbirds and plants in each community varied from 2 to 24 (mean ± SD: 8.2 ± 4.1) and from 5 to 68 (22 ± 14), respectively. The number of plant-hummingbird interactions ranged from 1 to 34 (6.7 ± 6.5) across communities. No hummingbird species occurred in more than eight communities and almost half (45%) of the hummingbird species occurred in a single community.

Overall, niche overlap varied widely among communities from 0.07 to 0.91, but cases of low niche overlap were more prevalent (mean ± SD: 0.3 ± 0.2, Fig. S2). Among all possible models, the best model explaining changes in niche overlap among hummingbird species was composed by mean WDL, mean pairwise distance of BL and NPP, that together explain 28.6% of niche overlap (see all models in Table S1). Each variable contributed, respectively, with 45%, 29% and 26%, of the explained variation in niche overlap.

Mean WDL value was positively related to niche overlap, while mean pairwise distance of BL values and NPP were negatively related to species' niche overlap (Table S2). This means that the niche overlap was greater in communities where hummingbirds have higher mean WDL values, lower BL variation and in places with lower productivity. On the other hand, communities with lower niche overlap have, on average, low WDL values and high variation in BL values, in addition to high NPP.

Discussion

Here we investigate the relationship between niche overlap and functional traits in local hummingbird communities. Our results demonstrated that the level of trophic niche overlap in hummingbird communities is partially explained by mean wing disc loading values, bill length variation and net primary productivity. Niche overlap was higher in communities with less resource availability (i.e. local productivity) and negatively related to the variation in the ability to obtain resources (i.e. bill length). Moreover, it is positively related to morphological traits associated to hummingbird defensive behavior. These findings show that hummingbird communities with greater niche overlap are also those with low resource availability, in which most species have greater dominance behavior over the food territory to avoid functionally similar species.

The variable that best explained niche overlap within hummingbird communities was mean WDL, a proxy for defensive behavior in hummingbirds. A dominant behavior occurs in hummingbirds species when they defend a territory, while subordinated species do not defend their territory. Species with subordinate behavior can act in two ways: i) foraging only on resources that are outside the territories defended by dominant species; or ii) foraging over resources that are defended by dominant species. In this last case, the intruder remains in the protected area looking for food until it is expelled by territorial dominant (Feinsinger & Colwell 1978; Ornelas 1994; Barbosa-Filho & de Araujo 2013). The defense of the territory carried out by hummingbird species with dominant behavior involves great energy expenditure that is compensated by the nectar provided by the protected plants (i.e. positive cost-benefit). Thus, the size of the territory can vary according to the availability of resources but it is restricted to the limit where the defense becomes energetically expensive (Justino *et al.* 2012). That is, in conditions of low availability of resources, communities can present a great number of territorial species, as we found here, but these species tend to have more extensive protected territory (Fonseca *et al.* 2015). The larger the size of a territory, the lower its efficiency in defending it, facilitating the occurrence of intrusive behavior and increasing trophic niche overlap, especially reported on the periphery of the territory (Walther & Brieschke 2001).

Although we found that hummingbirds consume similar resources in communities with low productivity, in general, they prefer to consume flowers that have characteristics that correspond to their bill morphology, as these flowers provide high foraging efficiency; that is, they can consume more nectar in less time, increasing their fitness (Temeles 1996; Dohzono *et al.* 2011; Maglianesi *et al.* 2014). However, this is not a mandatory relationship. It is known that hummingbird species feed on a variety of plant species. In this context, our results indicate that the use of a given resource may depend on its availability. According to Temeles *et al.* (2002), the scarcity of hummingbird ’favorite flowers combined with competition for these resources can result in the incorporation of new flowers into the diet, even though these flowers have little correspondence with the foraging morphology. It is quite common to observe hummingbirds that regularly visit flowers that are not morphologically suitable for them to feed (Feinsinger *et al.* 1982; Arizmendi 2001; Dziedzioch *et al.* 2003; Lara *et al.* 2009; Maruyama *et al.* 2013, 2015; Fonseca *et al.* 2015). These flowers can contribute to the acquisition of a considerable part of the hummingbirds' diet. *Phaethornis ruber*, for example, can have approximately 30% of its diet composed of them (Maruyama *et al.* 2015), and this percentage can be higher in communities with low availability of resources. In this context, our results suggest that species that are highly specialized in a given resource would have difficulty in acquiring the amount of resources sufficient to supply their energy needs in communities with low availability of resources and strong competitive interactions.

On the other hand, we found that communities with low niche overlap have less territorial species, and the hummingbirds tend to have more dissimilar bill morphology (i.e. ability to obtain different resources) and more resource available. It is expected that species will have interspecific interactions reduced in communities with greater abundance of resources, facilitating their coexistence (Abrahamczyk & Kessler 2010; Malhi *et al.* 2011). In this scenario, the energy needs of all species that make up the community are met, which reduces competitive interactions, and keeps niche overlap low. In addition, species with different bill morphology tend to consume flowers that provide a better cost-benefit balance, while territorial species, with less occurrence, tend to defend smaller areas, which in this case are sufficient to meet their energy costs (as discussed earlier). Species with subordinate behavior, that are majority, also follow a similar pattern, where the increase in available resources allows species to take smaller areas to acquire resources (Tello-Ramos *et al.* 2015), which can make the intrusive behavior reduced or non-existent. In a context of high availability of resources, hummingbirds can focus on plant species and behaviors that increase their fitness, but without increasing the risk of confrontation with other species, reducing interspecific competition. This is in line with the Optimal Foraging Theory (MacArthur & Pianka 1966), which assumes that animals tend to maximize their fitness through the way they forage, that is, they select their diet and structure their foraging activities to maximize gain and minimize energy losses per unit of time, which increases the efficiency of foraging (Charnov 1976; Pyke *et al.* 1977). In hummingbirds, the net energy gain depends on the energy value of the flower nectar, the time used to handle the flowers and ingest the nectar (handling time), the time to fly from flower to flower and the presence of negative interspecific interactions during foraging. Thus, to optimize foraging, hummingbirds can use information contained in the environment to restrict their effort to those flowers that offer a greater net amount of energy. Flowers that have higher volume and concentration/quality of nectar as well as those with shorter handling times (Maglianesi *et al.* 2014; Temeles *et al.* 2016, 2017) can be selected by the morphological characteristics of the flowers, such as length and corolla curvature, angle of inclination of the flower and number of inflorescences per plant (Sandlin 2000; Sapir & Dudley 2013; Maglianesi *et al.* 2014; Temeles *et al.* 2016; Weinstein & Graham 2017), which makes foraging faster and compensatory.

In summary, hummingbird communities with high dietary overlap are mainly structured by territorial behavior, which is directly affected by the low availability of resources. Although several studies have found that the differences in bill morphology can be determinant for the partition of food resources among hummingbirds due to correspondence with the specific floral morphology (Araujo 1996; Temeles *et al.* 2009; Maglianesi *et al.* 2014), our study shows that, contrary to our theoretical expectation, bill's morphology contributed to increase niche overlap in communities with less resources available. In productive communities, on the other hand, the species will not depend heavily on the niche partition. The partition occurs naturally due to the foraging restricted to small areas and the preference of hummingbirds for the consumption of flowers that optimize their fitness, without increasing energy expenditure, which reduces the trophic niche overlap.

References

Abrahamczyk, S. & Kessler, M. (2010). Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *J. Ornithol.*, 151, 615–625.

Abrahamczyk, S. & Kessler, M. (2015). Morphological and behavioural adaptations to feed on nectar: how feeding ecology determines the diversity and composition of hummingbird assemblages. *J. Ornithol.*, 156, 333–347.

Araujo, A.C. (1996). Beija-flores e seus recursos florais numa área de planicie costeira do litoral norte de São Paulo. Campinas State University, Brazil.

Araujo, A.C. & Sazima, M. (2003). The assemblage of flowers visited by hummingbirds in the “capões” of Southern Pantanal, Mato Grosso do Sul, Brazil. *Flora - Morphol. Distrib. Funct. Ecol. Plants*, 198, 427–435.

Arizmendi, M.C. (2001). Multiple ecological interactions: nectar robbers and hummingbirds in a highland forest in Mexico. *Can. J. Zool.*, 79, 997–1006.

Barbosa-Filho, W.G. & Araujo, A.C. (2013). Flores visitadas por beija-flores em um fragmento urbano de Cerrado, Mato Grosso do Sul, Brasil. *Biota Neotrop.*, 13, 21–27.

Bartoń, K. (2018). Package “MuMIn”: Multi-Model Inference. *Cran-R*, 1–74.

de Bello, F., Carmona, C.P., Lepš, J., Szava-Kovats, R. & Pärtel, M. (2016). Functional diversity through the mean trait dissimilarity: resolving shortcomings with existing paradigms and algorithms. *Oecologia*, 180, 933–940.

Burnham, K.P. & Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. In: *Model Selection and Multimodel Inference*. Springer New York, New York, USA.

Cade, B.S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, 96, 2370–2382.

Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.*, 9, 129–136.

Chesson, P. & Case, T.J. (1986). Overview: Nonequilibrium community theories: Chance, variability, history, and coexistence. In: *Community ecology* (eds. Diamond, J. & Case, T.J.). Harper & Row, New York, pp. 229–239.

Cotton, P.A. (1998a). Coevolution in an Amazonian hummingbird-plant community. *Ibis*, 140, 639–646.

Cotton, P.A. (1998b). Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis*, 140, 647–653.

Cotton, P.A. (2007). Seasonal resource tracking by Amazonian hummingbirds. *Ibis*, 149, 135–142.

Dalsgaard, B., Martín González, A.M., Olesen, J.M., Ollerton, J., Timmermann, A., Andersen, L.H., *et al.* (2009). Plant-hummingbird interactions in the West Indies: Floral specialisation gradients associated with environment and hummingbird size. *Oecologia*, 159, 757–766.

Dayan, T. & Simberloff, D. (1994). Morphological relationships among coexisting heteromyids: An incisive dental character. *Am. Nat.*, 143, 462–477.

Díaz, S., Cabido, M. & Casanoves, F. (1999). Functional implications of trait–environment linkages in plant communities. In: *Ecological Assembly Rules – Perspectives, Advances, Retreats* (eds. Weiher, E. & Keddy, P.). Cambridge University Press, Cambridge, pp. 338–362.

Dohzono, I., Takami, Y. & Suzuki, K. (2011). Is Bumblebee Foraging Efficiency Mediated by Morphological Correspondence to Flowers? *Int. J. Insect Sci.*, 3, 1-3.

Dormann, C.F., Frund, J., Bluthgen, N. & Gruber, B. (2009). Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. *Open Ecol. J.*, 2, 7–24.

Dziedzioch, C., Stevens, A.D. & Gottsberger, G. (2003). The hummingbird plant community of a tropical montane rain forest in southern Ecuador. *Plant Biol.*, 5, 331–337.

Evans, K.L., Jackson, S.F., Greenwood, J.J.. & Gaston, K.J. (2006). Species traits and the form of individual species-energy relationships. *Proc. R. Soc. B Biol. Sci.*, 273, 1779–1787.

Feinsinger, P. (1976). Organization of a Tropical Guild of Nectarivorous Birds. *Ecol. Monogr.*, 46, 257–291.

Feinsinger, P. & Chaplin, S.B. (1975). On the relationship between wing disc loading and foraging strategy in hummingbirds. *Nat. Genet.*, 109, 217–224.

Feinsinger, P. & Colwell, R.K. (1978). *Community Organization Among Neotropical Nectar-Feeding Birds*.

Feinsinger, P., Wolfe, J.A. & Swarm, L.A. (1982). Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. *Ecology*, 63, 494–506.

Fonseca, L.C.N., Vizentin-Bugoni, J., Rech, A.R. & Alves, M.A.S. (2015). Plant-hummingbird interactions and temporal nectar availability in a restinga from Brazil. *An. Acad. Bras. Cienc.*, 87, 2163–2175.

Gass, C. & Montgomerie, R. (1981). Hummingbird foraging behavior: decision making and energy regulation. In: *Foraging behavior: ecological, ethological, and psychological approach* (eds. Kamil, A.C. & Sargent, T.D.). Garland STPM Press, New York**,** pp. 159–164.

Gómez, J.P., Bravo, G.A., Brumfield, R.T., Tello, J.G. & Cadena, C.D. (2010). A phylogenetic approach to disentangling the role of competition and habitat filtering in community assembly of Neotropical forest birds. *J. Anim. Ecol.*, 79, 1181–1192.

Grömping, U. (2006). Relative importance for linear regression in R: The package relaimpo.

J. Stat. Softw., 17, 1–27.

Guterres, A.P.M., Cunha, E.J., Godoy, B.S., Silva, R.R. & Juen, L. (2020). Co-occurrence patterns and morphological similarity of semiaquatic insects (Hemiptera: Gerromorpha) in streams of Eastern Amazonia. *Ecol. Entomol.*, 45, 155–166.

Hidasi-Neto, J., Barlow, J. & Cianciaruso, M. V. (2012). Bird functional diversity and wildfires in the Amazon: the role of forest structure. *Anim. Conserv.*, 15, 407–415.

Hijmans, R.J. (2012). Cross-validation of species distribution models: Removing spatial sorting bias and calibration with a null model. *Ecology*, 93, 679–688.

Hijmans, R.J. & Etten, J.V. (2019). raster: Geographic analysis and modeling with raster data. R package version 2.8-4.

Hubbell, S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Huey, R.B. (1974). Ecological character displacement in a lizard. *Integr. Comp. Biol.*, 14, 1127–1136.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.*, 22, 415–427.

Hutchinson, G.E. (1961). The paradox of the plankton. *Am. Nat.*, 95, 137–145.

Justino, D.G., Maruyama, P.K. & Oliveira, P.E. (2012). Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *J. Ornithol.*, 153, 189–197.

Keddy, P.A. (1992). Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.*, 3, 157–164.

Kelt, D.A. & Brown, J.H. (1999). Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. In: *Ecological Assembly Rules – Perspectives, Advances, Retreats* (eds. Weiher, E. & Keddy, P.). Cambridge University Press, pp. 75–106.

Krebs, C.J. (1989). *Ecological Methodology*. Harper Collins, New York.

Lara, C. (2006). Temporal dynamics of flower use by hummingbirds in a highland temperate forest in Mexico. *Ecoscience*, 13, 23–29.

Lara, C., Lumbreras, K. & González, M. (2009). Niche partitioning among hummingbirds foraging on Penstemon roseus (plantaginaceae) in central Mexico. *Ornitol. Neotrop.*, 20, 81–91.

Lara, C., Martínez-García, V., Ortiz-Pulido, R., Bravo-Cadena, J., Loranca, S. & Córdoba-Aguilar, A. (2011). Temporal-spatial segregation among hummingbirds foraging on honeydew in a temperate forest in Mexico. *Curr. Zool.*, 57, 56–62.

Lattanzio, M.S. & Miles, D.B. (2016). Trophic niche divergence among colour morphs that exhibit alternative mating tactics. *R. Soc. Open Sci.*, 3, 1-12.

Leibold, M.A. (1998). Similarity and local co-existence of species in regional biotas. *Evol. Ecol.*, 12, 95–110.

Lyon, D.L. (1976). A Montane Hummingbird Territorial System in Oaxaca, Mexico. *Wilson Bull.*, 88, 280–299.

MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence, ans divergence of coexisting species. *Am. Nauralist*, 101, 377–384.

Maglianesi, M.A., Blüthgen, N., Böhning-Gaese, K. & Schleuning, M. (2015a). Functional structure and specialization in three tropical plant-hummingbird interaction networks across an elevational gradient in Costa Rica. *Ecography*, 38, 1119–1128.

Maglianesi, M.A., BlüThgen, N., BöHning-Gaese, K. & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, 95, 3325–3334.

Maglianesi, M.A., Böhning-Gaese, K. & Schleuning, M. (2015b). Different foraging preferences of hummingbirds on artificial and natural flowers reveal mechanisms structuring plant-pollinator interactions. *J. Anim. Ecol.*, 84, 655–664.

Malhi, Y., Doughty, C. & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philos. Trans. R. Soc. B Biol. Sci.*, 366, 3225–3245.

Maruyama, P.K., Oliveira, G.M., Ferreira, C., Dalsgaard, B. & Oliveira, P.E. (2013). Pollination syndromes ignored: Importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften*, 100, 1061–1068.

Maruyama, P.K., Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I. & Sazima, M. (2015). Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. *Oecologia*, 178, 783–793.

Mason, N.W.H., De Bello, F., Doležal, J. & Lepš, J. (2011). Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *J. Ecol.*, 99, 788–796.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

Nychka, D., Furrer, R., Paige, J., & Sain, S. (2017). fields: Tools for spatial data. R package version 11.6.

Ornelas, J.F. (1994). *Serrate Tomia: An Adaptation for Nectar Robbing in Hummingbirds?. Auk*, 111, 703-710.

Ornelas, J.F., Ordano, M., Hernández, A., López, J.C., Mendoza, L. & Perroni, Y. (2002). Nectar oasis produced by Agave marmorata Roezl. (Agavaceae) lead to spatial and temporal segregation among nectarivores in the Tehuacán Valley, México. *J. Arid Environ.*, 52, 37–51.

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

Petchey, O.L., Evans, K.L., Fishburn, I.S. & Gaston, K.J. (2007). Low functional diversity and no redundancy in British avian assemblages. *J. Anim. Ecol.*, 76, 977–985.

Pianka, E.R. (1974). Niche Overlap and Diffuse Competition. *Proc. Natl. Acad. Sci.*, 71, 2141–2145.

Pigot, A.L., Tobias, J.A. & Jetz, W. (2016). Energetic Constraints on Species Coexistence in Birds. *PLoS Biol.*, 14, e1002407.

Pyke, G.H., Pulliam, H.R., Charnov, E. & Charnov, E.L. 1977. (1977). Optimal foraging: A selective review of theory and tests Recommended Citation Optimal foraging: A selective review of theory and tests. *Q. Rev. Biol., 52, 137-154.*

R Development Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

del Rio, C.M. & Eguiarte, L.E. (1987). Bird Visitation to Agave salmiana: Comparisons among Hummingbirds and Perching Birds. *Condor*, 89, 357–363.

Rios, P.A.F., Da Silva, J.B. & Moura, F.D.B.P. (2010). Visitantes florais de Aechmea constantinii (Mez) L. B. Sm.(Bromeliaceae) em um remanescente da Mata Atlântica do Nordeste Oriental. *Biotemas*, 23, 29–36.

Running, S., Mu, Q. & Zhao, M. (2017). MOD17A3H, MODIS/Terra Net Primary Production Yearly L4 Global 500m SIN Grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/modis/mod17a3h.006.

Safi, K., Cianciaruso, M. V., Loyola, R.D., Brito, D., Armour-Marshall, K. & Diniz-Filho, J.A.F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos. Trans. R. Soc. B Biol. Sci.*, 366, 2536–2544.

Sandlin, E.A. (2000). Cue use affects resource subdivision among three coexisting hummingbird species. *Behav. Ecol.*, 11, 550–559.

Sapir, N. & Dudley, R. (2013). Implications of floral orientation for flight kinematics and metabolic expenditure of hover-feeding hummingbirds. *Funct. Ecol.*, 27, 227–235.

Sazima, I., Buzato, S. & Sazima, M. (1996). An assemblage of hummingbird-pollinated flowers in a montane forest in southeastern Brazil. *Bot. Acta*, 109, 149–160.

Schoener, T.W. (1974). Resource partitioning in ecological communities. *Science.*, 185, 27–39.

Schuchmann, K.L. (1999). Family Trochilidae (hummingbirds). In: *Handbook of the birds ofthe world - Volume 5:Barn-owls to Hummingbirds* (eds. del Hoyo, J., Elliott, A. & Sargatal, J.). Lynx Editions, Barcelona, pp. 468–680.

Snow, B.K. & Snow, D.W. (1972). Feeding Niches of Hummingbirds in a Trinidad Valley. *J. Anim. Ecol.*, 41, 471–485.

Sobral, F.L., Lees, A.C. & Cianciaruso, M. V. (2016). Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. *Ecol. Lett.*, 19, 1091–1100.

Sottas, C., Reif, J., Kreisinger, J., Schmiedová, L., Sam, K., Osiejuk, T.S., *et al.* (2020). Tracing the early steps of competition-driven eco-morphological divergence in two sister species of passerines. *Evol. Ecol.*, 34, 501–524.

Stiles, F.G. & Altshuler, D.L. (2004). Conflicting Terminology for Wing Measurements in Ornithology and Aerodynamics. *Auk*, 121, 973–976.

Tello-Ramos, M.C., Hurly, T.A. & Healy, S.D. (2015). Traplining in hummingbirds: flying short-distance sequences among several locations. *Behav. Ecol.*, 26, 812–819.

Temeles, E.J. (1996). A new dimension to hummingbird - Flower relationships. *Oecologia*, 105, 517–523.

Temeles, E.J., Goldman, R.S. & Kudla, A.U. (2005). Foraging and Territory Economics of Sexually Dimorphic Purple-Throated Caribs (Eulampis Jugularis) on Three Heliconia Morphs. *Auk*, 122, 187–204.

Temeles, E.J., Koulouris, C.R., Sander, S.E. & Kress, W.J. (2009). Effect of flower shape and size on foraging performance and trade-offs in a tropical hummingbird. *Ecology*, 90, 1147–1161.

Temeles, E.J., Linhart, Y.B., Masonjones, M. & Masonjones, H.D. (2002). The Role of Flower Width in Hummingbird Bill Length-Flower Length Relationships. *Biotropica*, 34, 68–80.

Temeles, E.J., Mazzotta, A.R. & Williamson, A. (2017). Resource partitioning by color in a tropical hummingbird. *Behav. Ecol. Sociobiol.*, 71, 1–8.

Temeles, E.J., Newman, J.T., Newman, J.H., Cho, S.Y., Mazzotta, A.R. & Kress, W.J. (2016). Pollinator Competition as a Driver of Floral Divergence: An Experimental Test. *PLoS One*, 11, e0146431.

Van-Sluys, M. & Stotz, D.F. (1995). Padrões de visitação a Vriesea neoglutinosa por beija-flores no Espírito Santo, Sudeste de Brasil. *Bromélia*, 2, 27–35.

Vizentin-Bugoni, J., Maruyama, P.K., Debastiani, V.J., Duarte, L. da S., Dalsgaard, B. & Sazima, M. (2016). Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant-hummingbird network. *J. Anim. Ecol.,* 85, 262–272.

Walther, B.A. & Brieschke, H. (2001). Hummingbird-flower relationships in a mid-elevation rainforest near Mindo, Northwestern Ecuador. *Int. J. Ornithol.*, 4, 115–135.

Weinstein, B.G. & Graham, C.H. (2017). Persistent bill and corolla matching despite shifting temporal resources in tropical hummingbird-plant interactions. *Ecol. Lett.*, 20, 326–335.

Wright, D.H. (1983). Species-energy theory : an extension of species-area theory. *Oikos*, 41, 496–506.

Young, R.L., Sweeney, M.J. & Badyaev, A. V. (2010). Morphological diversity and ecological similarity: versatility of muscular and skeletal morphologies enables ecological convergence in shrews. *Funct. Ecol.*, 24, 556–565.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.*, 1, 3–14.

CAPÍTULO 3

A global synthesis on the Raunkiaeran shortfall for birds[3]

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A global synthesis on the Raunkiaeran shortfall for birds

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Abstract

Broad and accessible biodiversity-related knowledge is essential to understand the impacts of biodiversity loss and to make appropriate conservation decisions in the face of ongoing global changes. To guide global actions for data mobilization, many efforts have been made to identify gaps in species geographic distribution. However, knowledge gaps in digital accessible information regarding key species traits (i.e. Raunkiaeran shortfall) remain critically limited. Using birds as a study system, here we revise the literature to identify the ecologically most relevant traits and combine >97,000 records from public datasets to quantify and map their Raunkiaeran shortfall. We find that only 62% of the information about the possible species-trait combinations are freely available in published datasets. Major gaps exists for seabirds and small-ranged species from tropical countries, especially regarding morphological traits. Including two additional large data sources that did not meet our initial inclusion criteria reduces massively the shortfall but do not change the main gaps location, which may indicate important predictors of data limitation for less studied taxa. Our study provides a simple and intuitive approach for evaluating trait information that can be applied to study other clades, and highlights important data voids that will demand scientific cooperation and data management to effectively reduce the Raunkiaeran shortfall.

Key-words: Data availability, Information coverage, Functional traits, Knowledge bias, Maps of ignorance.

Introduction

Improvement of biodiversity-related knowledge is essential to understand patterns and processes that occur at different spatial and temporal scales and for making appropriate conservation decisions, so that the development of an advanced and shared biodiversity knowledge base is one of the global conservation targets (Aichi Target 19 - Convention on Biological Diversity; https://www.cbd.int/sp/targets/). Syntheses of information availability are therefore required to estimate the amount of knowledge that remains unknown and to comprehend how these data limitation may bias the interpretation of ecological processes or affect conservation initiatives. Relative progress to identify these knowledge gaps have been observed especially in terms of estimating the number of species that remain to be described (i.e. Linnean shortfall; Bini *et al.* 2006; Brown & Lomolino 1998; Mora *et al.* 2011) and estimating uncertainty in species' geographic distribution (i.e. Wallacean shortfall; Bini *et al.* 2006; Lomolino 2004; Menegotto & Rangel 2018). However, despite the growing number of studies with functional diversity due to its wide use in several research fields (Freitas & Mantovani 2018), the dimension of how much we don't know in terms of species traits, i.e. the dimension of the Raunkiaeran shortfall, remains relatively little explored (but see a few examples below).

The Raunkiaeran shortfall is defined as the lack of knowledge about species traits that are ecologically relevant, including the lack of knowledge about the variation of traits within and among species, the ecological function resulting from each trait, how these functions are affected by interactions with other traits, and which traits work together to perform ecosystem functions (Hortal *et al.* 2015). Quantifying how much information about relevant traits is already known for a determined set of species represents then a good starting point to evaluate the dimension of the Raunkiaeran shortfall, but quantifying scientific information is not a trivial task. After two centuries of biodiversity inventories with thousands of new publications each year, biological researchers have produced a tremendous amount of data dispersed over multiple small datasets (Oliveira *et al.* 2017). Without a proper data management and mobilization, this vast pool of high-value data could remain difficult to find or access by potential users or by anyone willing to quantify the raw product of the individual scientific effort (Hampton *et al.* 2013; Heidorn 2008; Nelson & Ellis 2018). For this reason, estimations of the biodiversity shortfalls usually rely on large and publicly open datasets (Conde *et al.* 2019; Cornwell *et al.* 2019; Etard *et al.* 2020; Meyer *et al.* 2015). On one hand, this choice implies that when estimating the biodiversity knowledge available there will be some degree of underestimation due to the fraction of scientific data that may continue hidden or inaccessible (i.e. the dark data; Heidorn 2008), indistinguishable in a practical sense from an unknown information (the unknown knowns *sensu* Hortal *et al.* 2015). On the other hand, quantifying the information that anyone in the community can easily find, access without restrictions, integrate and re-use (following the FAIR Data Principles; Wilkinson *et al.* 2016) reveals the amount of – and the gaps in the – data at the disposal of researchers and policy makers, which is more in accordance with the international targets.

There is a great effort by plant ecologists to collect, measure and make data on functional attributes available. Since 2003, there are protocols for measurement of plant functional traits that gather traits known to be functional in a standardized way (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013), as well as a database of functional traits that concentrate most of the information available in the literature (TRY - Plant trait database, Kattge *et al.* 2011). Yet, estimates show that we do not know any functional traits for 64.5% of the plant species (Cornwell *et al.* 2019). For most animal groups, the main limitations that prevent us from determining the dimension of the Raunkiaeran shortfall are the lack of definition about the most relevant set of traits and a unified database where trait data can be aggregated and shared (Brousseau *et al.* 2018; Schneider *et al.* 2019, but see recent initiatives in Gallagher *et al.* 2020; Kissling *et al.* 2018; Moretti *et al.* 2017; Oliveira *et al.* 2017; Parr *et al.* 2016). Five categories of species traits have been suggested recently as essential biological variables for detecting and reporting biodiversity changes (morphology, movement, phenology, physiology, and reproduction; Kissling *et al.* 2018), but a narrower definition about which traits should be assessed for each biological group still does not exist. Consequently, estimates of gaps in trait availability are mainly restricted to a region (Tiler *et al.* 2012) and/or to a specific trait (Freitas *et al.* 2020). The broadest gap estimation until the moment was with a subset of traits that are transversal to terrestrial tetrapods (Etard *et al.* 2020). This study revealed an average trait completeness higher than 84% for birds and mammals species, but lower than 50% for amphibians and reptiles. A similar taxonomic bias have also been observed in tetrapods by population ecologists regarding public availability of demographic information (Conde *et al.* 2019). Although transversal traits are highly important to conduct studies combining different taxa, they may not necessarily represent the most ecologically relevant traits for specific groups, i.e. those that ecologists actually use to evaluate functional changes. Therefore, the amount of information about relevant species traits that is freely available to scientists and practitioners still remains unknown for most, if not all, animal clades.

Here, we provide, as a case study, an overview of the Raunkiaeran shortfall for birds considering only datasets published as data papers or deposited in public data repositories. Birds are among the most well-studied organisms and, therefore, the large set of existing data for this group may indicate an upper bound of the knowledge available for other animal clades. To achieve this goal, we first revised the literature to identify the most used traits in studies of bird functional ecology. By doing so, we assumed that the most used traits are also the most relevant ones to test ecological hypotheses. Then, we searched for digital accessible information about each identified trait in public datasets. After compiling the information freely available, we estimated the proportion of species for which trait data are available (trait coverage Etard *et al.* 2020). Finally, we mapped the lack of trait data using worldwide species distribution range maps to identify regions where this knowledge is more scarce and to investigate the underlying causes of such geographic bias. Specifically, we evaluated the influence of different socio-environmental variables on trait knowledge gaps based on the hypotheses that information coverage should increase in regions with relatively few species, regions composed by widely distributed species, regions with higher potential for funding scientific activities, and easily accessible regions close to major cities (Meyer *et al.* 2015).

Methods

Defining literature traits

To identify the most used bird traits in functional diversity studies, we first searched in Web of Science for trait-based articles published over the last 20 years (1999-12/12/2019). We searched for articles containing the words “functional diversity” AND (aves OR avian OR bird*) in the title, abstract, or keywords, and selected only those in the ecology subarea. The search was carried out in this way with the aim of restricting the terms found to those used in studies focusing on functional diversity. The literature search yielded 235 articles, of which 87 were disregarded as they were not dealing with birds or were outside of the search scope (n = 148; see a detailed list in Appendix A). After screening, we identified 55 different traits used in functional diversity studies with birds, from which only 14 were frequently used (≥ 10% of the studies): diet (78%), body mass (76%), foraging strategy (66%), nesting strategy (30%), migratory status (28%), clutch size (25%), wing length (24%), bill length (23%), habitat preference (18%), tarsus length (16%), bill width (14%), activity period (13%), tail length (12%), and Kipp’s distance (10%). Foraging strategy was commonly used to describe the location and/or the method used by the species to obtain their food, representing two different traits (López-Ordoñez *et al.* 2015). Therefore, we converted foraging strategy into foraging stratum and foraging mode (see Appendix B for the standardized list of traits terms and definitions). We also eliminated habitat preference because the definition of habitat varied widely in the literature, depending totally on the objective of the study. Researchers obtained data for these traits from 325 different data sources, composed mainly by books (64% of the studies), articles (51%), web sites (32%), museums (14%), unpublished data (5%), and field collected data (3%). Data from mobile applications, other online resources, private collections, and dissertations accounted for less than 1%. Overall, 94% of the studies used secondary data sources and only 18% collected primary data (9% did not inform the origin of some or all the used traits).

Searching for trait data

To assess the availability of the 14 traits investigated here we first searched for data papers on bird traits. We searched for (“functional diversity” OR traits) AND (avian OR bird*) in Web of Science, selecting only data papers. We also screened journals that publish biodiversity-related data papers using the same search terms (see https://www.gbif.org/en/data-papers). We found 13 datasets that compile species traits for birds. Datasets presented from 2 to 9 (6 ± 2) of the selected traits, with an average information coverage of 92.12% (± 7.50%). The geographic coverage of the datasets varied from regional to global scale, ranging from 95 to 9844 species (Table S1). Overall, they totaled 28,807 records for 10,274 of the 10,949 species evaluated here. We also searched for trait data in the public repositories Dryad, Zenodo, Figshare, Pangea and Senckenberg (search in January 2020), as well as in the supplemental material of the 148 articles investigated from Web of Science. This additional search resulted in a total of 324 datasets with 68,338 records for 10,226 species.

Because our initial goal of estimating knowledge gaps considering only datasets published as data papers or in data repositories may be too restrictive, we also accounted for the contribution of two large and available datasets in independent analyses: Pigot *et al.* (2020) and the Handbook of Birds of the World (del Hoyo *et al.* 1992-2011). The first one assemble data on all the seven morphological traits considered in our analyses for 9,810 bird species (90% of our species after synonyms verification), while the second one provides description of body mass, clutch size, diet, forage mode, forage stratum, migratory status and nesting strategy for all species over the world. Regarding the Handbook, some species may still have a few traits undescribed. Therefore, the results of this exercise should be seen as an overestimated extrapolation.

We standardized all scientific names to the species level following the nomenclature accepted by Handbook of the Birds of the World & BirdLife International (2019) taxonomic checklist. For this purpose, we developed an algorithm to search for synonyms of unaccepted names in The World Bird Database (Avibase; Lepage *et al.* 2014), and used the R packages '*taxize'* (Chamberlain & Szocs 2020) and '*rredlist*' (Chamberlain 2020) to verify ambiguous names not corrected by our algorithm. Then we removed all names considered invalid, names of hybrid species and species already extinct (including those extinct in the wild and potentially extinct). After nomenclature correction, our merged dataset totaled information on 10,328 species of the 10,949 species with mapped range on BirdLife International & Handbook of the Birds of the World (2019) (94%; see details below).

Estimating the Raunkiaerian shortfall

To evaluate the extent of the Raunkiaerian shortfall, we first calculate the trait coverage, i.e. percentage of species for which trait information is available. Then, we used the species range available in BirdLife (BirdLife International & Handbook of the Birds of the World, 2019) to map this knowledge estimation by substituting the presence information of each species by its respective trait coverage and calculating the average coverage of each cell. For this purpose, we converted the range maps into a presence-absence matrix using a global grid of 1° resolution. We selected only ranges were the species are native, extant, resident throughout the year or during the breeding season. From a total of 11,145 species with range available on BirdLife, our map end up with 10,949 species, which represents the total number of species in all subsequent analyses presented here. We did not include non-breeding ranges to avoid overestimating the trait coverage of regions that receive temporary species coming for well-studied regions, though the inclusion of these range does not alter our main results (see Fig. S1). It is also noteworthy that selecting or not non-breeding ranges produces a similar total number of mapped species, with the exception of two birds that have their known distribution reduced to non-breeding ranges (*Acrocephalus sorghophilus* and *Leucocarbo carunculatus*). The whole procedure was conducted in the software R (R, Core Team 2019) using the packages '*raster*' (Hijmans 2019), '*rgdal*' (Bivand *et al.* 2019) and '*letsR*' (Vilela & Villalobos 2015).

Statistical analyses

We analyzed the relationship of four biologic, geographic and economic factors with trait coverage. We considered as biologic variables (i) the number of species and (ii) the average range size of the species in a cell, used here as a measure of endemism. The range size of a species was defined as its number of occupied cells in the world grid map. (iii) As geographic variable we used the on-ground accessibility, included here as the time required to travel to the nearest urban center (population > 50,000; Weiss *et al.* 2018). This variable also includes topographic features, such as slope angle and elevation. (iv) Finally, we used regional GDP per capita, an economic variable, as a proxy of research investment. Data referent to 2015 was obtained from a gridded global dataset at one-twelfth-degree resolution and averaged within 1° cells (Kummu *et al.* 2018).

To investigate the effects of the predictor variables on the Raunkiaerian shortfall we conducted a multiple regression analysis (n = 15,492 cells). However, we removed species diversity from the model due to its collinearity with average range size. All predictor variables were transformed by $\log_{(x+1)}$ before analysis to meet the normality assumption. Because we detected spatial autocorrelation in the model's residuals (Moran's $I = 0.17$, p-value < 0.01), we incorporated spatial predictors into our model using the principal coordinates of neighbor matrices (PCNM) approach (Borcard & Legendre 2002; Dray *et al.* 2006). To overcome the challenge of conducting the PCNM for such large dataset, we used the method proposed by Paula-Souza & Diniz-Filho (2020), which consists in to randomly sample the matrix thousands of times and evaluate the statistical distribution of parameters to be estimated. We tested the regression with different sample sizes, from 50 to 2000 grid cells, in order to find the smallest sample size that represents the coverage traits pattern. In our study case, the distribution of the parameters remained relatively stable after 1000 grid cells (Fig. S2; similar to Paula-Souza & Diniz-Filho, 2020). Finally, we calculated the variance partition component to estimate the relative contribution of each predictor variable using the package '*vegan*' (Oksanen *et al.* 2020).

Results

Based on a search conducted in January 2020, we found a moderate but variable knowledge deficit in bird traits, with information about only 62 ± 27% (mean ± standard deviation) of the 14 traits explored in the 10,949 bird species investigated here. Surprisingly, we found more information for traits related to life history (70% ± 25%) than morphology (54% ± 35%). Most complete traits, i.e. with information available for more than 90% of the species, were migratory status, body mass and period of activity, while Kipp's distance, foraging mode and bill width had the lowest information coverage (Table 1). A large amount of the data available was already present in a few data papers (46%), with additional resources found on data repositories and some supplementary materials accounting for 16% of new information – only two datasets accounted for 6% and the ten most important datasets accounted for 12% of new information. These additional data contributed with information mostly related to migratory status (increment of 79%), nesting strategy (26%) and foraging mode (20%; Table 1). An analysis of the frequency that unique species-trait combinations are available revealed that 26% of the combinations appeared only once in our data search, while 36% of the combinations presented some level of redundancy, i.e. appeared in more than one data source (Fig. 1). Traits with redundant information were mainly body mass (85% of the species), migratory status (72%) and diet (64%; Fig. 1). These are the same traits with higher coverage, indicating that the redundancy of information tends to increase for more complete traits ($r = 0.76$).

Despite our focus on public information, we also calculated trait coverage after virtually including records from two large data sources currently available, but that did not meet our initial inclusion criteria, in order to better estimate the scientific knowledge accumulated so far (del Hoyo *et al.* 1992-2011; Pigot *et al.* 2020; see details in the Methods). According to our results, this addition greatly improves coverage estimate, reaching to an impressive value of 95% ± 14%. Remaining gaps would still occur for nearly 10% of the species, especially in morphological traits (Table 1).

Table 1. Summary description of all the 14 bird traits investigated in our study showing their classification by trait type (LH: life history; M: morphological) and their estimated coverage based only on the 13 data papers currently available for birds traits, based on a robust search in public data repositories, the total completeness based on these digital accessible information, and the total completeness estimated after accounting for information from relatively restricted data sources. We also estimated the average and the maximum number of times that each trait was found for the same species in the public datasets (considering only those species for which the trait was found more than once). Estimates for additional traits are available in Table S2.

Trait	**Type**	**Coverage**				**Redundancy**	
		Data papers	**Repositories**	**Total (DAI)**	**Total (estimated)**	**Mean**	**Max**
Activity period	LH	89.86	15.40	90.04	90.04	2.76	9
Bill length	M	46.75	35.07	58.88	91.05	3.01	12
Bill width	M	23.61	32.66	38.28	90.53	2.87	13
Body mass	M	88.36	79.62	91.88	100	6.72	61
Clutch size	LH	61.25	61.23	70.99	100	4.06	36
Diet	LH	72.15	69.42	85.63	100	4.17	37
Foraging mode	LH	3.44	19.86	23.14	100	3.12	13
Foraging	LH	87.57	31.10	88.2	100	2.95	20
Kipp’s distance	M	5.43	11.43	14.79	89.89	2.44	5
Migratory	LH	14.49	92.96	93.05	100	3.84	30
Nesting	LH	14.07	36.46	39.68	100	3.78	22
Tail length	M	44.35	31.86	53.89	90.98	2.82	15
Tarsus length	M	45.91	35.88	58.63	91.02	2.93	17
Wing length	M	48.41	37.39	60.76	91.06	3.05	17

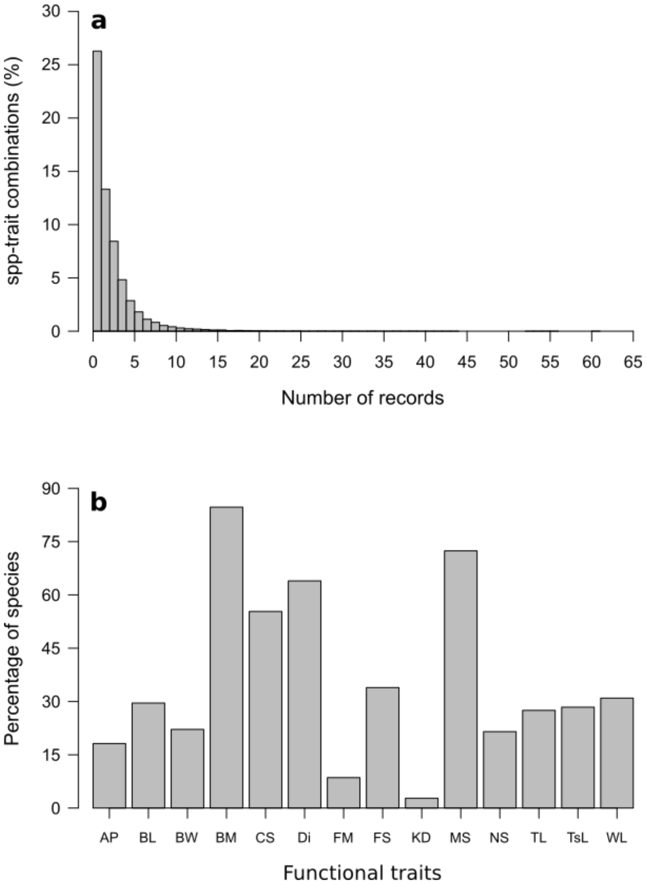

Fig. 1. Redundancy of information in bird traits available in the literature. (a) Histogram showing the frequency that information for unique species-trait combination appears in different datasets. (b) Percentage of species with information appearing more than once for each trait. AP: Activity period; BL: Bill length; BW: Bill width, BM: Body mass; CS: Clutch size; Di: Diet; FM: Foraging mode; FS: Foraging stratum; KD: Kipp's distance; MS: Migratory status; NS: Nesting strategy; TL: Tail length; TsL: Tarsus length; WL: Wing length.

The amount of trait information available for birds was also highly variable through the space. On average, trait coverage was higher for species in the northern hemisphere, with the highest values in Europe, extending to West Asia, and east of North America. Conversely, the Neotropic (especially Amazon and Andes), Afrotropic and Indo-Malaya regions exhibited lower coverage values, with the lowest estimates in Southeast Asia (Fig. 2; see Fig. S3 for the spatial distribution of the coverage estimation for each trait). Coverage was also strongly reduced for seabirds compared to continental birds, with the lowest values in the Pacific east coast, Sargasso Sea, Bay of Bengal and in the Sea of Japan (Fig. S1). Despite the different estimates of life history and morphological traits, we found a very similar geographical pattern between both trait categories, either considering the entire domain (r = 0.87 and r = 0.97, respectively; Fig. S4) or only the continental realm (r = 0.90; Fig. 2). Species without any trait information (n = 625) were more common in the tropics, especially in the Amazon rain forest and in the Andes (Fig. 3a). Together with the Southeast Asia, these are also the regions where probably are the poorest known species in terms of functional traits, i.e. species with information still incomplete even after considering the inclusion of other large additional data sources (Fig. 3b).

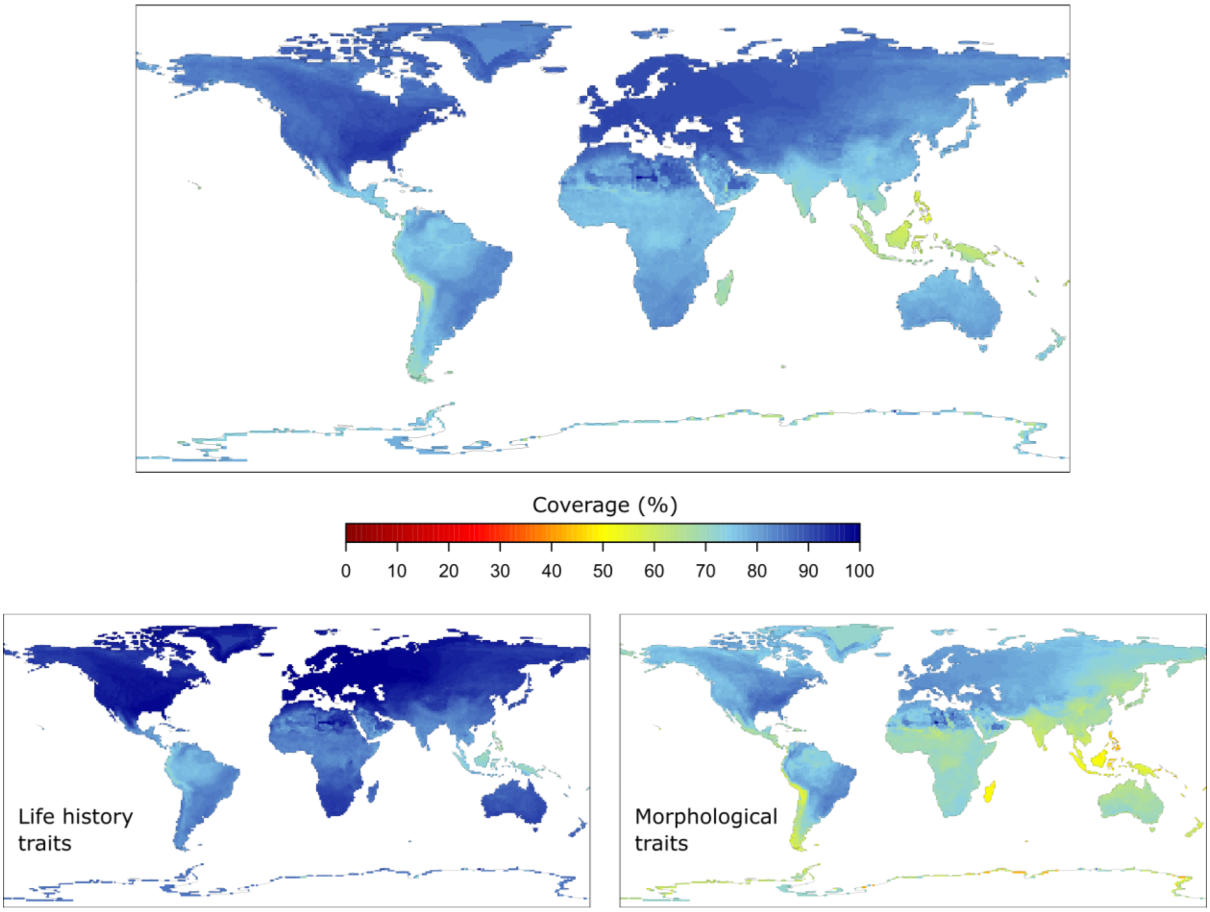

Fig. 2. Spatial variation of average trait coverage in birds considering all the 14 bird traits evaluated in our study (top), only life history traits (bottom-left), and only morphological traits (bottom-right).

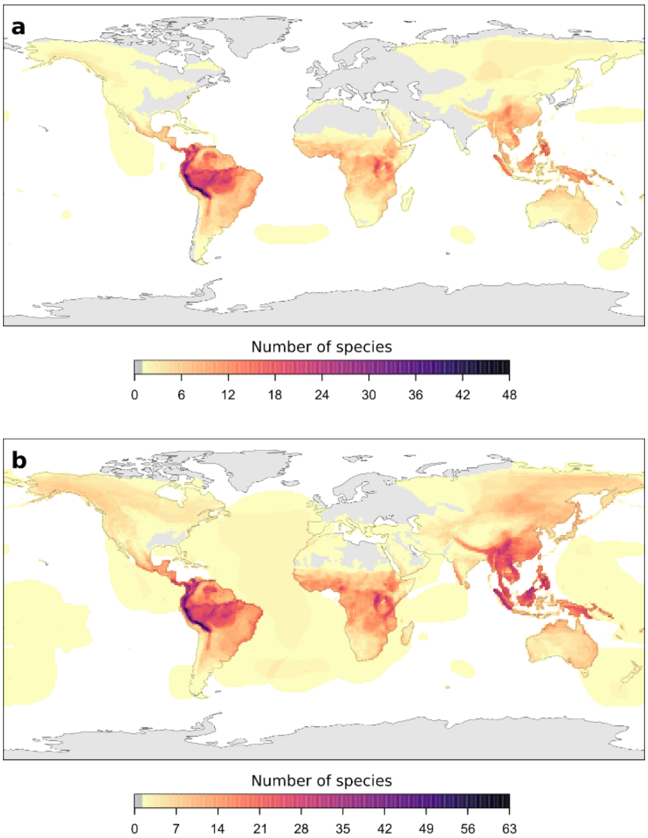

Fig. 3. Global distribution of the species of birds for which digital information about all the 14 traits investigated in our study remain unknown or inaccessible (a), and the species for which at least one trait information would still be missing after accounting for data of Pigot *et al.* (2020) and the Handbook of Birds of the World (del Hoyo *et al.* 1992-2011) (b).

To understand what could explain the spatial variation in trait coverage, we used a multiple regression analysis to identify its main geographic and economic drivers. Our initial predictors were species diversity, average range size of the species, regional Gross Domestic Product (GPD) per capita and on-ground accessibility. However, we excluded species diversity because of its collinearity with average range size. Our results showed that the predictors explained 54% of the spatial variation in trait coverage, and that this pattern is highly structured in geographic space. Pure spatial fraction still accounted for additional 32% of the total explained variation (see Fig. S2c). Average range size was the most important predictor variable, accounting alone for 30% of the explained fraction (Fig. S2d). GDP per capita was the second most important predictor, and similar to the average range size, it was positively associated with trait coverage. Distance to major cities, as expected, was negatively associated with trait coverage, but accounted for only 8% of the total variation. It is noteworthy that distance to major cities did not exhibit any relationship with traits coverage when analyzed individually ($R^2 < 0.001$), contributing only to the full model. The increase in coverage after including information from other large additional data sources reduces its spatial variability and, consequently, the explanatory power of socio-environmental predictors ($R^2 = 0.16$). But since the regions and species with most gaps remain practically the same, average range size continued as the main predictor of information gaps (Fig. S5).

Discussion

In our evaluation of the Raunkiaeran shortfall we found that birds have, overall, a high information coverage. However, contrary to previous estimates (Etard *et al.* 2020), the public data about bird traits accounts for only 62% of the expected information. More importantly, we show here that this knowledge deficit is not equally distributed through the globe, species and even between trait categories. Despite the increasing interest in functional ecology (Freitas & Mantovani 2018), as far as we know only few studies have ventured to assess the extent of the Raunkiaeran shortfall (Tiler *et al.* 2012; Cornwell *et al.* 2019; Etard *et al.* 2020; Freitas *et al.* 2020). Such studies represent important advances in the field, but they are still limited in terms of geographic extent or number of traits analyzed. In line with the guiding steps for achieving international targets on biodiversity knowledge, our approach contributes to the identification of important data voids across different regions, species, and key functional traits.

All 14 traits investigated here were classified as morphological, those that are measured directly on the body of the organism, and as life history, when they are defined by observing the characteristics of organisms in the field over time. Considering that morphological traits may be obtained from preserved museum specimens while the record of life history traits demands *in situ* observation and monitoring effort, one would expect a higher information completeness for morphological traits. Curiously, our results revealed the opposite. Information for life history traits were more complete in both data papers and data repositories (Table 1). We suspect that this pattern arise due to the historical compilation of such traits by large-scale guidebooks through the last decades, subsequently available in a machine readable format for a large number of species as published datasets (e.g. Wilman *et al.* 2014). Guidebooks and data papers providing different morphological traits also exist, but they are commonly restricted to specific continents (Hockey *et al.* 2005), biogeographic regions (Cramp *et al.* 1977-1994), countries (Montoya *et al*. 2018) or biomes (Rodrigues *et al*. 2019). In support of this hypothesis, an analysis of the sources used in the functional diversity studies revised here showed that, on average, 93% of the studies that used life history traits gathered data from secondary sources and only 3% collected the data (Table S3). Most of these data were retrieved exactly from a few guidebooks and large data papers (Table S4). Conversely, an average of only 40% of the studies that used morphological traits gathered data from secondary sources, while 58% collected primary data. This fraction is even higher for traits not commonly present in guidebooks such as Kipp’s distance and bill width, and lowest for body mass, commonly present in secondary data sources (Table S3). Assembling a large dataset of morphological traits from preserved specimens worldwide is a challenging but not impossible task (Pigot *et al.* 2020), important to increase findability and accessibility of birds data. Fortunately, the necessity for such information is stimulating the collection and sharing of morphological traits in these last years (Table S1), reducing the knowledge gaps in the freely accessible information.

One of the most important outcomes of our analyses was how the global unevenness in publicly accessible trait information may affect ecological investigations in the biodiversity richest regions of the world. Similar to previous studies (González-Suárez *et al.* 2012; Etard *et al.* 2020), mapping the average information of trait coverage revealed a clear spatial pattern with higher knowledge level in the northern hemisphere and relatively less information about species in tropical regions. Even after expanding the analysis to include records from Pigot *et al.* (2020) and the Handbook of Birds of the World (del Hoyo *et al.* 1992-2011), the tropics were the regions still presenting the remaining data gaps. Among the variables evaluated to explain this variation in traits coverage, the average range size of the species was the most important one, accounting for nearly 48% of the total explained variation. This result is not surprising as research effort in birds is strongly related to the range size of the species (Ducatez & Lefebvre 2014). Species with wide distribution can be studied by different research groups and, consequently, will integrate different datasets sharing traits description. Considering that each dataset may focus on specific sets of traits, these species will have most of their traits measured and shared somewhere. In the data papers investigated here, for example, we observe that even datasets compiled for a specific territory such as Japan (Takagawa *et al.* 2011) are composed by many species occurring all over Eurasia, and even species from other regions all over the world (Fig. S6). Therefore, regions that accumulate widely distributed species such as the high latitudes in the northern hemisphere will necessarily be more complete, especially if they have relatively reduced species richness. The second most important variable was GDP per capita, which accounted for 30% of the explained variation in traits completeness. It is not new that research funding is directly correlated to the level of knowledge in biodiversity, especially for birds (Meyer *et al.* 2015; Titley *et al.* 2017). Consequently, biodiversity research is commonly carried out by institutions of developed countries, particularly in western Europe (Titley *et al.* 2017). Developing countries, on the other hand, have relatively fewer resources to invest in research, which limits local scientific activities and local data availability exactly in those regions of elevated biodiversity and number of endemic species since most of they are located in the tropics (Orme *et al.* 2005). Such poor data availability for small-ranged species in regions of high diversity is not a phenomenon restricted to birds or traits **(**González-Suárez *et al.* 2012; Etard *et al.* 2020; Moura & Jetz 2020), but probably a general tendency in biodiversity knowledge limitation that may guide future endeavors in data collection and mobilization. Finally, on-ground accessibility from cities exhibited only a modest contribution. Its relatively low importance makes sense given that traits may be collected at any place across the species range, independent of the distance to major urban centers. However, it is interesting to note that the contribution of accessibility increases in the model including average range size and GDP per capita, suggesting that distance to major cities may still constrain field collections and data availability once other important variables are held constant. This importance could probably be higher than estimated here if only the distance to the research institutions were considered (Meyer *et al.* 2015).

It is noteworthy that we only quantified here the presence of information about each trait. We did not evaluate qualitatively how much the traits are comparable among datasets (i.e. due to differences in how morphological traits are measured and categorical traits are defined), which certainly may reduce or even inhibit the aggregation of different data sources in studies encompassing large scales (Kissling *et al.* 2018). This problem becomes more evident when we observe the low frequency with which records for most species-trait combinations appear in the data compilation, indicating that alternatives to how some traits are measured or categorized may probably not be available for a large number of species and many different traits. Protocols are important exactly to reduce this information incompatibility (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013; Moretti *et al.* 2017; Dawson *et al.* 2019). Aggregating trait data from multiple sources requires not only comprehensive definitions of measurement protocols but also standardized lists of trait terms or controlled vocabularies (Kissling *et al.* 2018). However, such comprehensive definitions are still missing or remain little-known even for birds (López-Ordoñez *et al.* 2015). We also would like to emphasize that there is no definitive list or ranking of which traits must be used in functional ecology, even because the choice of traits should depend on the research question (Brousseau *et al.* 2018), but our approach allowed us to identify those traits considered most relevant by the peers. Accordingly, all morphological traits identified here are recognized as those well-connected to important niche structures of ecological bird communities (Pigot *et al.* 2020). To investigate how the inclusion of other important traits would impact our results, we included into our data search the set of traits proposed in a regional bird survey protocol (López-Ordoñez *et al.* 2015). As would be expected, increasing the number of traits reduces the overall completeness estimate (47% ± 23%; Table S2) but, on the other hand, it does not change our spatial result (r = 0.94; Fig. S1), indicating a consistently poor trait availability for regions of reduced information coverage.

In conclusion, our results reveal important limitations in the public information of key traits for birds. The prevalence of gaps for small-ranged species from tropical regions in these well-studied groups (González-Suárez *et al.* 2012; Ducatez & Lefebvre 2014;_Etard *et al.* 2020), even after including information from other large data sources available highlights the need for major efforts to acquire and compile traits for other taxa that commonly receive less attention in the literature. Reducing the Raunkiaeran shortfall will demand great effort and cooperation of the scientific community both in collecting primary information and by sharing existing datasets following the FAIR principles of scientific data management (Findability, Accessibility, Interoperability, and Reusability; Wilkinson *et al.* 2016). Such effective data mobilization is of central importance, especially in the current scenario, where traits are essential to understand ecological patterns and processes in different fields of ecology (Freitas & Mantovani 2018), including our ability to manage and conserve species in the face of climate change.

References

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Bastos, R.P. & Pinto, M.P. (2006). Challenging Wallacean and Linnean shortfalls: Knowledge gradients and conservation planning in a biodiversity hotspot. *Divers. Distrib.*, 12, 475–482.

BirdLife International & Handbook of the Birds of the World (2019) Bird species distribution maps of the world. Version 2019.1. Available at http://datazone.birdlife.org/species/requestdis.

Bivand, R., Keitt, T. & Rowlingson, B. (2019). rgdal: Bindings for the "Geospatial" Data Abstraction Library. R package version 1.4-8. https://CRAN.R-project.org/package=rgdal.

Borcard, D. & Legendre, P. (2002) All-scale spatial analyses of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153, 51–68.

Brown, J.H., & Lomolino, M.V. (1998). Biogeography. Second edition. Sunderland, Massachussets: Sinauer Associates, Inc.

Brousseau, P.-M., Gravel, D. & Handa, I.T. (2018). On the development of a predictive functional trait approach for studying terrestrial arthropods. *J. Anim. Ecol.*, 87, 1209–1220.

Chamberlain, S. (2020). rredlist: "IUCN" Red List Client. R package version 0.7.0. https://CRAN.R-project.org/package=rredlist.

Chamberlain, S. & Szocs, E. (2020). taxize - taxonomic search and retrieval in R. package version 0.9.99. https://CRAN.R-project.org/package=taxize

Conde, D.A., Staerk, J., Colchero, F., da Silva, R., Schöley, J., Baden, H.M., *et al.* (2019). Data gaps and opportunities for compara- tive and conservation biology. *PNAS*, 116, 9658–9664.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.*, 51, 335–380.

Cornwell, W.K., Pearse, W.D., Dalrymple, R.L. & Zanne, A.E. (2019). What we (don't) know about global plant diversity. *Ecography*, 42, 1819–1831.

Cramp, S., Brooks, D.J. & Perrins, C.M. (Eds.). (1977-1994). *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic Vol. 1-*

9. Oxford University Press.

Dray, S., Legendre, P. & Peres-Neto, P.R. (2006) Spatial modeling: a comprehensive framework for principal coordinate analyses of neighbor matrices (PCNM). *Ecological Modelling*, 196, 483–493.

Dawson, S.K., Boddy, L., Halbwachs, H., Bässler, C., Andrew, C., Crowther, T.W., *et al.* (2019). Handbook for the measurement of macrofungal functional traits: A start with basidiomycete wood fungi. *Funct. Ecol.*, 33, 372-387.

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. (Eds.). (1992-2011) *Handbook of the Birds of the World Vol. 1–16*. Lynx Edicions.

Ducatez, S. & Lefebvre, L. (2014). Patterns of Research Effort in Birds. *PLoS One*, 9, e89955.

Freitas, J.R., & Mantovani, W. (2018). An overview of the applicability of functional diversity in biological conservation. *Brazilian J. Biol.*, 78, 517–524.

Freitas, T.M.S., Stropp, J., Calegari, B.B., Calatayud, J., De Marco Jr., P., Montag, L.F.A., *et al.* (2020). Quantifying shortfalls in the knowledge on Neotropical Auchenipteridae fishes. *Fish fish., in press.*

Gallagher, R. V., Falster, D.S., Maitner, B.S., Salguero-Gómez, R., Vandvik, V., Pearse, W.D., *et al.* (2020). Open Science principles for accelerating trait-based science across the Tree of Life. *Nat. Ecol. Evol.*, 4, 294–303.

González-Suárez, M., Lucas, P.M. & Revilla, E. (2012). Biases in comparative analyses of extinction risk: mind the gap. *J. Anim. Ecol.*, 81, 1211–1222.

Grömping, U. (2006). Relative importance for linear regression in R: The package relaimpo. *J. Stat. Softw.*, 17, 1–27.

Hampton, S.E., Strasser, C.A., Tewksbury, J.J., Gram, W.K., Budden, A.E., Batcheller, A.L., *et al.* (2013). Big data and the future of ecology. *Front. Ecol. Environ.*, 11, 156–162.

Handbook of the Birds of the World & BirdLife International (2019). Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 4.

Heidorn, P.B. (2008). Shedding Light on the Dark Data in the Long Tail of Science. *Libr. Trends*, 57, 280–299.

Hijmans, R.J. (2019). raster: Geographic Data Analysis and Modeling. R package version 3.0-7. https://CRAN.R-project.org/package=raster.

Hockey, P.A., Dean, W.R.J. & Ryan, P.G. (2005). *Roberts birds of southern Africa*. VII. Jacana Publishers.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 46, 523–549.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., *et al.* (2011). TRY - a global database of plant traits. *Glob. Chang. Biol.*, 17, 2905–2935.

Kissling, W.D., Walls, R., Bowser, A., Jones, M.O., Kattge, J., Agosti, D., *et al.* (2018). Towards global data products of essential biodiversity variables on species traits. *Nat. Ecol. Evol.*, 2, 1531-1540.

Kummu, M., Taka, M. & Guillaume, J.H.A. (2018). Gridded global datasets for Gross Domestic Product and Human Development Index over 1990-2015. *Sci. Data*, 5, 180004.

Lepage, D., Vaidya, G. & Guralnick, R. (2014). Avibase - A database system for managing and organizing taxonomic concepts. *Zookeys*, 420, 117–135.

Lomolino, M.V. (2004). Conservation Biogeography. In: *Frontiers of Biogeography: New directions in the geography of nature* (ed. M.V. Lomolino & L.R. Heaney). Sunderland, Massachussets: Sinauer Associates, Inc., pp. 293-296.

López-Ordoñez, J.P., Stiles, G. & Parra-Vergara, J.L. (2015). Protocolo para la medición de rasgos funcionales en aves. In: *La Ecología funcional como aproximación al estudio, manejo y conservación de la biodiversidad: protocolos y aplicaciones* (ed. Salgado-Negret, B.). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, pp. 80–125.

Menegotto, A. & Rangel, T.F. (2018). Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nat. Commun.*, 9, 4713.

Meyer, C., Kreft, H., Guralnick, R. & Jetz, W. (2015). Global priorities for an effective information basis of biodiversity distributions. *Nat. Commun.*, 6, 8221.

Montoya, P.M., González, A., Tenorio, E.A., López-Ordóñez, J.P., Pinto, A., Cueva, D., *et al.* (2018). A morphological database for 606 Colombian bird species. *Ecology*, 99, 1693–1693.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011). How Many Species Are There on Earth and in the Ocean? *PLoS Biol*, 9, e1001127.

Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., *et al.* (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Funct. Ecol.*, 31, 558–567.

Moura, M.R. & Jetz, W. (2020). Shortfalls and opportunities in terrestrial vertebrate species discovery. bioRxiv, doi: 10.1101/2020.10.23.352690.

Nelson, G. & Ellis, S. (2019). The history and impact of digitization and digital data mobilization on biodiversity research. *Philos. Trans. R. Soc. B Biol. Sci.*, 374, 20170391.

Oksanen, J., Blanchet, F.G., Friendly, M., et al. (2020) Vegan: community ecology package. R package version 2.5-7.

Oliveira, B.F., São-Pedro, V.A., Santos-Barrera, G., Penone, C., & Costa, G.C. (2017). AmphiBIO, a global database for amphibian ecological traits. *Scientific Data, 4*, 170123.Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., *et al.* (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436, 1016–1019.

Parr, C.S., Schulz, K.S., Hammock, H., Wilson, N., Leary, P., Rice, *et al.* (2016). TraitBank: practical semantics for organism attribute data. *Semant. Web,* 7, 577–588.

De Paula-Souza, L.B., & Diniz Filho, J.A.F. (2019) Variance partitioning and spatial eigenvector analyses with large macroecological datasets. *Frontiers of Biogeography,* 12, e47295.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., *et al.* (2013). New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.*, 61, 167–234.

Pigot, A.L., Sheard, C., Miller, E.T., Bregman, T., Freeman, B., Roll, U., *et al*. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nat. Ecol. Evol*., 4, 230–239.

R, Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rodrigues, R.C., Hasui, É., Assis, J.C., Pena, J.C.C., Muylaert, R.L., Tonetti, V.R., *et al.* (2019). Atlantic Bird Traits: A dataset of bird morphological traits from the Atlantic Forests of South America. *Ecology*, 100, e02647.

Schneider, F.D., Fichtmuller, D., Gossner, M.M., Güntsch, A., Jochum, M., Konig-Ries, B., *et al.* (2018). Towards an ecological trait-data standard. *Methods Ecol. Evol.*, 10, 2006-2019.Takagawa, S., Ueta, M., Amano, T., Okahisa, Y., Kamioki, M., Amamo, T., *et al.* (2011). JAVIAN Database: a species-level database of life history, ecology and morphology of bird species in Japan. *Bird Res.*, 7, R9–R12.

Titley, M.A., Snaddon, J.L. & Turner, E.C. (2017). Scientific research on animal biodiversity is systematically biased towards vertebrates and temperate regions. *PLoS One,* 12, e0189577.

Vilela, B. & Villalobos, F. (2015). LetsR: A new R package for data handling and analysis in macroecology. *Methods Ecol. Evol.*, 6, 1229–1234.

Weiss, D.J., Nelson, A., Gibson, H.S., Temperley, W., Peedell, S., Lieber, A., *et al.* (2018). A global map of travel time to cities to assess inequalities in accessibility in 2015. *Nature*, 553, 333–336.

Wilkinson, M.D., Dumontier, M., Aalbersberg, I.J.J., Appleton, G., Axton, M., Baak, A., et al. (2016). The FAIR Guiding Principles for scientific data management and stewardship. Scientific Data, 3, 160018.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027–2027.

Conclusão geral

Essa tese contribui para compreender melhor como diferentes metodologias podem afetar a distribuição das espécies e os fatores que estruturam as comunidades. Além disso, ampliamos também o diagnóstico da lacuna Raunkiaeriana para aves e os fatores que a influenciam.

No primeiro capítulo mostramos que o poder preditivo e a acurácia dos modelos de distribuição de espécies são pouco afetados pela adição de preditores bióticos. No entanto, encontramos que a adição de preditores pode influenciar o range estimado das espécies, principalmente daquelas amplamente distribuídas. Nós argumentamos que para o nosso sistema de estudo (i.e. beija-flores como espécies focais e plantas produtoras de néctar como espécies interatoras) a influência dos preditores bióticos representa apenas um ruído no *output* dos modelos de espécies espacialmente restritas, mas que pode gerar uma dissimilaridade espacial considerável em espécies com ampla distribuição devido a um possível efeito estatístico. Portanto, apesar de diversos estudos suportarem a relevância de preditores bióticos para modelar a distribuição das espécies (contrário a hipótese do ruído Eltoniano), o resultado do nosso estudo indica que a força de interação pode não ser suficiente para representar a importância de preditores bióticos, e que algum nível de dependência entre a espécie foco e a interatora pode ser necessário para afetar a distribuição das espécies em grandes escalas.

No segundo capítulo mostramos que a partição de nicho das espécies de beija-flores em comunidades tidas como sobrepostas de acordo com as redes de interações tróficas podem apresentar partição dos recursos, principalmente a partir de características funcionais mais finas e difíceis de detectar, como por exemplo o comportamento de forrageio. Esse resultado destaca que a partição de nicho pode ocorrer de forma sutil, e a aquisição e disponibilização de dados de história de vida pode ser essencial para melhor compreensão da estruturação das comunidades.

No terceiro capítulo mostramos que, para aves, cerca de 38% dos dados de atributos continuam inacessíveis ou desconhecidos, principalmente para espécies de regiões tropicais e com pequena distribuição geográfica. Nesse estudo utilizamos inicialmente apenas dados irrestritos, mas analisamos também a dimensão da lacuna Raunkiaerana considerando grandes conjuntos de dados que são conhecidos pela ciência mas que continuam com acesso restrito e/ou imobilizados. Encontramos que a disponibilização aberta desses dados geraria uma completude de 95%. Mesmo assim, nosso resultado mostrou que a distribuição das espécies com algum dado desconhecido se mantém nas mesmas condições (i.e. regiões tropicais com predomínio de espécies com limitada distribuição geográfica). A consistência desse resultado e sua similaridade com outros estudos sugere que o mesmo padrão pode ser esperado para outros grupos de animais, mas isso ainda precisa ser avaliado no futuro próximo.

Capítulo 1: Additional Information

Supplementary Material

Table S1. Unique interactions between 100 hummingbirds and 202 plant species.

Hummingbirds	Plants
Adelomyia melanogenys	*Bomarea multiflora*
Adelomyia melanogenys	*Guzmania gracilior*
Adelomyia melanogenys	*Palicourea lineata*
Adelomyia melanogenys	*Tropaeolum deckerianum*
Aglaeactis cupripennis	*Barnadesia spinosa*
Aglaeactis cupripennis	*Monnina salicifolia*
Aglaeactis cupripennis	*Oreocallis grandiflora*
Aglaiocercus coelestis	*Guzmania jaramilloi*
Amazilia beryllina	*Penstemon roseus*
Amazilia beryllina	*Phaseolus coccineus*
Amazilia beryllina	*Salvia iodantha*
Amazilia beryllina	*Salvia mexicana*
Amazilia brevirostris	*Calliandra guildingii*
Amazilia fimbriata	*Bauhinia forficata*
Amazilia fimbriata	*Ceiba speciosa*
Amazilia fimbriata	*Erythrina speciosa*
Amazilia fimbriata	*Esterhazya splendida*
Amazilia fimbriata	*Genipa americana*
Amazilia fimbriata	*Geissomeria schottiana*
Amazilia fimbriata	*Helicteres brevispira*
Amazilia fimbriata	*Hippeastrum stylosum*
Amazilia fimbriata	*Ipomoea hederifolia*
Amazilia fimbriata	*Palicourea crocea*
Amazilia fimbriata	*Psittacanthus cucullaris*
Amazilia fimbriata	*Sinningia douglasii*
Amazilia fimbriata	*Stachytarpheta gesnerioides*
Amazilia lactea	*Abutilon bedfordianum*
Amazilia lactea	*Anisacanthus brasiliensis*
Amazilia lactea	*Erythrina speciosa*
Amazilia lactea	*Palicourea rigida*
Amazilia lactea	*Stachytarpheta glabra*
Amazilia leucogaster	*Heliconia richardiana*
Amazilia rutila	*Combretum farinosum*
Amazilia rutila	*Crusea coccinea*
Amazilia rutila	*Lobelia laxiflora*
Amazilia rutila	*Psittacanthus ramiflorus*
Amazilia rutila	*Salvia iodantha*
Amazilia rutila	*Salvia mexicana*
Amazilia versicolor	*Aechmea cylindrata*

Amazilia versicolor	*Aechmea nudicaulis*
Amazilia versicolor	*Erythrina falcata*
Amazilia versicolor	*Justicia ramulosa*
Amazilia versicolor	*Macrocarpaea rubra*
Amazilia versicolor	*Vriesea altodaserrae*
Amazilia violiceps	*Salvia iodantha*
Amazilia violiceps	*Salvia mexicana*
Anopetia gounellei	*Anisacanthus brasiliensis*
Anopetia gounellei	*Lychnophora salicifolia*
Anthracothorax aurulentus	*Cordia rickseckeri*
Anthracothorax nigricollis	*Citharexylum myrianthum*
Anthracothorax nigricollis	*Erythrina fusca*
Anthracothorax nigricollis	*Handroanthus chrysotrichus*
Anthracothorax nigricollis	*Jacaranda puberula*
Anthracothorax nigricollis	*Norantea guianensis*
Aphantochroa cirrochloris	*Ceiba speciosa*
Aphantochroa cirrochloris	*Ruellia angustiflora*
Aphantochroa cirrochloris	*Vriesea procera*
Atthis heloisa	*Salvia elegans*
Atthis heloisa	*Salvia lavanduloides*
Augastes scutatus	*Stachytarpheta glabra*
Boissonneaua flavescens	*Aetanthus nodosus*
Boissonneaua flavescens	*Palicourea lineata*
Calothorax lucifer	*Bouvardia ternifolia*
Calothorax lucifer	*Castilleja tenuiflora*
Calothorax lucifer	*Fouquieria splendens*
Calothorax lucifer	*Myrtillocactus geometrizans*
Campylopterus largipennis	*Palicourea crocea*
Chalcostigma herrani	*Brachyotum lindenii*
Chlorostilbon lucidus	*Aechmea distichantha*
Chlorostilbon lucidus	*Bauhinia ungulata*
Chlorostilbon lucidus	*Buddleja brasiliensis*
Chlorostilbon lucidus	*Citharexylum myrianthum*
Chlorostilbon lucidus	*Corymborkis flava*
Chlorostilbon lucidus	*Coussarea hydrangeifolia*
Chlorostilbon lucidus	*Fridericia speciosa*
Chlorostilbon lucidus	*Helicteres brevispira*
Chlorostilbon lucidus	*Inga vera*
Chlorostilbon lucidus	*Ipomoea hederifolia*
Chlorostilbon lucidus	*Lychnophora salicifolia*
Chlorostilbon lucidus	*Pyrostegia venusta*
Chlorostilbon lucidus	*Stachytarpheta glabra*
Chlorostilbon lucidus	*Styrax ferrugineus*
Chlorostilbon lucidus	*Vochysia emarginata*
Chlorostilbon lucidus	*Vochysia tucanorum*
Chlorostilbon mellisugus	*Palicourea crocea*

Chlorostilbon notatus	*Bomarea edulis*
Chlorostilbon notatus	*Calliandra guildingii*
Chlorostilbon notatus	*Erythrina fusca*
Chlorostilbon notatus	*Gurania acuminata*
Chrysuronia oenone	*Besleria aggregata*
Chrysuronia oenone	*Combretum llewelynii*
Chrysuronia oenone	*Palicourea crocea*
Clytolaema rubricauda	*Fuchsia regia*
Clytolaema rubricauda	*Inga sessilis*
Clytolaema rubricauda	*Siphocampylus sulfureus*
Clytolaema rubricauda	*Spirotheca rivieri*
Coeligena iris	*Barnadesia arborea*
Coeligena iris	*Fuchsia vulcanica*
Coeligena iris	*Oreocallis grandiflora*
Coeligena lutetiae	*Fuchsia corollata*
Coeligena torquata	*Aetanthus nodosus*
Coeligena torquata	*Bomarea multiflora*
Coeligena torquata	*Psammisia columbiensis*
Coeligena wilsoni	*Aetanthus nodosus*
Coeligena wilsoni	*Mezobromelia capituligera*
Coeligena wilsoni	*Psammisia ulbrichiana*
Colibri coruscans	*Castilleja fissifolia*
Colibri coruscans	*Macleania rupestris*
Colibri coruscans	*Palicourea demissa*
Colibri coruscans	*Salvia corrugata*
Colibri serrirostris	*Helicteres velutina*
Colibri serrirostris	*Inga vera*
Colibri serrirostris	*Lobelia fistulosa*
Colibri serrirostris	*Sinningia elatior*
Colibri serrirostris	*Stachytarpheta gesnerioides*
Colibri serrirostris	*Stachytarpheta glabra*
Colibri serrirostris	*Vochysia cinnamomea*
Colibri serrirostris	*Vochysia tucanorum*
Colibri serrirostris	*Zeyheria montana*
Cynanthus latirostris	*Castilleja toluccensis*
Cynanthus latirostris	*Cylindropuntia imbricata*
Cynanthus latirostris	*Ipomoea wolcottiana*
Doryfera ludovicae	*Cavendishia bracteata*
Doryfera ludovicae	*Guzmania gracilior*
Doryfera ludovicae	*Palicourea acetosoides*
Ensifera ensifera	*Brugmansia sanguinea*
Ensifera ensifera	*Passiflora mixta*
Ensifera ensifera	*Tristerix longebracteatus*
Eriocnemis derbyi	*Barnadesia spinosa*
Eriocnemis luciani	*Barnadesia arborea*
Eriocnemis luciani	*Oreocallis grandiflora*

Eriocnemis mosquera	*Brachyotum lindenii*
Eriocnemis vestita	*Vaccinium floribundum*
Eugenes fulgens	*Bouvardia ternifolia*
Eugenes fulgens	*Calliandra grandiflora*
Eugenes fulgens	*Cirsium ehrenbergii*
Eugenes fulgens	*Fuchsia fulgens*
Eugenes fulgens	*Penstemon gentianoides*
Eugenes fulgens	*Phaseolus coccineus*
Eugenes fulgens	*Salvia mexicana*
Eupetomena macroura	*Anisacanthus brasiliensis*
Eupetomena macroura	*Bauhinia ungulata*
Eupetomena macroura	*Erythrina falcata*
Eupetomena macroura	*Erythrina speciosa*
Eupetomena macroura	*Esterhazya splendida*
Eupetomena macroura	*Handroanthus chrysotrichus*
Eupetomena macroura	*Heliconia psittacorum*
Eupetomena macroura	*Inga vera*
Eupetomena macroura	*Lobelia fistulosa*
Eupetomena macroura	*Lundia cordata*
Eupetomena macroura	*Mandevilla guanabarica*
Eupetomena macroura	*Psittacanthus cordatus*
Eupetomena macroura	*Stachytarpheta glabra*
Eupetomena macroura	*Vochysia tucanorum*
Eupetomena macroura	*Vriesea procera*
Eupetomena macroura	*Zeyheria montana*
Eupherusa nigriventris	*Psychotria elata*
Eutoxeres aquila	*Centropogon granulosus*
Florisuga fusca	*Aechmea nudicaulis*
Florisuga fusca	*Aechmea pectinata*
Florisuga fusca	*Ceiba speciosa*
Florisuga fusca	*Erythrina speciosa*
Florisuga fusca	*Inga sessilis*
Florisuga fusca	*Schwartzia brasiliensis*
Florisuga fusca	*Pavonia viscosa*
Florisuga mellivora	*Erythrina fusca*
Florisuga mellivora	*Isertia hypoleuca*
Florisuga mellivora	*Norantea guianensis*
Florisuga mellivora	*Palicourea demissa*
Florisuga mellivora	*Warszewiczia coccinea*
Glaucis dohrnii	*Centropogon cornutus*
Glaucis hirsutus	*Besleria aggregata*
Glaucis hirsutus	*Centropogon cornutus*
Glaucis hirsutus	*Heliconia bihai*
Glaucis hirsutus	*Heliconia richardiana*
Glaucis hirsutus	*Palicourea crocea*
Haplophaedia aureliae	*Elleanthus aurantiacus*

Haplophaedia lugens	*Drymonia tenuis*
Heliactin bilophus	*Lychnophora salicifolia*
Heliactin bilophus	*Sacoila lanceolata*
Heliangelus exortis	*Aetanthus nodosus*
Heliangelus exortis	*Guzmania gracilior*
Heliangelus mavors	*Vaccinium floribundum*
Heliangelus mavors	*Vallea stipularis*
Heliangelus strophianus	*Palicourea lineata*
Heliangelus viola	*Gaultheria tomentosa*
Heliangelus viola	*Oreocallis grandiflora*
Heliangelus viola	*Salvia corrugata*
Heliodoxa imperatrix	*Guzmania jaramilloi*
Heliodoxa imperatrix	*Tropaeolum deckerianum*
Heliodoxa jacula	*Centropogon solanifolius*
Heliodoxa jacula	*Heliconia lankesteri*
Heliodoxa jacula	*Pitcairnia brittoniana*
Heliomaster constantii	*Ceiba aesculifolia*
Heliomaster squamosus	*Costus spiralis*
Heliomaster squamosus	*Erythrina speciosa*
Heliomaster squamosus	*Tacinga palmadora*
Heliomaster squamosus	*Qualea parviflora*
Hylocharis chrysura	*Aechmea distichantha*
Hylocharis chrysura	*Handroanthus chrysotrichus*
Hylocharis chrysura	*Inga vera*
Hylocharis chrysura	*Lepidagathis floribunda*
Hylocharis chrysura	*Luehea divaricata*
Klais guimeti	*Hamelia patens*
Lafresnaya lafresnayi	*Barnadesia spinosa*
Lafresnaya lafresnayi	*Macleania rupestris*
Lafresnaya lafresnayi	*Tristerix longebracteatus*
Lampornis amethystinus	*Phaseolus coccineus*
Lampornis amethystinus	*Salvia elegans*
Lampornis clemenciae	*Bouvardia ternifolia*
Lampornis clemenciae	*Castilleja toluccensis*
Lampornis clemenciae	*Cirsium nivale*
Lampornis clemenciae	*Penstemon gentianoides*
Lampornis clemenciae	*Penstemon roseus*
Lampornis clemenciae	*Salvia mexicana*
Lampornis hemileucus	*Psychotria elata*
Leucochloris albicollis	*Erythrina speciosa*
Leucochloris albicollis	*Fuchsia regia*
Leucochloris albicollis	*Handroanthus chrysotrichus*
Leucochloris albicollis	*Inga sessilis*
Leucochloris albicollis	*Mutisia speciosa*
Leucochloris albicollis	*Pyrostegia venusta*
Leucochloris albicollis	*Siphocampylus sulfureus*

Lophornis chalybeus	*Aechmea nudicaulis*
Lophornis chalybeus	*Erythrina speciosa*
Lophornis chalybeus	*Inga luschnathiana*
Lophornis chalybeus	*Spirotheca rivieri*
Lophornis magnificus	*Helicteres brevispira*
Lophornis magnificus	*Qualea multiflora*
Lophornis magnificus	*Styrax pohlii*
Lophornis magnificus	*Vochysia tucanorum*
Metallura baroni	*Saracha quitensis*
Metallura tyrianthina	*Aetanthus nodosus*
Metallura tyrianthina	*Berberis lutea*
Metallura tyrianthina	*Disterigma codonanthum*
Metallura tyrianthina	*Echeveria bicolor*
Metallura tyrianthina	*Elleanthus aurantiacus*
Metallura tyrianthina	*Gaiadendron punctatum*
Metallura tyrianthina	*Gaultheria erecta*
Metallura tyrianthina	*Gaultheria tomentosa*
Metallura tyrianthina	*Salvia corrugata*
Metallura tyrianthina	*Viola arguta*
Oxypogon lindenii	*Castilleja fissifolia*
Panterpe insignis	*Cavendishia bracteata*
Panterpe insignis	*Macleania rupestris*
Phaethornis bourcieri	*Aphelandra macrostachya*
Phaethornis bourcieri	*Besleria aggregata*
Phaethornis bourcieri	*Gurania rhizantha*
Phaethornis bourcieri	*Monotagma secundum*
Phaethornis eurynome	*Aechmea distichantha*
Phaethornis eurynome	*Aegiphila obducta*
Phaethornis eurynome	*Alstroemeria inodora*
Phaethornis eurynome	*Camptosema scarlatinum*
Phaethornis eurynome	*Canistrum cyathiforme*
Phaethornis eurynome	*Collaea speciosa*
Phaethornis eurynome	*Erythrina speciosa*
Phaethornis eurynome	*Hippeastrum puniceum*
Phaethornis eurynome	*Justicia brasiliana*
Phaethornis eurynome	*Justicia carnea*
Phaethornis eurynome	*Lobelia fistulosa*
Phaethornis eurynome	*Mutisia speciosa*
Phaethornis eurynome	*Nidularium marigoi*
Phaethornis eurynome	*Sinningia cooperi*
Phaethornis eurynome	*Sinningia douglasii*
Phaethornis eurynome	*Siphocampylus westinianus*
Phaethornis guy	*Cavendishia bracteata*
Phaethornis guy	*Heliconia atropurpurea*
Phaethornis guy	*Heliconia bihai*
Phaethornis hispidus	*Aechmea contracta*

Phaethornis hispidus	*Besleria aggregata*
Phaethornis hispidus	*Costus scaber*
Phaethornis hispidus	*Palicourea crocea*
Phaethornis idaliae	*Aechmea nudicaulis*
Phaethornis idaliae	*Quesnelia quesneliana*
Phaethornis idaliae	*Tillandsia gardneri*
Phaethornis longirostris	*Renealmia cernua*
Phaethornis longuemareus	*Palicourea crocea*
Phaethornis malaris	*Isertia hypoleuca*
Phaethornis pretrei	*Aechmea distichantha*
Phaethornis pretrei	*Ananas ananassoides*
Phaethornis pretrei	*Geissomeria schottiana*
Phaethornis pretrei	*Centropogon cornutus*
Phaethornis pretrei	*Dicliptera squarrosa*
Phaethornis pretrei	*Geissomeria longiflora*
Phaethornis pretrei	*Heliconia psittacorum*
Phaethornis pretrei	*Helicteres velutina*
Phaethornis pretrei	*Hololepis pedunculata*
Phaethornis pretrei	*Ipomoea hederifolia*
Phaethornis pretrei	*Lepidagathis floribunda*
Phaethornis pretrei	*Lobelia fistulosa*
Phaethornis pretrei	*Lundia cordata*
Phaethornis pretrei	*Manettia cordifolia*
Phaethornis pretrei	*Neoregelia bahiana*
Phaethornis pretrei	*Opuntia monacantha*
Phaethornis pretrei	*Ruellia angustiflora*
Phaethornis pretrei	*Ruellia brevifolia*
Phaethornis pretrei	*Sinningia rupicola*
Phaethornis pretrei	*Vriesea procera*
Phaethornis ruber	*Erythrina speciosa*
Phaethornis ruber	*Gurania acuminata*
Phaethornis ruber	*Ischnosiphon lasiocoleus*
Phaethornis ruber	*Palicourea crocea*
Phaethornis ruber	*Passiflora speciosa*
Phaethornis squalidus	*Aechmea ornata*
Phaethornis squalidus	*Geissomeria schottiana*
Phaethornis squalidus	*Passiflora speciosa*
Phaethornis squalidus	*Ruellia brevifolia*
Phaethornis squalidus	*Vriesea rodigasiana*
Phaethornis striigularis	*Gurania coccinea*
Phaethornis striigularis	*Renealmia cernua*
Phaethornis syrmatophorus	*Centropogon solanifolius*
Phaethornis yaruqui	*Columnea mastersonii*
Phaethornis yaruqui	*Heliconia griggsiana*
Pterophanes cyanopterus	*Barnadesia arborea*
Pterophanes cyanopterus	*Macleania rupestris*

Pterophanes cyanopterus	*Oreocallis grandiflora*
Pterophanes cyanopterus	*Puya clava-herculis*
Pterophanes cyanopterus	*Tristerix longebracteatus*
Ramphodon naevius	*Erythrina speciosa*
Ramphodon naevius	*Vriesea ensiformis*
Ramphodon naevius	*Vriesea incurvata*
Ramphodon naevius	*Vriesea vagans*
Ramphomicron microrhynchum	*Gaiadendron punctatum*
Selasphorus flammula	*Disterigma humboldtii*
Selasphorus flammula	*Fuchsia microphylla*
Selasphorus sasin	*Prunella vulgaris*
Selasphorus scintilla	*Disterigma humboldtii*
Stephanoxis lalandi	*Aechmea distichantha*
Stephanoxis lalandi	*Buddleja brasiliensis*
Stephanoxis lalandi	*Cestrum corymbosum*
Stephanoxis lalandi	*Collaea speciosa*
Stephanoxis lalandi	*Nematanthus fornix*
Stephanoxis lalandi	*Salvia arenaria*
Stephanoxis loddigesii	*Aechmea distichantha*
Stephanoxis loddigesii	*Bougainvillea glabra*
Stephanoxis loddigesii	*Gaylussacia brasiliensis*
Stephanoxis loddigesii	*Lantana camara*
Thalurania furcata	*Besleria aggregata*
Thalurania furcata	*Dicliptera squarrosa*
Thalurania furcata	*Gurania rhizantha*
Thalurania furcata	*Gurania spinulosa*
Thalurania furcata	*Heliconia psittacorum*
Thalurania furcata	*Helicteres brevispira*
Thalurania furcata	*Palicourea marcgravii*
Thalurania furcata	*Psychotria platypoda*
Thalurania furcata	*Ruellia brevifolia*
Thalurania glaucopis	*Abutilon bedfordianum*
Thalurania glaucopis	*Aechmea nudicaulis*
Thalurania glaucopis	*Geissomeria schottiana*
Thalurania glaucopis	*Erythrina speciosa*
Thalurania glaucopis	*Fuchsia regia*
Thalurania glaucopis	*Psychotria nuda*
Thalurania glaucopis	*Spirotheca rivieri*
Threnetes leucurus	*Cuphea melvilla*
Threnetes leucurus	*Erythrina fusca*
Threnetes leucurus	*Heliconia stricta*
Threnetes leucurus	*Passiflora quadriglandulosa*
Threnetes ruckeri	*Calathea inocephala*
Tilmatura dupontii	*Salvia iodantha*
Tilmatura dupontii	*Salvia mexicana*
Topaza pyra	*Isertia hypoleuca*

Urosticte benjamini	*Palicourea demissa*

Table S2. Abiotic variables used to build the species distribution models.

Climatic properties	**Soil properties***
Annual Mean Temperature	Bulk density
Mean Diurnal Range	Clay content
Isothermality	Coarse fragments
Temperature Seasonality	Sand
Maximum Temperature of Warmest Month	Silt
Minimum Temperature of Coldest Month	Cation exchange capacity (at pH 7)
Temperature Annual Range	Nitrogen
Mean Temperature of Wettest Quarter	Soil organic carbon
Mean Temperature of Driest Quarter	pH water
Mean Temperature of Warmest Quarter	
Mean Temperature of Coldest Quarter	
Annual Precipitation	
Precipitation of Wettest Month	
Precipitation of Driest Month	
Precipitation Seasonality	
Precipitation of Wettest Quarter	
Precipitation of Driest Quarter	
Precipitation of Warmest Quarter	
Precipitation of Coldest Quarter	

* Each soil property has data for six different soil depths (0-5, 5-15, 15-30, 30-60, 60-100, 100-200 cm).

Table S3. Results of the species distribution models generated using only abiotic variables and combined variables (abiotic and biotic), and the best fit of each model according to the second-order Akaike information criterion (AICc) for all 100 hummingbird species evaluated. NP: number of predictors, Se: Sensitivity, Sp: Specificity

	Abiotic				**Combined**			
Species	NP	AICc	Se	Sp	NP	AICc	Se	Sp
Glaucis dohrnii	4	283.70	1.00	0.84	5	286.83	1.00	0.84
Oxypogon lindenii	5	106.68	1.00	0.92	5	107.34	1.00	0.92

Metallura baroni	4	121.60	1.00	0.98	6	635.43	1.00	0.84
Stephanoxis lalandi	6	1074.42	0.99	0.91	5	112.55	1.00	0.99
Eriocnemis derbyi	5	1227.63	0.98	0.88	5	1229.14	0.99	0.86
Ramphodon naevius	6	3586.69	0.97	0.93	8	4766.12	0.99	0.82
Stephanoxis loddigesii	6	4697.52	0.97	0.85	7	3564.97	0.98	0.93
Lophornis chalybeus	6	1426.37	0.97	0.94	5	5231.18	0.97	0.88
Coeligena torquata	6	10652.44	0.97	0.86	7	1358.78	0.97	0.96
Lafresnaya lafresnayi	6	8727.31	0.97	0.87	8	2535.38	0.97	0.87
Lampornis hemileucus	5	643.35	0.96	0.85	12	9383.80	0.97	0.87
Panterpe insignis	5	916.15	0.96	0.88	10	18536.77	0.96	0.86
Heliangelus exortis	5	5226.94	0.96	0.85	7	937.49	0.96	0.87
Eriocnemis vestita	5	5251.33	0.96	0.89	5	699.98	0.96	0.90
Ensifera ensifera	5	7143.74	0.96	0.89	6	5243.58	0.96	0.86
Aglaeactis cupripennis	6	9896.79	0.96	0.88	6	4056.38	0.96	0.92
Boissonneaua flavescens	5	5260.31	0.96	0.86	7	1869.39	0.96	0.89
Chalcostigma herrani	5	2091.57	0.96	0.81	10	18097.36	0.96	0.91
Eriocnemis mosquera	5	1948.33	0.96	0.86	6	777.66	0.96	0.83
Selasphorus flammula	5	721.17	0.96	0.90	6	725.37	0.96	0.90
Heliodoxa imperatrix	5	1212.83	0.96	0.85	9	16430.83	0.95	0.80
Ramphomicron microrhynchum	5	4121.54	0.95	0.90	6	9410.99	0.95	0.75
Haplophaedia aureliae	5	5422.83	0.95	0.80	7	2171.40	0.95	0.88
Metallura tyrianthina	5	18068.39	0.95	0.90	6	5196.66	0.95	0.86
Coeligena lutetiae	5	3108.77	0.95	0.88	7	10619.17	0.95	0.87
Haplophaedia lugens	5	588.86	0.95	0.86	7	8736.13	0.95	0.89
Colibri coruscans	6	34921.41	0.95	0.84	7	9933.81	0.95	0.89
Leucochloris albicollis	6	16556.66	0.95	0.81	6	639.54	0.95	0.88
Atthis heloisa	5	4054.11	0.94	0.81	6	5329.85	0.95	0.81
Phaethornis eurynome	6	9330.28	0.94	0.90	7	3802.59	0.95	0.77
Selasphorus scintilla	5	1134.79	0.94	0.85	8	6353.34	0.94	0.91
Clytolaema rubricauda	6	3978.32	0.94	0.89	6	7116.28	0.94	0.92
Pterophanes cyanopterus	5	6390.23	0.94	0.90	8	3850.47	0.94	0.91
Phaethornis squalidus	6	2601.23	0.94	0.92	6	3076.44	0.94	0.89
Augastes scutatus	6	610.20	0.93	0.93	6	1135.67	0.94	0.88
Heliangelus viola	5	1951.61	0.93	0.88	8	1475.26	0.94	0.75
Coeligena iris	5	2190.08	0.93	0.87	9	11844.85	0.94	0.88
Heliangelus mavors	5	695.17	0.92	0.94	7	7921.23	0.94	0.87
Thalurania glaucopis	6	18768.98	0.92	0.88	8	1041.40	0.93	0.94
Doryfera ludovicae	5	9525.65	0.92	0.89	6	1235.01	0.92	0.90
Heliomaster constantii	7	14833.31	0.92	0.77	6	4044.03	0.92	0.83
Adelomyia melanogenys	5	18896.39	0.92	0.88	6	2084.94	0.92	0.86
Phaethornis yaruqui	5	3885.45	0.92	0.73	6	1204.83	0.92	0.90
Eupherusa nigriventris	5	782.81	0.91	0.87	8	34731.76	0.92	0.87
Tilmatura dupontii	6	5907.10	0.91	0.74	7	7215.08	0.92	0.84
Phaethornis syrmatophorus	6	7949.53	0.91	0.89	6	1925.82	0.91	0.91
Amazilia beryllina	7	21307.34	0.91	0.75	9	21275.93	0.91	0.74

Eriocnemis luciani	5	1260.61	0.90	0.92	8	17158.15	0.91	0.86
Florisuga fusca	6	15228.00	0.90	0.82	8	19191.18	0.91	0.87
Calothorax lucifer	6	9974.84	0.90	0.71	7	9395.43	0.91	0.90
Amazilia rutila	6	35109.29	0.89	0.77	7	14886.68	0.91	0.77
Aglaiocercus coelestis	6	2461.37	0.89	0.82	7	5885.12	0.90	0.75
Phaethornis idaliae	4	673.11	0.89	0.82	10	23622.26	0.90	0.80
Anopetia gounellei	6	1477.70	0.89	0.78	9	34960.34	0.90	0.79
Phaethornis guy	6	17789.65	0.89	0.81	10	15010.29	0.89	0.86
Phaethornis longuemareus	6	2037.08	0.89	0.83	7	9581.22	0.88	0.82
Amazilia lactea	6	11948.47	0.89	0.92	7	602.01	0.88	0.97
Chrysuronia oenone	5	9666.80	0.88	0.81	11	11666.25	0.87	0.84
Lampornis amethystinus	6	6404.92	0.88	0.82	6	9289.60	0.87	0.80
Lampornis clemenciae	6	14463.49	0.88	0.81	6	2400.39	0.87	0.87
Aphantochroa cirrochloris	6	7275.14	0.88	0.85	8	5119.01	0.87	0.78
Cynanthus latirostris	6	44048.25	0.87	0.86	6	585.60	0.87	0.83
Florisuga mellivora	6	45817.76	0.87	0.65	7	29051.93	0.87	0.72
Topaza pyra	6	1402.07	0.86	0.72	8	44393.90	0.87	0.85
Eutoxeres aquila	5	7604.91	0.86	0.77	9	9830.42	0.87	0.76
Glaucis hirsutus	6	32535.52	0.86	0.56	9	14341.62	0.85	0.83
Phaethornis hispidus	5	12862.87	0.86	0.67	8	3639.26	0.84	0.74
Hylocharis chrysura	6	35120.81	0.85	0.77	8	35076.00	0.84	0.76
Coeligena wilsoni	5	1914.86	0.84	0.87	8	5989.18	0.84	0.72
Colibri serrirostris	6	11797.65	0.84	0.88	17	25449.93	0.84	0.79
Heliomaster squamosus	6	5998.25	0.84	0.75	6	20390.40	0.84	0.76
Phaethornis longirostris	6	20525.83	0.83	0.77	7	6383.23	0.84	0.83
Phaethornis pretrei	6	25676.39	0.82	0.80	6	13730.29	0.84	0.75
Heliangelus strophianus	5	765.39	0.82	0.89	8	19121.01	0.84	0.87
Chlorostilbon lucidus	6	86188.77	0.82	0.71	6	7565.61	0.83	0.81
Amazilia leucogaster	6	3998.60	0.82	0.92	14	86098.10	0.83	0.70
Phaethornis malaris	5	13686.35	0.82	0.78	6	2056.59	0.83	0.90
Heliodoxa jacula	6	5118.05	0.82	0.82	8	8248.15	0.83	0.67
Selasphorus sasin	6	24238.34	0.82	0.91	6	741.90	0.82	0.89
Amazilia violiceps	7	19176.42	0.82	0.87	15	40327.70	0.82	0.81
Phaethornis striigularis	6	29571.01	0.81	0.74	7	1940.02	0.82	0.89
Urosticte benjamini	6	1390.18	0.81	0.81	8	3053.19	0.81	0.86
Klais guimeti	6	9739.67	0.81	0.82	6	3727.29	0.81	0.82
Eupetomena macroura	5	41386.73	0.81	0.78	7	1411.77	0.81	0.73
Amazilia brevirostris	5	3717.20	0.80	0.84	9	31808.20	0.80	0.60
Lophornis magnificus	6	3101.12	0.80	0.88	8	12681.97	0.80	0.78
Eugenes fulgens	6	23802.17	0.79	0.84	14	49517.48	0.80	0.59
Chlorostilbon notatus	5	13948.15	0.77	0.74	6	1391.79	0.80	0.83
Threnetes ruckeri	6	9618.18	0.77	0.82	9	13599.50	0.79	0.78
Heliactin bilophus	6	3702.52	0.76	0.77	7	4021.53	0.78	0.94
Threnetes leucurus	5	7115.98	0.73	0.89	6	24437.23	0.78	0.72
Phaethornis bourcieri	6	8241.18	0.71	0.73	9	44521.87	0.77	0.83
Phaethornis ruber	5	32259.45	0.69	0.69	9	31542.76	0.77	0.78

Anthracothorax aurulentus	3	853.17	0.69	0.43	6	16588.33	0.75	0.69
Campylopterus largipennis	5	16584.08	0.69	0.76	7	24771.30	0.75	0.93
Chlorostilbon mellisugus	5	24600.80	0.66	0.76	7	7031.61	0.75	0.88
Thalurania furcata	6	43777.51	0.62	0.70	3	853.24	0.68	0.44
Amazilia versicolor	5	23169.66	0.61	0.86	9	22925.07	0.67	0.82
Amazilia fimbriata	6	49976.70	0.56	0.79	11	43338.93	0.67	0.69
Anthracothorax nigricollis	6	63355.81	0.54	0.84	8	62058.78	0.61	0.84

Table S4. Results of the spatial similarity in environmental suitability and binary geographic projection between the species distribution models generated using only abiotic variables and those with abiotic and biotic variables for all 100 hummingbird species evaluated.

Species	Suitability Similarity	Geographic Similarity
Anthracothorax aurulentus	1.00	0.98
Oxypogon lindenii	1.00	0.92
Glaucis dohrnii	1.00	0.93
Eriocnemis vestita	1.00	0.94
Anopetia gounellei	1.00	0.85
Eriocnemis derbyi	1.00	0.81
Boissonneaua flavescens	1.00	0.94
Heliomaster constantii	1.00	0.88
Urosticte benjamini	1.00	0.84
Topaza pyra	1.00	0.89
Tilmatura dupontii	0.99	0.87
Chalcostigma herrani	0.99	0.73
Hylocharis chrysura	0.99	0.82
Amazilia brevirostris	0.99	0.68
Selasphorus flammula	0.99	0.88
Chlorostilbon mellisugus	0.99	0.57
Amazilia rutila	0.99	0.79
Heliangelus exortis	0.99	0.89
Heliangelus mavors	0.99	0.64
Aglaeactis cupripennis	0.99	0.83
Campylopterus largipennis	0.99	0.57
Phaethornis malaris	0.99	0.73
Coeligena torquata	0.99	0.84
Atthis heloisa	0.99	0.79
Phaethornis syrmatophorus	0.98	0.79
Amazilia violiceps	0.98	0.75
Amazilia beryllina	0.98	0.85

Heliodoxa jacula	0.98	0.72
Phaethornis longirostris	0.98	0.78
Lampornis amethystinus	0.98	0.77
Coeligena lutetiae	0.98	0.85
Ensifera ensifera	0.98	0.77
Thalurania furcata	0.98	0.49
Phaethornis ruber	0.98	0.51
Heliomaster squamosus	0.98	0.73
Lophornis magnificus	0.98	0.65
Lampornis clemenciae	0.98	0.76
Stephanoxis loddigesii	0.98	0.85
Heliactin bilophus	0.98	0.68
Lampornis hemileucus	0.98	0.81
Doryfera ludovicae	0.98	0.74
Amazilia leucogaster	0.98	0.60
Eriocnemis mosquera	0.98	0.62
Phaethornis bourcieri	0.98	0.63
Lafresnaya lafresnayi	0.98	0.80
Calothorax lucifer	0.98	0.64
Eupherusa nigriventris	0.98	0.73
Chlorostilbon notatus	0.98	0.54
Panterpe insignis	0.97	0.77
Eugenes fulgens	0.97	0.65
Aphantochroa cirrochloris	0.97	0.67
Phaethornis hispidus	0.97	0.50
Haplophaedia aureliae	0.97	0.75
Metallura tyrianthina	0.97	0.84
Leucochloris albicollis	0.97	0.81
Coeligena wilsoni	0.97	0.70
Amazilia fimbriata	0.97	0.35
Threnetes leucurus	0.97	0.52
Selasphorus scintilla	0.97	0.82
Florisuga fusca	0.97	0.61
Chrysuronia oenone	0.97	0.63
Pterophanes cyanopterus	0.97	0.83
Amazilia versicolor	0.96	0.48
Eriocnemis luciani	0.96	0.74
Phaethornis striigularis	0.96	0.69
Heliodoxa imperatrix	0.96	0.61
Chlorostilbon lucidus	0.96	0.77
Anthracothorax nigricollis	0.96	0.37
Colibri serrirostris	0.96	0.67
Thalurania glaucopis	0.96	0.71
Coeligena iris	0.96	0.71
Colibri coruscans	0.96	0.72
Cynanthus latirostris	0.96	0.68

Florisuga mellivora	0.96	0.42
Phaethornis yaruqui	0.96	0.68
Glaucis hirsutus	0.96	0.43
Amazilia lactea	0.95	0.59
Ramphomicron microrhynchum	0.95	0.69
Phaethornis squalidus	0.95	0.53
Aglaiocercus coelestis	0.95	0.57
Heliangelus strophianus	0.95	0.55
Phaethornis pretrei	0.94	0.65
Eutoxeres aquila	0.94	0.50
Eupetomena macroura	0.94	0.53
Heliangelus viola	0.93	0.73
Adelomyia melanogenys	0.93	0.63
Phaethornis longuemareus	0.93	0.47
Threnetes ruckeri	0.93	0.57
Ramphodon naevius	0.93	0.52
Clytolaema rubricauda	0.92	0.68
Stephanoxis lalandi	0.92	0.54
Selasphorus sasin	0.92	0.49
Augastes scutatus	0.91	0.38
Phaethornis guy	0.91	0.54
Phaethornis eurynome	0.91	0.61
Lophornis chalybeus	0.89	0.52
Haplophaedia lugens	0.89	0.53
Phaethornis idaliae	0.88	0.48
Klais guimeti	0.84	0.37
Metallura baroni	0.83	0.35

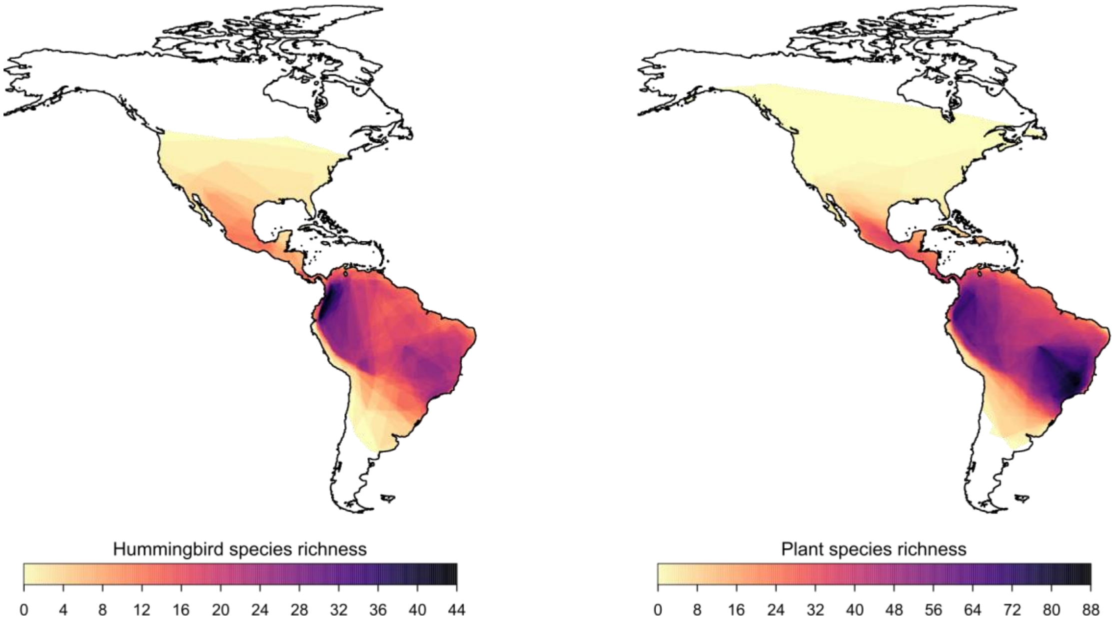

Fig. S1. Distribution of hummingbird and plant species analyzed in our study.

Capítulo 2: Additional Information

Supplementary Material

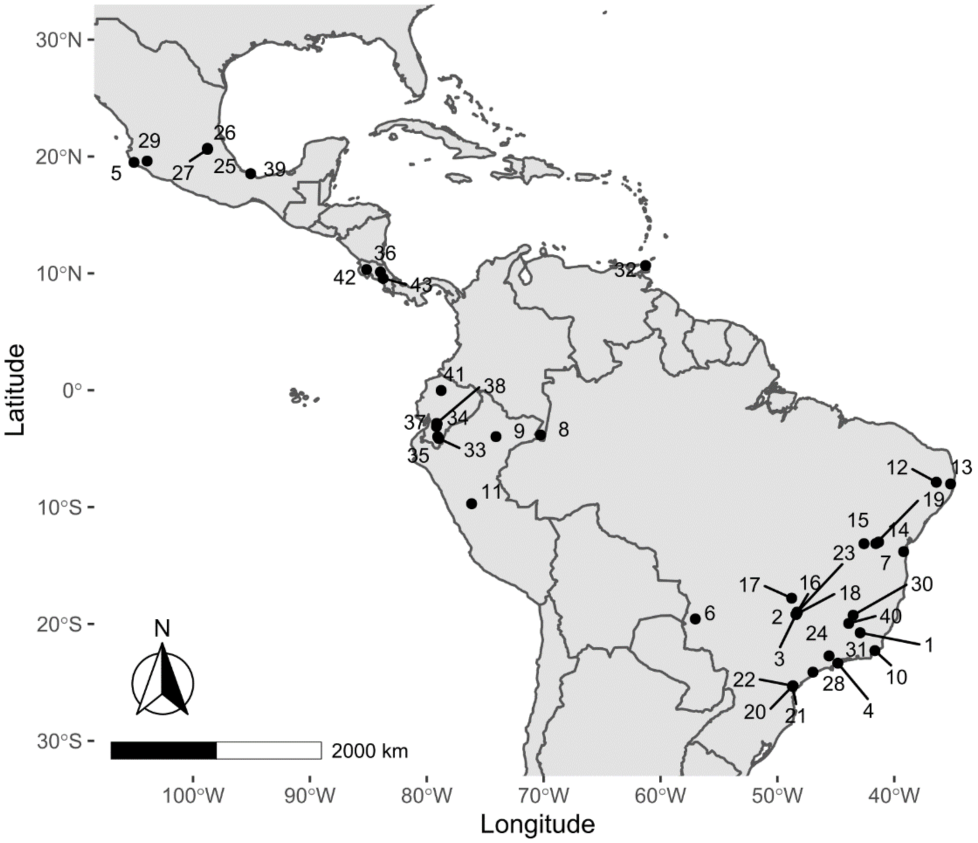

Fig. S1. Location map of the hummingbird-plant interaction networks used in this study. See Table A1 for codes meaning and references.

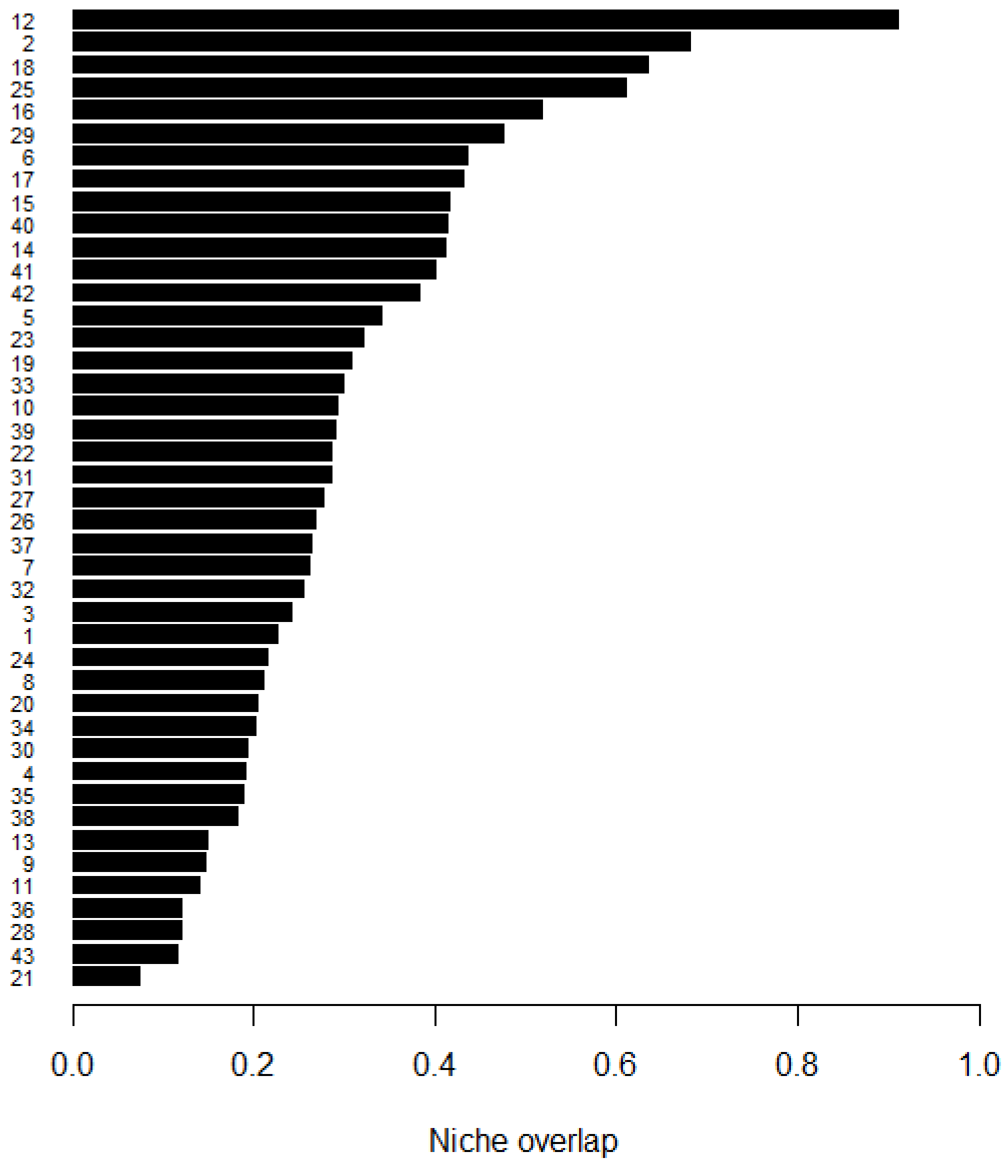

Fig. S2. Overlap values in each community. To access the code with the name of the networks, see Appendix A.

Table S1. All regression models generated. Net Primary Productivity (NPP), Mean Wing Disc Loading ($\bar{X}$WDL), Mean Pairwise Distance of the Bill Length (MPD.BL) and ratio between the species richness of hummingbirds and plants (RAT).

Models	df	AICc	△AICc	R^2
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$	5.0	-34.0	0.00	0.29
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$	4.0	-33.0	1.00	0.22
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$	3.0	-33.0	1.10	0.18
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$	4.0	-33.0	1.60	0.21
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$	4.0	-32.0	2.00	0.21
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$	6.0	-32.0	2.20	0.29
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$+ $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	6.0	-32.0	2.40	0.29
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$	5.0	-32.0	2.40	0.24
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$	4.0	-32.0	2.50	0.20
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	4.0	-31.0	3.30	0.18
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	5.0	-31.0	3.40	0.23
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$	5.0	-31.0	3.50	0.23
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$	5.0	-30.0	4.00	0.22
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	5.0	-30.0	4.10	0.21
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	5.0	-30.0	4.20	0.21
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	7.0	-30.0	4.50	0.30
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	6.0	-30.0	4.60	0.25
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	5.0	-29.0	5.00	0.20
NO ~ $\mathrm{Log}_{(\mathrm{NPP}+1)}$	3.0	-28.0	5.90	0.08
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$	3.0	-28.0	5.90	0.08
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	6.0	-28.0	6.00	0.23
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$	4.0	-28.0	6.40	0.12
NO ~ $\mathrm{Log}_{(\bar{x}\mathrm{WDL}+1)}$ + $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	6.0	-28.0	6.50	0.22
NO ~ $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	4.0	-28.0	6.80	0.11
Intercept	2.0	-27.0	7.20	0.00
NO ~ $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$	4.0	-27.0	7.40	0.10
NO ~ $\mathrm{Log}_{(\mathrm{RAT}+1)}$	3.0	-27.0	7.60	0.04
NO ~ $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	3.0	-26.0	8.30	0.03
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	4.0	-26.0	8.40	0.08
NO ~ $\mathrm{Log}_{(\mathrm{MPD.BIL}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	5.0	-25.0	8.80	0.12
NO ~ $\mathrm{Log}_{(\mathrm{NPP}+1)}$ + $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	5.0	-25.0	8.90	0.12
NO ~ $\mathrm{Log}_{(\mathrm{RAT}+1)}$ + $\mathrm{Log}_{(\mathrm{MPD.WDL}+1)}$	4.0	-25.0	9.30	0.06

Table S2: Coefficient values of the regression model used in our study (niche.overlap ~ log (MPD.BL + 1) + log ($\bar{x}$WDL + 1) + log (NPP + 1). Mean Wing Disc Loading ($\bar{x}$WDL), Mean Pairwise Distance of the Bill Length (MPD.BL) and Net Primary Productivity (NPP).

	Estimate	Std. Error	t-value
MPD.BIL	-0.30	0.15	-2.09
$\bar{x}$WDL	0.29	0.15	1.99
NPP	-0.28	0.15	-1.84

Appendix A

Appendix A: Details on the interaction networks used.

Table A1. Network data used in the study.

Code	Latitude	Longitude	Humming-bird richness	Plant richness	NPP	Data Source Reference
1	-20.75	-42.92	8	14	114.38	(Abreu & Vieira 2004)
2	-18.99	-48.3	6	5	84.01	(de Araújo *et al.* 2011)
3	-19.18	-48.4	7	36	84.28	(Araújo *et al.* 2013)
4	-23.35	-44.83	12	44	150.78	(Araújo 1996)
5	19.5	-105.05	5	23	129.52	(Arizmendi & Ornelas 1990)
6	-19.57	-57.02	3	15	94.35	(Bogiani 2012)
7	-13.81	-39.2	13	18	150.17	(Coelho 2013)
8	-3.82	-70.27	14	29	145.77	(Cotton 1998)
9	-3.97	-74.08	24	63	153.52	(Dziedzioch *et al.* 2003)
10	-22.28	-41.66	3	10	122.11	(Fonseca *et al.* 2015)
11	-9.71	-76.16	12	27	65.83	(Gonzalez & Loiselle 2016)
12	-7.87	-36.4	5	31	88.22	(Las-Casas *et al.* 2012)
13	-8.02	-35.18	8	27	103.47	(Lopes & Sazima 2002)
14	-12.99	-41.34	7	36	90.92	(Machado *et al.* 2007)
15	-13.13	-42.59	7	29	83.7	(Machado 2009)
16	-18.98	-48.3	10	10	84.01	(Machado 2012)
17	-17.79	-48.78	8	12	87.27	(Machado 2012)
18	-19.17	-48.39	6	17	84.28	(Machado 2012)
19	-13.12	-41.58	8	10	86.52	(Machado 2014)
20	-25.32	-48.71	7	13	139.81	(Malucelli 2014)
21	-25.32	-48.71	4	13	139.81	(Malucelli 2014)
22	-25.29	-48.66	4	13	139.81	(Malanotte 2018)
23	-18.99	-48.3	7	9	84.01	(Maruyama *et al.* 2013)
24	-19.17	-48.4	6	17	84.28	(Maruyama *et al.* 2013)
25	20.68	-98.76	3	7	158.21	(Martínez-García & Ortiz-Pulido 2014)

26	20.69	-98.77	2	9	158.21	(Martínez-García & Ortiz-Pulido 2014)
27	20.61	-98.76	5	11	158.21	(Martínez-García & Ortiz-Pulido 2014)
28	-24.12	-46.96	13	38	151.62	(Rocca de Andrade 2006)
29	19.61	-103.93	11	14	120.34	(Rodríguez Flores 2009)
30	-19.25	-43.52	6	45	120.53	(Rodrigues & Rodrigues 2014)
31	-22.73	-45.58	4	23	147.71	(Sazima *et al.* 1996)
32	10.67	-61.28	9	58	100.38	(Snow & Snow 1972)
33	-4.13	-78.97	7	16	183.1	(Sonne *et al.* 2019)
34	-3.1	-79.17	8	17	93.58	(Sonne *et al.* 2019)
35	-3.97	-79.07	9	13	93.58	(Sonne *et al.* 2019)
36	10.12	-83.97	13	51	153.76	(Stiles 1985)
37	-2.87	-79.12	8	20	72.79	(Tinoco *et al.* 2017)
38	-2.84	-79.16	12	19	72.79	(Tinoco *et al.* 2017)
39	18.53	-95.07	10	18	98.87	(Toledo 1975)
40	-19.95	-43.9	6	10	120.53	(Vasconcelos & Lombardi 1999)
41	-0.02	-78.77	13	28	94.51	(Walther & Brieschke 2001)
42	10.33	-85.15	9	11	89.67	(Wolf 1970)
43	9.57	-83.73	4	18	134.86	(Wolf *et al.* 1976)

Network references

Abreu, C.R.M. & Vieira, M.F. (2004). Os beija-flores e seus recursos florais em um fragmento florestal de Viçosa, sudeste brasileiro. *Lundiana*, 5, 129–134.

Araújo, A.C. (1996). Beija-flores e seus recursos florais numa área de planicie costeira do litoral norte de São Paulo. Campinas State University, Brazil.

Araújo, F.P., Barbosa, A.A.A. & Oliveira, P.E. (2011). Floral resources and hummingbirds on an island of flooded forest in Central Brazil. *Flora - Morphol. Distrib. Funct. Ecol. Plants*, 206, 827–835.

Araújo, F.P., Sazima, M. & Oliveira, P.E. (2013). The assembly of plants used as nectar sources by hummingbirds in a Cerrado area of Central Brazil. *Plant Syst. Evol.*, 299, 1119–1133.

Arizmendi, M.C. & Ornelas, J.F. (1990). Hummingbirds and Their Floral Resources in a Tropical Dry Forest in Mexico. *Biotropica*, 22, 172–180.

Bogiani, P.A. (2012). Rede de interações entre beija-flores (aves: Trochilidae) e as flores que visitam no Pantanal do Miranda, Mato Grosso do Sul. Federal University of Mato Grosso do Sul, Brazil.

Coelho, A.G. (2013). Aline Goes Coelho Beija-Flores No Sub-Bosque De Um Fragmento De Mata Atlântica Da Bahia , Brasil. Campinas State University, Brazil.

Cotton, P.A. (1998). Coevolution in an Amazonian hummingbird-plant community. *Ibis*, 140, 639–646.

Dziedzioch, C., Stevens, A.D. & Gottsberger, G. (2003). The hummingbird plant community of a tropical montane rain forest in southern Ecuador. *Plant Biol.*, 5, 331–337.

Fonseca, L.C.N., Vizentin-Bugoni, J., Rech, A.R. & Alves, M.A.S. (2015). Plant-hummingbird interactions and temporal nectar availability in a restinga from Brazil. *An. Acad. Bras. Cienc.*, 87, 2163–2175.

Gonzalez, O. & Loiselle, B.A. (2016). Species interactions in an andean bird-flowering plant network: Phenology is more important than abundance or morphology. *PeerJ*, 2016, 1–22.

Las-Casas, F.M.G., Azevedo Júnior, S.M. & Dias Filho, M.M. (2012). A comunidade de beija-flores (Aves: Trochilidae) e a assembleia de flores em uma área de Caatinga. *Brazilian J. Biol.*, 72, 51–58.

Lopes, A.V.F. & Sazima, M. (2002). Polinização por Beija-Flores em Remanescentes da Mata Atlântica Pernambucana, Nordeste do Brasil. Campinas State University, Brazil.

Machado, A.O. (2012). Diversidade de recursos florais para beija-flores nos cerrados do Triângulo Mineiro e região. Federal University of Uberlandia, Brazil.

Machado, C.G. (2009). Beija-flores (aves: Trochilidae) e seus recursos florais em uma área de caatinga da chapada diamantina, bahia, brasil. *Zoologia*, 26, 255–265.

Machado, C.G. (2014). The hummingbird community and the plants which they visit at a savannah in the Chapada Diamantina, Bahia, Brazil. *Biosci. J.*, 30, 1578–1587.

Machado, C.G., Coelho, A.G., Santana, C.S. & Rodrigues, M. (2007). Beija-flores e seus recursos florais em uma área de campo rupestre da Chapada Diamantina, Bahia. *Rev. Bras. Ornitol.*, 15, 267–279.

Malanotte, M.L. (2018). Ligando flores e polinizadores : como os padrões de floração estruturam as comunidades de beija-flores?, Federal University of Paraná, Brazil.

Malucelli, T.S. (2014). Fatores envolvidos na estruturação das redes de polinização beja-flor-planta em um gradiente sucessional. Federal University of Paraná, Brazil.

Martínez-García, V. & Ortiz-Pulido, R. (2014). Redes mutualistas colibrí-planta: Comparación en dos escalas espaciales. *Ornitol. Neotrop.*, 25, 273–289.

Maruyama, P.K., Oliveira, G.M., Ferreira, C., Dalsgaard, B. & Oliveira, P.E. (2013). Pollination syndromes ignored: Importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften*, 100, 1061–1068.

Rocca de Andrade, M.A. (2006). Recurso floral para aves de uma comunidade de Mata Atlântica de encosta: sazonalidade e distribuição vertical. Campinas State University, Brazil, Campinas.

Rodrigues, L.C. & Rodrigues, M. (2014). Flowers visited by hummingbirds in the open habitats of the southeastern brazilian mountaintops: species composition and seasonality. *Brazilian J. Biol.*, 74, 659–676.

Rodríguez Flores, C.I. (2009). Dinámica de las estrategias de forrajeo por néctar en colibríes (Aves: Trochilidae) en la Reserva de la Biósfera Sierra de Manantlán (Jalisco, México). Universidad Nacional Autónoma de México.

Sazima, I., Buzato, S. & Sazima, M. (1996). An assemblage of hummingbird-pollinated flowers in a montane forest in southeastern Brazil. *Bot. Acta*, 109, 149–160.

Snow, B.K. & Snow, D.W. (1972). Feeding Niches of Hummingbirds in a Trinidad Valley. *J. Anim. Ecol.*, 41, 471–485.

Sonne, J., Zanata, T.B., Martín González, A.M., Cumbicus Torres, N.L., Fjeldså, J., Colwell, R.K., *et al.* (2019). The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. *Biotropica*, 51, 205–218.

Stiles, F.G. (1985). Seasonal Patterns and Coevolution in the Hummingbird-Flower Community of a Costa Rican Subtropical Forest. *Ornithol. Monogr.*, 36, 757–787.

Tinoco, B.A., Graham, C.H., Aguilar, J.M. & Schleuning, M. (2017). Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos*, 126, 52–60.

Toledo, V.M. (1975). La Estacionalidad de las Flores Utilizadas por los Colibries de una Selva Tropical Humeda en Mexico. *Biotropica*, 7, 63–70.

Vasconcelos, M.F. De & Lombardi, J.A. (1999). Padrão sazonal na ocorrência de seis espécies de beija-flores (Apodiformes: Trochilidae) em uma localidade de campo rupestre na Serra do Curral, Minas Gerais. *Ararajuba*,7, 71–79.

Walther, B.A. & Brieschke, H. (2001). Hummingbird-flower relationships in a mid-elevation rainforest near Mindo, Northwestern Ecuador. *Int. J. Ornithol.*, 4, 115–135.

Wolf, L.L. (1970). The Impact of Seasonal Flowering on the Biology of Some Tropical Hummingbirds. *Condor*, 72, 1–14.

Wolf, L.L., Stiles, F.G. & Hainsworth, F.R. (1976). Ecological Organization of a Tropical, Highland Hummingbird Community. *J. Anim. Ecol.*, 45, 349–479.

Appendix B

Appendix B: Details about the collected traits.

The species traits were obtained from 25 different sources (references below). We prioritized obtaining data that contained information for both female and male adult individuals. Most of the acquired data presented these characteristics, 95% for bill length values and 96% for mass and wing length values. The rest of the values were filled with data from adult males. The species *Lophornis magnificus*, *Phaethornis subochraceus* and *Oxypogon lindenii*, were excluded from the interaction networks, as some of their traits were not available in the literature.

Traits references:

Arquez-Luna, U.M., Lara, C., Corcuera, P. & Valverde, P.L. (2019). Factors affecting the dominance hierarchy dynamics in a hummingbird assemblage. *Curr. Zool.*, 65, 261–268.

Brown, J.H. & Bowers, M.A. (1985). Community organization in hummingbirds: relationships between morphology an ecology. *Auk*, 102, 251–269.

Colwell, R.K. (2000). Rensch’s rule crosses the line: Convergent allometry of sexual size dimorphism in hummingbirds and flower mites. *Am. Nat.*, 156, 495–510.

Da Cruz Rodrigues, L. & Rodrigues, M. (2011). Size Dimorphism, Juvenal Plumage, and Timing of Breeding of the Hyacinth Visorbearer (Augastes scutatus). *Wilson J. Ornithol.*, 123, 726–733.

Feinsinger, P., Colwell, R.K., Terborgh, J. & Chaplin, S.B. (1979). Elevation and the morphology, flight energetics and foraging ecology of tropical hummingbirds. *Am. Nat.*, 113, 481–497.

Fernandez, M.J. (2010). Flight Performance and Comparative Energetics of the Giant Andean Hummingbird (Patagona gigas). University of California, Berkeley.

Graves, G.R. (1980). A new species of metaltail hummingbird from northern Peru. *Wilson Bull.*, 92, 1–148.

Groom, D.J.E., Toledo, M.C.B., Powers, D.R., Tobalske, B.W. & Welch, K.C. (2018). Integrating morphology and kinematics in the scaling of hummingbird hovering metabolic rate and efficiency. *Proc. R. Soc. B Biol. Sci.*, 285, 20172011.

Gutiérrez-Zamora, A. (2008). Ecological interactions and structure of a high Andean community of hummingbirds and flowers in the Eastern Andes of Colombia. *Ornitol. Colomb.*, 1, 17–42.

Hasui, É., Metzger, J.P., Pimentel, R.G., Silveira, L.F., Bovo, A.A. d. A., Martensen, A.C., *et al.* (2018). ATLANTIC BIRDS: a data set of bird species from the Brazilian Atlantic Forest. *Ecology*, 99, 497.

Lara, C., Curiel-Durán, H.A. & Castillo-Guevara, C. (2020). Coexistence among morphologically similar hummingbird species is promoted via density compensation in a Mexican temperate forest. *Ecol. Res.*, 416–427.

López-Segoviano, G., Bribiesca, R. & Arizmendi, M.D.C. (2018). The role of size and dominance in the feeding behaviour of coexisting hummingbirds. *Ibis.*, 160, 283–292.

Montoya, P., Gonzalez, M.A., Tenorio, E.A., López-Ordóñez, J.P., Pinto Gómez, A., Cueva, D., *et al.* (2018). A morphological database for 606 Colombian bird species. *Ecology*, 99, 1693–1693.

Nascimento, J.L.X.(2000). Estudo comparativo da avifauna em duas Estações Ecológicas da Caatinga: Aiuaba e Seridó. *Melopsittacus*, 3, 12–35.

Piacentini, V.Q. (2011). Taxonomia e distribuição geográfica dos representantes do gênero Phaethornis Swainson, 1827 (Aves: Trochilidae), University of São Paulo, Brazil.

Rico-Guevara, A. (2014). Morphology and Function of the Drinking Apparatus in Hummingbirds. University of Connecticut, EUA.

Rodríguez-Flores, C.I., Ornelas, J.F., Wethington, S. & Arizmendi, M.C. (2019). Are hummingbirds generalists or specialists? Using network analysis to explore the mechanisms influencing their interaction with nectar resources. *PLoS One*, 14, e0211855.

Salama, P., Donegan, T.M., Davison, D. & Ochoa, J.M. (2007). Birds of Serranía de los Churumbelos, their conservation and elevational distribution. *Conserv. Colomb.*, 3, 29–58.

Souza, E.A., Nunes, M.F.C., Simão, I., Sousa, A.E.B.A., Las-Casas, F.M.G., Rodrigues, R.C., *et al.* (2010). Ampliação de área de ocorrência do Beija-flor-de-gravatinha-vermelha Augastes lumachella (Lesson, 1838)(Trochilidae). *Ornithologia*, 3, 145–148.

Stiles, F.G., Altshuler, D.L. & Dudley, R. (2005). Wing Morphology and Flight Behavior of Some North American Hummingbird Species. *Auk*, 122, 872–886.

Tovilla-Sierra, R.D., Herrera-Alsina, L., Bribiesca, R. & Arita, H.T. (2019). The spatial analysis of biological interactions: morphological variation responding to the co-occurrence of competitors and resources. *J. Avian Biol.*, 50, jav.02223.

Weinstein, B.G., Tinoco, B., Parra, J.L., Brown, L.M., McGuire, J.A., Stiles, F.G., *et al.* (2014). Taxonomic, Phylogenetic, and Trait Beta Diversity in South American Hummingbirds. *Am. Nat.*, 184, 211–224.

Wolf, L.L., Stiles, F.G. & Hainsworth, F.R. (1976). Ecological Organization of a Tropical, Highland Hummingbird Community. *J. Anim. Ecol.*, 45, 349–379.

Zanata, T.B., Dalsgaard, B., Carsten, R. & Varassin, I.G. (2019). Bill measurements of hummingbirds in the ecological network database. figshare. Dataset.

Capítulo 3: Additional Information

Supplementary Material

Table S1. Basic description about the 13 data papers found with bird traits. These 13 datasets together account for 46% of all information available for the 10,949 species investigated here (see the main text). S: number of 10,949 species that are present in the dataset; N° Traits: number of morphological (M) and life history (H) traits evaluated in this study that are present in the dataset; Dataset completeness: percentage of information completeness considering the number of species (S) and traits (N° Traits) in the dataset; Dataset contribution: percentage of information completeness in the dataset considering the total number of species and traits evaluated in this study. See Appendix A for references.

Reference	S	N° Traits (M - H)	Dataset coverage (%)	Dataset contribution (%)
Burgio *et al.* 2019	394	5 - 3	96.86	1.99
Garnett *et al.* 2015	930	1 - 4	83.76	2.54
Lislevand *et al.* 2007	3729	5 - 1	75.48	11.02
Montoya *et al.* 2018	604	7 - 0	98.30	2.71
Myhrvold *et al.* 2015	9435	1 - 1	83.83	10.32
Razafindratsima *et al.* 2018	242	1 - 6	95.81	1.06
Renner & van Hoesel 2017	98	6 - 2	90.94	0.47
Ricklefs 2017	1684	5 - 0	100	5.49
Rodrigues *et al.* 2019	763	6 - 0	89.30	2.67
Storchová & Horák 2018	497	5 - 4	99.73	2.91
Takagawa *et al.* 2011	492	1 - 4	92.68	1.49
Willians *et al.* 2010	95	1 - 3	99.47	0.25
Wilman *et al.* 2014	9844	1 - 3	91.34	23.46

Table S2. Summary description of eight additional traits investigated here to evaluate the consistency of our results. These traits integrate a list of 19 bird functional traits (most already present in our initial list based on ecologists preference) suggested by a regional bird survey protocol (López-Ordoñez *et al.* 2015). See Table 1 for caption and the main text for reference.

Trait	**Type**	**Coverage Data papers**	**Coverage Repositories**	**Coverage Total**	**Mean redundancy**	**Max redundancy**
Bill curvature	M	0	0.80	0.80	0	0
Bill height	M	23.55	31.24	37.25	2.63	9
Hallux length	M	19.8	7.11	24.72	2.03	3
Nesting behavior	H	12.46	45.79	47.05	3.02	13
Social behavior	H	10.69	19.99	25.64	2.48	7
Tail graduation	M	4.2	9.78	13.62	2.02	3
Wing area	M	1.83	3.55	4.89	2.02	3
Wingspan	M	1.74	6.78	7.74	2.07	3

Table S3. Relative contribution of primary (field and museum) and secondary (articles, books, etc.) data sources for each one of the 14 traits most frequently used in the ecological literature. To calculate this source contribution, we considered only those articles that explicitly cited the data source of each trait (86% of the 148 analyzed articles). Note that an article can use more than one source for the same trait, and, for this reason, the sum of the columns may be higher than 100%.

Life history traits	**Primary Source**	**Secondary Source**	**No Reference**
Activity period	0.12	1.00	0
Clutch size	0	0.93	0.07
Diet	0.02	0.96	0.04
Foraging strategy	0.02	0.95	0.05
Habitat preference	0	0.81	0.19
Migratory status	0.03	0.93	0.03
Nesting strategy	0	0.94	0.06
Average	*0.03*	*0.93*	*0.06*

Morphological traits	**Primary Source**	**Secondary Source**	**No Reference**
Body mass	0.08	0.91	0.05
Bill length	0.58	0.39	0.06
Bill width	0.95	0.05	0.05
Kipp’s distance	0.93	0	0.07
Tail length	0.53	0.47	0.06
Tarsus length	0.50	0.45	0.09
Wing length	0.47	0.50	0.06
Average	*0.58*	*0.40*	*0.06*

Table S4. Relative contribution of the five most cited data sources for each one of the 14 traits most frequently used in the ecological literature. To calculate this source contribution, we considered only those articles that explicitly cited the data source of each trait (86% of the 148 analyzed articles). Note that an article can use more than one source for the same trait, and, for this reason, the sum of the rows may be higher than 100%. See references of the data sources below.

Source	**AP**	**BL**	**BW**	**BM**	**CS**	**Di**	**FS**	**HP**	**KD**	**MS**	**NS**	**TL**	**TsL**	**WL**
Batisteli *et al.* 2018								0.06						
Garnett *et al.* 2015					0.07			0.12		0.1				0.06
BoA		0.06										0.12	0.09	0.06
BTO		0.03											0.05	
BWP	0.18			0.07	0.14	0.12	0.11			0.13	0.24			
BirdsNA	0.12					0.07	0.11			0.13	0.06	0.06		
HBW	0.24			0.1	0.14	0.18	0.17				0.09	0.06		
Devictor *et al.* 2010	0.12				0.11					0.1	0.09			
HABM				0.22										
HANZAB								0.12						0.06
BoSA		0.12		0.12	0.14	0.13	0.1	0.19		0.17	0.27	0.12	0.14	0.18
Matthews *et al.* 2017			0.05						0.07					
Museum		0.55	0.9						0.86			0.47	0.45	0.44
No reference		0.06	0.05					0.19	0.07				0.09	
Particular collection			0.05						0.07					
Trisos *et al.* 2014			0.05											
Wilman *et al.* 2014	0.35			0.22		0.24	0.28							

AP: Activity period; BL: Bill length; BW: Bill width, BM: Body mass; CS: Clutch size; Di: Diet; FS: Forage strategy; HP: Habitat preference; KD: Kipp's distance; MS: Migratory status; NS: Nesting strategy; TL: Tail length; TsL: Tarsus length; WL: Wing length.

BoA: The Birds of Africa (Brown *et al.* 1982-2013); BTO: British Trust for Ornitology ("BTO - British Trust for Ornithology"); BWP: The Birds of Western Palearctic (Cramp *et al.* 1977-1994); BirdsNA: The Birds of North America (Rodewald 2019); HBW: Handbook of the Birds of the World (del Hoyo *et al.* 1992-2013); HABM: Handbook of Avian Body Mass (Dunning 2007); HANZAB: Handbook of Australian, New Zealand and Antarctic Birds (Marchant *et al.* 1990-2006); BoSA: Birds of Southern Africa (Hockey *et al.* 2005).

References

Batisteli, A.F., Tanaka, M.O., & Souza, A.L. (2018). Bird Functional Traits Respond to Forest Structure in Riparian Areas Undergoing Active Restoration. *Diversity, 10*, 90.

Brown, L.H., Urban, E.K., Newman, K.B., Fry, C.H., Keith, S., Safford, R., *et al.* (1982-2013). *The Birds of Africa. Vol. 1-8 (1982-2013)*. Helm and Academic Press (Via A & C Black).

BTO - British Trust for Ornithology. Available at: https://www.bto.org/.

Cramp, S., Brooks, D.J. & Perrins, C.M. (1977-1994). *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic Vol. 1- 9 (1977-1994)*. Oxford University Press.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.*, 13, 1030–1040.

Dunning, J.B. (2007). *CRC handbook of avian body masses*. Taylor and Francis, Boca Raton.

Garnett, S., Duursma, D., Ehmke, G., Patrick-Jean G., Stewart, A., Szabo, J.K. *et al.* (2015). Biological, ecological, conservation and legal information for all species and subspecies of Australian bird. *Sci Data 2*, 150061

Hockey, P.A., Dean, W.R.J. & Ryan, P.G. (2005). *Roberts birds of southern Africa*. VII. Jacana Publishers.

del Hoyo, J., Elliott, A., Sargatal, J. & Christie, D.A. (1992-2013). *Handbook of the Birds of the World - Vol. 1-16 (1992-2013). Lynx Edicions, Barcelona*. Lynx Edicions.

Marchant, S., Higgins, P.J., Davies, S., Steele, W. & Peter, J. (1990-2006). *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1-7 (1990-2006)*. Oxford University Press.

Matthews, T.J., Cottee-Jones, H.E.W., Bregman, T.P. & Whittaker, R.J. (2017). Assessing the relative importance of isolated Ficus trees to insectivorous birds in an Indian human-modified tropical landscape. *Biodivers. Conserv.*, 26, 2803–2819.

Rodewald, P. (2019). *Birds of North America*. Cornell Lab of Ornithology.

Trisos, C.H., Petchey, O.L. & Tobias, J.A. (2014). Unraveling the Interplay of Community Assembly Processes Acting on Multiple Niche Axes across Spatial Scales. *Am. Nat.*, 184, 593–608.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

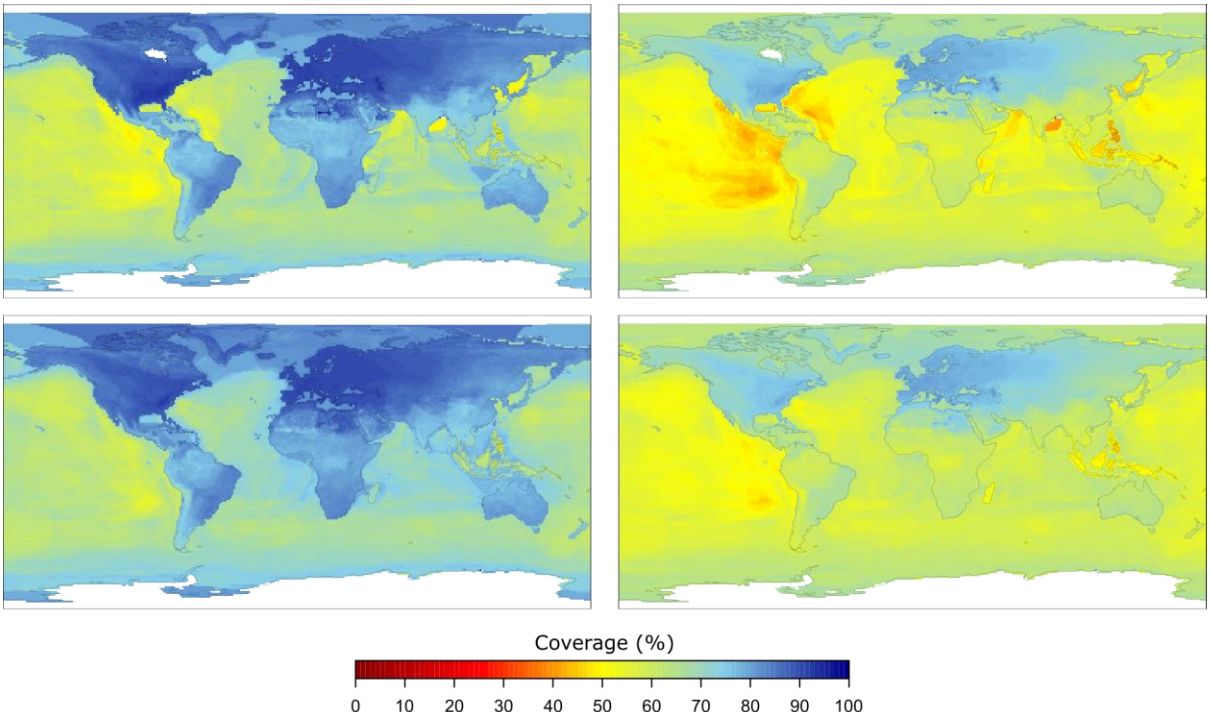

Fig. S1. Spatial variation of average trait completeness in birds considering only breeding ranges to map species distribution (top), the option adopted in our study, and including non-breeding ranges (bottom), for our initial list with the 14 most relevant functional traits according to the ecological literature (left) and after the addition of eight traits proposed by López-Ordoñez *et al.* (2015) (right). See the main text for reference.

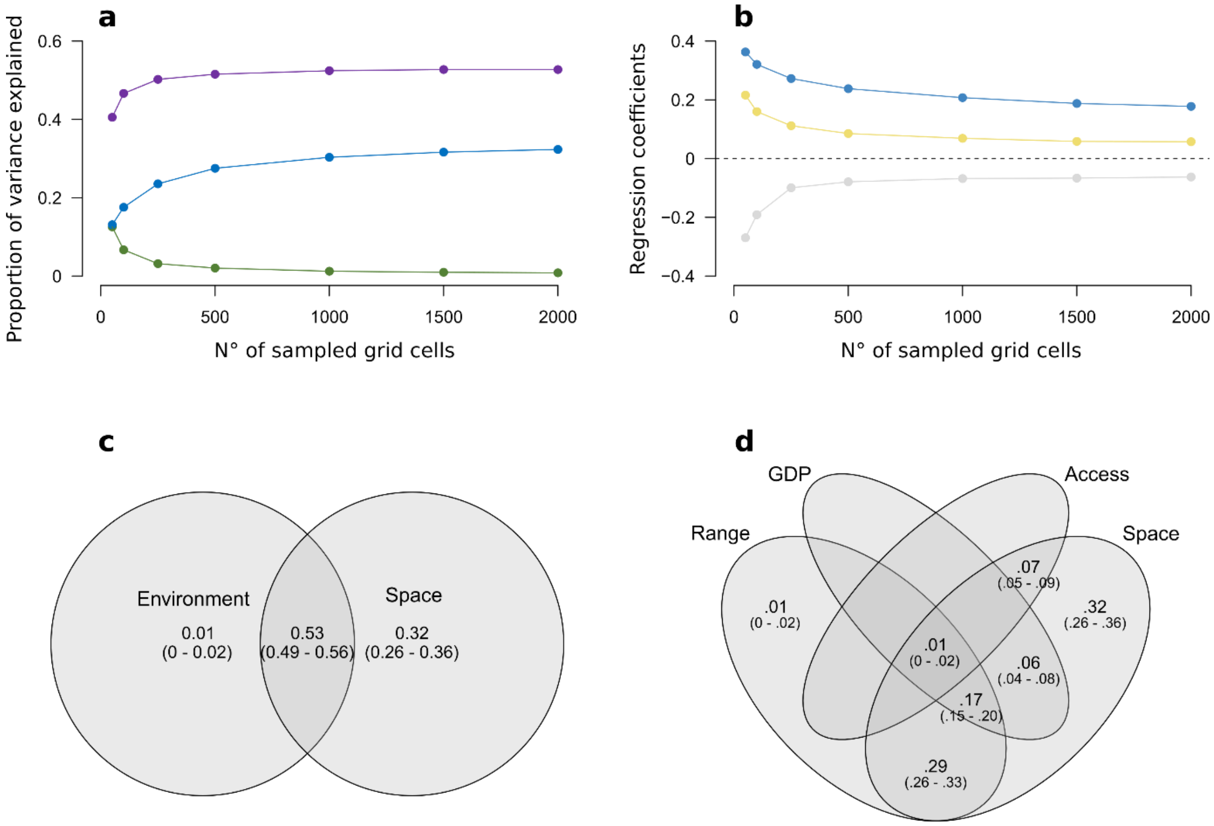

Fig. S2. Results of the resampling approach used to estimate the statistical distribution of the variation partitioning components and the multiple regression coefficients of the model explaining trait information coverage for birds considering only public datasets. a) Tendency lines of variance partitioning components: median values for unique environmental (or socio-environmental, green line), shared (purple line), and unique geographical (blue line) effects on birds trait coverage worldwide at different samples sizes. b) Tendency lines of the standardized regression coefficients: median values for average range size (blue line), GDP (yellow line) and accessibility (grey line) at different samples sizes. c) Variance partitioning of the effects of environmental and geographical variables on birds trait coverage, with median values and 95% CI limits for the 1000 samples. d) Variance partitioning of the effects of average range size, GDP per capita, on-ground accessibility and geographical variables, with median values and 95% CI limits for the 1000 samples (values < 0.01 are not shown). The median value and 95% CI limits of the standardized regression coefficients at the sample size of 1000 grid cells was 0.19 (0.04, 0.32) for average range size, 0.06 (-0.01, 0.16) for GDP per capita and -0.07 (-0.13, 0) for on-ground accessibility.

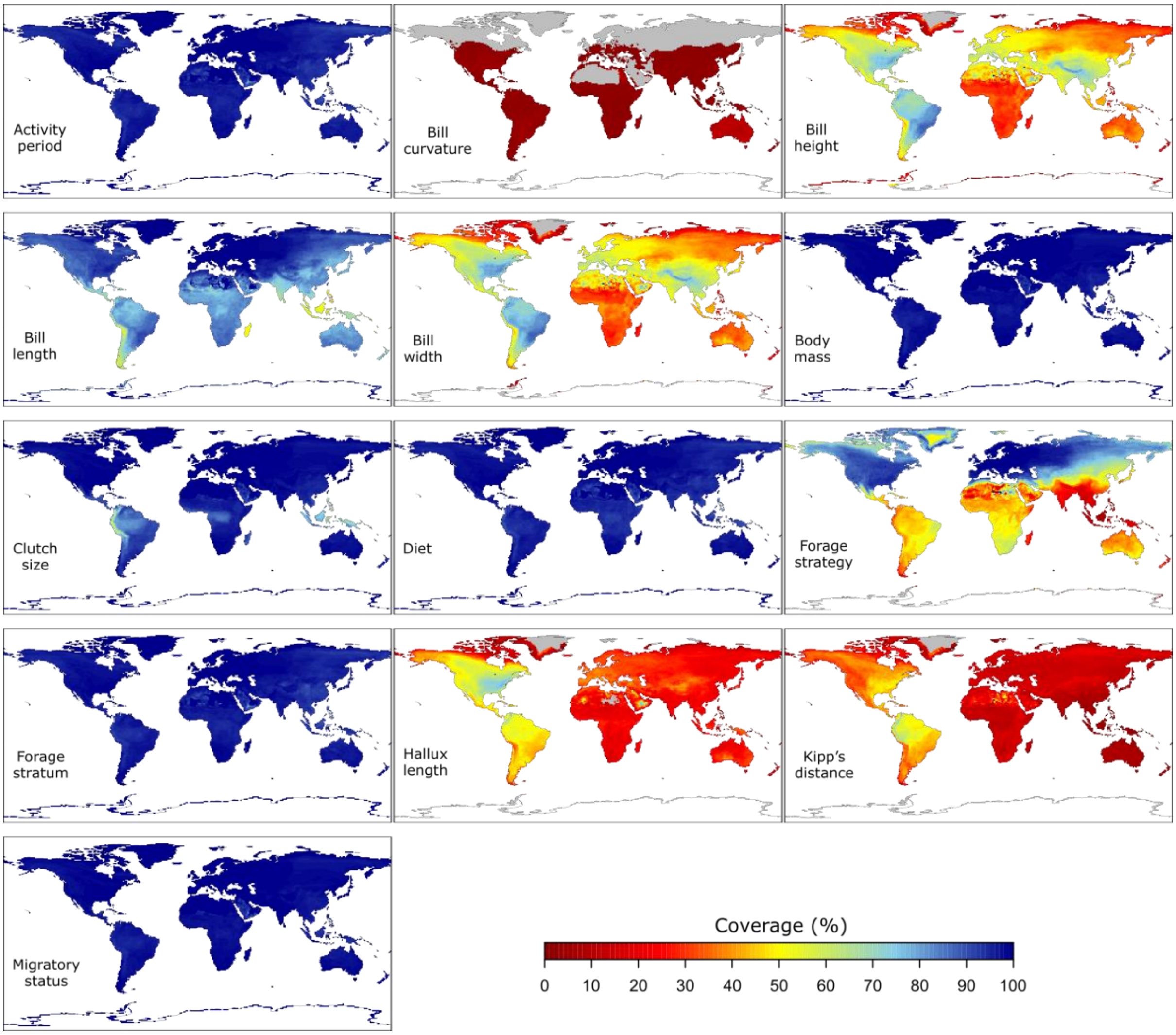

Fig. S3. Spatial variation of average coverage for each bird trait investigated in our study. Grey cells indicate regions where the trait remains unknown for all species. Figure continues to the next page.

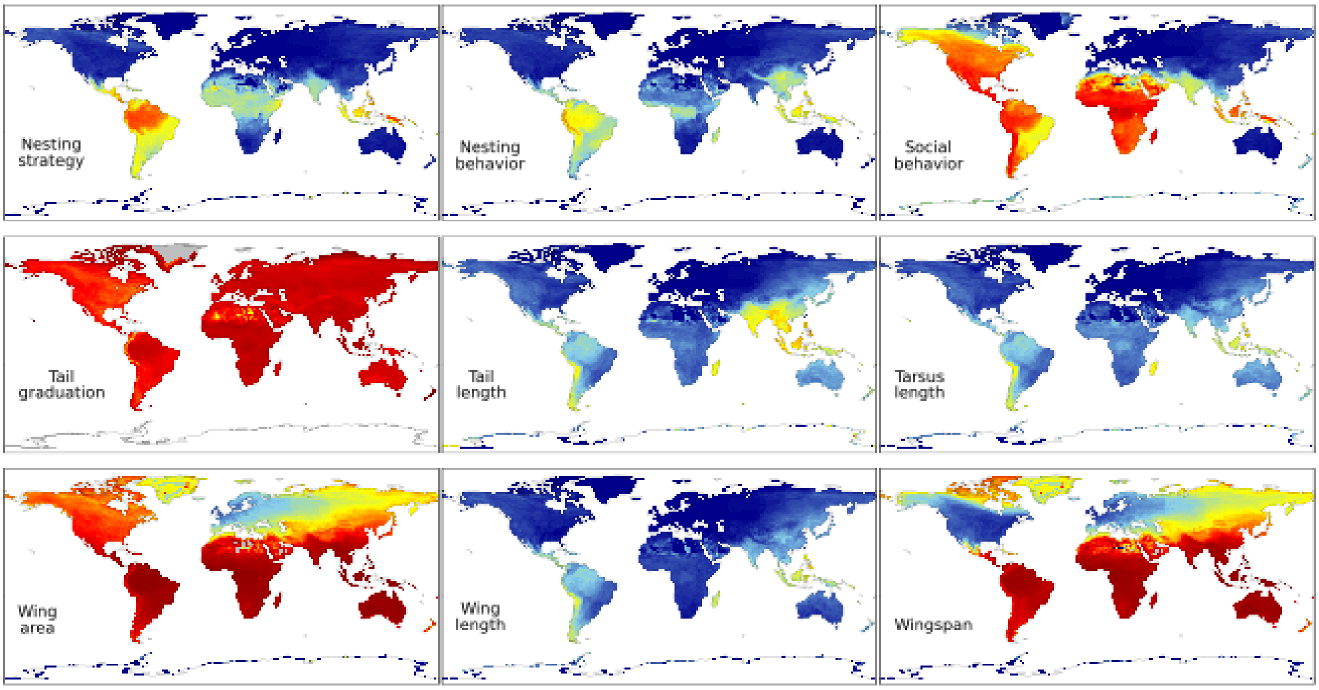

Fig. S3. Continued.

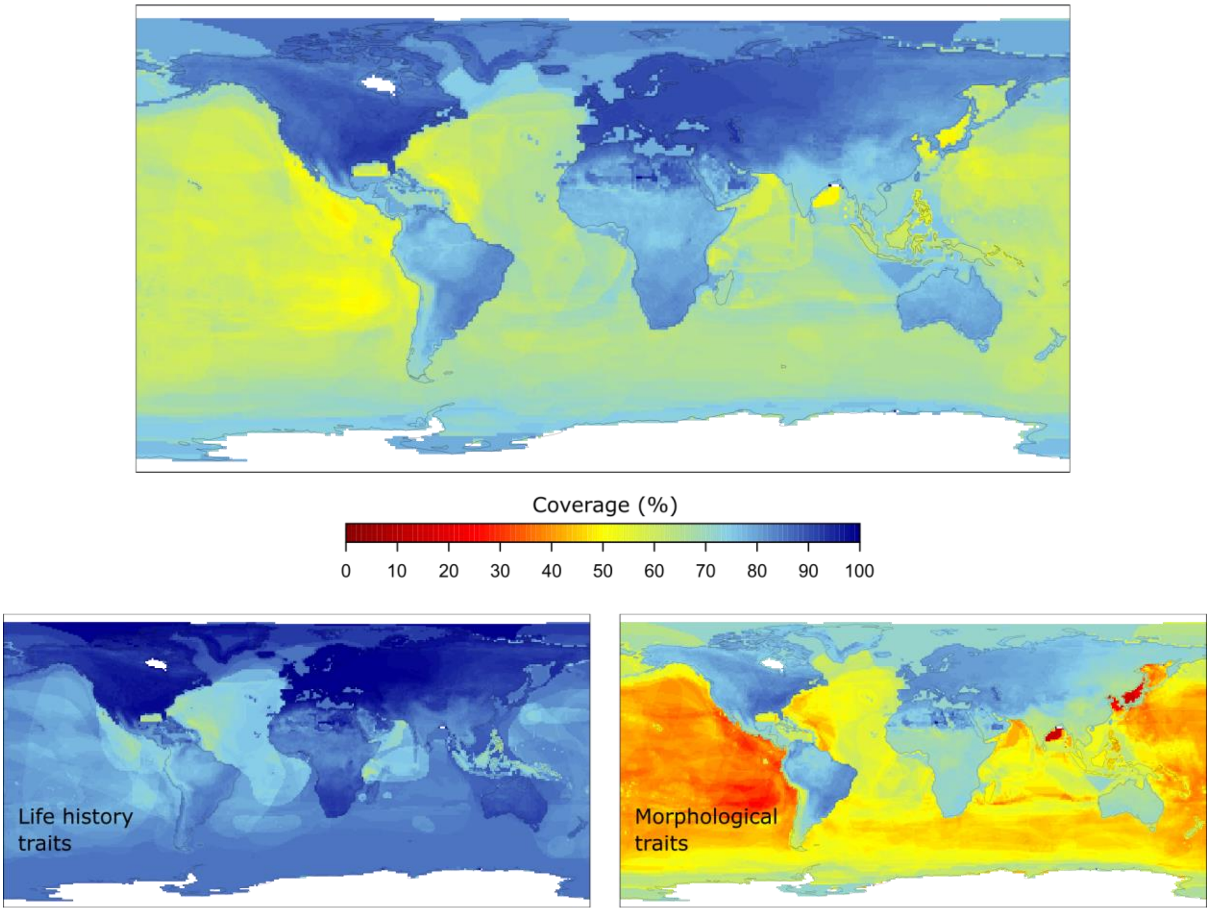

Fig. S4. Spatial variation of average trait coverage in birds considering all the 14 functional traits evaluated in our study (top), only life history traits (bottom-left), and only morphological traits (bottom-right) without masking ocean grid cells.

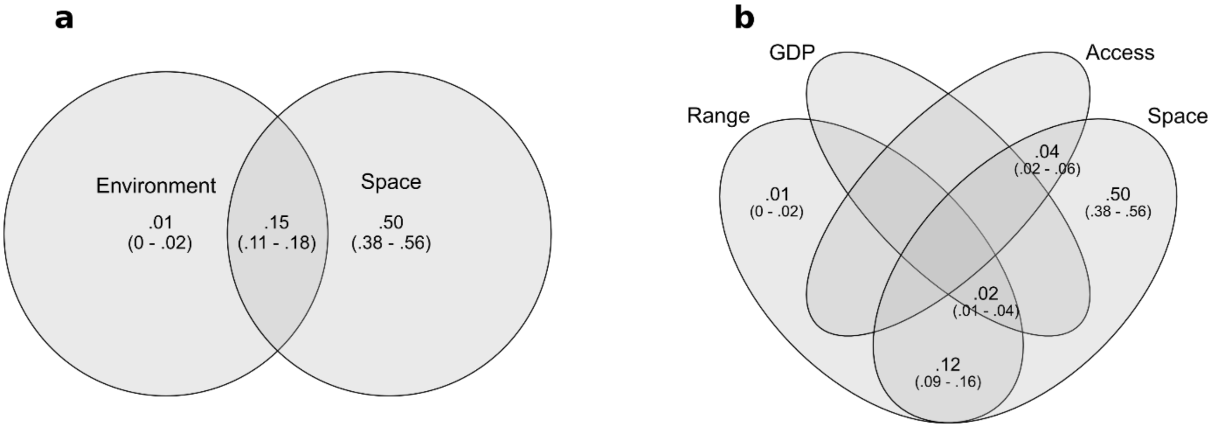

Fig. S5. Results of the resampling approach used to estimate the statistical distribution of the variation partitioning components and the multiple regression coefficients of the model explaining trait information coverage for birds considering public datasets plus the additional information from the Handbook of Birds of the World (del Hoyo et al. 1992-2011) and Pigot *et al.* (2020). a) Variance partitioning of the effects of environmental and geographical variables on birds trait coverage, with median values and 95% CI limits for the 1000 samples. d) Variance partitioning of the effects of average range size, GDP per capita, on-ground accessibility and geographical variables, with median values and 95% CI limits for the 1000 samples (values < 0.01 are not shown). The median value and 95% CI limits of the standardized regression coefficients at the sample size of 1000 grid cells was 0.14 (0.02, 0.29) for average range size, -0.01 (-0.10, 0.09) for GDP per capita and -0.05 (-0.14, 0.04) for on-ground accessibility.

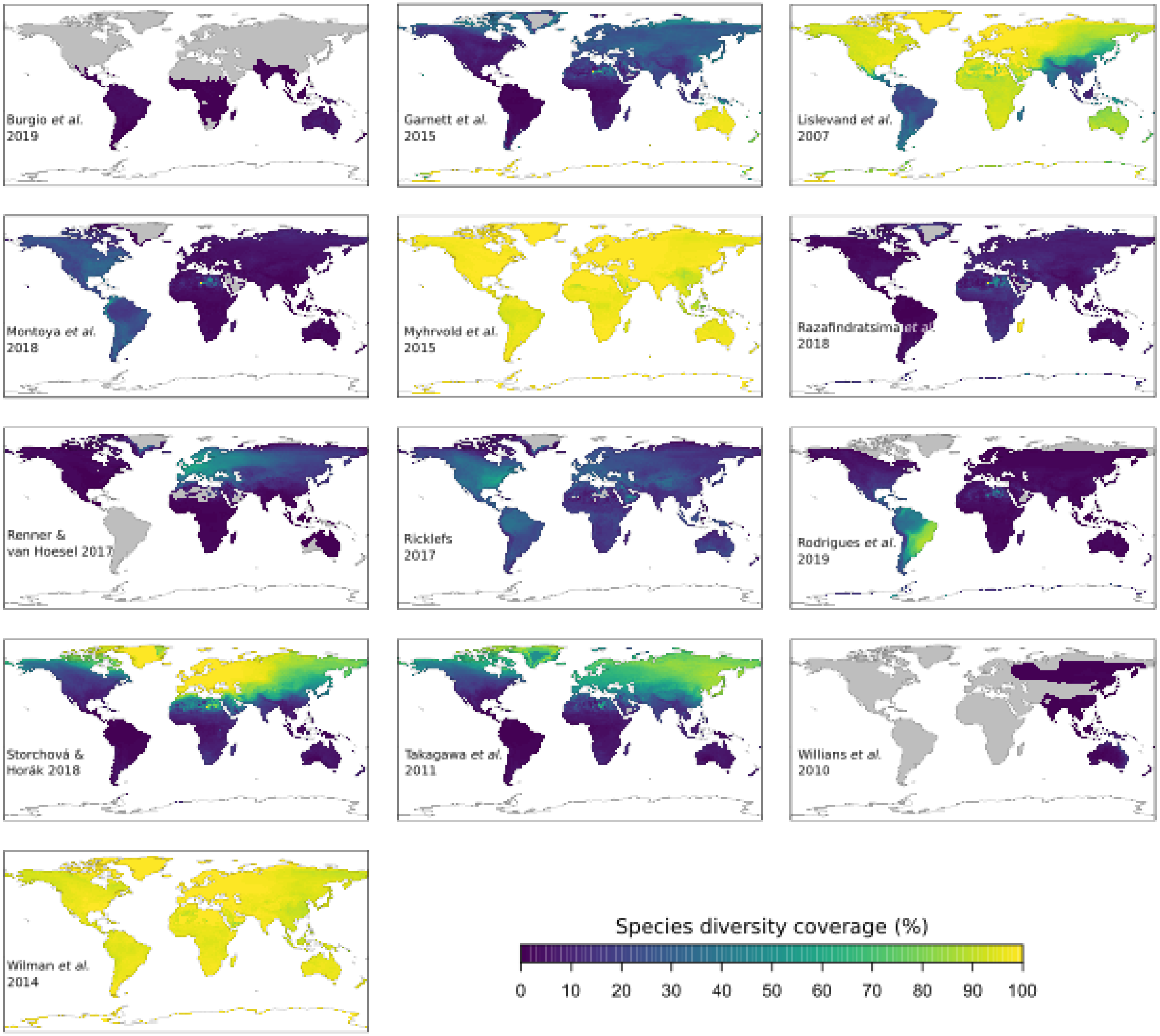

Fig. S6. Spatial diversity coverage of 13 data papers with bird traits. Grey cells indicate regions not covered by the data paper.

Appendix A

Appendix A1. List of the 148 references reviewed in this study to select the most relevant functional traits according to the ecological literature.

Alexander, J., Ehlers Smith, D.A., Ehlers Smith, Y.C. & Downs, C.T. (2019a). A multi-taxa functional diversity assessment of the effects of eco-estate development in the mixed land-use mosaic of the KwaZulu-Natal North Coast, South Africa. *Landsc. Urban Plan.*, 192, 103650.

Alexander, J., Ehlers Smith, D.A., Ehlers Smith, Y.C. & Downs, C.T. (2019b). Drivers of fine-scale avian functional diversity with changing land use: an assessment of the effects of eco-estate housing development and management. *Landsc. Ecol.*, 34, 537–549.

Almeida, S.M., Juen, L., Sobral, F.L. & Santos, M.P.D. (2018). The influence of biogeographic history on the functional and phylogenetic diversity of passerine birds in savannas and forests of the Brazilian Amazon. *Ecol. Evol.*, 8, 3617–3627.

Almeida, S.M., Silva, L., Cardoso, M., Cerqueira, P., Paraense, M. & Goeldi -Mpeg, E. (2016). The effects of oil palm plantations on the functional diversity of Amazonian birds Bird telemetry monitoring to evaluate loss of habitat in mining area in the northeastern Amazon. View project Rede Amazônia Sustentável View project. *Artic. J. Trop. Ecol.*

dos Anjos, L., Bochio, G.M., Medeiros, H.R., Almeida, B. de A., Lindsey, B.R.A., Calsavara, L.C., *et al.* (2019). Insights on the functional composition of specialist and generalist birds throughout continuous and fragmented forests. *Ecol. Evol.*, 9, ece3.5204.

de Arruda Almeida, B., Gimenes, M.R. & dos Anjos, L. (2017). Wading bird functional diversity in a floodplain: Influence of habitat type and hydrological cycle. *Austral Ecol.*, 42, 84–93.

Barbaro, L., Allan, E., Ampoorter, E., Castagneyrol, B., Charbonnier, Y., De Wandeler, H., *et al.* (2019). Biotic predictors complement models of bat and bird responses to climate and tree diversity in European forests. *Proc. R. Soc. B Biol. Sci.*, 286, 20182193.

Barbaro, L., Brockerhoff, E.G., Giffard, B. & van Halder, I. (2012). Edge and area effects on avian assemblages and insectivory in fragmented native forests. *Landsc. Ecol.*, 27, 1451–1463.

Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I. & Brockerhoff, E.G. (2014). Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. *Divers. Distrib.*, 20, 149–159.

Barbaro, L. & van Halder, I. (2009). Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography*, 32, 321–333.

Barbaro, L., Rusch, A., Muiruri, E.W., Gravellier, B., Thiery, D. & Castagneyrol, B. (2017).

Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. *J. Appl. Ecol.*, 54, 500–508.

Barbet-Massin, M. & Jetz, W. (2015). The effect of range changes on the functional turnover, structure and diversity of bird assemblages under future climate scenarios. *Glob. Chang. Biol.*, 21, 2917–2928.

Barnagaud, J.-Y., Gaüzère, P., Zuckerberg, B., Princé, K. & Svenning, J.-C. (2017a). Temporal changes in bird functional diversity across the United States. *Oecologia*, 185, 737–748.

Barnagaud, J.-Y., Kissling, W.D., Tsirogiannis, C., Fisikopoulos, V., Villéger, S., Sekercioglu, C.H., *et al.* (2017b). Biogeographical, environmental and anthropogenic determinants of global patterns in bird taxonomic and trait turnover. *Glob. Ecol. Biogeogr.*, 26, 1190–1200.

Barros, F.M., Martello, F., Peres, C.A., Pizo, M.A. & Ribeiro, M.C. (2019). Matrix type and landscape attributes modulate avian taxonomic and functional spillover across habitat boundaries in the Brazilian Atlantic Forest. *Oikos*, 128, 1600–1612.

Batisteli, A., Tanaka, M. & Souza, A. (2018). Bird Functional Traits Respond to Forest Structure in Riparian Areas Undergoing Active Restoration. *Diversity*, 10, 90.

Belmaker, J. & Jetz, W. (2015). Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecol. Lett.*, 18, 563–571.

Boesing, A.L., Nichols, E. & Metzger, J.P. (2018). Biodiversity extinction thresholds are modulated by matrix type. *Dryad*.

Boyer, A.G. & Jetz, W. (2014). Extinctions and the loss of ecological function in island bird communities. *Glob. Ecol. Biogeogr.*, 23, 679–688.

Bregman, T.P., Lees, A.C., MacGregor, H.E.A., Darski, B., de Moura, N.G., Aleixo, A., *et al.* (2016). Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc. R. Soc. B Biol. Sci.*, 283, 20161289.

Calba, S., Maris, V. & Devictor, V. (2014). Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds: separating ecological drivers from methodological choices. *Glob. Ecol. Biogeogr.*, 23, 669–678.

de Camargo, U., Roslin, T. & Ovaskainen, O. (2019). Spatio-temporal scaling of biodiversity in acoustic tropical bird communities. *Ecography*, 42, 1936–1947.

Cannon, P.G., Gilroy, J.J., Tobias, J.A., Anderson, A., Haugaasen, T. & Edwards, D.P. (2019). Land-sparing agriculture sustains higher levels of avian functional diversity than land sharing. *Glob. Chang. Biol.*, 25, 1576–1590.

Chalmandrier, L., Münkemüller, T., Devictor, V., Lavergne, S. & Thuiller, W. (2015). Decomposing changes in phylogenetic and functional diversity over space and time. *Methods Ecol. Evol.*, 6, 109–118.

Chapman, P.M., Tobias, J.A., Edwards, D.P. & Davies, R.G. (2018). Contrasting impacts of land-use change on phylogenetic and functional diversity of tropical forest birds. *J. Appl. Ecol.*, 55, 1604–1614.

Charbonnier, Y.M., Barbaro, L., Barnagaud, J.-Y., Ampoorter, E., Nezan, J., Verheyen, K., *et al.* (2016). Bat and bird diversity along independent gradients of latitude and tree composition in European forests. *Oecologia*, 182, 529–537.

Che, X., Chen, D., Zhang, M., Quan, Q., Møller, A.P. & Zou, F. (2019). Seasonal dynamics of waterbird assembly mechanisms revealed by patterns in phylogenetic and functional diversity in a subtropical wetland. *Biotropica*, 51, 421–431.

Chevalier, M., Lindström, Å., Pärt, T. & Knape, J. (2019). Changes in forest bird abundance, community structure and composition following a hurricane in Sweden. *Ecography*, 42, 1862–1873.

Child, M.F., Cumming, G.S. & Amano, T. (2009). Assessing the broad-scale impact of agriculturally transformed and protected area landscapes on avian taxonomic and functional richness. *Biol. Conserv.*, 142, 2593–2601.

Chiron, F., Chargé, R., Julliard, R., Jiguet, F. & Muratet, A. (2014). Pesticide doses, landscape structure and their relative effects on farmland birds. *Agric. Ecosyst. Environ.*, 185, 153–160.

Coetzee, B.W.T. & Chown, S.L. (2016). Land-use change promotes avian diversity at the expense of species with unique traits. *Ecol. Evol.*, 6, 7610–7622.

Concepción, E.D., Götzenberger, L., Nobis, M.P., de Bello, F., Obrist, M.K. & Moretti, M. (2017). Contrasting trait assembly patterns in plant and bird communities along environmental and human-induced land-use gradients. *Ecography*, 40, 753–763.

Cosset, C.C.P. & Edwards, D.P. (2017). The effects of restoring logged tropical forests on avian phylogenetic and functional diversity. *Ecol. Appl.*, 27, 1932–1945.

Costantini, D., Edwards, D.P. & Simons, M.J.P. (2016). Life after logging in tropical forests of Borneo: A meta-analysis. *Biol. Conserv.*, 196, 182–188.

De Coster, G., Banks-Leite, C. & Metzger, J.P. (2015). Atlantic forest bird communities provide different but not fewer functions after habitat loss. *Proc. R. Soc. B Biol. Sci.*, 282, 20142844.

Dehling, D.M., Jordano, P., Schaefer, H.M., Böhning-Gaese, K. & Schleuning, M. (2016). Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. *Proc. R. Soc. B Biol. Sci.*, 283, 20152444.

Dehling, D.M., Töpfer, T., Schaefer, H.M., Jordano, P., Böhning-Gaese, K. & Schleuning, M. (2014). Functional relationships beyond species richness patterns: trait matching in plant-bird mutualisms across scales. *Glob. Ecol. Biogeogr.*, 23, 1085–1093.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.*, 13, 1030–1040.

Dias, D.F.C., Ribeiro, M.C., Felber, Y.T., Cintra, A.L.P., de Souza, N.S. & Hasui, É. (2016). Beauty before age: landscape factors influence bird functional diversity in naturally regenerating fragments, but regeneration age does not. *Restor. Ecol.*, 24, 259–270.

Ding, Z., Feeley, K.J., Wang, Y., Pakeman, R.J. & Ding, P. (2013). Patterns of bird functional diversity on land-bridge island fragments. *J. Anim. Ecol.*, 82, 781–790.

Doohan, B., Kemp, J. & Fuller, S. (2019). Diversity favours the old: Metrics of avian diversity increase in aging regrowth Acacia woodlands of semi-arid eastern Australia. *Glob. Ecol. Conserv.*, 20, e00798.

Echeverri, A., Frishkoff, L.O., Gomez, J.P., Zook, J.R., Juárez, P., Naidoo, R., *et al.* (2019). Precipitation and tree cover gradients structure avian alpha diversity in North-western Costa Rica. *Divers. Distrib.*, 25, 1222–1233.

Ehlers Smith, D.A., Ehlers Smith, Y.C. & Downs, C.T. (2019). Promoting functional connectivity of anthropogenically-fragmented forest patches for multiple taxa across a critically endangered biome. *Landsc. Urban Plan.*, 190, 103579.

Ehlers Smith, D.A., Si, X., Ehlers Smith, Y.C. & Downs, C.T. (2018a). Seasonal variation in avian diversity and tolerance by migratory forest specialists of the patch-isolation gradient across a fragmented forest system. *Biodivers. Conserv.*, 27, 3707–3727.

Ehlers Smith, D.A., Si, X., Ehlers Smith, Y.C., Kalle, R., Ramesh, T. & Downs, C.T. (2018b). Patterns of avian diversity across a decreasing patch-size gradient in a critically endangered subtropical forest system. *J. Biogeogr.*, 45, 2118–2132.

Ehlers Smith, Y.C., Ehlers Smith, D.A., Seymour, C.L., Thébault, E. & van Veen, F.J.F. (2015). Response of avian diversity to habitat modification can be predicted from life-history traits and ecological attributes. *Landsc. Ecol.*, 30, 1225–1239.

Emer, C., Galetti, M., Pizo, M.A., Guimarães, P.R., Moraes, S., Piratelli, A., *et al.* (2018). Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. *Ecol. Lett.*, 21, 484–493.

Endenburg, S., Mitchell, G.W., Kirby, P., Fahrig, L., Pasher, J. & Wilson, S. (2019). The homogenizing influence of agriculture on forest bird communities at landscape scales. *Landsc. Ecol.*, 34, 2385–2399.

Evans, B.S., Reitsma, R., Hurlbert, A.H. & Marra, P.P. (2018). Environmental filtering of avian communities along a rural-to-urban gradient in Greater Washington, D.C. *Ecosphere*, 9, e02402.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., *et al.* (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.*, 12, 22–33.

Godet, L., Gaüzere, P., Jiguet, F. & Devictor, V. (2015). Dissociating several forms of commonness in birds sheds new light on biotic homogenization. *Glob. Ecol. Biogeogr.*, 24, 416–426.

Gove, A.D., Hylander, K., Nemomissa, S., Shimelis, A. & Enkossa, W. (2013). Structurally complex farms support high avian functional diversity in tropical montane Ethiopia. *J.*

Trop. Ecol., 29, 87–97.

Guerrero, I., Morales, M.B., Oñate, J.J., Aavik, T., Bengtsson, J., Berendse, F., *et al.* (2011). Taxonomic and functional diversity of farmland bird communities across Europe: effects of biogeography and agricultural intensification. *Biodivers. Conserv.*, 20, 3663–3681.

Hamer, K.C., Newton, R.J., Edwards, F.A., Benedick, S., Bottrell, S.H. & Edwards, D.P. (2015). Impacts of selective logging on insectivorous birds in Borneo: The importance of trophic position, body size and foraging height. *Biol. Conserv.*, 188, 82–88.

Hanz, D.M., Böhning-Gaese, K., Ferger, S.W., Fritz, S.A., Neuschulz, E.L., Quitián, M., *et al.* (2019). Functional and phylogenetic diversity of bird assemblages are filtered by different biotic factors on tropical mountains. *J. Biogeogr.*, 46, 291–303.

Hausner, V.H., Yoccoz, N.G. & Ims, R.A. (2003). Selecting indicator traits for monitoring land use impacts: birds in northern coastal birch forests. *Ecol. Appl.*, 13, 999– 1012.

Heath, S.K. & Long, R.F. (2019). Multiscale habitat mediates pest reduction by birds in an intensive agricultural region. *Ecosphere*, 10.

Hevia, V., Carmona, C.P., Azcárate, F.M., Torralba, M., Alcorlo, P., Ariño, R., *et al.* (2016). Effects of land use on taxonomic and functional diversity: a cross-taxon analysis in a Mediterranean landscape. *Oecologia*, 181, 959–970.

Hidasi-Neto, J., Barlow, J. & Cianciaruso, M. V. (2012). Bird functional diversity and wildfires in the Amazon: The role of forest structure. *Anim. Conserv.*, 15, 407–415.

Hořák, D., Ferenc, M., Sedláček, O., Motombi, F.N., Svoboda, M., Altman, J., *et al.* (2019). Forest structure determines spatial changes in avian communities along an elevational gradient in tropical Africa. *J. Biogeogr.*, 46, 2466–2478.

Ibarra, J.T. & Martin, K. (2015). Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. *Biol. Conserv.*, 192, 418–427.

Imai, H. & Nakashizuka, T. (2010). Environmental factors affecting the composition and diversity of avian community in mid- to late breeding season in urban parks and green spaces. *Landsc. Urban Plan.*, 96, 183–194.

Jacoboski, L.I., Debastiani, V.J., de Mendonça-Lima, A. & Hartz, S.M. (2016). How do diversity and functional nestedness of bird communities respond to changes in the landscape caused by eucalyptus plantations? *Community Ecol.*, 17, 107–113.

Jarzyna, M.A. & Jetz, W. (2017). A near half-century of temporal change in different facets of avian diversity. *Glob. Chang. Biol.*, 23, 2999–3011.

Jia, Q., Wang, X., Zhang, Y., Cao, L. & Fox, A.D. (2018). Drivers of waterbird communities and their declines on Yangtze River floodplain lakes. *Biol. Conserv.*, 218, 240–246.

Jonason, D., Ekroos, J., Öckinger, E., Helenius, J., Kuussaari, M., Tiainen, J., *et al.* (2017). Weak functional response to agricultural landscape homogenisation among plants, butterflies and birds. *Ecography*, 40, 1221–1230.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R. & Daily, G.C. (2012).

Intensive agriculture erodes β-diversity at large scales. *Ecol. Lett.*, 15, 963–970.

Ke, A., Sibiya, M.D., Reynolds, C., McCleery, R.A., Monadjem, A. & Fletcher, R.J. (2018). Landscape heterogeneity shapes taxonomic diversity of non-breeding birds across fragmented savanna landscapes. *Biodivers. Conserv.*, 27, 2681–2698.

Klingbeil, B.T. & Willig, M.R. (2016). Matrix composition and landscape heterogeneity structure multiple dimensions of biodiversity in temperate forest birds. *Biodivers. Conserv.*, 25, 2687–2708.

Kühnert, K., Grass, I. & Waltert, M. (2019). Sacred groves hold distinct bird assemblages within an Afrotropical savanna. *Glob. Ecol. Conserv.*, 18, e00656.

Kupsch, D., Vendras, E., Ocampo-Ariza, C., Batáry, P., Motombi, F.N., Bobo, K.S., *et al.* (2019). High critical forest habitat thresholds of native bird communities in Afrotropical agroforestry landscapes. *Biol. Conserv.*, 230, 20–28.

Laiolo, P., Pato, J. & Obeso, J.R. (2018). Ecological and evolutionary drivers of the elevational gradient of diversity. *Ecol. Lett.*, 21, 1022–1032.

Lee, M.-B. & Carroll, J.P. (2018). Effects of patch size and basal area on avian taxonomic and functional diversity in pine forests: Implication for the influence of habitat quality on the species-area relationship. *Ecol. Evol.*, 8, 6909–6920.

Lee, M., Gates, B.J., Cooper, R.J. & Carroll, J.P. (2020). Avian taxonomic and functional diversity in early stage of longleaf pine (Pinus palustris) stands restored at agricultural lands: variations in scale dependency. *Restor. Ecol.*, 28, 147–155.

Lees, A.C. & Moura, N.G. (2017). Taxonomic, phylogenetic and functional diversity of an urban Amazonian avifauna. *Urban Ecosyst.*, 20, 1019–1025.

Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., *et al.* (2016). Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. R. Soc. B Biol. Sci.*, 283, 20160084.

Leveau, L.M. (2019). Urbanization induces bird color homogenization. *Landsc. Urban Plan.*, 192, 103645.

Li, C., Zhang, Y., Zha, D., Yang, S., Huang, Z.Y.X. & Boer, W.F. (2019). Assembly processes of waterbird communities across subsidence wetlands in China: A functional and phylogenetic approach. *Divers. Distrib.*, 25, 1118–1129.

Lindenmayer, D., Blanchard, W., Tennant, P., Barton, P., Ikin, K., Mortelliti, A., *et al.* (2015). Richness is not all: How changes in avian functional diversity reflect major landscape modification caused by pine plantations. *Divers. Distrib.*, 21, 836–847.

Lindenmayer, D.B., MacGregor, C., Wood, J., Westgate, M.J., Ikin, K., Foster, C., *et al.* (2016). Bombs, fire and biodiversity: Vertebrate fauna occurrence in areas subject to military training. *Biol. Conserv.*, 204, 276–283.

Lindenmayer, D.B., Wood, J., MacGregor, C., Hobbs, R.J. & Catford, J.A. (2017). Non-target impacts of weed control on birds, mammals, and reptiles. *Ecosphere*, 8, e01804.

Martin, A.E., Desrochers, A. & Fahrig, L. (2017). Homogenization of dispersal ability across bird species in response to landscape change. *Oikos*, 126, 996–1003.

Martin, E.A., Viano, M., Ratsimisetra, L., Laloë, F. & Carrière, S.M. (2012). Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. *Agric. Ecosyst. Environ.*, 149, 1–9.

Martínez-Salinas, A., DeClerck, F., Vierling, K., Vierling, L., Legal, L., Vílchez-Mendoza, S., *et al.* (2016). Bird functional diversity supports pest control services in a Costa Rican coffee farm. *Agric. Ecosyst. Environ.*, 235, 277–288.

Maseko, M.S.T., Zungu, M.M., Ehlers Smith, D.A., Ehlers Smith, Y.C. & Downs, C.T. (2019). High microhabitat heterogeneity drives high functional traits in forest birds in five protected forest areas in the urban mosaic of Durban, South Africa. *Glob. Ecol. Conserv.*, 18, e00645.

Matthews, T.J., Cottee-Jones, H.E.W., Bregman, T.P. & Whittaker, R.J. (2017). Assessing the relative importance of isolated Ficus trees to insectivorous birds in an Indian human-modified tropical landscape. *Biodivers. Conserv.*, 26, 2803–2819.

Maure, L.A., Rodrigues, R.C., Alcântara, Â. V., Adorno, B.F.C.B., Santos, D.L., Abreu, E.L., *et al.* (2018). Functional Redundancy in bird community decreases with riparian forest width reduction. *Ecol. Evol.*, 8, 10395–10408.

McCleery, R., Monadjem, A., Baiser, B., Fletcher, R., Vickers, K. & Kruger, L. (2018). Animal diversity declines with broad-scale homogenization of canopy cover in African savannas. *Biol. Conserv.*, 226, 54–62.

Mendez, V., Gill, J.A., Burton, N.H.K., Austin, G.E., Petchey, O.L. & Davies, R.G. (2012). Functional diversity across space and time: trends in wader communities on British estuaries. *Divers. Distrib.*, 18, 356–365.

Méndez, V., Wood, J.R. & Butler, S.J. (2018). Resource diversity and provenance underpin spatial patterns in functional diversity across native and exotic species. *Ecol. Evol.*, 8, 4409–4421.

Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F. & Mouquet, N. (2011). Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Glob. Ecol. Biogeogr.*, 20, 893–903.

Monnet, A.-C., Jiguet, F., Meynard, C.N., Mouillot, D., Mouquet, N., Thuiller, W., *et al.* (2014). Asynchrony of taxonomic, functional and phylogenetic diversity in birds. *Glob. Ecol. Biogeogr.*, 23, 780–788.

Moreno-Contreras, I., Gómez de Silva, H., Andrade-González, V., Vital-García, C. & Ortiz-Ramírez, M.F. (2019). Disentangling an avian assemblages' evolutionary and functional history in a Chihuahuan desert city. *Urban Ecosyst.*, 22, 893–906.

Muñoz, M.C., Schaefer, H.M., Böhning-Gaese, K., Neuschulz, E.L. & Schleuning, M. (2017). Phylogenetic and Functional Diversity of Fleshy-Fruited Plants Are Positively Associated with Seedling Diversity in a Tropical Montane Forest. *Front. Ecol. Evol.*, 5.

Murray, B.D., Holland, J.D., Summerville, K.S., Dunning, J.B., Saunders, M.R. & Jenkins, M.A. (2017). Functional diversity response to hardwood forest management varies across taxa and spatial scales. *Ecol. Appl.*, 27, 1064–1081.

Nell, C.S., Abdala-Roberts, L., Parra-Tabla, V. & Mooney, K.A. (2018). Tropical tree diversity mediates foraging and predatory effects of insectivorous birds. *Proc. R. Soc. B Biol. Sci.*, 285, 20181842.

Norfolk, O., Jung, M., Platts, P.J., Malaki, P., Odeny, D. & Marchant, R. (2017). Birds in the matrix: the role of agriculture in avian conservation in the Taita Hills, Kenya. *Afr. J. Ecol.*, 55, 530–540.

Norfolk, O., Power, A., Eichhorn, M.P. & Gilbert, F. (2015). Migratory bird species benefit from traditional agricultural gardens in arid South Sinai. *J. Arid Environ.*, 114, 110–115.

Nowak, L., Kissling, W.D., Bender, I.M.A., Dehling, D.M., Töpfer, T., Böhning-Gaese, K., *et al.* (2019). Projecting consequences of global warming for the functional diversity of fleshy-fruited plants and frugivorous birds along a tropical elevational gradient. *Divers. Distrib.*, 25, 1362–1374.

Oliveira Hagen, E., Hagen, O., Ibáñez-Álamo, J.D., Petchey, O.L. & Evans, K.L. (2017). Impacts of Urban Areas and Their Characteristics on Avian Functional Diversity. *Front. Ecol. Evol.*, 5.

Oliveira, J. de, Almeida, S.M., Florêncio, F.P., Pinho, J.B., Oliveira, D.M.M., Ligeiro, R., *et al.* (2019). Environmental structure affects taxonomic diversity but not functional structure of understory birds in the southwestern Brazilian Amazon. *Acta Amaz.*, 49, 232–241.

Park, D.S. & Razafindratsima, O.H. (2019). Anthropogenic threats can have cascading homogenizing effects on the phylogenetic and functional diversity of tropical ecosystems. *Ecography*, 42, 148–161.

Pauw, A. & Louw, K. (2012). Urbanization Drives a Reduction in Functional Diversity in a Guild of Nectar-feeding Birds. *Ecol. Soc.*, 17, art27.

Pavoine, S. & Izsák, J. (2014). New biodiversity measure that includes consistent interspecific and intraspecific components. *Methods Ecol. Evol.*, 5, 165–172.

Pellissier, V., Barnagaud, J.-Y., Kissling, W.D., Şekercioğlu, Ç. & Svenning, J.-C. (2018). Niche packing and expansion account for species richness-productivity relationships in global bird assemblages. *Glob. Ecol. Biogeogr.*, 27, 604–615.

Petchey, O.L., Evans, K.L., Fishburn, I.S. & Gaston, K.J. (2007). Low functional diversity and no redundancy in British avian assemblages. *J. Anim. Ecol.*, 76, 977–985.

Phillips, A.G., Töpfer, T., Rahbek, C., Böhning-Gaese, K. & Fritz, S.A. (2018). Effects of phylogeny and geography on ecomorphological traits in passerine bird clades. *J. Biogeogr.*, 45, 2337–2347.

Philpott, S.M. & Bichier, P. (2012). Effects of shade tree removal on birds in coffee agroecosystems in Chiapas, Mexico. *Agric. Ecosyst. Environ.*, 149, 171–180.

Philpott, S.M., Soong, O., Lowenstein, J.H., Pulido, A.L., Lopez, D.T., Flynn, D.F.B., *et al.*

(2009). Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. *Ecol. Appl.*, 19, 1858–1867.

Pigot, A.L., Bregman, T., Sheard, C., Daly, B., Etienne, R.S. & Tobias, J.A. (2016). Quantifying species contributions to ecosystem processes: a global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. *Dryad*.

van der Plas, F., van Klink, R., Manning, P., Olff, H. & Fischer, M. (2017). Sensitivity of functional diversity metrics to sampling intensity. *Methods Ecol. Evol.*, 8, 1072–1080.

Plein, M., Längsfeld, L., Neuschulz, E.L., Schultheiß, C., Ingmann, L., Töpfer, T., *et al.* (2013). Constant properties of plant–frugivore networks despite fluctuations in fruit and bird communities in space and time. *Ecology*, 94, 1296–1306.

Prescott, G.W., Gilroy, J.J., Haugaasen, T., Medina Uribe, C.A., Foster, W.A. & Edwards, D.P. (2016). Reducing the impacts of Neotropical oil palm development on functional diversity. *Biol. Conserv.*, 197, 139–145.

Pringle, S., Chiweshe, N., Steward, P.R., Mundy, P.J. & Dallimer, M. (2019). Rapid redistribution of agricultural land alters avian richness, abundance, and functional diversity. *Ecol. Evol.*, 9, 12259–12271.

Pryde, E.C., Nimmo, D.G., Holland, G.J. & Watson, S.J. (2016). Species' traits affect the occurrence of birds in a native timber plantation landscape. *Anim. Conserv.*, 19, 526–538.

Quitián, M., Santillán, V., Espinosa, C.I., Homeier, J., Böhning-Gaese, K., Schleuning, M., *et al.* (2019). Direct and indirect effects of plant and frugivore diversity on structural and functional components of fruit removal by birds. *Oecologia*, 189, 435–445.

Rapacciuolo, G., Marin, J., Costa, G.C., Helmus, M.R., Behm, J.E., Brooks, T.M., *et al.* (2017). The signature of human pressure history on the biogeography of body mass in tetrapods. *Glob. Ecol. Biogeogr.*, 26, 1022–1034.

Rocha, J., Laps, R.R., Machado, C.G. & Campiolo, S. (2019). The conservation value of cacao agroforestry for bird functional diversity in tropical agricultural landscapes. *Ecol. Evol.*, 9, 7903–7913.

Rogers, A.M. & Chown, S.L. (2014). Novel ecosystems support substantial avian assemblages: the case of invasive alien Acacia thickets. *Divers. Distrib.*, 20, 34–45.

Rolo, V., Olivier, P.I. & van Aarde, R. (2017). Tree and bird functional groups as indicators of recovery of regenerating subtropical coastal dune forests. *Restor. Ecol.*, 25, 788–797.

Ross, S.R.P.-J., Hassall, C., Hoppitt, W.J.E., Edwards, F.A., Edwards, D.P. & Hamer, K.C. (2017). Incorporating intraspecific trait variation into functional diversity: Impacts of selective logging on birds in Borneo. *Methods Ecol. Evol.*, 8, 1499–1505.

Ross, S.R.P. -J., Friedman, N.R., Janicki, J. & Economo, E.P. (2019). A test of trophic and functional island biogeography theory with the avifauna of a continental archipelago. *J. Anim. Ecol.*, 88, 1392–1405.

Saavedra, F., Hensen, I., Beck, S.G., Böhning-Gaese, K., Lippok, D., Töpfer, T., *et al.*

(2014). Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. *Oecologia*, 176, 837–848.

Santillán, V., Quitián, M., Tinoco, B.A., Zárate, E., Schleuning, M., Böhning-Gaese, K., *et al.* (2019). Different responses of taxonomic and functional bird diversity to forest fragmentation across an elevational gradient. *Oecologia*, 189, 863–873.

Sattler, T., Pezzatti, G.B., Nobis, M.P., Obrist, M.K., Roth, T. & Moretti, M. (2014). Selection of Multiple Umbrella Species for Functional and Taxonomic Diversity to Represent Urban Biodiversity. *Conserv. Biol.*, 28, 414–426.

Schipper, A.M., Belmaker, J., de Miranda, M.D., Navarro, L.M., Böhning-Gaese, K., Costello, M.J., *et al.* (2016). Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Glob. Chang. Biol.*, 22, 3948–3959.

Schumm, M., Edie, S.M., Collins, K.S., Gómez-Bahamón, V., Supriya, K., White, A.E., *et al.* (2019). Common latitudinal gradients in functional richness and functional evenness across marine and terrestrial systems. *Proc. R. Soc. B Biol. Sci.*, 286, 20190745.

Schütz, C. & Schulze, C.H. (2015). Functional diversity of urban bird communities: effects of landscape composition, green space area and vegetation cover. *Ecol. Evol.*, 5, 5230–5239.

Seymour, C.L., Simmons, R.E., Joseph, G.S. & Slingsby, J.A. (2015). On Bird Functional Diversity: Species Richness and Functional Differentiation Show Contrasting Responses to Rainfall and Vegetation Structure in an Arid Landscape. *Ecosystems*, 18, 971–984.

Sitters, H., Di Stefano, J., Christie, F., Swan, M. & York, A. (2016). Bird functional diversity decreases with time since disturbance: Does patchy prescribed fire enhance ecosystem function? *Ecol. Appl.*, 26, 115–127.

Skórka, P., Żmihorski, M., Grzędzicka, E., Martyka, R. & Sutherland, W.J. (2018). The role of churches in maintaining bird diversity: A case study from southern Poland. *Biol. Conserv.*, 226, 280–287.

Sobral, F.L., Lees, A.C. & Cianciaruso, M. V. (2016). Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. *Ecol. Lett.*, 19, 1091–1100.

La Sorte, F.A., Lepczyk, C.A., Aronson, M.F.J., Goddard, M.A., Hedblom, M., Katti, M., *et al.* (2018). The phylogenetic and functional diversity of regional breeding bird assemblages is reduced and constricted through urbanization. *Divers. Distrib.*, 24, 928–938.

Suri, J., Anderson, P.M., Charles-Dominique, T., Hellard, E. & Cumming, G.S. (2017). More than just a corridor: A suburban river catchment enhances bird functional diversity. *Landsc. Urban Plan.*, 157, 331–342.

Tinoco, B.A., Santillán, V.E. & Graham, C.H. (2018). Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. *Ecol. Evol.*, 8, 3478–3490.

Trindade-Filho, J., Sobral, F.L., Cianciaruso, M.V. & Loyola, R.D. (2012). Using indicator groups to represent bird phylogenetic and functional diversity. *Biol. Conserv.*, 146, 155–162.

Trisos, C.H., Petchey, O.L. & Tobias, J.A. (2014). Unraveling the Interplay of Community Assembly Processes Acting on Multiple Niche Axes across Spatial Scales. *Am. Nat.*, 184, 593–608.

Tscharntke, T., Sekercioglu, C.H., Dietsch, T. V., Sodhi, N.S., Hoehn, P. & Tylianakis, J.M. (2008). Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, 89, 944–951.

Vaccaro, A.S., Filloy, J. & Bellocq, M.I. (2019). What land use better preserves taxonomic and functional diversity of birds in a grassland biome? *Avian Conserv. Ecol.*, 14, art1.

Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Dolédec, S., Dubs, F., *et al.* (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodivers. Conserv.*, 19, 2921–2947.

Virkkala, R. & Lehikoinen, A. (2017). Birds on the move in the face of climate change: High species turnover in northern Europe. *Ecol. Evol.*, 7, 8201–8209.

Vollstädt, M.G.R., Ferger, S.W., Hemp, A., Howell, K.M., Töpfer, T., Böhning-Gaese, K., *et al.* (2017). Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. *Glob. Ecol. Biogeogr.*, 26, 963–972.

Walker, S.C., Poos, M.S. & Jackson, D.A. (2008). Functional rarefaction: estimating functional diversity from field data. *Oikos*, 117, 286–296.

Wang, J.W., Poh, C.H., Tan, C.Y.T., Lee, V.N., Jain, A. & Webb, E.L. (2017). Building biodiversity: drivers of bird and butterfly diversity on tropical urban roof gardens. *Ecosphere*, 8, e01905.

Weideman, E.A., Slingsby, J.A., Thomson, R.L. & Coetzee, B.T.W. (2020). Land cover change homogenizes functional and phylogenetic diversity within and among African savanna bird assemblages. *Landsc. Ecol.*, 35, 145–157.

White, H.J., Montgomery, W.I., Storchová, L., Hořák, D. & Lennon, J.J. (2018). Does functional homogenization accompany taxonomic homogenization of British birds and how do biotic factors and climate affect these processes? *Ecol. Evol.*, 8, 7365–7377.

Yen, J.D.L., Thomson, J.R., Keith, J.M., Paganin, D.M., Fleishman, E., Bennett, A.F., *et al.* (2018). Linking species richness and size diversity in birds and fishes. *Ecography*, 41, 1979–1991.

Zapponi, L., Luiselli, L., Cento, M., Catorci, A. & Bologna, M.A. (2014). Disentangling patch and landscape constraints of nested assemblages. *Basic Appl. Ecol.*, 15, 712–719.

Zeng, Q., Reid, J., Saintilan, N., Colloff, M.J., Lei, G. & Wen, L. (2019). Contrasting diversity patterns of breeding Anatidae in the Northern and Southern Hemispheres. *Ecol. Evol.*, 9, 9990–10003.

Zhang, Q., Holyoak, M., Chen, C., Liu, Z., Liu, J., Che, X., *et al.* (2020). Trait-mediated filtering drives contrasting patterns of species richness and functional diversity across montane bird assemblages. *J. Biogeogr.*, 47, 301–312.

Appendix A2. Data papers with birds functional traits found in our data search.

Burgio, K.R., Davis, K.E., Dreiss, L.M., Klingbeil, B.T., Cisneros, L.M., Presley, S.J., *et al.* (2019). Phylogenetic supertree and functional trait database for all extant parrots. *Data in Brief*, 24, 103882. https://doi.org/10.1016/j.dib.2019.103882.

Garnett, S., Duursma, D., Ehmke, G., Patrick-Jean G., Stewart, A., Szabo, J.K. *et al.* (2015). Biological, ecological, conservation and legal information for all species and subspecies of Australian bird. *Sci Data 2*, 150061. https://doi.org/10.1038/sdata.2015.61.

Lislevand, T., Figuerola, J. & Székely, T. (2007). Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. *Ecology*, 88-1605.https://doi.org/10.1890/06-2054

Montoya, P.M., González, A., Tenorio, E.A., López-Ordóñez, J.P., Pinto, A., Cueva, D., *et al.* (2018). A morphological database for 606 Colombian bird species. *Ecology*, 99, 1693. https://doi.org/10.1002/ecy.2368.

Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L. & Ernest, S.K. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109-3109. https://doi.org/10.1890/15-0846R.1.

Razafindratsima, O.H., Yacoby, Y. & Park, D.S. (2018). MADA: Malagasy Animal trait Data Archive. Ecology, 99, 990. https://doi.org/10.1002/ecy.2167.

Renner, S.C., & van Hoesel, W. (2017). Ecological and functional traits in 99 bird species over a large-scale gradient in Germany. *DATA*, 2, 12. https://doi.org/10.3390/data2020012.

Ricklefs, R.E. (2017). Passerine morphology: external measurements of approximately one-quarter of passerine bird species. *Ecology*, 98, 1472-1472. https://doi.org/10.1002/ecy.1783.

Rodrigues, R.C., Hasui, É., Assis, J.C., Pena, J.C.C., Muylaert, R.L., Tonetti, V.R., *et al.* (2019). Atlantic Bird Traits: A dataset of bird morphological traits from the Atlantic Forests of South America. *Ecology*, 100, e02647. https://doi.org/10.1002/ecy.2647.

Storchová, L., Hořák, D., & Hurlbert, A. (2018). Life-history characteristics of European birds. *Glob. Ecol. Biogeogr.*, 27, 400-406. https://doi.org/10.1111/geb.12709.

Takagawa, S., Ueta, M., Amano, T., Okahisa, Y. & Kamioka, M. (2011). JAVIAN Database: a species-level database of life history,ecology and morphology of bird species in Japan. *Bird Res.*,7, R9-R12. 10.11211/birdresearch.7.R9.

Williams, S.E., VanDerWal, J., Isaac, J., Shoo, L.P., Storlie, C., Fox, S., *et al.* (2010). Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology*, 91, 2493. https://doi.org/10.1890/09-1069.1.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

Appendix A3. Datasets published in public repositories with birds functional traits found in our data search.

Acker, P., Grégoire, A., Rat, M., Spottiswoode, C.N., van Dijk, R.E., Paquet, M., et al. (2015). Disruptive viability selection on a black plumage trait associated with dominance. *Dryad*. Dataset. https://doi.org/10.5061/dryad.b5837.

Adamkova, M., Bilkova, Z., Tomasek, O., Simek, Z., Simek, Z. & Albrecht, T. (2019). Feather steroid hormone concentrations in relation to age, sex, and moulting time in a long distance migratory passerine. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.v4bf803.

Araya-Ajoy, Y.G., Ranke, P.S.S., Kvalnes, T., Rønning, B., Holand, H., Myhre, A.M., *et al.* (2020). Characterizing morphological (co)variation using structural equation models: body size, allometric relationships and evolvability in a house sparrow metapopulation. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.s654mf6.

Armstrong, C., Richardson, D.S., Hipperson, H., Horsburgh, G.J., Kuepper, C., Percival-Alwyn, L., *et al.* (2018). Genomic associations with bill length and disease reveal drift and selection across island bird populations. *Dryad*. Dataset. https://doi.org/10.5061/dryad.9642b.

Arnold, S.J. & Houck, L.D. (2016). Can the Fisher-Lande process account for birds of paradise and other sexual radiations?. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.66ft5.

Atwell, J.W., Cardoso, G.C., Whittaker, D.J., Price, T.D. & Ketterson, E.D. (2014). Hormonal, behavioral, and life-history traits exhibit correlated shifts in relation to population establishment in a novel environment. *Dryad*. Dataset. https://doi.org/10.5061/dryad.b6h36 .

Badás, E.P., Autor, A., Martínez, J., Rivero-de Aguilar, J. & Merino, S. (2020). Individual quality and extra-pair paternity in the blue tit: sexy males bear the costs. *Dryad*. v3. Dataset. https://doi.org/10.5061/dryad.pzgmsbcgf.

Balasubramaniam, P. & Rotenberry, J.T. (2017). Elevation and latitude interact to drive life-history variation in precocial birds: a comparative analysis using Galliformes. *Dryad*. Dataset. https://doi.org/10.5061/dryad.38s8g.

Barbaro, L., Allan, E., Ampoorter, E., Castagneyrol, B., Charbonnier, Y., De Wandeler, H., *et al.* (2018). Biotic predictors complement models of bat and bird responses to climate and tree diversity in European forests. *Dryad*. Dataset. https://doi.org/10.5061/dryad.t48p8c0.

Bellier, E., Kéry, M. & Schaub, M. (2019). Relationships between vital rates and ecological traits in an avian community. *Dryad*. Dataset. https://doi.org/10.5061/dryad.474jc10.

Bentz, A.B., Andreasen, V.A. & Navara, K.J. (2018). An experimental test of the relationship between yolk testosterone and the social environment in a colonial passerine. *Dryad*. Dataset. https://doi.org/10.5061/dryad.42tv030.

Bertrand, J.A.M., Delahaie, B., Bourgeois, Y.X.C., Duval, T., García-Jiménez, R., Cornuault, J., *et al.* (2016). The role of selection and historical factors in driving population differentiation along an elevational gradient in an island bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.50b93.

Bishop, P.J., Graham, D.F., Lamas, L.P., Hutchinson, J.R., Rubenson, J., Hancock, J.A., *et al.* (2018). The influence of speed and size on avian terrestrial locomotor biomechanics: Predicting locomotion in extinct theropod dinosaurs. PLoS ONE, 13, e0192172. Dataset. https://doi.org/10.1371/journal.pone.0192172.

Björklund, M. & Gustafsson, L. (2017). Subtle but ubiquitous selection on body size in a natural population of collared flycatchers over 33 years. *Dryad*. Dataset. https://doi.org/10.5061/dryad.24tm0.

Björklund, M., Husby, A. & Gustafsson, L. (2012). Rapid and unpredictable changes of the G-matrix in a natural bird population over 25 years. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s55c4.

Bowers, E.K., Forsman, A.M., Masters, B.S., Johnson, B.G.P., Johnson, L.S., Sakaluk, S.K., et al. (2015). Increased extra-pair paternity in broods of aging males and enhanced recruitment of extra-pair young in a migratory bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.v4b8n.

Boyle, W.A., Sandercock, B.K., & Martin, K. (2016). Patterns and drivers of intraspecific variation in avian life history along elevational gradients: a meta-analysis. *Dryad*. Dataset. https://doi.org/10.5061/dryad.h13vg.

Bregman, T.P., Lees, A.C., Seddon, N., MacGregor, H.E.A., Darski, B., Aleixo, A., *et al.* (2015). Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Figshare*. Dataset. https://doi.org/10.6084/m9.figshare.3563157.v1.

Brown, C.R. & Brown, M.B. (2017). Parasites favor intermediate nestling masses and brood sizes in cliff swallows. *Dryad*. Dataset. https://doi.org/10.5061/dryad.bt11p.

Brown, L.M. & Graham, C.H. (2016). Demography, traits, and vulnerability to urbanization: can we make generalizations?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.m3d4d.

Buckley, L.B., Khaliq, I., Swanson, D.L. & Hof, C. (2019). Does metabolism constrain bird and mammal ranges and predict shifts in response to climate change?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.68fr52p.

Buehler, D.M., Vézina, F., Goymann, W., Schwabl, I., Versteegh, M., Tieleman, B.I., *et al.*

(2012). Independence among physiological traits suggests flexibility in the face of ecological demands on phenotypes. *Dryad*. Dataset. https://doi.org/10.5061/dryad.4q6f1.

Caizergues, A.E., Gregoire, A. & Charmantier, A. (2018). Urban versus forest ecotypes are not explained by divergent reproductive selection. *Dryad*. Dataset. https://doi.org/10.5061/dryad.tv45802.

Calhim, S. & Montgomerie, R. (2014). Testis asymmetry in birds: the influences of sexual and natural selection. *Dryad*. Dataset. https://doi.org/10.5061/dryad.75t05.

Callan, L.M., La Sorte, F.A., Martin, T.E. & Rohwer, V.G. (2019). Higher nest predation favors rapid fledging at the cost of plumage quality in nestling birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.p6m33p3.

Camacho, C., Canal, D. & Potti, J. (2014). Nonrandom dispersal drives phenotypic divergence within a bird population. *Dryad*. Dataset. https://doi.org/10.5061/dryad.h22n9.

Cardoso, G.C. & Hu, Y. (2011). Birdsong performance and the evolution of simple (rather than elaborate) sexual signals. *Dryad*. Dataset. https://doi.org/10.5061/dryad.1q424.

Casagrande, S., Pinxten, R., Zaid, E. & Eens, M. (2015). Carotenoids, birdsong and oxidative status: administration of dietary lutein is associated with an increase in song rate and circulating antioxidants (albumin and cholesterol) and a decrease in oxidative damage. *Dryad*. Dataset. https://doi.org/10.5061/dryad.36bv0.

Castaño, M.I., Cadena, C.D. & Avendaño, J.E. (2019). Home-range size of an Andean bird: assessing the role of physical condition. *Dryad*. Dataset. https://doi.org/10.5061/dryad.j15b535.

Catry, T., Moreira, F., Alcazar, R. & Rocha, P.A. & Catry, I. (2016). Mechanisms and fitness consequences of laying decisions in a migratory raptor. *Dryad*. Dataset. https://doi.org/10.5061/dryad.9r6b3.

Chakarov, N., Jonker, R.M., Boerner, M., Hoffman, J.I. & Krüger, O. (2013). Variation at phenological candidate genes correlates with timing of dispersal and plumage morph in a sedentary bird of prey. *Dryad*. Dataset. https://doi.org/10.5061/dryad.r058p.

Chen, C., Holyoak, M., Si, X., Wang, Y. & Ding, P. (2018). Spatiotemporal distribution of seasonal bird assemblages on land-bridge islands: linking dynamic and static views of metacommunities. *PANGAEA*. Dataset. https://doi.org/10.1594/PANGAEA.885964.

Chira, A.M., Cooney, C.R., Bright, J.A., Capp, E.J.R., Hughes, E.C., Moody, C.J.A. *et al.* (2019). Correlates of rate heterogeneity in avian ecomorphological traits. *Dryad*. Dataset. https://doi.org/10.5061/dryad.4006fm8.

Class, B. & Brommer, J.E. (2018). Shared environmental effects bias phenotypic estimates of assortative mating in a wild bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.g983j23.

Cockburn, Andrew. 2006. Prevalence of different modes of parental care in birds. 273. Proc. R. Soc. Bhttp://doi.org/10.1098/rspb.2005.3458.

Corti, M., Romano, A., Costanzo, A., Bentz, A.B., Navara, K., Parolini, M., *et al.* (2018).

Protoporphyrin-based eggshell pigmentation is associated with female plumage colouration and predicts offspring sex ratio in the barn swallow. *Dryad*. Dataset. https://doi.org/10.5061/dryad.rc41072.

Cosset, C., Gilroy, J., Srinivasan, U., Hethcoat, M., Edwards, D. (2020). Mass-abundance scaling in avian communities is maintained after tropical selective logging. *Figshare*. Dataset. https://doi.org/10.15131/shef.data.11590902.v1.

Cramer, E.R.A., Kaiser, S.A., Webster, M.S., Sillett, T. S., Ryder, T. B.; Cramer, E.R.A., *et al.* (2017). Characterizing selection in black-throated blue warblers using a sexual network approach. *Dryad*. Dataset. https://doi.org/10.5061/dryad.r5nj3.

Crino, O.L., Prather, C.T. Driscoll, S.C., Good, J.M. & Breuner, C.W. (2014). Developmental stress increases reproductive success in male zebra finches. *Dryad*. Dataset. https://doi.org/10.5061/dryad.ct121.

Cubo, J., Le Roy, N., Martinez-Maza, C. & Montes, L. (2011). Paleohistological estimation of bone growth rate in extinct archosaurs. *Dryad*. Dataset. https://doi.org/10.5061/dryad.j2m25n82.

Cunha, F.C.R., Fontenelle, J.C.R. & Griesser, M. (2017). Predation risk drives the expression of mobbing across bird species. *Dryad*. Dataset. https://doi.org/10.5061/dryad.1j79t.

Davidson, G., Thornton, A., Clayton, N., Davidson, G.L. & Clayton, N.S. (2016). Evolution of iris colour in relation to cavity nesting and parental care in passerine birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.ks824.

de Lima, H.S., Las-Casas, F.M.G., Ribeiro, J.R.; Gonçalves-Souza, T. & Naka, L.N. (2019). Ecological and phylogenetic predictors of mobbing behavior in a tropical dry forest. *Dryad*, Dataset. https://doi.org/10.5061/dryad.4bp16g2.

de Magalhães, J.P., Costa, J.A. (2009). Database of vertebrate longevity records and their relation to other life-history traits. J. Evol. Biol., 22, 1770-1774. https://doi.org/10.1111/j.1420-9101.2009.01783.x.

de Zwaan, D.R., Greenwood, J.L. & Martin, K. (2016). Feather melanin and micro-structure variation in dark-eyed junco (Junco hyemalis) across an elevational gradient in the Selkirk Mountains. *Dryad*. Dataset. https://doi.org/10.5061/dryad.ks53j.

Dececchi, T.A. & Larsson, H.C.E. (2016). Assessing Arboreal Adaptations of Bird Antecedents: Testing the Ecological Setting of the Origin of the Avian Flight Stroke. PLoS ONE, 6, e22292. Dataset. https://doi.org/10.1371/journal.pone.0022292.

Dehnhard, N., Eens, M., Demongin, L., Quillfeldt, P. & Poisbleau, M. (2016). Individual consistency and phenotypic plasticity in rockhopper penguins: female but not male body mass links environmental conditions to reproductive investment. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s6f0p.

Dokter, A.M., Fokkema, W., Fokkema, W., Bekker, S.K., Bouten, W., Ebbinge, B.S., *et al.* (2018). Body stores persist as fitness correlate in a long-distance migrant released from food constraints. *Dryad*. Dataset. https://doi.org/10.5061/dryad.6b55m22.

DuBay, S., Wu, Y., Scott, G., Qu, Y., Liu, Q., Smith, J., et al. (2020). Life history predicts flight muscle phenotype and function in birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.jsxksn05s.

DuBay, S.G. & Witt, C.C. (2014). Differential high-altitude adaptation and restricted gene flow across a mid-elevation hybrid zone in Andean tit-tyrant flycatchers. *Dryad*. Dataset. https://doi.org/10.5061/dryad.f5t28.

Duursma, D.E. (2018). Avian breeding phenology and functional traits in relation to climatic variation. *figshare*. Dataset. https://doi.org/10.6084/m9.figshare.5413189.v4.

Echeverri, A., Karp, D., Naidoo, R., Tobias, J., Zhao, J. & Chan, K. (2019). Can avian functional traits predict cultural ecosystem services?. *Dryad*. v3. Dataset. https://doi.org/10.5061/dryad.cjsxksn1p.

Edme, Anais; Munclingwe, Pavel; Krist, Miloš; Munclinger, Pavel (2016). Female collared flycatchers choose neighbouring and older extra-pair partners from the pool of males around their nests, Dryad, Dataset, https://doi.org/10.5061/dryad.043tn.

Eliason, C.M. & Clarke, J.A. (2018). Metabolic physiology explains macroevolutionary trends in the melanic colour system across amniotes. *Dryad*. Dataset. https://doi.org/10.5061/dryad.qv871g8.

Elliott, K.H., Ricklefs, R.E., Gaston, A.J., Hatch, S.A., Speakman, J.R. & Davoren, G.K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Dryad*. Dataset. https://doi.org/10.5061/dryad.23td2.

Emaresi, G., Richter, H., Ducrest, A.; Bize, P., Simon, C. & Roulin, A. (2013). Pleiotropy in the melanocortin system: expression levels of this system are associated with melanogenesis and pigmentation in the tawny owl (Strix aluco). *Dryad*. Dataset. https://doi.org/10.5061/dryad.6f4g4.

Eyres, A., Böhning-Gaese, K. & Fritz, S.A. (2017). Quantification of climatic niches in birds: adding the temporal dimension. *Senckenberg*. Database. http://dataportal-senckenberg.de/database/metacat/bikf.10058.1/bikf.

Farwig, N., Schabo, D.G. & Albrecht, J. (2017). Trait-associated loss of frugivores in fragmented forest does not affect seed removal rates. *Dryad*. Dataset. https://doi.org/10.5061/dryad.2784g.

Forstmeier, W., Ihle, M., Opatova, P., Martin, K., Knief, U., Albrechtová, J., *et al.* (2017). Testing the phenotype-linked fertility hypothesis in the presence and absence of inbreeding. *Dryad*. Dataset. https://doi.org/10.5061/dryad.515c6.

Forstmeier, W., Schielzeth, H., Mueller, J.C., Ellegren, H. & Kempenaers, B. (2012). Heterozygosity-fitness correlations in zebra finches: microsatellite markers can be better than their reputation. *Dryad*. Dataset. https://doi.org/10.5061/dryad.6v0h65g3.

Fowler, M.A.; Paquet, M., Legault, V., Cohen, A.A. & Williams, T.D. (2018). Physiological predictors of reproductive performance in the European Starling (Sturnus vulgaris). *Dryad*. Dataset. https://doi.org/10.5061/dryad.j0s643c.

Francis, C.D. (2016). Vocal traits and diet explain avian sensitivities to anthropogenic noise.

Dryad. Dataset. https://doi.org/10.5061/dryad.7v6q3.

Friedman, N.R., Miller, E.T., Ball, J.R., Kasuga, H., Remeš, V. & Economo, E.P. (2019). Evolution of a multifunctional trait: shared effects of foraging ecology and thermoregulation on beak morphology, with consequences for song evolution. *Dryad*. v3. Dataset. https://doi.org/10.5061/dryad.crjdfn312.

Fuentes-G., J.A., Housworth, E.A., Weber, A. & Martins, E.P. (2016). Phylogenetic ANCOVA: estimating changes in evolutionary rates as well as relationships between traits. *Dryad*. Dataset. https://doi.org/10.5061/dryad.2r504

Galen, S.C., Speer, K.A., Perkins & S.L. (2019). Evolutionary lability of host associations promotes phylogenetic overdispersion of co-infecting blood parasites. *Dryad*. Dataset. https://doi.org/10.5061/dryad.3r88b02

Galván, I. & Møller, A.P. (2011). Brain size and the expression of pheomelanin-based colour in birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.8262

Galván, I., Bonisoli-Alquati, A., Jenkinson, S., Ghanem, G., Wakamatsu, K., Mousseau, Timothy A., *et al.* (2015). Chronic exposure to low-dose radiation at Chernobyl favours adaptation to oxidative stress in birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.rb5hr

García Peña. G.E. (2019). West Nile Virus evolves at the pace of its avian hosts' life-history. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.xgxd254c0

Garcia-Longoria, L., Marzal, A., de Lope, F. & Garamszegi, L. (2019). Host-parasite interaction explains variation in the prevalence of avian haemosporidians at the community level. *PLoS ONE*. Dataset. https://doi.org/10.1371/journal.pone.0205624

García-Navas, V., Rodriguez-Rey, M. & Christidis, L. (2017). Ecological opportunity and ecomorphological convergence in Australasian robins (Petroicidae). *Dryad*. Dataset. https://doi.org/10.5061/dryad.tq76n

Gilsenan, C., Valcu, M. & Kempenaers, B. (2019). Timing of arrival in the breeding area is repeatable and affects reproductive success in a non-migratory population of blue tits. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.2rbnzs7hz

Giraudeau, M. & Ducatez, S. (2016). Co-adjustment of yolk antioxidants and androgens in birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.7gk6d

Gleditsch, J.M. & Sperry, J.H. (2020). Rapid morphological change of non-native frugivores on the Hawaiian island of O'ahu. *Dryad*. Dataset. https://doi.org/10.5061/dryad.3f2bm54

González, A.D., Matta, N.E., Ellis, V.A.; Miller, E.T., Ricklefs, R.E. & Gutiérrez, H.R. (2014). Mixed Species Flock, Nest Height, and Elevation Partially Explain Avian Haemoparasite Prevalence in Colombia. *PLoS ONE*. Dataset. https://doi.org/10.1371/journal.pone.0100695

Gonzalez-Voyer, A., den Tex, R.-J., Castelló, A. & Leonard, J.A (2012). Evolution of Acoustic and Visual Signals in Asian Barbets. *Dryad*. Dataset. https://doi.org/10.5061/dryad.kd73k

Gowen, F.C, Maley, J.M., Cicero, C., Peterson, A.T., Faircloth, B.C., Warr, T.C. *et al.* 2014. Speciation in Western Scrub-Jays, Haldane's rule, and genetic clines in secondary contact. *Dryad*. Dataset. https://doi.org/10.5061/dryad.57f48

Grunst, A.S., Grunst, M.L., Formica, V.A., Korody, M.L., Betuel, A.M.; Barcelo-Serra, M., *et al.* (2017). Morph-specific patterns of reproductive senescence: connections to discrete reproductive strategies. *Dryad*. Dataset. https://doi.org/10.5061/dryad.vj5pn

Grunst, A.S., Grunst, M.L.; Thys, B., Raap, T., Daem, N., Pinxten, R., *et al.* (2019). Variation in animal personality traits across a metal pollution gradient in a free-living songbird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.dc611p0

Grunst, M., Grunst, A., Pinxten, R., Bervoets, L. & Eens, M. (2019). Carotenoid- but not melanin-based plumage coloration is negatively related to metal exposure and proximity to the road in an urban songbird. *Dryad.* v2. Dataset. https://doi.org/10.5061/dryad.zgmsbcc6h

Gutiérrez, J.S., Piersma, T. & Thieltges, D.W. (2019). Micro- and macroparasite species richness in birds: the role of host life history and ecology. *Dryad*. Dataset. https://doi.org/10.5061/dryad.sk5972v

Habel, J.C., Tobias, J.A. & Fischer, C. (2019). Movement ecology of Afrotropical birds: Functional traits provide complementary insights to species identity. *Dryad*. Dataset. https://doi.org/10.5061/dryad.22mq8g2

Halfwerk, W., Both, C. & Slabbekoorn, H. (2016). Noise affects nest box choice of 2 competing songbird species, but not their reproduction. *Dryad*. Dataset. https://doi.org/10.5061/dryad.tb5d8

Hasegawa, M. & Arai, E. (2018). Differential visual ornamentation between brood-parasitic and parental cuckoos. *Dryad*. Dataset. https://doi.org/10.5061/dryad.7sh2h-10.1111/jeb.13240

Hau, M., Haussmann, M.F., Greives, T.J., Matlack, C., Costantini, D., Quetting, M., *et al.* (2015). Repeated stressors in adulthood increase the rate of biological ageing. *Dryad*. Dataset. https://doi.org/10.5061/dryad.5sv61

Heinen, J.H., van Loon, E.E., Hansen, D.M. & Kissling, W.D. (2017). Extinction-driven changes in frugivore communities on oceanic islands. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s522m

Hennin, H., Legagneux, P., Gilchrist, H., Bêty, J., McMurtry, J. & Love, O.P. (2019). Plasma mammalian leptin analogue predicts reproductive phenology, but not reproductive output in a capital-income breeding seaduck. *Dryad*. Dataset. https://doi.org/10.5061/dryad.283n1c6

Hosner, P.A., Tobias, J.A., Braun, E.L. & Kimball, R.T. (2017). How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes). *Dryad*. Dataset. https://doi.org/10.5061/dryad.kr96h

Husby, A. & Husby, M. (2014). Interspecific analysis of vehicle avoidance behavior in birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.jv387

Husby, A., Gustafsson, L. & Qvarnström, A. (2011). Low genetic variance in the duration of the incubation period in a collared flycatcher (Ficedula albicollis) population. *Dryad*. Dataset. https://doi.org/10.5061/dryad.3hq60- 10.1086/663193

Husby, A., Kawakami, T., Rönnegård, L., Smeds, L., Ellegren, H., Qvarnström, A., *et al.* (2015). Genome-wide association mapping in a wild avian population identifies a link between genetic and phenotypic variation in a life-history trait. *Dryad*. Dataset. https://doi.org/10.5061/dryad.sm1vt

Husby, A., Schielzeth, H., Forstmeier, W., Gustafsson, L. & Qvarnström, A. (2012). Sex chromosome linked genetic variance and the evolution of sexual dimorphism of quantitative traits. *Dryad*. Dataset. https://doi.org/10.5061/dryad.451n7

Iglesias-Carrasco, M., Duchene, D., Head, M., Møller, A. & Cain, K. (2019). Sex in the city: sexual selection and urban colonisation in passerines. *Dryad*. Dataset. https://doi.org/10.5061/dryad.5bp74q1

Iglesias-Carrasco, M., Jennions, M., Ho, S. & Duchene, D. (2019). Sexual selection, body mass, and molecular evolution interact to predict diversification in birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.p39d12d

Ikin, K., Barton, P.S., Blanchard, W., Crane, M., Stein, J. & Lindenmayer, D.B. (2019). Avian functional responses to landscape recovery. *Dryad*. Dataset. https://doi.org/10.5061/dryad.d6k0804

Illera, J.C., Palmero, A.M., Laiolo, P., Rodríguez, F., Moreno, Á.C. & Navascués, M. (2014). Genetic, morphological and acoustic evidence reveals lack of diversification in the colonization process in an island bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.q42p7

Inostroza-Michael, O., Hernández, C.E., Rodríguez-Serrano, E., Avaria-Llautureo, J. & Rivadeneira, M.M. (2018). Interspecific geographic range size–body size relationship and the diversification dynamics of Neotropical Furnariid birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.975k5j8

Jacob, S., Parthuisot, N., Vallat, A., Ramon-Portugal, F., Helfenstein, F. & Heeb, P. (2015). Microbiome affects egg carotenoid investment, nestling development and adult oxidative costs of reproduction in Great tits. *Dryad*. Dataset. https://doi.org/10.5061/dryad.9n741

Jamwal, P.S., Chandan, P., Rattan, R., Anand, A., Kannan, P.M. & Parsons, M.H. (2017). Survey of avifauna of the Gharana wetland reserve: implications for conservation in a semi-arid agricultural setting on the Indo-Pakistan border. *PANGAEA.* Dataset. https://doi.org/10.1594/PANGAEA.874857

Jenkins, B.R., Vitousek, M.N., Hubbard, J.K. & Safran, R.J. (2014). An experimental analysis of the heritability of variation in glucocorticoid concentrations in a wild avian population. *Dryad*. Dataset. https://doi.org/10.5061/dryad.h14kk

Jetz, W., Sekercioglu, C.H. & Böhning-Gaese, K. (2008). The worldwide variation in avian clutch size across species and space. PLoS Biol. 6, 2650–2657.

https://doi.org/10.1371/journal.pbio.0060303

Johnson, A.E., Mitchell, J.S. & Brown, M.B. (2017). Convergent evolution in social swallows (Aves: Hirundinidae). *Dryad*. Dataset. https://doi.org/10.5061/dryad.m07t1

Jones, M.R., Witt, C.C., Jones, M.R. & Witt, C.C. (2014). Migrate small, sound big: functional constraints on body size promote tracheal elongation in cranes. *Dryad*. Dataset. https://doi.org/10.5061/dryad.p8g3r

Jønsson, K.A., Fabre, P.H., Fritz, S.A., Etienne, R.S., Ricklefs, R.E.; Jørgensen, T.B., *et al.* (2012). Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas, Dryad, Dataset, https://doi.org/10.5061/dryad.mh2qf615

Jønsson, K.A., Lessard, J.P., Ricklefs, R.E.& Lessard, J.P (2015). The evolution of morphological diversity in continental assemblages of Passerine birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.qk461

Kennedy, C. M., Marra, P.P., Fagan, W.F. & Neel, M.C. (2016). Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *figshare*. Dataset. https://doi.org/10.6084/m9.figshare.c.3309585.v1

Kennedy, J. (2019). The association between morphological and ecological characters across a global passerine radiation. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.fbg79cnr6

Kernbach, M., Newhouse, D., Miller, J., Hall, R., Gibbons, J., Oberstaller, J., et al. (2019). Light pollution increases West Nile virus competence of a ubiquitous passerine reservoir species. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.7v72n64

Kervinen, M., Lebigre, C., Alatalo, R.,V., Siitari, H. & Soulsbury, C.D. (2014). Life history differences in age-dependent expressions of multiple ornaments and behaviors in a lekking bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.rg8d4

Khaliq, I., Fritz, S.A., Prinzinger, R., Pfenninger, M., Böhning-Gaese, K. & Hof, C. (2015). Global variation in thermal physiology of birds and mammals: evidence for phylogenetic niche conservatism only in the tropics. J. Biogeogr., 42, 2187– 2196. https://doi.org/10.1111/jbi.12573

Kikuchi, D.W., Kattan, G.H. & Velez, K.C.N. (2018). A continent-scale test of multiple hypotheses on the abundances of Neotropical birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.k5912k6

Knief, U., Schielzeth, H., Backstrom, N., Hemmrich-Stanisak, G., Wittig, M., Franke, A., *et al.* (2016). Association mapping of morphological traits in wild and captive zebra finches: reliable within but not between populations. *Dryad*. Dataset. https://doi.org/10.5061/dryad.10pv6

Knief, U., Schielzeth, H., Kempenaers, B., Ellegren, H. & Forstmeier, W. (2012). QTL and quantitative genetic analysis of beak morphology reveals patterns of standing genetic variation in an Estrildid finch. *Dryad*. Dataset. https://doi.org/10.5061/dryad.9vq45n5s

Koivula, M.J., Chamberlain, D.E., Fuller, R.J., Palmer, S.C.F., Bankovics, A., Bracken, F., *et al.* (2017). Breeding bird species diversity across gradients of land use from forest to agriculture in Europe. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.ts57v

Kok, E.M.A., Burant, J.B., Dekinga, A., Manche, P., Saintonge, D., Piersma, T., *et al.* (2019). Within-individual canalization contributes to age-related increases in trait repeatability: a longitudinal experiment in red knots. *Dryad*. Dataset. https://doi.org/10.5061/dryad.dn28cn6

Krist, M. & Munclinger, P. (2011). Superiority of extra-pair offspring: maternal but not genetic effects as revealed by a mixed cross-fostering design. *Dryad*. Dataset. https://doi.org/10.5061/dryad.984b0528

Kvalnes, T., Røberg, A.Å., Jensen, H., Holand, H., Pärn, H., Sæther, B.E, *et al.* (2018). Offspring fitness and the optimal propagule size in a fluctuating environment. *Dryad*. Dataset. https://doi.org/10.5061/dryad.m74c7m9

Langin, K.M., Sillett, T.S., Morrison, S.A. & Ghalambor, C.K. (2017). Bill morphology and neutral genetic structure both predict variation in acoustic signals within a bird population. *Dryad*. Dataset. https://doi.org/10.5061/dryad.jk578

Latimer, C., Smith, O., Taylor, J., Edworthy, A., Owen, J., Snyder, W., et al. (2020), Landscape context mediates the physiological stress response of birds to farmland diversification. *Dryad*. v2. Dataset, https://doi.org/10.5061/dryad.zgmsbcc70

Lavergne, S., Evans, M.E.K., Burfield, I.J., Jiguet, F. & Thuiller, W. (2013). Are species' responses to global change predicted by past niche evolution?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.rk775

Legagneux, P., Berzins, L.L., Forbes, M., Harms, N.J., Hennin, Holly L., *et al.* (2014). No selection on immunological markers in response to a highly virulent pathogen in an Arctic breeding bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.7d0k4

Leighton, G.M. (2017). Cooperative breeding influences the number and type of vocalizations in avian lineages. Dryad. Dataset. https://doi.org/10.5061/dryad.53924

Leung, T.L.F. & Koprivnikar, J. (2017). Nematode parasite diversity in birds: the role of host ecology, life history and migration. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s1m40

Lifjeld, J.T., Anmarkrud, J.A., Calabuig, P., Cooper, J.E.J., Johannessen, L.Erik, Johnsen, A., *et al.* (2016). Species-level divergences in multiple functional traits between the two endemic subspecies of Blue Chaffinches Fringilla teydea in Canary Islands. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.9j616

Lindenmayer, D., Blanchard, W., Blair, D., Westgate, M. & Scheele, B. (2019). Spatio-temporal effects of logging and fire on tall, wet temperate eucalypt forest birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.4c44hq3

Lindenmayer, D.B., Blanchard, W., Westgate, M.J., Foster, C., Banks, S.C., Barton, P., *et al.* (2019). Novel bird responses to successive large-scale, landscape transformations. *Dryad*. Dataset. https://doi.org/10.5061/dryad.ct677k9

Lindsay, W.R., Barron, D.G., Webster, M.S. & Schwabl, H. (2016). Testosterone activates sexual dimorphism including male-typical carotenoid but not melanin plumage pigmentation in a female bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.gf46s

Liu, J., Slik, F., Coomes, D., Corlett, R.T., Wang, Y., Wilson, M., *et al.* (2019). The distribution of plants and seed dispersers in response to habitat fragmentation in an artificial island archipelago. *Dryad*. Dataset. https://doi.org/10.5061/dryad.dg03kv8

Lodjak, J., Mand, R. & Mägi, M. (2018). Insulin-like growth factor 1 and life-history evolution of passerine birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.mv755

Lundblad, C. & Conway, C. (2019). Variation in selective regimes drives intraspecific variation in life-history traits and migratory behaviour along an elevational gradient. *Dryad*. v3. Dataset. https://doi.org/10.5061/dryad.2547d7wmj

Lutz, H.L., Hochachka, W.M., Engel, J.I., Jeffrey, A.B., Tkach, V.V.; Bates, J.M., *et al.* (2016). Parasite Prevalence Corresponds to Host Life History in a Diverse Assemblage of Afrotropical Birds and Haemosporidian Parasites. *PLoS ONE*. Dataset. https://doi.org/10.1371/journal.pone.0121254

Maas, B., Tscharntke, T., Shahabuddin, S., Dwi P.D. & Clough, Y. (2015). Avian species identity drives predation success in tropical cacao agroforestry. *PANGAEA*. Dataset. https://doi.org/10.1594/PANGAEA.841264

Madonia, C., Hutton, P., Giraudeau, M. & Sepp, T. (2018). Carotenoid coloration is related to fat digestion efficiency in a wild bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s7q28

Mangini, G.G. & Areta, J.I. (2018). Bird mixed-species flock formation is driven by low temperatures between and within seasons in a Subtropical Andean-foothill forest. *Dryad*. Dataset. https://doi.org/10.5061/dryad.t5m5662

Marrot, P., Charmantier, A., Blondel, J. & Garant, D. (2018). Current spring warming as a driver of selection on reproductive timing in a wild passerine. *Dryad*. Dataset. https://doi.org/10.5061/dryad.95486

Martin, A.E., Desrochers, A. & Fahrig, L. (2016). Homogenization of dispersal ability across bird species in response to landscape change. *Dryad*. Dataset. https://doi.org/10.5061/dryad.2522c

Martin, L.B., Kilvitis, H.J., Brace, A.J., Cooper, L, Haussmann, M.F., Mutati, A., *et al.* (2017). Costs of immunity and their role in the range expansion of the house sparrow in Kenya. *Dryad*. Dataset. https://doi.org/10.5061/dryad.fn0f4

Martin, P., Kenyon, H. & Hayes, L. (2020). Size-dependent costs of migration: migrant bird species are subordinate to residents, but only at small body sizes. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.8kprr4xjj

Martin, T.E. (2016). Age-related mortality explains life history strategies of tropical and temperate songbirds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.2m15n

Martínez, A.E., Gomez, J.P., Ponciano, J.M. & Robinson, S.K. (2016). Functional traits, flocking propensity and perceived predation risk in an Amazonian understory bird community. *Dryad*. Dataset. https://doi.org/10.5061/dryad.18v4b

Martin-Silverstone, E., Vincze, O., McCann, R., Jonsson, C.H.W., Palmer, C., Kaiser, G., *et al.* (2016). Exploring the Relationship between Skeletal Mass and Total Body Mass in Birds. *PLoS ONE*. Dataset. https://doi.org/10.1371/journal.pone.0141794

Mason, N.A., Burns, K.J., Tobias, J.A., Claramunt, S., Seddon, N. & Derryberry, E.P. (2016). Song evolution, speciation, and vocal learning in passerine birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.r99p7

Mathot, K., Kok, E., Burant, J., Dekinga, A., Manche, P., Saintonge, D., *et al.* (2019). Evolutionary design of a flexible, seasonally migratory, avian phenotype: why trade gizzard mass against pectoral muscle mass?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.48894fk

Matysiokova, B., Friedman, N., Turčoková, L. & Remes, V. (2017). The evolution of feather coloration and song in Old World orioles (genus Oriolus). *Dryad*. Dataset. https://doi.org/10.5061/dryad.c3c51

McLean, N., van der Jeugd, H.P. & van de Pol, M. (2019). High intra-specific variation in avian body condition responses to climate limits generalisation across species. *Dryad*. Dataset. https://doi.org/10.5061/dryad.8r882

Medina, I. & Langmore, N.E. (2015). Coevolution is linked with phenotypic diversification but not speciation in avian brood parasites. *Dryad*. Dataset. https://doi.org/10.5061/dryad.c79vc

Medina, I., Langmore, N.E., Lanfear, R. & Kokko, H. (2017). The evolution of clutch size in hosts of avian brood parasites. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s20hm

Messina, S., Eens, M., Casasole, G., AbdElgawad, H., Asard, H., Pinxten, R., *et al.* (2018). Experimental inhibition of a key cellular antioxidant affects vocal communication. *Dryad*. Dataset. https://doi.org/10.5061/dryad.4g313

Mikula, P., Tószögyová, A., Hořák, D., Petrusková, T., Storch, D. & Albrecht, T. (2019). Female solo song and duetting are associated with different territoriality in songbirds. *Dryad*. v3. Dataset. https://doi.org/10.5061/dryad.fn2z34tpr

Miller, E.T., Wagner, S.K., Harmon, L.J. & Ricklefs, R.E. (2016). Radiating despite a lack of character: ecological divergence among closely related, morphologically similar honeyeaters (Aves: Meliphagidae) co-occurring in arid Australian environments. *Dryad*. Dataset. https://doi.org/10.5061/dryad.r82jg

Miller, J.R., Wiens, J.A., Hobbs, N.T. & Theobald, D.M. (2003). Effects of human settlement on bird communities in lowland riparian areas of colorado (USA). *Figshare*. Dataset. https://doi.org/10.6084/m9.figshare.3511508.v1

Minias, P., Włodarczyk, R. & Meissner, W. (2018). Leukocyte profiles are associated with longevity and survival, but not migratory effort: a comparative analysis of shorebirds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.7v37m

Minias, Piotr (2019). Evolution of heterophil/lymphocyte ratios in response to ecological and life-history traits: a comparative analysis across the avian tree of life. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s3cc172

Moiron, M., Araya A., Yimen G., Mathot, K.J., Mouchet, A., Dingemanse, N.J., *et al.* (2018). Functional relations between body mass and risk-taking behavior in wild great tits. *Dryad*. Dataset. https://doi.org/10.5061/dryad.14cn58v

Moller, A.P., Erritzoe, J. & Van Dongen, S. (2018). Body size, developmental instability and climate change. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s0n86hq

Montoya, B., Valverde, M., Rojas, E. & Torres, R. (2016). Oxidative stress during courtship affects male and female reproductive effort differentially in a wild bird with biparental care. *Dryad*. Dataset. https://doi.org/10.5061/dryad.pn358- 10.1242/jeb.141325

Montreuil-Spencer, C., Schoenemann, K., Lendvai, Á. & Bonier, F. (2019). Winter corticosterone and body condition predict subsequent breeding investment in nonmigratory bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.4pf04c0

Morales, J., Cuervo, J.J., Moreno, J. & Soler, J.J. (2019). Juvenile plumage whiteness is associated with the evolution of clutch size in passerines. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s88fv55

Morelli, F., Benedetti, Y., Diaz, M., Grim, T., Ibáñez-Álamo, J., Jokimäki, J., *et al.* (2019). Contagious fear: escape behaviour increases with flock size in European gregarious birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.3q25r77

Morganti, M., Rubolini, D., Akesson, S., Bermejo, A., De la Puente, J., Lardelli, R., *et al.* (2017). Effect of light-level geolocators on apparent survival of two highly aerial swift species. *Dryad*. Dataset. https://doi.org/10.5061/dryad.b1t42 10.1111/jav.01521

Morrison, K.W. (2015). Individual repeatability in laying behaviour does not support the migratory carry-over effect hypothesis of egg-size dimorphism in Eudyptes penguins. *Dryad*. Dataset. https://doi.org/10.5061/dryad.d4196

Munoz, M. (2016). Plant and bird interactions in Colombia. *Senckenberg*. Database. http://dataportal-senckenberg.de/database/metacat/bikf.10043.1/bikf

Nabholz, B., Lanfear, R. & Fuchs, J. (2016). Body mass-corrected molecular rate for bird mitochondrial DNA. *Dryad*. Dataset. https://doi.org/10.5061/dryad.1040d

Naguib, M., Diehl, J., van Oers, K. & Snijders, L. (2019). Repeatability of signalling traits in the avian dawn chorus. *Dryad*. Dataset. https://doi.org/10.5061/dryad.r1s93g8

Nwaogu, C., Galema, A., Cresswell, W., Dietz, M. & Tieleman, I. (2019). A fruit diet rather than invertebrate diet maintains a robust innate immunity in an omnivorous tropical songbird. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.bg79cnp77

O'Connell, D.P., Kelly, D.J., Lawless, N., O'Brien, K., Marcaigh, F. Ó.; Karya, A., *et al.* (2019). A sympatric pair of undescribed white-eye species (Aves: Zosteropidae: Zosterops) with different origins. *figshare*. Dataset. https://doi.org/10.6084/m9.figshare.7998299.v1

Ocampo, D., Barrantes, G. & Uy, J.A.C. (2019). Morphological adaptations for relatively larger brains in hummingbird skulls. *Dryad*. Dataset. https://doi.org/10.5061/dryad.9s364g3

Odom, K.J., Omland, K.E. & Price, J.J. (2014). Differentiating the evolution of female song and male-female duets in the New World blackbirds: can tropical natural history traits explain duet evolution?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.jd068

Olalla-Tárraga, M.Á., Amado, T., Bini, L.M., Martínez, P., Morales-Castilla, I., Torres-Romero, Erik J., *et al.* (2019). Biological traits, phylogeny and human footprint signatures on the geographic range size of passerines (Order Passeriformes) worldwide. *Dryad*. Dataset. https://doi.org/10.5061/dryad.4q0c65c

Olsen, A.M. (2016). Exceptional avian herbivores: multiple transitions toward herbivory in the bird order Anseriformes and its correlation with body mass. *Dryad*. Dataset. https://doi.org/10.5061/dryad.6b5n7

Ortega, J.C.G., Machado, N., Diniz-Filho, J.A.F., Rangel, T.F., Araújo, M.B., Loyola, R., et al. (2019). Meta-analyzing the likely cross-species responses to climate change. *Dryad*. Dataset. https://doi.org/10.5061/dryad.qv5p3r8

Ouyang, J.Q., Sharp, P., Quetting, M. & Hau, M. (2013). Endocrine phenotype, reproductive success and survival in the great tit, Parus major. *Dryad*. Dataset. https://doi.org/10.5061/dryad.cv003

Pap, P.L., Fülöp, A., Adamkova-Kotasova, M., Cepak, J., Michalkova, R., Safran, R.J., *et al.* (2019). Selection on multiple sexual signals in two Central- and Eastern-European populations of the barn swallow. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.64p7k2f

Pardal, S., Alves, J.A., Mota, P.G. & Ramos, J.A. (2018). Dressed to impress: breeding plumage as a reliable signal of innate immunity. *Dryad*. Dataset. https://doi.org/10.5061/dryad.m21m300

Pattinson, N., Thompson, M., Griego, M., Russell, G., Mitchell, N., Martin, R., *et al.* (2019). Heat dissipation behaviour of birds in seasonally hot, arid-zones: are there global patterns?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.t76hdr7xb

Peel, A. (2018). Interspecific alterations in avian physiology across a gradient of fragmentation. *Zenodo*. v1. Dataset. http://doi.org/10.5281/zenodo.1327557

Pellerin, S., Rioux Paquette, S., Pelletier, F., Garant, D. & Bélisle, M. (2015). The trade-off between clutch size and egg mass in tree swallows (Tachycineta bicolor) is modulated by female body mass. *Dryad*. Dataset. https://doi.org/10.5061/dryad.76735

Pérez-Camacho, L., Martínez-Hesterkamp, S., Rebollo, S., García-Salgado, G. & Morales-Castilla, I. (2018). Structural complexity of hunting habitat and territoriality increase the reversed sexual size dimorphism in diurnal raptors. *Dryad*. Dataset. https://doi.org/10.5061/dryad.0n226hs

Pérez-Rodríguez, L., Jovani, R. & Mougeot, F. (2013). Fractal geometry of a complex plumage trait reveals bird's quality. *Dryad*. Dataset. https://doi.org/10.5061/dryad.83873

Pigeault, R., Cozzarolo, C.S., Choquet, R., Strehler, M., Jenkins, T., Delhaye, J., *et al.* (2019). Haemosporidian infection and co-infection affect host survival and reproduction in wild populations of great tits. *Dryad*. Dataset. https://doi.org/10.5061/dryad.0f8n6sj

Pigot, A.L., Trisos, C.H. & Tobias, J.A. (2015). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.fd986

Pirrello, S., Pilastro, A., Rubolini, D., Cecere, J., Romano, A., Andreotti, A., *et al.* (2016). Early exposure to a bacterial endotoxin advances the onset of moult in the European starling. *Dryad*. Dataset. https://doi.org/10.5061/dryad.c3g3b

Plard, F., Schindler, S., Arlettaz, R. & Schaub, M. (2017). Sex-specific heterogeneity in fixed morphological traits influences individual fitness in a monogamous bird population. *Dryad*. Dataset. https://doi.org/10.5061/dryad.61cf7

Poissant, J., Morrissey, M.B., Gosler, A.G., Slate, J. & Sheldon, B.C. (2016). Multivariate selection and intersexual genetic constraints in a wild bird population. *Dryad*. Dataset. https://doi.org/10.5061/dryad.qt745

Price, T., Schumm, M., White, A. & Supriya, K. (2019). Ecological limits as the driver of bird species richness patterns along the east Himalayan elevational gradient. *Dryad*. v4. Dataset. https://doi.org/10.5061/dryad.hmgqnk9bx

Pryke, S.R., Astheimer, L.B., Griffith, S.C. & Buttemer, W.A. (2011). Covariation in life-history traits: differential effects of diet on condition, hormones, behavior and reproduction in genetic finch morphs. *Dryad*. Dataset. https://doi.org/10.5061/dryad.v3b42mv1

Quinard, A., Cezilly, F., Motreuil, S., Rossi, J.M. & Biard, C. (2016). Reduced sexual dichromatism, mutual ornamentation, and individual quality in the monogamous Zenaida dove, Zenaida aurita. *Dryad*. Dataset. https://doi.org/10.5061/dryad.7120d

Quitián, M., Santillán, V., Bender, I.M. A., Espinosa, C.I., Homeier, J., Böhning-Gaese, K., *et al.* (2019). Functional responses of avian frugivores to variation in fruit resources between natural and fragmented forests. *Senckenberg*. Database. http://dataportal-senckenberg.de/database/metacat/bikf.10268.47/bikf

Ramakers, J.J.C., Cobben, M.M.P., Bijma, P., Reed, T.E., Visser, M.E. & Gienapp, P. (2017). Maternal effects in a wild songbird are environmentally plastic but only marginally alter the rate of adaptation. *Dryad*. Dataset. https://doi.org/10.5061/dryad.4fv71

Récapet, C., Daniel, G., Taroni, J., Bize, P. & Doligez, B. (2016). Food supplementation mitigates dispersal-dependent differences in nest defence in a passerine bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.n3k7f

Redondo, T., Romero, J.M., Díaz-Delgado, R. & Nagy, J. (2019). Broodmate aggression and life history variation in accipitrid birds of prey. *Dryad*. Dataset. https://doi.org/10.5061/dryad.8h07878

Reed, T.E., Gienapp, P. & Visser, M.E. (2016). Testing for biases in selection on avian reproductive traits and partitioning direct and indirect selection using quantitative genetic models. *Dryad*. Dataset. https://doi.org/10.5061/dryad.1255v

Rees J.D., Kingsford R.T. & Letnic M. (2019) Changes in desert avifauna associated with the functional extinction of a terrestrial top predator. *Ecography*, 42:67–76

Rodríguez-Gómez, F. & Ornelas, J.F. (2018). Genetic structuring and secondary contact in the white-chested Amazilia hummingbird species complex. *Dryad*. Dataset.

https://doi.org/10.5061/dryad.kf01h4b

Rohwer, V.G., Bonier, F. & Martin, P.R. (2015). Conflict between biotic and climatic selective pressures acting on an extended phenotype in a subarctic, but not temperate, environment. *Dryad*. Dataset. https://doi.org/10.5061/dryad.c65d8

Romano, A., Nodari, R., Bandi, C., Caprioli, M., Costanzo, A., Ambrosini, R., *et al.* (2019). Haemosporidian parasites depress breeding success and plumage coloration in female barn swallows (Hirundo rustica). *Dryad*. Dataset. https://doi.org/10.5061/dryad.b33k48m

Roulin, A., Uva, V. & Romano, A. (2018). A melanin-based trait is more strongly related to body size in the tropics than in temperate regions in the globally distributed barn owl family. *Dryad*. Dataset. https://doi.org/10.5061/dryad.mc085g9

Ruuskanen, S., Gienapp, P., Groothuis, T.G.G., Schaper, S.V., Darras, V.M., Pereira, C., et al. (2016). Heritable variation in maternally-derived yolk androgens, thyroid hormones and immune factors. *Dryad*. Dataset. https://doi.org/10.5061/dryad.vr666

Ruuskanen, S., Groothuis, T.G.G., Baugh, A.T., Schaper, S.V., deVries, B., van Oers, K., *et al.* (2018). Maternal egg hormones in the mating context: the effect of pair personality. *Dryad*. Dataset. https://doi.org/10.5061/dryad.5781r

Saino, N., Bazzi, G., Gatti, E., Caprioli, M., Cecere, J.G., Possenti, C.D., *et al.* (2015). Polymorphism at the Clock gene predicts phenology of long-distance migration in birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.j22j1

Sakamoto, M., Ruta, M. & Venditti, C. (2018). Extreme and rapid bursts of functional adaptations shape bite force in amniotes. *Dryad*, v2, Dataset. https://doi.org/10.5061/dryad.q12c06f

Sánchez-Clavijo, L.M., Bayly, N.J. & Quintana-Ascencio, P.F. (2019). Habitat selection in transformed landscapes and the role of forest remnants and shade coffee in the conservation of resident birds. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.mp5rn5b

Saraux, C., Chiaradia, A., Le Maho, Y. & Ropert-Coudert, Y. (2011). Everybody needs somebody: unequal parental effort in little penguins. *PANGAEA*. Dataset. https://doi.org/10.1594/PANGAEA.834278

Sayol, F., Lapiedra, O., Ducatez, S. & Sol, D. (2020). Larger brains spur species diversification in birds. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.p4v4n0s

Schepers, M.J. & Proppe, D.S. (2016). Song playback increases songbird density near low to moderate use roads. *Dryad*. Dataset. https://doi.org/10.5061/dryad.26127

Schielzeth, H., Forstmeier, W., Kempenaers, B. & Ellegren, H. (2011). QTL linkage mapping of wing length in zebra finch using genome-wide single nucleotide polymorphisms markers. *Dryad*. Dataset. https://doi.org/10.5061/dryad.5fj1310p

Schmitt, C., Garant, D., Bélisle, M. & Pelletier, F. (2017). Linking innate immunogenetic variation with phenotypic traits in a wild population of tree swallows, Tachycineta bicolor. *Dryad*. Dataset. https://doi.org/10.5061/dryad.5k5k0

Scholer, M.N., Arcese, P., Puterman, M.L., Londono, G.A. & Jankowski, J.E. (2019). Survival is negatively related to basal metabolic rate in tropical Andean birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.sf2gt4k

Scordato, E., Smith, C.C.R., Semenov, G.A., Liu, Y., Wilkins, M.R., Liang, W., *et al.* (2019). Migratory divides coincide with reproductive barriers across replicated avian hybrid zones above the Tibetan Plateau. *Dryad*. v5. Dataset. https://doi.org/10.5061/dryad.pvmcvdngk

Scordato, E.S.C. (2018). Male competition drives song divergence along an ecological gradient in an avian ring species, Dryad, Dataset, https://doi.org/10.5061/dryad.1pj4302

Scordato, E.S.C., Wilkins, M.R., Semenov, G., Rubtsov, A.S., Kane, N.C., Safran, R.J., *et al.* (2017). Genomic variation across two barn swallow hybrid zones reveals traits associated with divergence in sympatry and allopatry. *Dryad*. Dataset. https://doi.org/10.5061/dryad.0g6k1

Sebastián-González, E. (2017), Drivers of species' role in avian seed-dispersal mutualistic networks. *figshare*. Dataset. https://doi.org/10.6084/m9.figshare.4829524.v1

Sekercioglu, C., Daily, G. & Ehrlich, P. (2004). Ecosystem consequences of bird declines. Proc. Natl. Acad. Sci. 101, 18042–18047. https://doi.org/10.1073/pnas.0408049101

Seneviratne, S.S., Davidson, P., Martin, K. & Irwin, D.E. (2018). Low levels of hybridization across two contact zones among three species of woodpeckers (Sphyrapicus sapsuckers). *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.66jt1

Sepp, T., Rattiste, K., Saks, L., Meitern, R., Urvik, J., Kaasik, A., *et al.* (2016). A small badge of longevity: opposing survival selection on the size of white and black wing markings. *Dryad*. Dataset. https://doi.org/10.5061/dryad.gc60p

Shultz, A.J. & Burns, K.J. (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Dryad*. Dataset. https://doi.org/10.5061/dryad.g4k83

Sibly, R.M, Witt, C.C., Wright, N.A., Venditti, C., Jetz, W. & Brown, J.H. (2012). Energetics, lifestyle, and reproduction in birds. PNAS, 109, 10937-10941. https://doi.org/10.1073/pnas.1206512109

Silva, C.N.S., McFarlane, S.E., Hagen, I.J., Rönnegård, L., Billing, A.M., Kvalnes, T., *et al.* (2017). Insights into the genetic architecture of morphological traits in two passerine bird species. *Dryad*. Dataset. https://doi.org/10.5061/dryad.786m4

Simpson, R.K. & McGraw, K.J. (2019). Interspecific covariation in courtship displays, iridescent plumage, solar orientation, and their interactions in hummingbirds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.t53g6p1

Sitters, H., Di Stefano, J., Christie, F.J., Swan, M., York, A. & Christie, F. (2015). Bird functional diversity decreases with time since disturbance: does patchy prescribed fire enhance ecosystem function?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.6336b

Snell-Rood, E.C., Swanson, E.M. & Young, R.L. (2015). Life history as a constraint on plasticity: developmental timing is correlated with phenotypic variation in birds. *Dryad*.

Dataset. https://doi.org/10.5061/dryad.c5s06

Sofaer, H.R., Sillett, T.S., Langin, K.M., Morrison, S.A., Ghalambor, C.K. & Sillett, T.S. (2015). Partitioning the sources of demographic variation reveals density-dependent nest predation in an island bird population. *Dryad*. Dataset. https://doi.org/10.5061/dryad.m4fs7

Sreekar, R., Zhang, K., Xu, J., Harrison, R.D. & Sreekar, R (2016). Yet another empty forest: considering the conservation value of a recently established tropical nature reserve. *Dryad*. Dataset. https://doi.org/10.5061/dryad.76mg6

Stokke, B.G., Ratikainen, I.I., Moksnes, A., Røskaft, E., Schulze-Hagen, K., Leech, D.I., *et al.* (2019). Characteristics determining host suitability for a generalist parasite. *Dryad*. Dataset. https://doi.org/10.5061/dryad.9r0n681

Støstad, H.N., Rekdal, S.L., Kleven, O., Laskemoen, T., Marthinsen, G., Johnsen, A., *et al.* (2016). Weak geographical structure in sperm morphology across the range of two willow warbler Phylloscopus trochilus subspecies in Scandinavia. *Dryad*. Dataset. https://doi.org/10.5061/dryad.td453

Sulloway, F.J. & Kleindorfer, S. (2013). Adaptive divergence in Darwin's small ground finch (Geospiza fuliginosa): divergent selection along a cline. *Dryad*. Dataset. https://doi.org/10.5061/dryad.d4g94

Sun, L., Zhou, T., Stone, G., Wan, Q.H. & Fang, S.G. (2019). Seeing-good-gene-based mate choice: from genes to behavioural preferences. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s75p458

Svagelj, W.S., Laich, A.G. & Quintana, F. (2018). Richards’s equation and nonlinear mixed models applied to avian growth: why use them?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.s448n5d

Taff, C.C.J., Freeman-Gallant, C.R. & Taff, C.C. (2015). An experimental test of the testosterone mediated oxidation handicap hypothesis in a wild bird. *Dryad*. Dataset. https://doi.org/10.5061/dryad.d5d6b

Tamburello, N., Côté, I.M. & Dulvy, N.K. (2015). Energy and the scaling of animal space use. *Dryad*. Dataset. https://doi.org/10.5061/dryad.q5j65

Teerikorpi, P.E., Sirkiä, P.M. & Laaksonen, T. (2018). Ecological crossovers of sexual signalling in a migratory bird. Dryad. v2. Dataset. https://doi.org/10.5061/dryad.s27v5b0

Tellería, J.L., De La Hera, I. & Perez-Tris, J. (2014). Morphological variation as a tool for monitoring bird populations: a review. *Dryad*. Dataset. https://doi.org/10.5061/dryad.c6qm2- 10.13157/arla.60.2.2013.191

Teplitsky, C., Mouawad, N.G., Balbontín, J., de Lope, F. & Møller, A.P. (2011). Quantitative genetics of migration syndromes: a study of two barn swallow populations. *Dryad*. Dataset. https://doi.org/10.5061/dryad.41np7

Toews, D.P.L., Streby, H.M., Burket, L., Taylor, S.A. & Toews, D.P.L. (2018). A wood-warbler produced through both interspecific and intergeneric hybridization. *Dryad*. Dataset. https://doi.org/10.5061/dryad.qb3sq2s

Tomasek, O., Bobek, L., Kralova, T., Adamkova, M. & Albrecht, T. (2018). Fuel for the pace of life: baseline blood glucose concentration coevolves with life history traits in songbirds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.jc56n4r

Tsai, P., Ko, C., Hsieh, C., Su, Y., Lu, Y. & Tuanmu, M. (2019). A trait database for Taiwan's breeding birds. *Zenodo*. v 1.1. Dataset. http://doi.org/10.5281/zenodo.3580768

Tschirren, B. (2016). Differential effects of maternal yolk androgens on male and female offspring: a role for sex-specific selection?. *Dryad*. Dataset. https://doi.org/10.5061/dryad.85k6p

Velando, A., Beamonte-Barrientos, R. & Torres, R. (2014). Data from: Enhanced male coloration after immune challenge increases reproductive potential. *Dryad*. Dataset. https://doi.org/10.5061/dryad.p534s

Versteegh, M.A., Schwabl, I., Jacqier, S., Tieleman, B.I. & Jaquier, S. (2012). Do immunological, endocrine and metabolic traits fall on a single Pace-of-Life axis? Covariation and constraints among physiological systems. *Dryad*. Dataset. https://doi.org/10.5061/dryad.kf320

Walker, L.K., Ewen, J.G., Brekke, P. & Kilner, R.M. (2014). Sexually selected dichromatism in the hihi Notiomystis cincta: multiple colours for multiple receivers. *Dryad*. Dataset. https://doi.org/10.5061/dryad.58q4d

Wang, Y., Si, X., Bennett, P.M., Chen, C., Zeng, D., Zhao, Y., *et al.* (2017). Ecological correlates of extinction risk in Chinese birds. *Dryad*. Dataset. https://doi.org/10.5061/dryad.18bd8

Wei, C., Price, T.D., Liu, J., Alström, P. & Zhang, Y. (2017). The evolutionary origin of variation in song length and frequency in the avian family Cettiidae. *Dryad*. Dataset. https://doi.org/10.5061/dryad.r14ch

Werner, J. & Griebeler, E.M. (2016). New Insights into Non-Avian Dinosaur Reproduction and Their Evolutionary and Ecological Implications: Linking Fossil Evidence to Allometries of Extant Close Relatives. *PLoS ONE*. Dataset. https://doi.org/10.1371/journal.pone.0072862

Wheelwright, N.T., Keller, L.F. & Postma, E. (2015). The effect of trait type and strength of selection on heritability and evolvability in an island bird population. *Dryad*. v2. Dataset. https://doi.org/10.5061/dryad.dv0qt

Whittingham, L.A. & Dunn, P.O. (2016). Experimental evidence that brighter males sire more extra-pair young in tree swallows. *Dryad*. Dataset. https://doi.org/10.5061/dryad.8qp00

Winger, B.M. & Bates, J.M. (2015). The tempo of trait divergence in geographic isolation: avian speciation across the Marañon valley of Peru. *Dryad*. Dataset. https://doi.org/10.5061/dryad.p0v93

Wood, J.R., MacLeod, C.J., Gormley, A.M., T., Daniel M., Butler, S.J. (2016). Ecological requirements of NZ birds. Landcare Research NZ Ltd. v1. Database. https://doi.org/10.7931/J27D2S27

Yoon, J., Jung, J.S., Joo, E.J., Kim, B.S. & Park, S.R. (2016). Parent birds assess nest predation risk: influence of cavity condition and avian nest predator activity. *Dryad*. Dataset. https://doi.org/10.5061/dryad.cr7s6

Yoshikawa, T., Kawakami, K. & Masaki, T. (2019). Allometric scaling of seed retention time in seed dispersers and its application to estimation of seed dispersal potentials of theropod dinosaurs. *Dryad*. Dataset. https://doi.org/10.5061/dryad.h622t6p

Zhang, S., Ma, Z., Feng, C.C., Melville, D., van Gils, J. & Piersma, T. (2019). Individual diet differences in a molluscivore shorebird are associated with the size of body instruments for internal processing rather than for feeding. *Dryad*. Dataset. https://doi.org/10.5061/dryad.8pp2rt0

Appendix B

Appendix B. List of the standardized definition for traits used in this study. Of which 14 bird were compiled from literature (†) and 8 suggested by a regional bird survey protocol (§, López-Ordoñez *et al.* 2015).

Trait	**Description**
Activity period (†)	Main period to which the individual restricts its activities: diurnal, crepuscular, nocturnal or cathemeral (i.e. irregularly active at any time of night or day; Wilman *et al.* 2014; Razafindratsima *et al.* 2018).
Bill curvature (§)	Bill shape can be classified as down curved, straight, up curved and flat (de Arruda Almeida *et al.* 2017; López-Ordoñez *et al.* 2015).
Bill height (§)	This measurement is taken as the length of an imaginary line perpendicular to the longitudinal axis of the bill, between the culmen and the lower jaw, with the bill completely closed. This measurement can be taken on the proximal end of operculum or in the most distal part of the nostrils (López-Ordoñez *et al.* 2015; Matthews *et al.* 2017; Oliveira *et al.* 2019).
Bill length (†,§)	Can be measured as the distance, from the closed bill and straight, from the tip of the bill to the base of the skull (i.e. total culmen), to the point at which the forehead feathers begin (i.e. exposed culmen; (López-Ordoñez *et al.* 2015; Pigot *et al.* 2016; Matthews *et al.* 2017), for the previous edge of the nostrils (Pigot *et al.* 2016; Matthews *et al.* 2017), or for the commissural point (i.e. gape length, Vollstädt *et al.* 2017).
Bill width (†,§)	Measured by the length between the commissures (corners located between the base of the maxilla and mandible, i.e. gape width; López-Ordoñez *et al.* 2015) or the bill width at proximal end of operculum (Oliveira *et al.* 2019; López-Ordoñez *et al.* 2015).
Body mass (†, §)	Body weight (Wilman *et al.* 2014; López-Ordoñez *et al.* 2015).
Clutch size (†)	Number of eggs or offspring produced in a single reproductive event/clutch (Lislevand *et al.* 2007; Williams *et al.* 2010; Myhrvold *et al.* 2015).

Diet (†, §)	Main food resources a bird consumes most of its life (López-Ordoñez *et al.* 2015). It can be divided into diet categories (i.e. seeds, fruits, nectar, invertebrates, vertebrates and others; Dias 2016), food guilds (i.e. Nectivore, granivore, frugivore, folivore, insectivore, carnivore, omnivore, among others; López-Ordoñez *et al.* 2015; Pringle *et al.* 2019) or trophic position, estimated using stable isotope analysis (Edwards *et al.* 2013).
Foraging strategy (†)	Foraging strategy can be defined as the vertical stratum (foraging stratum) that the species occupies in vegetation during foraging (i.e. aquatic, semi-aquatic, ground, grassland, understory, midstrata, canopy; Wilman *et al.* 2014; López-Ordoñez *et al.* 2015; Prescott *et al.* 2016; Zhang *et al.* 2019), through the type of specific substrate (foraging substrate) in which the species usually seeks food (aquatic, trunk / bark, soil / litter, foliage or Air: prey items caught in the air; Prescott *et al.* 2016), or as the method used by species to find food (foraging mode) such as: Pursuit, Gleaning, Pouncing, Grazing, Digging, Scavenging, Probing (López-Ordoñez *et al.* 2015; Li *et al.* 2018). These three foraging strategies description are overlapping in the literature so, for simplicity, they were considered the same trait during the review and converted posteriorly in “Foraging mode” and “Foraging stratum”.
Foraging mode (†, §)	Defined as the method or mode used by species to find food (i.e. Pursuit, Gleaning, Pouncing, Grazing, Digging, Scavenging, Probing; López-Ordoñez et al. 2015; Li et al. 2018)
Foraging stratum (†, §)	Defined as the stratum (i.e. aquatic, ground, understory, canopy, air) or type of substrate (i.e. trunk / bark, soil / litter or foliage) on which species usually search for food (Wilman *et al.* 2014; López-Ordoñez *et al.* 2015; Prescott *et al.* 2016).
Hallux length (§)	Length of the nail present in the finger 1 (López-Ordoñez *et al.* 2015; Oliveira *et al.* 2019).
Kipp’s distance (†, §)	Linear distance from the tip of the longest primary feather to the longest secondary feather (López-Ordoñez *et al.* 2015; Phillips *et al.* 2018).

Migratory status (†, §)	Migration types can be grouped according to the geographic coverage of the trips. The main categories are: Altitudinal migration (species remain all year round in the same region, but move between different altitudinal ranges); local migration (species have a wide distribution, but a given population makes a cyclical movement within the same latitudinal belt in response to habitat availability or the presence of resources); continental migration (species migrate latitudinally each year; Residents: species that do not perform any type of migratory movement López-Ordoñez *et al.* 2015; Ehlers Smith *et al.* 2019).
Nesting behavior (§)	It is defined as the type of reproductive strategy, this includes several aspects such as the construction of the nest, surveillance, feeding and parental care of juveniles of the species. It can be divided into two categories. Colonial, where cooperative participation exists between individuals of the same species for the creation of juveniles. Individual, where species build nests and raise juveniles individually or in pairs (López-Ordoñez *et al.* 2015).
Nesting strategy (†)	The nest can be classified by type (e.g. open, built cavity, natural cavity, cavity in human constructions, closed, nest parasite), location (e.g. ground, rock, shrub, tree) or both (e.g. Open on ground, Open in tree; (Devictor *et al.* 2010; Leitão *et al.* 2016; White *et al.* 2018).
Social behavior (§)	Defined as the association behavior of an individual with others of the same or other species, to perform activities related to food and rest. Taking into account the number of species that make up the group and the number of individuals of each species, the main categories are: monoespecific flocking (groups of individuals of the same species that forage for a specific resource), mix flocking (groups of individuals of different species that forage together for food), association (individuals of different species that gather around a specific site, this is usually related to an environment, e.g. waterbirds associated with an estuary), solitary (species observed solitary most of the time) or in pairs (species that forage in pairs; Karp *et al.* 2012; López-Ordoñez *et al.* 2015).
Tail graduation (§)	It refers to the shape of the tail and can be measured by the difference in the length of the longest and shortest rectrix (López-Ordoñez *et al.* 2015).
Tail length (†, §)	Distance from the tip of the longest rectrix to the base of the tail (point at which the two central rectrices protrude from the skin; (Pigot *et al.* 2016).

Tarsus length (†, §)	Distance between the back of the intertarsal joint and the lower front edge of the last undivided scale before the beginning of the fingers (Eck *et al.* 2011; López-Ordoñez *et al.* 2015; Oliveira *et al.* 2019).
Wing area (§)	Area occupying the maximum wing extension limits (López-Ordoñez *et al.* 2015; Tinoco *et al.* 2018).
Wing length (§)	Length of the carpal (carpal junction) to the tip of the largest primary wing feather, measured with the wing closed (e.i. Wing chord; López-Ordoñez *et al.* 2015; Renner & Hoesel 2017; Storchová & Hořák 2018).
Wingspan (†, §)	Length between the tip of the largest left primary feather to the right, measured with flattened and stretched wings over a plane (López-Ordoñez *et al.* 2015; Renner & Hoesel 2017).

References

de Arruda Almeida, B., Gimenes, M.R. & dos Anjos, L. (2017). Wading bird functional diversity in a floodplain: Influence of habitat type and hydrological cycle. *Austral Ecol.*, 42, 84–93.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.*, no-no.

Dias, D.F.C., Ribeiro, M.C., Felber, Y.T., Cintra, A.L.P., de Souza, N.S. & Hasui, É. (2016). Beauty before age: landscape factors influence bird functional diversity in naturally regenerating fragments, but regeneration age does not. *Restor. Ecol.*, 24, 259–270.

Eck, S., Fiebig, J., Fiedler, W., Heynen, I., Nicolai, B., Töpfer, T., *et al.* (2011). *Measuring birds - Vögel vermessen*. *Dtsch. Ornithol.* DO-G Special Interest Group "Ornithological Collections."

Edwards, D.P., Woodcock, P., Newton, R.J., Edwards, F.A., Andrews, D.J.R., Docherty, T.D.S., *et al.* (2013). Trophic flexibility and the persistence of understory birds in intensively logged rainforest. *Conserv. Biol.*, 27, 1079–1086.

Ehlers Smith, D.A., Ehlers Smith, Y.C. & Downs, C.T. (2019). Promoting functional connectivity of anthropogenically-fragmented forest patches for multiple taxa across a critically endangered biome. *Landsc. Urban Plan.*, 190, 103579.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R. & Daily, G.C. (2012). Intensive agriculture erodes §-diversity at large scales. *Ecol. Lett.*, 15, 963–970.

Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., *et al.* (2016). Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. R. Soc. B Biol. Sci.*, 283, 20160084.

Li, D., Poisot, T., Waller, D.M. & Baiser, B. (2018). Homogenization of species composition and species association networks are decoupled. *Glob. Ecol. Biogeogr.*, 27, 1481–1491.

Lislevand, T., Figuerola, J. & Székely, T. (2007). Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. *Ecology*.

López-Ordoñez, J.P., Stiles, G. & Parra-Vergara, J.L. (2015). Protocolo para la medición de rasgos funcionales en aves. In: *La Ecología funcional como aproximación al estudio, manejo y conservación de la biodiversidad: protocolos y aplicaciones* (ed. Salgado-Negret, B.). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, pp. 80–125.

Matthews, T.J., Cottee-Jones, H.E.W., Bregman, T.P. & Whittaker, R.J. (2017). Assessing the relative importance of isolated Ficus trees to insectivorous birds in an Indian human-modified tropical landscape. *Biodivers. Conserv.*, 26, 2803–2819.

Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L. & Ernest, S.K.M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109–000.

Oliveira, J. de, Almeida, S.M., Florêncio, F.P., Pinho, J.B., Oliveira, D.M.M., Ligeiro, R., *et al.* (2019). Environmental structure affects taxonomic diversity but not functional structure of understory birds in the southwestern Brazilian Amazon. *Acta Amaz.*, 49, 232–241.

Phillips, A.G., Töpfer, T., Rahbek, C., Böhning-Gaese, K. & Fritz, S.A. (2018). Effects of phylogeny and geography on ecomorphological traits in passerine bird clades. *J. Biogeogr.*, 45, 2337–2347.

Pigot, A.L., Trisos, C.H. & Tobias, J.A. (2016). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Dryad*.

Prescott, G.W., Gilroy, J.J., Haugaasen, T., Medina Uribe, C.A., Foster, W.A. & Edwards, D.P. (2016). Reducing the impacts of Neotropical oil palm development on functional diversity. *Biol. Conserv.*, 197, 139–145.

Pringle, S., Chiweshe, N., Steward, P.R., Mundy, P.J. & Dallimer, M. (2019). Rapid redistribution of agricultural land alters avian richness, abundance, and functional diversity. *Ecol. Evol.*, 9, 12259–12271.

Razafindratsima, O.H., Yacoby, Y. & Park, D.S. (2018). MADA: Malagasy Animal trait Data Archive. *Ecology*, 99, 990.

Renner, S.C. & Hoesel, W. van. (2017). Ecological and Functional Traits in 99 Bird Species over a Large-Scale Gradient in Germany. *Data*, 2, 12.

Storchová, L. & Hořák, D. (2018). Life-history characteristics of European birds. *Glob. Ecol. Biogeogr.*, 27, 400–406.

Tinoco, B.A., Santillán, V.E. & Graham, C.H. (2018). Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. *Ecol. Evol.*, 8, 3478–3490.

Vollstädt, M.G.R., Ferger, S.W., Hemp, A., Howell, K.M., Töpfer, T., Böhning-Gaese, K., *et al.* (2017). Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. *Glob. Ecol. Biogeogr.*, 26, 963–972.

White, H.J., Montgomery, W.I., Storchová, L., Hořák, D. & Lennon, J.J. (2018). Does functional homogenization accompany taxonomic homogenization of British birds and how do biotic factors and climate affect these processes? *Ecol. Evol.*, 8, 7365–7377.

Williams, S.E., VanDerWal, J., Isaac, J., Shoo, L.P., Storlie, C., Fox, S., *et al.* (2010). Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology*, 91, 2493–2493.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027–2027.

Zhang, S., Ma, Z., Feng, C., Melville, D.S., van Gils, J.A. & Piersma, T. (2019). Individual diet differences in a molluscivore shorebird are associated with the size of body instruments for internal processing rather than for feeding. *J. Avian Biol.*, 50, jav.02255.