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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E EVOLUÇÃO

Fernando Landa Sobral

PADRÕES E PROCESSOS NA ORGANIZAÇÃO DE ASSEMBLEIAS DE AVES INSULARES

Orientador: Dr. Marcus Vinicius Cianciaruso

GOIÂNIA - GO

ABRIL – 2017

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Tese apresentada à Universidade Federal de Goiás, como parte das exigências do Programa de Pós-graduação em Ecologia e Evolução para obtenção do título de doutor em Ecologia e Evolução.

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ATA DA SESSÃO PÚBLICA DE DEFESA DE TESE Nº 56

Aos vinte dias do mês de abril de 2017 (20/04/2017), às oito horas (08h), no Auditório do ICB V, UFG, reuniram-se os componentes da banca examinadora: **Prof. Dr. Marcus Vinicius Cianciaruso, ICB-UFG; Dra. Margarita Patricia Florencio Diaz, Pós-Doc -ICB-UFG; Prof. Dr. José Alexandre Felizola Diniz Filho, ICB-UFG; Prof. Dr. Luis Mauricio Bini, ICB-UFG; Profa. Dra. Sandra Maria Hartz, UFRGS**; para, em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Padrões e processos de organização de assembleias de aves insulares"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria de **Fernando Landa Sobral**, discente do Programa de Pós-Graduação Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo(a) presidente(a), que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida a(o) autor(a) da tese que, em cerca de 31 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da tese. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a tese foi APROVADO, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Doutor(a) em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da tese na secretaria do programa, com as devidas correções sugeridas pela banca examinadora, no prazo de trinta dias a contar da data da defesa. Cumpridas as formalidades de pauta, às 11 h e 30 min.,

encerrou-se a sessão de defesa e, para constar, eu, Suely Ana Ribeiro, secretária executiva da Universidade Federal de Goiás - UFG, lavrei a presente ata que, após lida e aprovada, será assinada pelos membros da banca examinadora em três vias de igual teor.

Prof. Dr. Marcus Vinicius Cianciaruso
Presidente da banca
ICB-UFG

Dra. Margarita Patricia Florencio Diaz
Pós-Doc - ICB-UFG

Prof. Dr. José Alexandre Felizola Diniz Filho
ICB-UFG

Prof. Dr. Luis Mauricio Bini
ICB-UFG

Profa. Dra. Sandra Maria Hartz
UFRGS

À minha família,
pelo amor e incentivo

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Sumário

Resumo

A diversidade de espécies naturalmente habitando uma localidade insular é ultimamente moldada pelos processos combinados de colonização, especiação e extinção, e primeiramente pelo conjunto de fatores ambientais, ecológicos, históricos e evolutivos, que determinam o intercâmbio desses processos. Entretanto, a diversidade de espécies atualmente habitando muitas ilhas ao redor do globo também é moldada pelo processo de introdução. Usando os atributos funcionais e as relações de parentesco de espécies de aves, nós investigamos como diferentes mecanismos naturais e antrópicos têm moldada a diversidade de espécies em diferentes ilhas continentais e oceânicas distribuídas ao redor do globo. No primeiro capítulo, nós investigamos se a introdução de espécies compensa pelas informações ecológicas e evolutivas perdidas por meio da extinção de espécies. De maneira geral, nós encontramos que as espécies introduzidas possuem papéis ecológicos e histórias evolutivas diferentes das espécies extintas. Isso significa que as introduções verdadeiramente não compensam pelas extinções. No segundo capítulo, nós investigamos se determinados fatores biogeográficos, ambientais e antrópicos podem explicar a proporção de espécies de aves introduzidas ao longo de diferentes ilhas, e qual o impacto dessas introduções sobre a diversidade funcional e filogenética das assembleias. Nós encontramos que a proporção de espécies de aves introduzidas é mediada negativamente pela riqueza de espécies nativas, e positivamente pelo tamanho da população humana encontrada nas ilhas. Além disso, nós encontramos que a seletividade ecológica observada nas introduções de espécies de aves tem reduzido a diversidade funcional média, mas não a diversidade filogenética média, entre as espécies ocorrentes ao longo das assembleias insulares. Isso mostra que os padrões ecológicos nem sempre refletem os padrões evolutivos observados entre as espécies. Finalmente, no terceiro capítulo nós acessamos a distância funcional entre espécies de

aves visitantes e espécies de aves residentes para investigar o sucesso na colonização de localidades insulares. Nós encontramos que quando as espécies ocorrem como visitantes ao longo das ilhas, elas mostram uma distância funcional maior para as espécies residentes mais próximas do que quando elas ocorrem como residentes. Isso indica que a falha no processo de colonização de localidades insulares aumenta com a distância funcional para as espécies residentes mais próximas, o que corrobora a hipótese de pré-adaptação ao ambiente.

Palavras-chave: colonização natural, diversidade funcional, diversidade filogenética, extinção de espécies, falsa compensação, hipótese da pré-adaptação, introdução de espécies.

Introdução geral

Ilhas como sistema modelo em estudos de ecologia e evolução

As ilhas têm ditado um papel importante nos estudos de ecologia e evolução desde os tempos de Darwin e Wallace. Naquele período, a visão prevalente era de que as espécies eram imutáveis e sem nenhuma relação de parentesco entre si. As diferenças na composição das assembleias naturais eram explicadas por mecanismos criacionistas (por exemplo, pontos especiais de criação de espécies), e por fatores abióticos que potencialmente deveriam controlar a distribuição e ocorrência das espécies (Lomolino et al. 2010). Por meio das suas viagens a diferentes continentes e ilhas, Darwin e Wallace independentemente observaram que os padrões de co-ocorrência e riqueza de espécies aparentemente não eram congruentes com a predominante visão de imutabilidade e independência dos táxons (Darwin, 1859; Wallace, 1880, 1855). Durante as suas observações e reflexões, as localidades insulares ditaram um papel importante no processo de formulação das hipóteses de descendência a partir de ancestralidade comum, e descendência a partir de distintas áreas geográficas fontes (Darwin, 1859; Wallace, 1880, 1855).

As características das ilhas foram importantes não apenas para os estudos de Darwin e Wallace, mas também para um grande número de estudos desenvolvidos por outros pesquisadores (e.g. MacArthur and Wilson, 1967). Seus tamanhos pequenos comparados aos continentes, limites bem definidos e discretos, e biotas relativamente simplificadas, tornam mais fáceis de observar padrões ecológicos e evolutivos. Muitas ilhas também compartilham características similares, tais como área, isolamento, precipitação, temperatura e produtividade, funcionando como réplicas ecológicas e evolutivas naturais (Losos and Ricklefs, 2009; Warren et al., 2015). Além disso, ilhas

que surgem desprovidas de vida (e.g. vulcânicas ou completamente submergidas por água em algum ponto de suas histórias), podem servir como séries de tempo ecológicas e evolutivas. Todos esses fatores fazem das ilhas excelentes "laboratórios naturais" para o estudo do intercâmbio de processos ecológicos e evolutivos na geração da diversidade biológica (Losos and Ricklefs, 2009; Warren et al., 2015).

Mecanismos naturais que moldam a diversidade de espécies em sistemas insulares

Por muitos anos, os pesquisadores têm examinado os mecanismos naturais que produzem os padrões de diversidade biológica ao longo das regiões. O estudo de ilhas tem sido particularmente fértil, e tem levado a teorias de que os processos de colonização, extinção e especiação ditam um papel importante na determinação da diversidade de espécies em localidades insulares. Mais do que isso, essas teorias apontam que tais processos são esperados a serem influenciados pela área e isolamento geográfico das ilhas (Losos and Ricklefs, 2010; MacArthur and Wilson, 1967). Por exemplo, ilhas maiores e menos isoladas são esperadas a possuírem maior riqueza de espécies do que ilhas menores e menos isoladas porque são alvos de uma maior pressão de propágulos e, por isso, mais susceptíveis a colonização de diferentes espécies. Ilhas maiores e menos isoladas também são esperadas a possuírem maior riqueza de espécies porque os táxons ocorrentes localmente devem possuir populações maiores e, por isso, menos susceptíveis a extinção devido a eventos demográficos e climáticos estocásticos (Losos and Ricklefs, 2010; MacArthur and Wilson, 1967). Além disso, ilhas maiores ainda devem mostrar maior número de espécies porque áreas geográficas grandes possuem maior diversidade de habitats, e consequentemente, maiores oportunidades para eventos de especiação in situ (Losos and Ricklefs, 2010, 2009).

Igualmente importante, o sucesso no estabelecimento local das espécies é um fator fundamental na determinação da diversidade de espécies através das ilhas. Algumas teorias apontam que o sucesso na colonização de novas localidades pode ser determinado pela (i) capacidade de dispersão das espécies, (ii) capacidade de adaptação a novos ambientes, e (iii) capacidade de evitar fortes interações negativas por recursos compartilhados (Darwin, 1859; Diamond, 1974; Simberloff, 1978). De acordo com isso, espécies com maior capacidade de dispersão são esperadas a mostrar maior sucesso de colonização porque devem exibir maior pressão de propágulo e a chegar a um número maior de localidades (Diamond, 1974). Entretanto, diferentes evidências mostram que maior capacidade de dispersão nem sempre resulta em maior sucesso de colonização, especialmente em ilhas (Lees and Gilroy, 2014). Isso significa que outros fatores, como por exemplo, as interações bióticas e abióticas ocorrentes dentro das novas localidades também devem ditar um papel importante no estabelecimento das espécies (Blackburn et al., 2009; Blackburn and Duncan, 2001; Darwin, 1859). Para espécies introduzidas, alguns trabalhos mostram que essas interações ditam um papel importante no sucesso de colonização (Ma et al., 2016; Thuiller et al., 2010). Entretanto, pouco se sabe se essas interações também são fundamentais no estabelecimento de espécies que se dispersam naturalmente até novas localidades. Estudos explorando as relações entre as interações (bióticas e abióticas) ocorrentes dentro das novas localidades e o sucesso de colonização natural devem esclarecer um pouco mais sobre os mecanismos responsáveis pela diversidade biológica em localidades insulares.

Mecanismos antrópicos que moldam a diversidade de espécies em sistemas insulares

As atividades humanas têm uma profunda influência sobre a diversidade biológica global. A magnitude, variedade e longevidade das mudanças induzidas pelos humanos

têm impactos diferentes sobre táxons e localidades distintos. Existem múltiplas formas pelos quais as atividades humanas afetam a composição das assembleias naturais ao longo do tempo. Enquanto que as mudanças no uso do solo têm causado não apenas a perda como também o ganho local de espécies particulares (Flynn et al., 2009). As mudanças climáticas têm gerado uma perda desproporcional na diversidade de espécies (Thuiller et al., 2011). Particularmente em localidades insulares, a introdução de espécies tem marcadamente alterado o processo de colonização natural das assembleias locais (Dyer et al., 2017). Os humanos têm intencionalmente ou acidentalmente transportado e introduzido um grande número de espécies a diferentes ilhas (Blackburn and Duncan, 2001). Esses eventos de introdução tem causado uma redução na riqueza de espécies em algumas localidades (devido à extinção de espécies nativas), e um aumento no número de espécies em outras, alterando a composição das assembleias ao longo do tempo (Sax et al., 2002).

As evidências mostram que as espécies escolhidas para introdução não são aleatórias com relação as suas taxonomias e aos seus atributos de história de vida (Blackburn and Duncan, 2001). No período histórico, os eventos de introdução eram amplamente ligados a liberações planejadas associadas com a expansão colonial europeia (principalmente britânica). Nesse período, as introduções tinham como objetivo melhorar a aclimatação dos novos colonizadores às novas ilhas colonizadas. Por isso, as espécies mais introduzidas nessa época pertencem as principais famílias de aves de caça (e.g. Anatidae, Phasianidae e Columbidae) (Dyer et al., 2017). Por outro lado, os padrões na introdução de espécies de aves têm mudado ao longo dos anos. No período recente, as introduções são na grande maioria não planejadas e ligadas ao aumento dos níveis de atividade econômica das localidades. Atualmente, as introduções ocorrem em maior número em regiões com economia emergente, e estão associadas

com o comércio de aves. Por isso, as espécies mais introduzidas atualmente pertencem a famílias de aves de gaiola (e.g. Psittacidae, Estrildidae e Sturnidae) (Dyer et al., 2017). Muitos estudos têm investigado os padrões na introdução de espécies em escalas insulares, continentais e até globais (Dyer et al., 2017; Fridley et al., 2007; Stohlgren et al., 2006). Entretanto, a maioria deles têm explorado as causas e os efeitos das introduções apenas sobre a simples riqueza de espécies (Blackburn et al., 2016; Dyer et al., 2017). Estudos investigando os potenciais impactos da introdução de espécies sobre outras facetas da biodiversidade devem ajudar a esclarecer as verdadeiras consequências das atividades humanas sobre diversidade natural de espécies.

Mecanismos antrópicos substituem a diversidade biológica originalmente moldada pelos mecanismos naturais?

A diversidade de espécies atualmente observada ao longo da maioria das assembleias biológicas é moldada pela combinação de diferentes processos naturais e antrópicos (Blackburn et al., 2016; Losos and Ricklefs, 2010; MacArthur and Wilson, 1967). O efeito combinado de ambos os tipos de processos tem resultado não apenas na introdução como também na extinção de um grande número de táxons ao longo de diferentes localidades, incluindo ilhas (Blackburn et al., 2016; Boyer and Jetz, 2014). Em conjunto, os processos de introdução e extinção potencialmente podem levar a diferentes padrões na riqueza de espécies das assembleias locais (Sax et al., 2002; Sax and Gaines, 2008). Por exemplo, em assembleias onde a taxa de introdução supera a taxa de extinção, a riqueza de espécies é esperada a aumentar ao longo do tempo. Enquanto que em localidades onde as taxas de introdução e extinção são similares, a riqueza de espécies potencialmente deve se manter em equilíbrio. Por outro lado, em

assembleias onde a taxa de extinção supera a taxa de introdução, a riqueza de espécies é esperada a diminuir ao longo do tempo.

Em localidades insulares, o número de espécies de aves introduzidas, na média, tem sido similar ao número de aves extintas (Sax et al., 2002; Sax and Gaines, 2008), sugerindo que as introduções têm compensado pelas extinções ao longo dos anos. Entretanto, as introduções têm causado o ganho de grupos particulares de espécies, muitas vezes generalistas (Blackburn and Cassey, 2007; Sol et al., 2012), enquanto que as extinções têm levado a perda de guildas ecológicas e linhagens evolutivas específicas (Boyer, 2010). Isso significa que uma compensação na riqueza de espécies não necessariamente se traduz em uma compensação nos papéis ecológicos e nas histórias evolutivas das espécies. Na literatura existem poucos estudos investigando essas potenciais mudanças na composição das assembleias naturais (Boyer, 2010; Boyer and Jetz, 2014). Dados os potenciais impactos negativos que essas mudanças podem acarretar sobre a biodiversidade (Boyer and Jetz, 2014; Helmus et al., 2014; Whittaker et al., 2014), investigar como as introduções e as extinções alteram a diversidade ecológica e evolutiva das assembleias é importante para garantir os processos que geram e mantêm os serviços e funções do ecossistema.

Objetivos gerais dos capítulos da tese

O objetivo geral do primeiro capítulo foi testar pelos potenciais impactos da introdução e extinção de espécies sobre os componentes alfa e beta da diversidade funcional e filogenética das assembleias de aves insulares. Usando um conjunto de 32 ilhas distribuídas em todo o mundo, nós investigamos se as introduções e extinções tem afetado a diversidade funcional e filogenética das assembleias, se as espécies

introduzidas, nativas existentes e extintas são funcionalmente e filogeneticamente similares, e se as introduções têm compensado pelos papéis ecológicos e pelas histórias evolutivas perdidos por meio das extinções. Diferentemente, o objetivo geral do segundo capítulo foi testar se diferentes fatores biogeográficos, ambientais e antrópicos podem explicar a proporção de espécies de aves introduzidas ao longo de 32 diferentes assembleias insulares, e o impacto dessas introduções sobre a diversidade funcional e filogenética das assembleias. Por fim, o objetivo do terceiro capítulo foi acessar a distância funcional entre espécies de aves visitantes e espécies de aves residentes para investigar o sucesso de colonização em 49 assembleias de aves insulares. Especificamente, nós investigamos se a falha na colonização natural de ilhas continentais e oceânicas por espécies de aves está relacionada à falta de pré-adaptações às condições ambientais locais ou a forte competição por recursos compartilhados com espécies residentes.

Referências

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CAPÍTULO I

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Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages

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ABSTRACT

The ratio of species extinctions to introductions has been comparable for many insular assemblages, suggesting that introductions could have 'compensated' for extinctions. However, the capacity for introduced species to replace ecological roles and evolutionary history lost following extinction is unclear. We investigated changes in bird functional and phylogenetic diversity in the wake of extinctions and introductions across a sample of 32 islands worldwide. We found that extinct and introduced species have comparable functional and phylogenetic alpha diversity. However, this was distributed at different positions in functional space and in the phylogeny, indicating a 'false compensation'. Introduced and extinct species did not have equivalent functional roles nor belong to similar lineages. This makes it unlikely that novel island biotas composed of introduced taxa will be able to maintain ecological roles and represent the evolutionary histories of pre-disturbance assemblages and highlights the importance of evaluating changes in alpha and beta diversity concurrently.

Keywords: alpha diversity, beta diversity, biological conservation, community assembly, compensation, functional diversity, phylogenetic diversity, species gain, species loss, turnover.

INTRODUCTION

Humans have colonized most habitable islands across the globe, leading to major biophysical changes to these typically fragile ecosystems (Blackburn *et al.* 2004; Steadman 2006). Land conversion for agriculture, livestock and settlement has led to habitat loss, fragmentation and degradation, which coupled with hunting and the introduction of non-native species has led to dramatic changes to assemblages of insular species. As a consequence, thousands of species have become extinct following human colonization whilst many others have been left on the brink of extinction (Steadman 1995; Sax & Gaines 2008; Triantis *et al.* 2010). Such changes in species composition may modify the underlying ecological functions and evolutionary history of insular assemblages (Boyer 2010). Accordingly, there is evidence that the extinction of native species leads to a disproportionate loss of both functional and phylogenetic diversity in natural assemblages (Vamosi & Wilson 2008; Boyer & Jetz 2014).

Functional diversity is a representation of how species are distributed in a multidimensional niche space defined by functional traits and, therefore, provides a way to assess the effects and responses of species interactions with the environment and with other co-occurring species (Pavoine & Bonsall 2011). On the other hand, phylogenetic diversity is a biodiversity measure that accounts for the relatedness among species and captures the evolutionary history of a given assemblage (Pavoine & Bonsall 2011). Understanding the effect of extinctions on the functional and phylogenetic diversity of assemblages is fundamental to ensure the maintenance of ecological (e.g. seed dispersal and pollination) and evolutionary (e.g. coevolution and speciation) processes (Weiher *et al.* 2011). These facets of biodiversity are thus frequently used to understand not only the consequences of changes in species assemblage composition (for example, due to

species extinctions or introduction) (Boyer & Jetz 2014; Helmus *et al.* 2014) but also in conservation planning exercises (Sobral *et al.* 2014).

The human-mediated dispersal of species and concomitant anthropogenic disturbances have favoured the introduction and naturalization of non-native species, leading to variable impacts on natural assemblages (Strauss *et al.* 2006; Sax *et al.* 2007). Although a large number of studies have highlighted the negative effects of introduced species there are still uncertainties about the true impacts of these introductions (Baker *et al.* 2014). For example, introduced species may ensure the ecosystem functioning when they compensate for ecological roles lost after the extinction of native species (Lees & Bell 2008; García *et al.* 2014). In addition, at both regional and local scales, species richness increases when the number of introductions is greater than the number of extinctions (Sax *et al.* 2002; Sax & Gaines 2008; Winter *et al.* 2009). In this case, the introduction of species could increase the functional and phylogenetic diversity of assemblages (Whittaker *et al.* 2014), considering that introduced species can often be functionally and phylogenetically distinct from native species (Strauss *et al.* 2006; Sullivan *et al.* 2015).

The relative temporal stability of insular bird richness suggests that introductions have, on average, compensated for extinctions (Sax *et al.* 2002; Sax & Gaines 2008). Nevertheless, extinctions have caused the loss of specific guilds and lineages of native birds (often flightless, large-bodied and endemic specialists; Boyer 2010; Thuiller *et al.* 2011), whereas introductions have resulted in the gain of particular groups of species (often generalists and with functional and phylogenetic traits distinct from native species; Cassey *et al.* 2004; Blackburn & Cassey 2007; Sol *et al.* 2012). Therefore, any potential compensation for species richness from introductions does not necessarily translate into compensation of functional and phylogenetic diversity (e.g. Villéger *et al.*

2014). For this to occur, introduced species need to compensate for ecological roles and evolutionary histories lost through extinction (e.g. García *et al.* 2014). This has important conceptual implications because extinctions and introductions may produce differential changes in alpha and beta components of functional and phylogenetic diversity (Devictor *et al.* 2008; Jackson *et al.* 2015). Although the alpha components of functional and phylogenetic diversity can show whether introductions compensate for the amount of diversity lost following extinction, they do not reveal the dissimilarity in functional or phylogenetic composition between assemblages (Leprieur *et al.* 2012; Villéger *et al.* 2013). Therefore, to understand if introductions really compensate for extinctions we must investigate not only the alpha but also the beta component of diversity (Fig. 1). Alpha diversity represents the space occupied by introduced and extinct species within the functional or phylogenetic dimensions defined by their functional traits or phylogenetic relatedness, respectively (Pavoine & Bonsall 2011). Therefore, it represents the amount of ecological or evolutionary information shown by the species within assemblages (Fig. 1). On the other hand, beta diversity indicates the position occupied by introduced and extinct species within these dimensions (Leprieur *et al.* 2012; Villéger *et al.* 2013), that is, it shows the dissimilarity in the functional or phylogenetic composition between assemblages (Fig. 1).

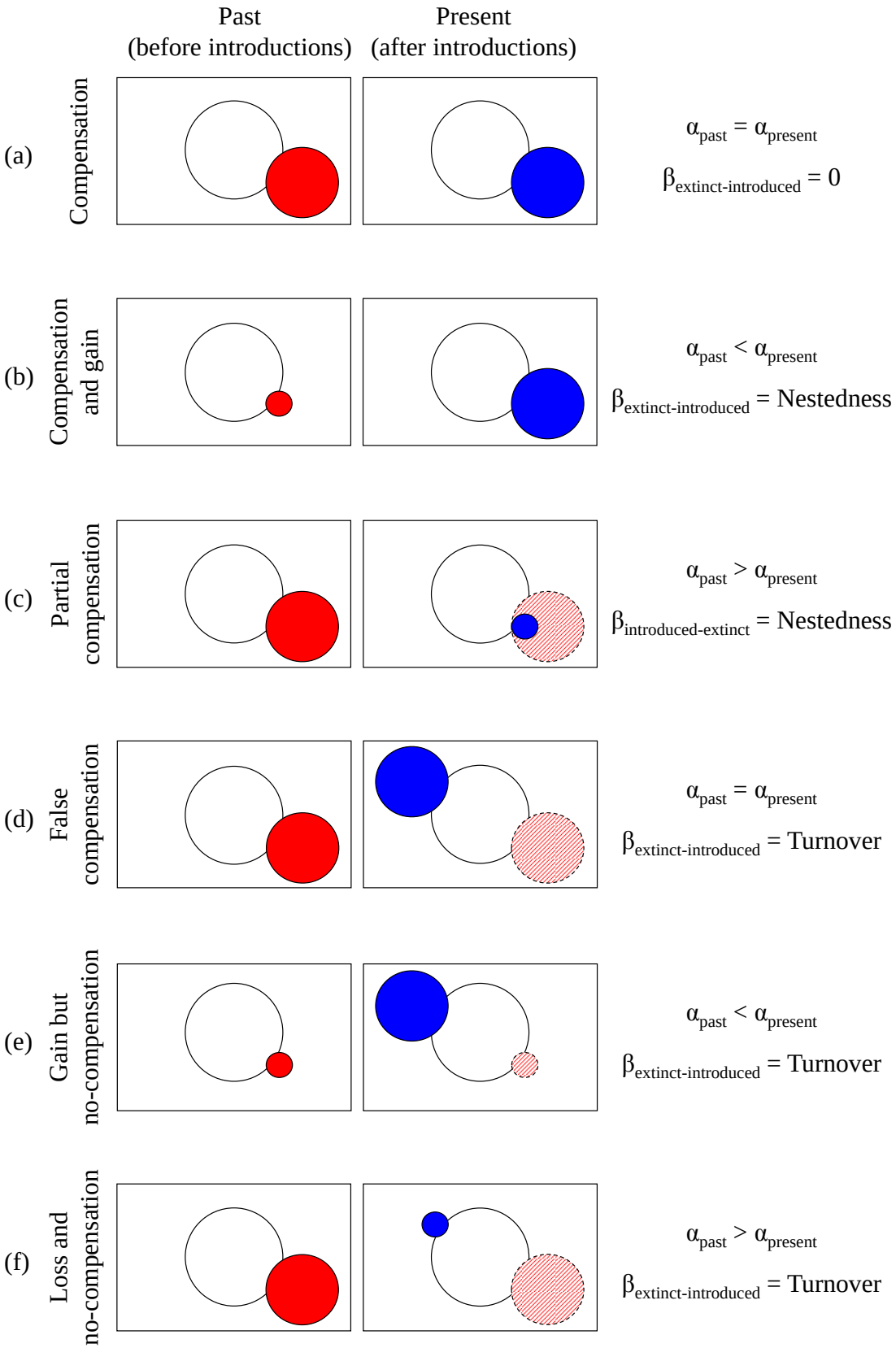

Figure 1 – Possible scenarios for alpha and beta functional or phylogenetic diversity of assemblages following species extinctions and introductions. 'Past' indicates

assemblages composed of extinct and extant native species whereas 'Present' represents assemblages composed of extant native and introduced species. The white circles represent the portion (volume and the position) occupied by the extant native species within the multidimensional functional or phylogenetic space. Solid red circles represent the portion of space occupied by the extinct species in the past, striped red circles represent the portion of space left vacant by the extinct species in the present, and blue circles represent the portion of space occupied by the introduced species in the present. We termed these scenarios as (a) Compensation: introduced species occupy similar volume and position in relation to the extinct species. Alpha diversity in the present is equal to that observed in the past, while beta diversity between introduced and extinct species is very low or none. (b) Compensation and gain: introduced species occupy a higher volume than extinct species but at a similar position in the multidimensional space. Alpha diversity in the present is higher than in the past, while beta diversity between extinct and introduced species shows a pattern of nestedness. (c) Partial compensation: introduced species occupy a lower volume than extinct species but a similar position in the multidimensional space. Alpha diversity in the present is lower than in the past, whereas the beta diversity between extinct and introduced species shows a pattern of nestedness. (d) False compensation: introduced species occupy a similar volume but at a distinct position in relation to the extinct species. Alpha diversity in the present is similar to that observed in the past, whereas the beta diversity between extinct and introduced species shows a pattern of turnover. (e) Gain but no-compensation: introduced species occupy a higher volume than extinct species but at a distinct position in the multidimensional space. Alpha diversity in the present is higher than in the past, whereas the beta diversity between extinct and introduced species shows a pattern of turnover. (f) Loss and no-compensation: introduced species occupy a lower volume than extinct species and at a distinct position in multidimensional space. Alpha diversity in the present is lower than in the past, whereas beta diversity between extinct and introduced species shows a pattern of turnover.

The impact of species extinctions and introductions on functional or phylogenetic diversity have been investigated separately, and even concomitantly, in previous studies (Matsuzaki *et al.* 2013; Boyer & Jetz 2014; Helmus *et al.* 2014).

However, the great majority of these studies have highlighted the effects of these processes quantifying only the alpha component of functional or phylogenetic diversity of assemblages (e.g. Matsuzaki *et al.* 2013), or less frequently, calculating only their beta components (e.g. Villéger *et al.* 2014). Investigating the impact of extinctions and introductions on both components (alpha and beta) of functional and phylogenetic diversity is a more robust way to predict the ecological and evolutionary consequences of changes in assemblage composition. For example, our framework (Fig. 1) allows us to answer with greater confidence if introduced species are really compensating for the loss of functional and phylogenetic diversity precipitated by extinctions.

Here, we used the historical record of bird extinctions and introductions across islands located in different zoogeographical zones to test the impact of these processes on the functional and phylogenetic alpha and beta components of insular bird assemblages. Based on evidence derived from 79 extinctions and 184 introductions of birds on 32 islands or island groups, we aim to answer the following questions: (1) how do extinctions and introductions affect the functional and phylogenetic diversity of assemblages?; (2) are extinct and introduced species functionally and phylogenetically distinct from the extant native species?; and (3) do introduced species compensate for the functional roles and evolutionary histories potentially lost due to the extinction of native species?

MATERIALS AND METHODS

Database

We investigated the role of extinctions and introductions of passerines and near-passerines land-bird assemblages on 32 islands and island groups located in different

climatic and geographical zones of the globe (Fig. 2). Our study included islands, atolls and close-knit archipelagos (for the sake of clarity, hereafter, 'islands') with a minimum separation distance of 60 km from other island groups or the nearest continental mainland coast. We excluded from the study newly formed volcanic islands, tidal islands, and island groups with more than 100,000 km^2 in land area. Our database included 16 islands with records of both species extinctions and introductions, and another 16 islands that only have records of introductions (Fig. 2). Occurrence data for extinct, extant native and introduced bird species were based on the revised data of Lees & Gilroy (2014).

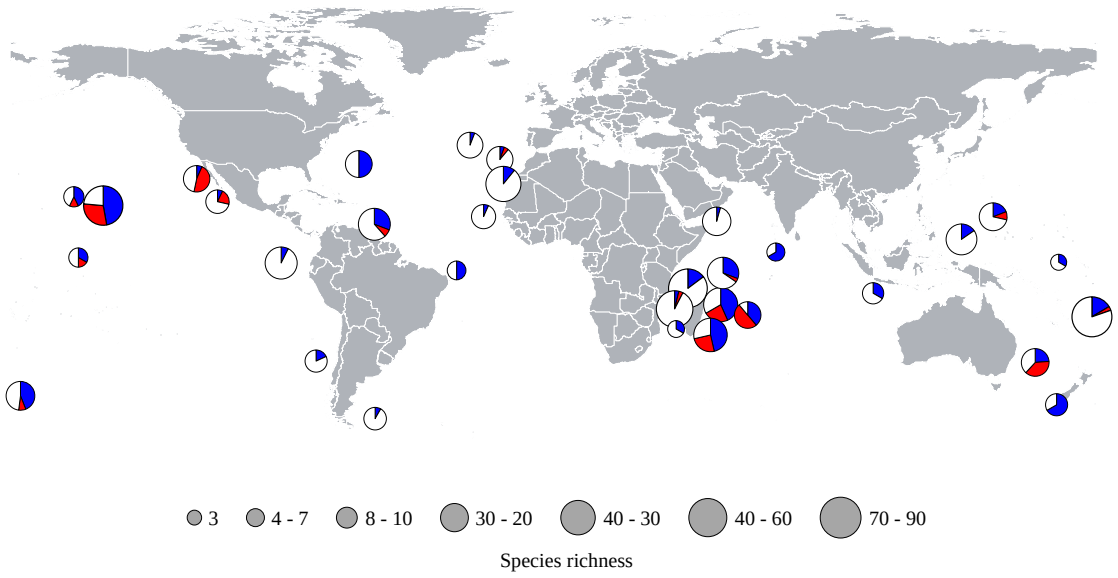

Figure 2 – Geographic distribution of 32 islands and island groups included in the study. Pie chart size is proportional to the richness of breeding bird species recorded on each island. The number of extant native species is represented in white, the number of extinct species in red, and the number of introduced species in blue.

The role of birds on ecological processes and ecosystem services are directly related to life-history traits, such as diet and foraging activity (Sekercioglu 2006). Thus,

to quantify the functional diversity of bird assemblages we used the following traits: diet, treated as the estimated percentage of each diet item (invertebrates, vertebrates, scavenger, fruits, nectar, seeds and plants); foraging niche, treated as the estimated percentage of time spent in each strata (ground, understory, midhigh, canopy and air), foraging period, treated as a binary categorical variable (diurnal and nocturnal); and body mass, as a continuous variable. We primarily used data from Wilman *et al.* (2014), but supplemented it with additional sources for 8% of species (Supporting Information 1). To quantify the phylogenetic diversity of assemblages we used the phylogenetic hypothesis presented in Jetz *et al.* (2012). Because these authors did not provide a consensus phylogeny we produced a maximum clade credibility tree (MCC) from 9,999 random, complete and dated phylogenies using the TreeAnnotator software v1.8.1 in BEAST (Drummond *et al.* 2012). Given that 8% of species in our study were absent from the Jetz *et al.* (2012) phylogeny we included them in the maximum clade credibility tree as polytomies at the genus (4.0%) or family (4.0%) level (Supporting Information 2). To verify the robustness of our results to phylogenetic uncertainty we repeated our analyses in 500 random trees (Supporting Information 3).

Functional and phylogenetic alpha diversity

To calculate the functional diversity of assemblages we constructed a functional distance matrix for each island including only the bird species present in each of them (extinct, extant native, and introduced). To calculate the distance matrices we used a modification of the Gower distance dedicated to the treatment of continuous and categorical traits (Pavoine *et al.* 2009). Then, using the distance matrices we quantified four measures of functional diversity that capture different aspects of the distribution of species in functional space: i) functional richness (FRic; Villéger *et al.* 2008), ii)

functional dispersion (FDis; Laliberté & Legendre 2010), iii) mean pairwise distance (MPD; Webb 2000), and iv) mean nearest taxon distance (MNTD; Webb 2000). Functional richness (FRic) quantifies the volume of the minimum convex hull that includes all species belonging to an assemblage in functional space (Villéger *et al.* 2008), whereas functional dispersion (FDis) quantifies the dispersion of species from the centre of the functional space filled by the assemblage (Laliberté & Legendre 2010). When used as a functional diversity measure, Mean Pairwise Distance (MPD_{FD}) quantifies the mean distance between all species pairs co-occurring in functional space (Sobral *et al.* 2014). Similarly, as a measure of functional diversity, Mean Nearest Taxon Distance ($MNTD_{FD}$) quantifies the mean distance between each species and its nearest neighbour in the functional space. We used these four measures because functional diversity is composed by multiple facets (Villéger *et al.* 2008) and no single measure is entirely able to capture the relative distribution of species in functional space (Podani & Schmera 2006; Boyer & Jetz 2014). This approach enables us to conduct a more robust investigation on the impacts of extinctions and introductions to the functional diversity of natural assemblages.

Considering that functional and phylogenetic data have similar structures, functional diversity measures can be used to estimate phylogenetic diversity of assemblages, and vice versa (Pavoine & Bonsall 2011). In this case, quantifying the phylogenetic diversity from FRic and FDis portrays the distribution of species in multidimensional space defined by the phylogenetic relatedness among species. On the other hand, MPD and MNTD characterize the distance between species based on a phylogenetic tree, as originally proposed by Webb (2000). To calculate the phylogenetic diversity we used the maximum clade credibility tree to produce a cophenetic distance matrix for each island, taking into account only the bird species present in each of them

(extinct, extant native, and introduced). Then, we used the same four measures to quantify the phylogenetic diversity of assemblages: Phylogenetic Richness (PRic), Phylogenetic Dispersion (PDis), Mean Pairwise Distance (MPD_{PD}) and Mean Nearest Taxon Distance ($MNTD_{PD}$). We used the first five PCoA axes to calculate FRic and PRic (Maire *et al.* 2015). All the analyses were carried out in R v.3.2.1 using the packages *FD* (Laliberté & Shipley 2011) and *Picante* (Kembel *et al.* 2008).

For the 16 islands that have records of both extinctions and introductions we investigated the impact of loss and gain of species quantifying the functional and phylogenetic diversity of all bird assemblages in three scenarios with different combinations of species: past (extinct + extant native species), native (only extant native species), and present (extant native + introduced species). Whereas 'past' is a representation of pre-disturbance bird assemblages, 'present' represents the actual composition of these assemblages after extinctions and introductions. Even if the native scenario is only an approximation to reality it is useful as an exercise to infer relative changes in functional and phylogenetic diversity due to loss or gain of species. We quantified the differences in the functional and phylogenetic diversity of assemblages among these three scenarios with repeated measures ANOVAs in R using the *aov*, *error*, and *pairwise.t.test* functions. For the other 16 islands in which only introductions were documented, we tested the impact of species gain comparing the functional and phylogenetic diversity of all bird assemblages in two scenarios: past (extant native species), and present (extant native + introduced species) using paired t tests in R using the *t.test* function.

We are aware that grouping single islands with archipelagos is a potential source of error. The same is true when grouping continental and oceanic islands. Therefore, we tested the potential influence of type (single islands or archipelagos) and category

(continental or oceanic islands) on functional and phylogenetic changes across scenarios (past, native and present) with generalized linear mixed models (GLMM) accounting for island type, category, and identity as random effects. Given that these categories did not explain much of the variance in functional and phylogenetic diversity (Supporting Information 4) we pooled islands and archipelagos and oceanic and continental islands in the same analysis. We carried out the GLMMs in R using the *lme* function.

Functional and phylogenetic beta diversity

To investigate the impacts of extinctions and introductions on the composition of assemblages we tested whether the extinct, extant native and introduced species were functionally and phylogenetically distinct. To achieve this, we used an additive partitioning framework of functional and phylogenetic beta diversity among these three species groups. This analysis allowed us to decompose beta diversity into two components: turnover and nestedness. Whereas the turnover component represents the functional and phylogenetic dissimilarity between assemblages due to distinct combinations of functional traits or phylogenetic lineages, the nestedness component represents the functional and phylogenetic dissimilarity between assemblages caused by the simple difference in functional and phylogenetic diversity (Leprieur *et al.* 2012). To quantify these components we used the UniFrac index, a measure derived from the Jaccard dissimilarity that quantifies the proportion of shared branch lengths of functional dendrograms or phylogenetic trees between pairs of assemblages (Lozupone & Knight 2005). The UniFrac index ranges from 0 to 1, where 0 indicates assemblages with identical functional and phylogenetic composition (sharing the same branches in the dendrogram or tree), and 1 indicates assemblages with totally different functional

and phylogenetic composition (sharing no branch in the dendrogram or tree). We carried out all these analyses in R using the functions available in Leprieur *et al.* (2012).

RESULTS

Across the 32 islands included in the study were recorded 508 passerine and near-passerine bird species, which included all recently extinct (post 1600), extant native and introduced species. For the 16 islands with documented extinctions and introductions, the number of extinct species varied from 1 to 26 (4.94 ± 6.35; mean ± standard deviation), whereas for all 32 islands, the number of extant native species varied from 2 to 49 (15.00 ± 13.69) and the number of introduced species varied from 1 to 42 (5.75 ± 7.60). In the past (prior to extinctions and introductions), the total richness within each island varied from 2 to 50 (17.47 ± 14.31), whereas in the present (after extinctions and introductions) it varied from 3 to 63 (20.75 ± 16.46). Although the proportion of both loss and gain of species varied from 2% to 47% across the 16 islands with records of both processes, there were on average more introductions than extinctions ($t = 2.131$, $P = 0.039$). For example, twice as many bird introductions were recorded on the island of Mauritius than extinctions (Fig. 3).

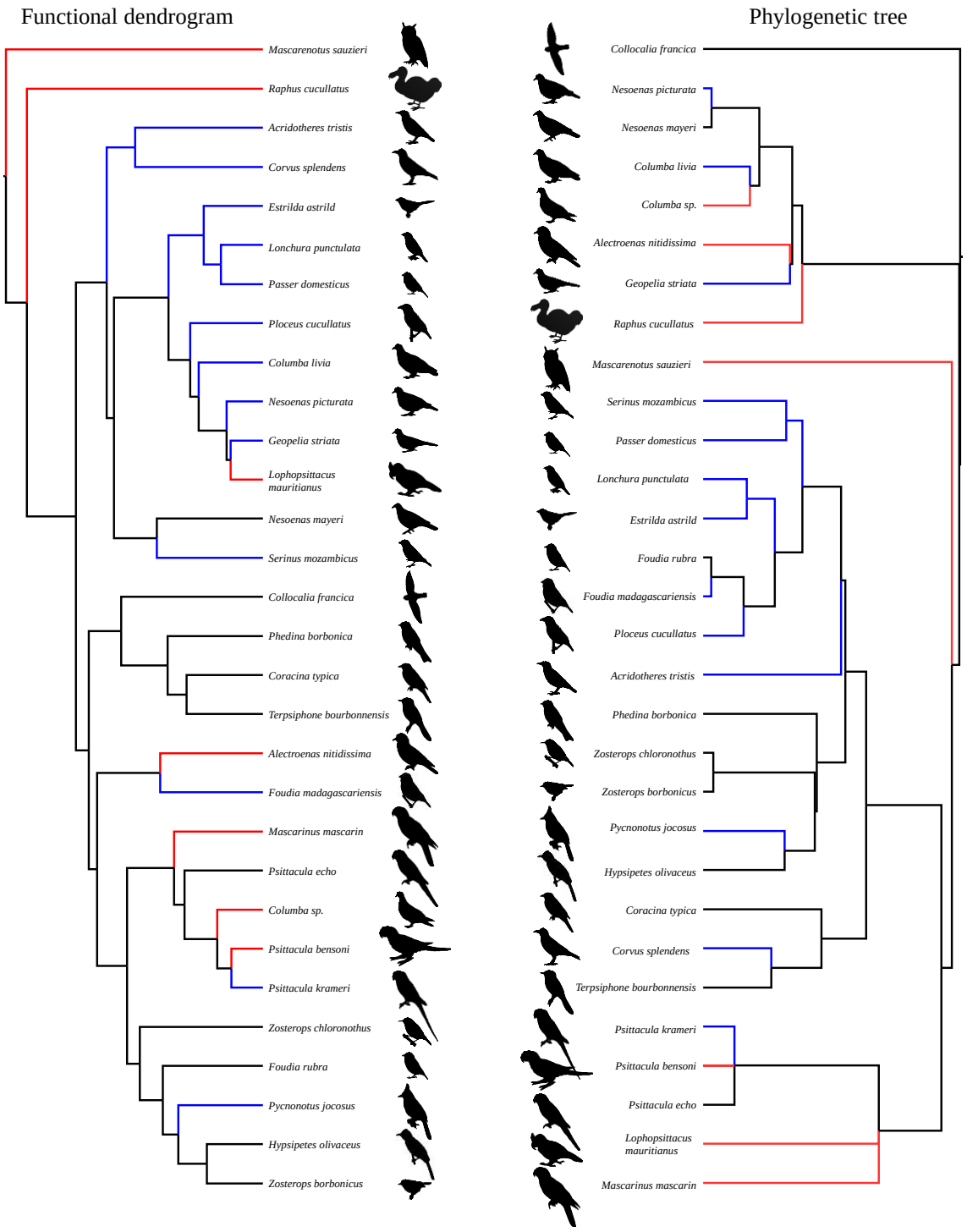

Figure 3 – Functional dendrogram and phylogenetic tree of the passerine and near-passerine inhabiting the island of Mauritius. Black branches indicate the extant native species, red branches indicate extinct species and blue branches indicate introduced species. The arrangement of species in the functional dendrogram and the phylogenetic tree is not the same because their ecological relationships are not equivalent to their respective evolutionary relationships.

Patterns of functional and phylogenetic alpha diversity

We found that neither extinctions nor introductions led to changes in the functional richness of assemblages (Table 1 and Table 2). On the other hand, extinctions led to a decrease and introductions led to an increase in functional dispersion (Table 1). Nevertheless, the functional dispersion of assemblages in the present (after extinctions and introductions) was similar to that observed in the past (before extinctions and introductions) (Table 1 and Table 2). Species loss also decreased the mean functional distance of assemblages but the gain in species in the present resulted in similar values to those observed in the past (Table 1 and Table 2). Our results also show that extinctions did not change the mean functional distance to the nearest species whereas introductions reduced it (Table 1). Despite this, the mean functional distance to the nearest species in the present was not different from that observed in the past for islands with records of both extinctions and introductions (Table 1). For islands with only introductions, the mean functional distance to the nearest species in the present was lower than that observed in the past (Table 2)

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Table 1 – Changes in the functional and phylogenetic diversity across the 16 island bird assemblages recording both extinctions and introductions. The 'past scenario' involves extinct + extant native species; the 'native scenario' extant native species, and the 'present scenario' is comprised of extant native + introduced species. The mean and standard deviation (in parentheses) of the functional and phylogenetic diversity measures for each scenario are also presented. *P*-values < 0.05 are in bold type. The repeated measures ANOVAs and paired t tests were done in R using the *aov*, *error* and *pairwise.t.test* functions. FRic = Functional richness; FDis = Functional dispersion; MPD_{FD} = Mean functional distance; $MNTD_{FD}$ = Mean functional distance to the nearest species; PRic = Phylogenetic richness; PDis = Phylogenetic dispersion; MPD_{PD} = Mean phylogenetic distance; $MNTD_{PD}$ = Mean phylogenetic distance to the nearest species.

Diversity	Measures	Scenarios			ANOVA			t test (*P*-value)		
		Past scenario (S1)	Native scenario (S2)	Present scenario (S3)	d.f.	F	*P*-value	S1-S2	S2-S3	S1-S3
Functional	FRic	0.041 (0.093)	0.023 (0.071)	0.042 (0.088)	2	1.930	0.164	-	-	-
	FDis	0.362 (0.035)	0.331 (0.052)	0.354 (0.034)	2	6.926	**0.003**	**0.018**	**0.004**	0.224
	MPD_{FD}	0.533 (0.052)	0.502 (0.060)	0.512 (0.052)	2	3.958	**0.030**	**0.034**	0.227	0.094
	$MNTD_{FD}$	0.278 (0.081)	0.292 (0.093)	0.261 (0.078)	2	3.881	**0.032**	0.224	**0.026**	0.095
Phylogenetic	PRic	11560 (10390)	7250 (8742)	9422 (9245)	2	1.419	0.262	-	-	-
	PDis	87.417 (19.210)	82.138 (19.992)	86.907 (12.731)	2	1.636	0.212	-	-	-
	MPD_{PD}	125. 222 (27.610)	120.971 (28.125)	124.749 (17.608)	2	0.584	0.564	-	-	-
	$MNTD_{PD}$	57.030 (18.981)	65.429 (26.598)	55.341 (19.111)	2	4.248	**0.024**	**0.016**	**0.027**	0.665

Table 2 – Changes in the functional and phylogenetic diversity across the 16 island bird assemblages recording only introductions. Here, the 'past scenario' is composed of extant native species, and the 'present scenario' is composed of extant native + introduced species. The mean and standard deviation (in parentheses) of the functional and phylogenetic diversity measures for each scenario are also presented. *P*-values < 0.05 are shown in bold type. The paired t tests were done in R using the *t.test* function. FRic = Functional richness; FDis = Functional dispersion; MPD_{FD} = Mean functional distance; $MNTD_{FD}$ = Mean functional distance to the nearest species; PRic = Phylogenetic richness; PDis = Phylogenetic dispersion; MPD_{PD} = Mean phylogenetic distance; $MNTD_{PD}$ = Mean phylogenetic distance to the nearest species.

Diversity	Measures	Scenarios		t test		
		Past scenario (S1)	Present scenario (S3)	d.f.	t	*P*-value
Functional	FRic	0.062 (0.106)	0.088 (0.133)	12	-1.827	0.093
	FDis	0.362 (0.061)	0.371 (0.044)	15	-1.023	0.322
	MPD_{FD}	0.578 (0.142)	0.557 (0.095)	15	1.273	0.222
	$MNTD_{FD}$	0.372 (0.238)	0.315 (0.171)	15	2.632	**0.019**
Phylogenetic	PRic	5951 (9387)	5960 (9381)	11	-1.103	0.293
	PDis	87.510 (12.006)	87.458 (11.659)	15	0.035	0.973
	MPD_{PD}	137.414 (24.077)	129.285 (17.878)	15	2.363	**0.032**
	$MNTD_{PD}$	90.190 (48.074)	72.968 (27.998)	15	2.669	**0.018**

Extinctions and introductions did not change the phylogenetic richness or the phylogenetic dispersion of assemblages (Table 1 and Table 2). In addition, for islands with records of extinctions and introductions there was no difference in the mean phylogenetic distance among the three scenarios (Table 1). However, for islands with only introductions, the species gain resulted in a decrease in the mean phylogenetic distance (Table 2). We also found that extinctions increased the mean phylogenetic distance to the nearest species, whereas introductions decreased it (Table 1 and Table 2). Despite this, the mean phylogenetic distance to the nearest species in the present did not differ from that observed in the past across islands (Table 1). These findings were robust to phylogenetic uncertainty (Supporting Information 3).

Patterns of functional and phylogenetic beta diversity

We found high levels of functional and phylogenetic turnover, and consequently low levels of nestedness, among extinct, extant native, and introduced species (Table 3). These results indicate that the three species groups occupy different positions within the multidimensional functional and phylogenetic space. An example of this pattern can be observed on the island of Mauritius, where most of the introduced species are clustered in the functional dendrogram and phylogenetic tree (Fig. 3). These findings were not influenced by phylogenetic uncertainty (Supporting Information 3).

Table 3 – Functional and phylogenetic turnover and nestedness components from comparisons among pairs of bird groups (extinct, extant native and introduced species) across all 32 islands. The mean and standard deviation (in parentheses) of the functional and phylogenetic beta diversity components for each pairwise comparison are also shown.

Beta diversity	Component	Pairwise comparisons		
		Extinct-Extant	Extant-Exotic	Extinct-Exotic
Functional	Total	0.903 (0.048)	0.886 (0.072)	0.900 (0.058)
	Turnover	0.701 (0.215)	0.706 (0.212)	0.833 (0.120)
	Nestedness	0.202 (0.225)	0.180 (0.205)	0.067 (0.097)
Phylogenetic	Total	0.837 (0.118)	0.870 (0.075)	0.857 (108)
	Turnover	0.593 (0.260)	0.676 (0.184)	0.728 (0.228)
	Nestedness	0.244 (0.218)	0.194 (0.188)	0.129 (0.170)

DISCUSSION

We found that, on average, islands experienced a higher number of introductions than extinctions, which have led to an increase in insular bird richness over time. This change in richness and consequently in species composition has caused varying impacts on both the functional and phylogenetic diversity of assemblages. For example, neither the loss nor the gain of species led to significant changes in functional richness. This shows that both extinct and introduced species are not distributed at the periphery of functional space, which maintains the convex hull volume relatively unchanged. On the other hand, for islands recording both extinctions and introductions, species loss decreased the functional dispersion and mean functional distance, whereas the gain in species from introductions returned the assemblages to values similar to those observed in the past. However, for islands with only introductions, species gain did not lead to

significant changes in functional dispersion or mean functional distance. At first glance, one would conclude that introductions have compensated for functional diversity lost through the extinctions (see Fig. 1a). However, introduced species have a distinct functional composition from extinct species (Table 3). This means that despite these species groups occupying a similar volume, they are located in different positions in functional space. This best agrees with our false functional compensation scenario (Fig. 1d).

This evidence for false functional compensation indicates that extinctions have led to a loss of functionally complementary species, which may impede ecosystem service provision, including the loss of specific ecological functions (Boyer 2010; Boyer & Jetz 2014) and result in cascade effects (e.g. Maron *et al.* 2006). On the other hand, this also indicates that introductions have led to a gain of functionally distinct species compared to the extinct and extant native species. Previous studies have shown that land cover change and disturbance may favour the naturalization of new functional guilds, particularly those with high dietary and foraging plasticity (Cassey *et al.* 2004; Sol *et al.* 2012; García *et al.* 2014). The introduction of exotic generalist species may lead to competition and replacement of native species and functional homogenization of natural assemblages (Devictor *et al.* 2008). Although extinctions did not cause significant changes in mean functional distance to the nearest species, introductions have decreased this facet of functional diversity; evidence that introduced species (functionally similar to each other) may indeed be causing functional homogenization of insular bird assemblages over time. For example, this seems to be the case on the islands of Rodrigues, Reunion and Kiritibati (see Supporting Information 5).

We also found that species extinctions and introductions did not change the phylogenetic richness and phylogenetic dispersion of insular assemblages. In addition,

for islands recording both extinctions and introductions, the mean phylogenetic distance was also not altered. Thus, extinct and introduced species are contributing with similar amounts of evolutionary history. However, for islands with only records of introductions, the gain in species decreased mean phylogenetic distance. This shows that introduced species in these islands are closely related to each other, on for example the islands of Fernando de Noronha, Bermuda and The Snares (see Supporting Information 5). For islands with extinctions and introductions, species loss reduced the mean phylogenetic distance to the nearest species, whereas species gain in the present led to similar values to that observed for assemblages in the past. Again, these results could be wrongly interpreted as introductions having compensated for phylogenetic diversity lost through extinctions (see Fig. 1a). However, we found that introduced species also have a distinct phylogenetic composition from extinct species (Table 3). This means that despite these groups retaining similar amounts of evolutionary history, they belong to distinct clades and lineages. That fits a false phylogenetic compensation scenario (Fig. 1d).

On the one hand, this scenario indicates that extinctions have caused the loss of evolutionarily unique species. This can have severe impacts on the capacity of the assemblages to respond to environmental changes, leading to further impoverishment and phylogenetic homogenization of native faunas (Webb *et al.* 2001; Jackson *et al.* 2015). On the other hand, this scenario also indicates that introductions have led to a gain of species with unique evolutionary histories. The successful introduction and establishment of evolutionarily divergent species indicates that some non-native lineages benefit from land-use and land-cover changes wrought by humans (Frishkoff *et al.* 2014). The proliferation of grassland habitats on many of our island samples creates novel habitats for non-native species, for example for members of the Passeridae

(sparrows and estrildid finches) which are known to proliferate on islands after introduction (Lockwood 1999). In addition, many taxa may be physically incapable of making the over-water crossings to remote island groups but proliferate if introduced there (Lees & Gilroy 2014). The introduction of exotic species, distantly-related from native species can also have significant negative impacts on biodiversity, because they may pose completely novel threats, for example, as competitors, parasites or disease vectors (Strauss *et al.* 2006) with unpredictable consequences for native biotas (Lees & Bell 2008).

For islands with only records of introductions, species gains have also decreased the mean phylogenetic distance to the nearest species, which suggests that introduced species are phylogenetically close to each other. For example, islands such as the Maldives, Bermuda, and Fernando de Noronha have gained closely related species over time (See Supporting Information 5). This is not surprising given that previous studies have already showed that bird introductions have typically involved just five families: Phasianidae, Passeridae, Psittacidae, Anatidae and Columbidae (Blackburn & Duncan 2001; Blackburn & Cassey 2007). In that sense, our findings show that the bird assemblages investigated have suffered more phylogenetic than functional homogenization. Nevertheless, it is important to highlight that such homogenization is taking place in different regions of functional or phylogenetic space from the original pre-disturbance scenario. These findings support other studies showing that non-native bird species occupy different portions of niche space than that occupied by native species (García *et al.* 2013, 2014). This means that non-native species play ecological (and potentially evolutionary) roles previously absent from these assemblages (e.g. prior to human disturbance), exploring portions of vacant (or novel) functional or phylogenetic space (Sullivan *et al.* 2015).

Although the general patterns show that introductions do not compensate for extinctions, we also observed particular cases of partial functional and phylogenetic compensation. For example the replacement of the frugivorous *Alectroenas nitidissima* (Mauritius Blue Pigeon) by the *Foudia madagascariensis* (Red Fody), and granivorous *Lophopsittacus mauritianus* (Broad-billed Parrot) by the *Geopelia striata* (Zebra Dove) in the Island of Mauritius are examples of partial functional compensation given our broad functional classes (Fig. 3). Although these species are not functionally identical, they share some similar ecological roles since they are closely clustered in the functional dendrogram. However, although these species show some functional compensation, they do not present the same phylogenetic compensation because are not closely related to each other (Fig. 3). In other cases, such as the *Raphus cucullatus* (Dodo) and *Mascarenotus sauzieri* (Mauritius Owl) on Mauritius, the functional space left vacant by the extinction of these species has not been filled by any introduced species (Fig. 3). However, the extinction of *Raphus cucullatus* has been partially compensated in phylogenetic space by the introduction of other less evolutionary unique pigeons such as *Geopelia striata*, and *Columba livia* var. *domesticus* (Rock Dove), but the extinction of *Mascarenotus sauzieri* remains uncompensated by any closely related species (Fig. 3). This shows that functional similarity does not always reflect phylogenetic similarity, thus it is important to evaluate these two facets of biodiversity when investigating the ecological roles and evolutionary histories of species (Losos 2008; Gerhold *et al.* 2015). An example of functional compensation that also reflects an evolutionary compensation is the replacement of *Psittacula bensoni* by *Psittacula krameri* on Mauritius (Fig. 3). Therefore, any plans to eradicate introduced bird species such as *Foudia madagascariensis*, *Geopelia striata* and *Psittacula krameri* from Mauritius (Fig. 3) should consider their part in partially compensating for ecological

roles and evolutionary histories lost with the extinction of native species (Tylianakis *et al.* 2010). Furthermore our results ought to be viewed conservatively given that many endemic insular bird species will have been lost before their discovery and scientific description was possible (e.g. Steadman 1995) and with them knowledge of the pre-disturbance regions of phylogenetic and functional space they occupied on their host islands.

We have shown that both the extinction of native species and subsequent reassembly with introduced species has led to variable impacts on the different facets and components of functional and phylogenetic diversity of insular faunal assemblages. Extinctions and introductions have led to both the loss and gain of ecologically and evolutionarily unique species. Although it is known that the number of introductions currently exceeds the number of extinctions across different islands (Sax *et al.* 2002; Sax & Gaines 2008), this balance may yet be readdressed when extinction debts are paid (Triantis *et al.* 2010). Nevertheless, we demonstrate that species introductions are not able to compensate for many ecological roles and evolutionary histories that have been lost over time. Thus, preventing extinctions and avoid introductions is still critical to guarantee the maintenance of ecological and evolutionary mechanisms responsible for community assembly and to ensure the persistence of ecosystem functions and services in a world increasingly governed by anthropogenic processes.

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Supporting Information 1

Table 1 – Functional traits for the 43 insular bird species not present in Wilman *et al.* (2014).

Scientific	Diet-Inv	Diet-Vend	Diet-Vect	Diet-Vfish	Diet-Vunk	Diet-Scav	Diet-Fruit	Diet-Nect	Diet-Seed	Diet-PlantO	ForStrat-watbelowsurf	ForStrat-wataroundsurf	ForStrat-ground	ForStrat-understory	ForStrat-midhigh	ForStrat-canopy	ForStrat-aerial	ForStrat-PelagicSpecialist	Nocturnal	BodyMass
Alectroenas nitidissima	10	0	0	0	0	0	50	0	40	0	0	0	0	0	40	60	0	0	n	165.33
Aplonis fusca	0	0	0	0	0	0	80	0	0	20	0	0	10	30	30	30	0	0	n	68.66
Carduelis cabaret	10	0	0	0	0	0	10	0	70	10	0	0	20	40	40	0	0	0	n	10.5
Chaetoptila angustipluma	0	0	0	0	0	0	0	100	0	0	0	0	0	50	50	0	0	0	n	40.57
Chloridops kona	10	0	0	0	0	0	0	0	90	0	0	0	0	50	50	0	0	0	n	37.85
Ciridops anna	90	0	0	0	0	0	0	10	0	0	0	0	0	10	0	90	0	0	n	27.69
*Columba sp.**	0	0	0	0	0	0	60	0	30	10	0	0	30	20	30	20	0	0	n	308.46
Drepanis funerea	20	0	0	0	0	0	0	80	0	0	0	0	0	100	0	0	0	0	n	18.3
Drepanis pacifica	20	0	0	0	0	0	0	80	0	0	0	0	0	0	0	100	0	0	n	18.3
Dysmorodrepanis munroi	20	0	0	0	0	0	80	0	0	0	0	0	33	33	33	0	0	0	n	28.62
Foudia delloni	20	0	0	0	0	0	0	10	70	0	0	0	0	33	33	33	0	0	n	18.248
Fregilupus varius	30	0	0	0	0	0	30	10	30	0	0	0	0	100	0	0	0	0	n	110
Hemignathus ellisianus	50	0	0	0	0	0	0	50	0	0	0	0	10	30	30	30	0	0	n	34
Hemignathus obscurus	50	0	0	0	0	0	0	50	0	0	0	0	10	30	30	30	0	0	n	27.5
Hemignathus sagittirostris	80	0	0	0	0	0	0	20	0	0	0	0	0	33	33	33	0	0	n	22.3
Hemignathus vorpalis	80	0	0	0	0	0	0	20	0	0	0	0	0	50	50	0	0	0	n	34
Hemiphaga chathamensis	0	0	0	0	0	0	80	0	0	20	0	0	10	20	50	20	0	0	n	800
Hypsipetes undescribed	40	0	0	0	0	0	40	10	0	10	0	0	20	40	40	0	0	0	n	52.39
Lophopsittacus mauritianus	0	0	0	0	0	0	0	0	100	0	0	0	100	0	0	0	0	0	n	1331
Loxioides kikuchi	0	0	0	0	0	0	20	0	20	60	0	0	0	50	50	0	0	0	n	37.85
Mascarenotus grucheti	0	20	80	0	0	0	0	0	0	0	0	0	80	10	10	0	0	0	y	368.3
Mascarenotus murivorus	0	20	80	0	0	0	0	0	0	0	0	0	80	10	10	0	0	0	y	289.38
Mascarenotus sauzieri	0	20	80	0	0	0	0	0	0	0	0	0	80	10	10	0	0	0	y	368.3
Mascarinus mascarin	0	0	0	0	0	0	100	0	0	0	0	0	0	40	40	20	0	0	n	186.24

Moho apicalis	20	0	0	0	0	0	0	80	0	0	0	0	0	50	50	0	0	0	n	49.5
Moho bishopi	20	0	0	0	0	0	20	60	0	0	0	0	0	50	50	0	0	0	n	50.5
Moho braccatus	60	0	0	0	0	0	0	40	0	0	0	0	0	50	50	0	0	0	n	38.5
Moho nobilis	20	0	0	0	0	0	20	60	0	0	0	0	0	50	50	0	0	0	n	55
Myadestes myadestinus	30	0	0	0	0	0	70	0	0	0	0	0	0	20	20	60	0	0	n	34.44
Necropsar rodericanus	90	0	0	0	0	10	0	0	0	0	0	0	100	0	0	0	0	0	n	91.67
Necropsittacus rodericanus	0	0	0	0	0	0	0	0	100	0	0	0	0	100	0	0	0	0	n	325
Nesoenas duboisi	0	0	0	0	0	0	0	0	0	100	0	0	40	10	40	10	0	0	n	302.76
Nesoenas rodericana	10	0	0	0	0	0	20	0	70	0	0	0	100	0	0	0	0	0	n	176.79
Pachycephala graeffii	70	0	0	0	0	0	20	0	10	0	0	0	33	33	33	0	0	0	n	30.36
Pachycephala vitiensis	70	0	0	0	0	0	20	0	10	0	0	0	33	33	33	0	0	0	n	30.36
Pezophaps solitaria	0	0	0	0	0	0	50	0	50	0	0	0	100	0	0	0	0	0	n	22500
Psittacula bensoni	0	0	0	0	0	0	50	10	20	20	0	0	20	30	30	20	0	0	n	214
Psittacula echo	0	0	0	0	0	0	40	20	20	20	0	0	0	33	33	33	0	0	n	163
Psittacula exsul	0	0	0	0	0	0	50	10	20	20	0	0	20	30	30	20	0	0	n	160.66
Psittacula wardi	0	0	0	0	0	0	40	20	20	20	0	0	0	50	50	0	0	0	n	214
Raphus cucullatus	0	0	0	0	0	0	60	0	20	20	0	0	100	0	0	0	0	0	n	14000
Rhodacanthis flaviceps	0	0	0	0	0	0	30	0	70	0	0	0	0	100	0	0	0	0	n	37.85
Rhodacanthis palmeri	20	0	0	0	0	0	0	0	80	0	0	0	0	100	0	0	0	0	n	37.85

* Data refers to average estimations at genus level.

Table 2 – Trait medatada for Table 1.

Variable	Description	Type	Variable codes
Diet-Inv	Percent use of: Invertebrates	Integer	estimated % use (categories sum to 100% total)
Diet-Vend	Percent use of: Mammals, Birds	Integer	estimated % use (categories sum to 100% total)
Diet-Vect	Percent use of: Reptiles, snakes, amphibians, salamanders	Integer	estimated % use (categories sum to 100% total)
Diet-Vfish	Percent use of: Fish	Integer	estimated % use (categories sum to 100% total)
Diet-Vunk	Percent use of: Vertebrates-general or unknown	Integer	estimated % use (categories sum to 100% total)
Diet-Scav	Percent use of: Scavenge, garbage, offal, carcasses, trawlers, carrion	Integer	estimated % use (categories sum to 100% total)
Diet-Fruit	Percent use of: Fruit, drupes	Integer	estimated % use (categories sum to 100% total)
Diet-Nect	Percent use of: Nectar, pollen, plant exudates, gums	Integer	estimated % use (categories sum to 100% total)
Diet-Seed	Percent use of: Seed, maize, nuts, spores, wheat, grains	Integer	estimated % use (categories sum to 100% total)
Diet-PlantO	Percent use of: Other plant material	Integer	estimated % use (categories sum to 100% total)
ForStrat-watbelowsurf	Prevalence of: Foraging below the water surfaces	Integer	estimated % use (categories sum to 100% total)
ForStrat-wataroundsurf	Prevalence of: Foraging on or just (<5 inches) below water surface	Integer	estimated % use (categories sum to 100% total)
ForStrat-ground	Prevalence of: Foraging on ground	Integer	estimated % use (categories sum to 100% total)
ForStrat-understory	Prevalence of: Foraging below 2m in understory in forest, forest edges, bushes or shrubs	Integer	estimated % use (categories sum to 100% total)
ForStrat-midhigh	Prevalence of: Foraging in mid to high levels in trees or high bushes (2m upward), but below canopy	Integer	estimated % use (categories sum to 100% total)
ForStrat-canopy	Prevalence of: Foraging in or just above (from) tree canopy	Integer	estimated % use (categories sum to 100% total)
ForStrat-aerial	Prevalence of: Foraging well above vegetation or any structures	Integer	estimated % use (categories sum to 100% total)
ForStrat-PelagicSpecialist	Foraging predominantly pelagic	Binary	0: no; 1: yes
Nocturnal	Main foraging activity at night	Binary	0: no; 1: yes
BodyMass	Body mass (g)	continuous	NA

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Supporting Information 2

Maximum clade credibility tree (MCC) from 9,999 random, complete and dated phylogenies in Jetz *et al.* (2012). Forty three species (Table 1) were added as polytomies at genus (22 species) and family (21 species) level.

Table 1 – Species included in the MCC tree, their respective category and taxonomic level where they were included.

Species	Category	Added in
Alectroenas nitidissima	Extinct	Genus
Aplonis fusca	Extinct	Genus
Carduelis cabaret	Introduced	Genus
Chaetoptila angustipluma	Extinct	Family
Chloridops kona	Extinct	Family
Ciridops anna	Extinct	Family
Columba sp.	Extinct	Genus
Drepanis funerea	Extinct	Genus
Drepanis pacifica	Extinct	Genus
Dysmorodrepanis munroi	Extinct	Family
Foudia delloni	Extinct	Genus
Fregilupus varius	Extinct	Family
Hemignathus ellisianus	Extinct	Genus
Hemignathus obscurus	Extinct	Genus
Hemignathus sagittirostris	Extinct	Genus
Hemignathus vorpalis	Extinct	Genus
Hemiphaga chathamensis	Extant native	Genus
Hypsipetes undescribed	Extinct	Genus
Lophopsittacus mauritianus	Extinct	Family
Loxioides kikuchi	Extinct	Family
Mascarenotus grucheti	Extinct	Family
Mascarenotus murivorus	Extinct	Family
Mascarenotus sauzieri	Extinct	Family
Mascarinus mascarin	Extinct	Family
Moho apicalis	Extinct	Family
Moho bishopi	Extinct	Family
Moho braccatus	Extinct	Family
Moho nobilis	Extinct	Family
Myadestes myadestinus	Extinct	Genus

Necropsar rodericanus	Extinct	Family
Necropsittacus rodericanus	Extinct	Family
Nesoenas duboisi	Extinct	Genus
Nesoenas rodericana	Extinct	Genus
Pachycephala graeffii	Extant native	Genus
Pachycephala vitiensis	Extant native	Genus
Pezophaps solitária	Extinct	Family
Psittacula bensoni	Extinct	Genus
Psittacula echo	Extant native	Genus
Psittacula exsul	Extinct	Genus
Psittacula wardi	Extinct	Genus
Raphus cucullatus	Extinct	Family
Rhodacanthis flaviceps	Extinct	Family
Rhodacanthis palmeri	Extinct	Family

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Maximum clade credibility tree in the newick format (508 species):

((((((Necropsittacus_rodericanus:58.12187884,Mascarinus_mascarin:58.12187884,Lophopsittacus_mauritianus:58.12187884,((((((Psittacula_wardi:10.36742702,Psittacula_exsul:10.36742702,Psittacula_echo:10.36742702,Psittacula_bensoni:10.36742702,(Psittacula_eques:3.288027525,Psittacula_krameri:3.288027525):7.079399495):6.076070206,Eclectus_roratus:16.44349723):21.09508643,(((Agapornis_canus:21.15285249,Agapornis_pullarius:21.15285249):10.95193419,(Melopsittacus_undulatus:21.75043744,((Phigys_solitarius:3.07141533,(Vini_kuhlii:1.670118835,Vini_australis:1.670118835):1.401296494):9.483243591,Charmosyna_amabilis:12.55465892):9.195778517):10.35434925):3.210324696,(((Prosopeia_tabuensis:3.372615521,Prosopeia_splendens:3.372615521):3.230855427,Prosopeia_personata:6.603470948):7.118081202,(Cyanoramphus_forbesi:3.038309026,Cyanoramphus_novaezelandiae:3.038309026):10.68324312):21.59355923):2.223472275):0.9892566494,(Coracopsis_nigra:8.308264029,Coracopsis_vasa:8.308264029):30.21957628):6.570277734,((((Aratinga_mitrata:8.552489376,Aratinga_erythrogenys:8.552489377):5.911176142,Aratinga_holochlora:14.46366552):22.03815464,((Amazona_viridigenalis:6.472185603,Amazona_amazonica:6.472185604):2.822470144,Amazona_ochrocephala:9.294655747):27.20716441):8.534753734,(Poicephalus_senegalus:7.595850278,Poicephalus_cryptoxanthus:7.595850278):37.44072361):0.06154414573):2.753138793,Cacatua_galerita:47.85125682):10.27062201):20.71122575,((((((Tyrannus_dominicensis:7.284083908,Pitangus_sulphuratus:7.284083909):1.268767905,Myiarchus_magnirostris:8.552851814):2.346819418,(Muscisaxicola_maclovianus:9.631203716,Pyrocephalus_rubinus:9.631203717):1.268467515):1.482205555,(Anairetes_fernandezianus:10.85124041,(Elaenia_ridleyana:6.532849815,Elaenia_martinica:6.532849816):4.318390593):1.530636378):39.59847297,(Aphrastura_masafuerae:13.66514074,(Cinclodes_antarcticus:1.24059032,Cinclodes_oustaleti:1.24059032):12.42455042):38.31520901):15.38214653,(Moho_nobilis:56.87801927,Moho_braccatus:56.87801927,Moho_bishopi:56.87801927,Moho_apicalis:56.87801927,Chaetoptila_angustipluma:56.87801927,(((((Gymnomyza_viridis:11.43589585,Foulehaio_carunculatus:11.43589585):20.22910892,Xanthotis_provocator:31.66500478):1.425579449,(Myzomela_jugularis:20.5720357,((Myzomela_cardinalis:6.797466925,Myzomela_rubratra:6.797466925):13.66408196,Myzomela_chermesina:20.46154888):0.1104868117):12.51854852):1.667381901,(Anthornis_melanura:29.28676853,Prosthemadera_novaeseelandiae:29.28676854):5.471197591):7.797741827,(Gerygone_albofrontata:16.9972726,Gerygone_igata:16.9972726):25.55843535):14.32231131,(((((Oriolus_auratus:24.93791908,((((((Rhipidura_fuliginosa:5.331036886,(Rhipidura_personata:4.330047547,Rhipidura_verreauxi:4.330047546):1.00098934):4.739622433,(Rhipidura_rufifrons:4.857943014,Rhipidura_lepida:4.857943014):5.212716305):9.288358982,Lamprolia_victoriae:19.3590183):2.688856965,((((Terpsiphone_mutata:3.474300112,Terpsiphone_viridis:3.474300112):0.03793648068,Terpsiphone_bourbonnensis:3.512236592):1.378442583,Terpsiphone_corvina:4.890679175):7.074306189,((((Myiagra_azureocapilla:3.940456462,Myiagra_oceanica:3.940456461):0.01790445922,Myiagra_vanikorensis:3.958360922):6.714309028,(Monarcha_takatsukasae:4.534415476,(Chasiempis_sandwichensis:3.735290483,((Clytorhynchus_vitiensis:1.949305708,Clytorhynchus_nigrogularis:1.949305708):0.2374102998,(Mayrornis_versicolor:0.8411487863,Mayrornis_lessoni:0.8411487863):1.345567221):1.548574475):0.7991249933):6.138254473):0.6490812033,Grallina_cyanoleuca:11.32175115):0.6432342125):10.0828899):0.4783272312,(Lanius_meridionalis:21.07300666,(((Corvus_splendens:6.42082129,(Corvus_kubaryi:6.135846209,((Corvus_hawaiiensis:4.380875573,Corvus_brachyrhynchos:4.380875573):0.841397347,(Corvus_corax:1.837690 96,Corvus_albus:1.83769096):3.384581959):0.9135732891):0.2849750823):1.208724901,Corvus_ruficollis:7.629546192):9.772310112,Pyrrhocorax_pyrrhocorax:17.4018563):3.671150353):1.453195841):1.972925766,(Dicrurus_macrocercus:4.826742369,(((Dicrurus_aldabranus:0.5981811615,Dicrurus_forficatus:0.5981811615):2.294607002,Dicrurus_waldenii:2.892788164):0.5988802237,Dicrurus_fuscipennis:3.491668387):1.335073981):19.6723859):0.4387908162):6.149760853,((Vireo_gracilirostris:8.680403165,Vireo_altiloquus:8.680403164):5.310736086,Vireo_griseus:13.99113925):17.09654069):3.784849604,(Pachycephala_vitiensis:12.56083148,Pachycephala_graeffii:12.56083148,(Pachycephala_pectoralis:9.145092073,Colluricincla_teneb

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Supporting Information 3

Methods to evaluate the sensibility of analyses to phylogenetic uncertainty

To test the sensitivity of our analyses to phylogenetic uncertainty we used 500 random phylogenetic trees from 9,999 used to produce the maximum clade credibility tree (MCC). Using these random trees we calculated Phylogenetic Richness (PRic), Phylogenetic Dispersion (PDis), Mean Pairwise Distance (MPD_{PD}) and Mean Nearest Taxon Distance ($MNTD_{PD}$) of all island bird assemblages across different scenarios. For islands recording extinctions and introductions, we used repeated measures ANOVAs to look for changes in the phylogenetic diversity (PRic, PDis, MPD_{PD} $MNTD_{PD}$) across the three scenarios (past, native and present). When ANOVAs were significant ($P < 0.05$), we performed paired t tests. For islands recording only introductions, we estimated the possible changes in the phylogenetic diversity (PRic, PDis, MPD_{PD} and $MNTD_{PD}$) of assemblages across two scenarios (past and present) using paired t tests. We compared the results from these 500 random trees with the results observed from the MCC tree (Figures 1 and 2). We also calculated the standardized effect size (z) and coefficient of variation (cv) for each phylogenetic diversity measure (PRic, PDis, MPD_{PD} and $MNTD_{PD}$) for each scenario (Table 1 below). The standardized effect size was quantified as follows: z = measure_MCC – average_500random / sd_500random. Where "measure_MCC" is the observed value for a given phylogenetic diversity measure (PRic, PDis, MPD_{PD} or $MNTD_{PD}$) quantified from the MCC tree, "average_500random" is the average for the 500 values of the phylogenetic diversity measure, and "sd_500random" is the standard deviation of the 500 values of phylogenetic diversity measure. We also quantified the coefficient of variation of the distribution of 500 values for each measure. Z-values close to zero or lower than |1.96| indicate low phylogenetic uncertainty (Tables 1 and 2). To test the sensitivity of our

beta diversity analyses to uncertainty phylogenetic, we also quantified the phylogenetic beta diversity among extinct, extant native and introduced species within each island using the same 500 random trees. For each tree we quantified the average value of each component (total, turnover and nestedness) taking into account all islands (Figure 3).

Results

Our findings using 500 random trees were consistent to those using the MCC tree. Even when our observed *P*-values from analyses using the MCC tree were not among the most frequent there was not any qualitative change in the interpretation of the results (Figures 1-3). Indeed, z-values and cv-values were low in almost all cases, indicating low phylogenetic uncertainty (Tables 1 and 2).

Figure 1 – Distribution of *P*-values for 500 repeated measures ANOVAs testing the changes in phylogenetic diversity (PRic, PDis, MPD_{PD} and $MNTD_{PD}$) between "past," "native" and "present" scenarios of assemblages recording species extinctions and introductions. Only the ANOVAs for $MNTD_{PD}$ presented *P*-values lower than 0.05. Therefore, we calculated 500 paired t tests testing the changes in $MNTD_{PD}$ among the pairwise scenarios. Black dots are the *P*-values from the ANOVAs and paired t tests quantified using the MCC tree (Table 1 in the manuscript). The results from the MCC tree overlap with the results from the 500 random trees or are qualitatively identical, indicating that our analyses were not affected by phylogenetic uncertainty.

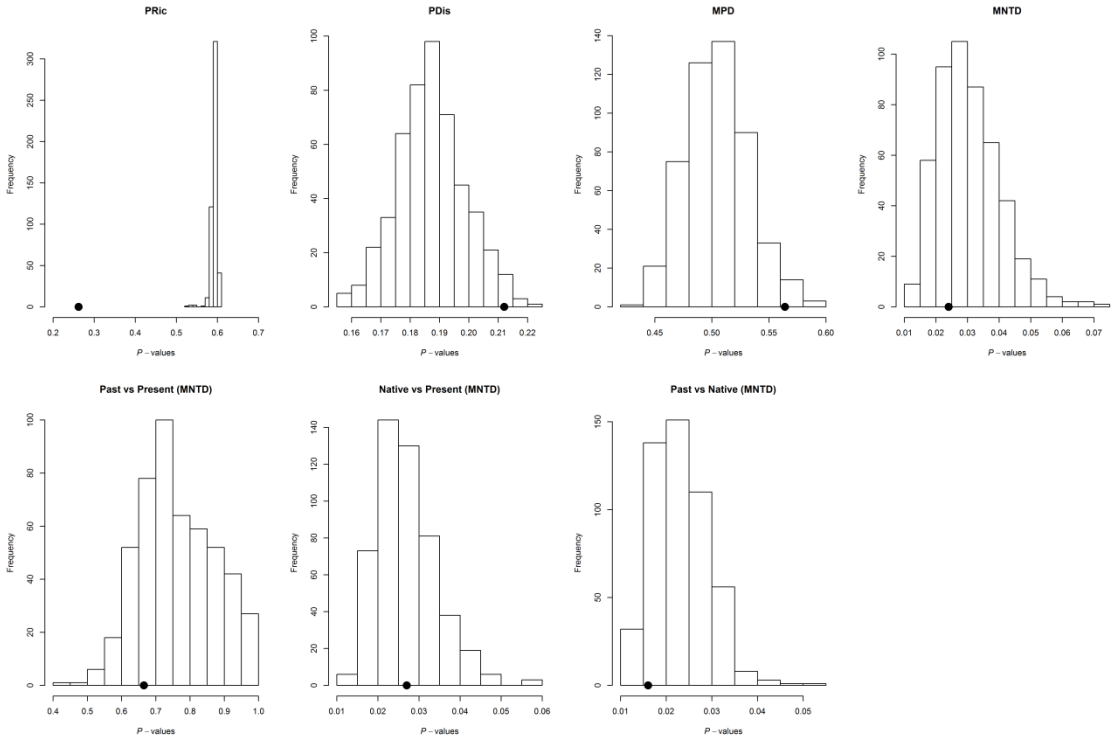


Table 1 – Standardized effect sizes (z) and coefficients of variation (cv) of each phylogenetic diversity measure (PRic, PDis, MPD_{PD} and $MNTD_{PD}$) and the respective scenario for islands with species extinctions and introductions. In general, z-values were close to zero and the cv-values were low, indicating that our analyses were not affected by phylogenetic uncertainty.

Measure	Island	Past		Native		Present	
		z	cv (%)	z	cv (%)	z	cv (%)
PRic	Barbados	0.97	30.00	0.66	31.20	0.44	27.73
	Chatham	0.81	18.00	0.81	17.73	0.68	16.79
	Fiji	-0.11	30.00	-0.11	30.26	-0.12	30.30
	Guadalupe	0.57	29.00	-0.18	41.33	-0.18	41.33
	Kiritibati	-1.01	28.00	-1.01	27.68	0.43	10.26
	Lord Howe	0.38	26.00	-0.13	44.51	-0.24	40.26
	Madeira	0.41	16.00	0.41	15.81	0.41	15.81
	Mariana	0.25	22.00	0.25	22.46	0.25	22.46
	Mauritius	0.67	16.00	0.69	16.36	0.69	16.36
	NW Hawaii	NA	NA	NA	NA	NA	NA
	Pemba	0.41	16.00	0.41	15.98	0.41	15.98
	Réunion	NA	NA	NA	NA	NA	NA
	Revillagigedo	0.39	10.00	0.39	10.28	0.39	10.28
	Rodrigues	NA	NA	NA	NA	NA	NA
	SE Hawaii	NA	NA	NA	NA	NA	NA
	Seychelles	0.46	22.00	0.37	22.79	0.46	22.38
PDis	Barbados	0.43	5.00	0.39	5.04	0.40	5.00
	Chatham	0.74	5.00	0.68	5.05	0.65	5.21
	Fiji	0.55	5.00	0.55	5.01	0.59	5.01
	Guadalupe	0.42	5.00	0.38	5.03	0.40	5.03
	Kiritibati	0.13	5.00	0.22	5.02	0.19	5.02
	Lord Howe	0.61	5.00	0.57	5.03	0.65	5.03
	Madeira	0.40	5.00	0.39	5.04	0.33	5.05
	Mariana	0.61	5.00	0.58	5.01	0.59	5.01
	Mauritius	0.50	5.00	0.78	5.04	0.63	5.03
	NW Hawaii	0.79	6.00	0.86	6.09	0.64	6.05
	Pemba	0.47	5.00	0.48	4.99	0.48	4.99
	Réunion	0.63	5.00	1.09	5.31	0.65	5.09
	Revillagigedo	0.52	5.00	0.58	5.02	0.54	4.99
	Rodrigues	0.43	5.00	0.86	6.09	0.32	5.15
	SE Hawaii	0.30	6.00	0.79	5.47	0.29	5.19
	Seychelles	0.53	5.00	0.54	4.99	0.51	4.98

MPD_{PD}	Barbados	0.33	5.03	-1.62	6.34	0.35	4.98
	Chatham	0.73	5.09	0.62	5.91	0.59	5.18
	Fiji	0.53	4.99	0.30	6.54	0.57	5.00
	Guadalupe	0.33	5.02	-0.33	5.51	0.30	5.03
	Kiritibati	0.09	5.28	-0.40	5.92	0.07	5.04
	Lord Howe	0.60	5.01	0.42	5.87	0.68	5.05
	Madeira	0.36	5.03	0.25	6.38	0.28	5.06
	Mariana	0.56	5.03	-0.15	6.52	0.56	5.01
	Mauritius	0.51	4.85	0.81	5.48	0.61	5.03
	NW Hawaii	0.59	6.13	0.42	6.33	0.52	6.03
	Pemba	0.46	4.98	-0.08	5.80	0.46	4.99
	Réunion	0.65	4.92	0.84	6.18	0.63	5.09
	Revillagigedo	0.53	4.99	0.54	5.55	0.54	4.99
	Rodrigues	0.45	4.90	0.86	6.09	0.26	5.19
	SE Hawaii	0.06	5.82	0.11	6.71	0.22	5.17
	Seychelles	0.54	4.97	0.10	5.96	0.50	4.97
$MNTD_{PD}$	Barbados	-1.34	6.28	-1.62	6.34	-0.67	6.28
	Chatham	0.50	6.52	0.62	5.91	-0.20	5.94
	Fiji	0.34	6.91	0.30	6.54	0.49	6.44
	Guadalupe	-0.77	5.10	-0.33	5.51	-0.64	5.69
	Kiritibati	0.17	8.23	-0.40	5.92	-0.41	5.65
	Lord Howe	0.17	6.13	0.42	5.87	0.43	5.78
	Madeira	0.31	6.42	0.25	6.38	0.11	6.43
	Mariana	-0.79	7.23	-0.15	6.52	-0.15	6.83
	Mauritius	0.55	4.58	0.81	5.48	-0.18	6.37
	NW Hawaii	0.19	6.54	0.42	6.33	-0.08	7.77
	Pemba	-0.07	5.68	-0.08	5.80	-0.07	5.84
	Réunion	0.71	4.99	0.84	6.18	0.35	6.17
	Revillagigedo	0.58	6.61	0.54	5.55	0.27	5.74
	Rodrigues	0.80	4.29	0.86	6.09	-0.66	6.93
	SE Hawaii	-0.47	6.74	0.11	6.71	0.47	6.21
	Seychelles	0.26	6.20	0.10	5.96	0.31	6.26

Figure 2 – Distribution of *P*-values for 500 paired t test testing changes in phylogenetic diversity (PRic, PDis, and MPD_{PD} $MNTD_{PD}$) between "past" and "present" scenarios of assemblages recording only species introductions. Black dots indicate the *P*-values from paired t tests quantified using MCC tree (Table 2 in the manuscript). The results from the MCC tree overlap with the results from the 500 random trees, indicating that our analyses were not sensitive to phylogenetic uncertainty.

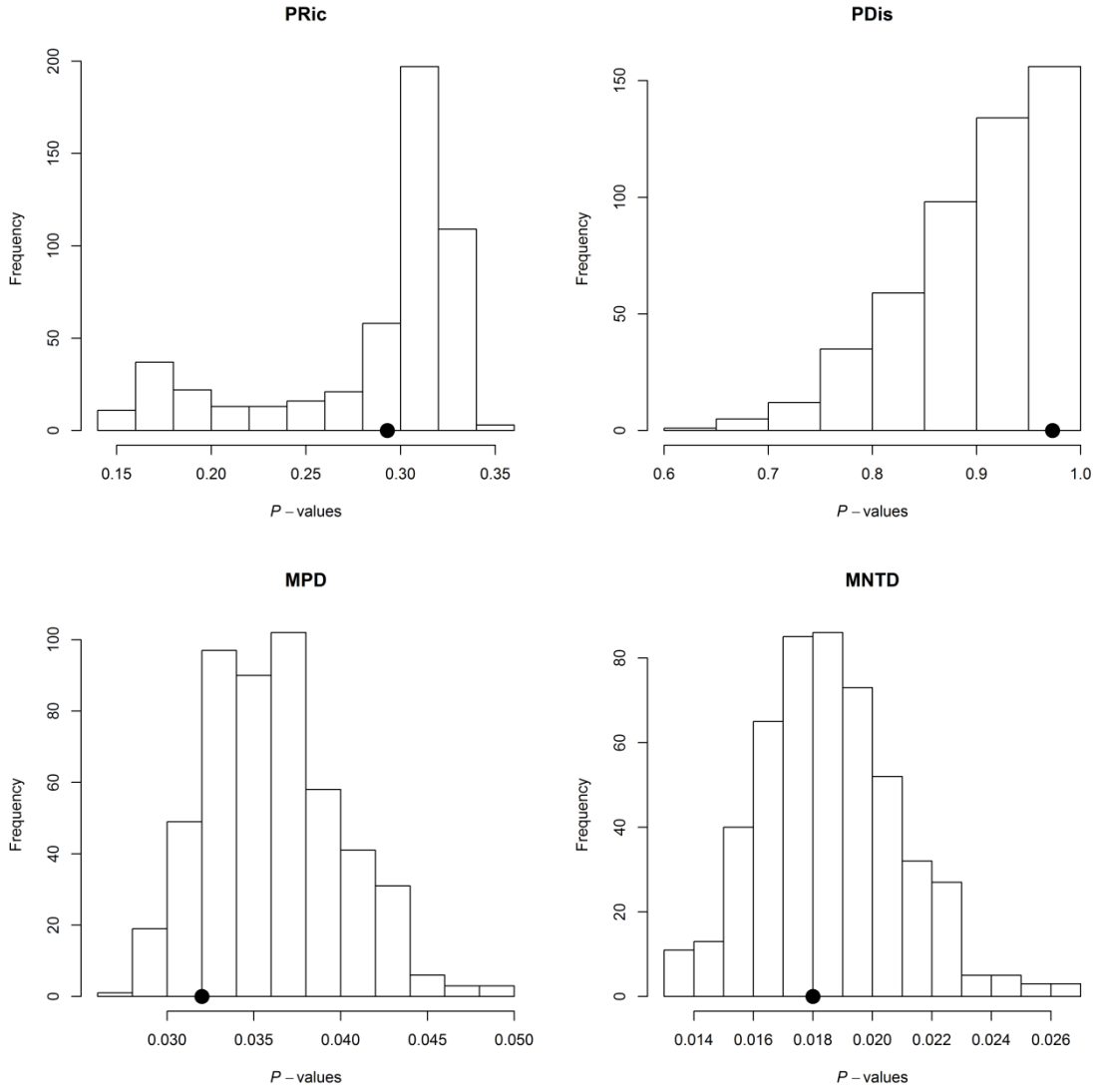
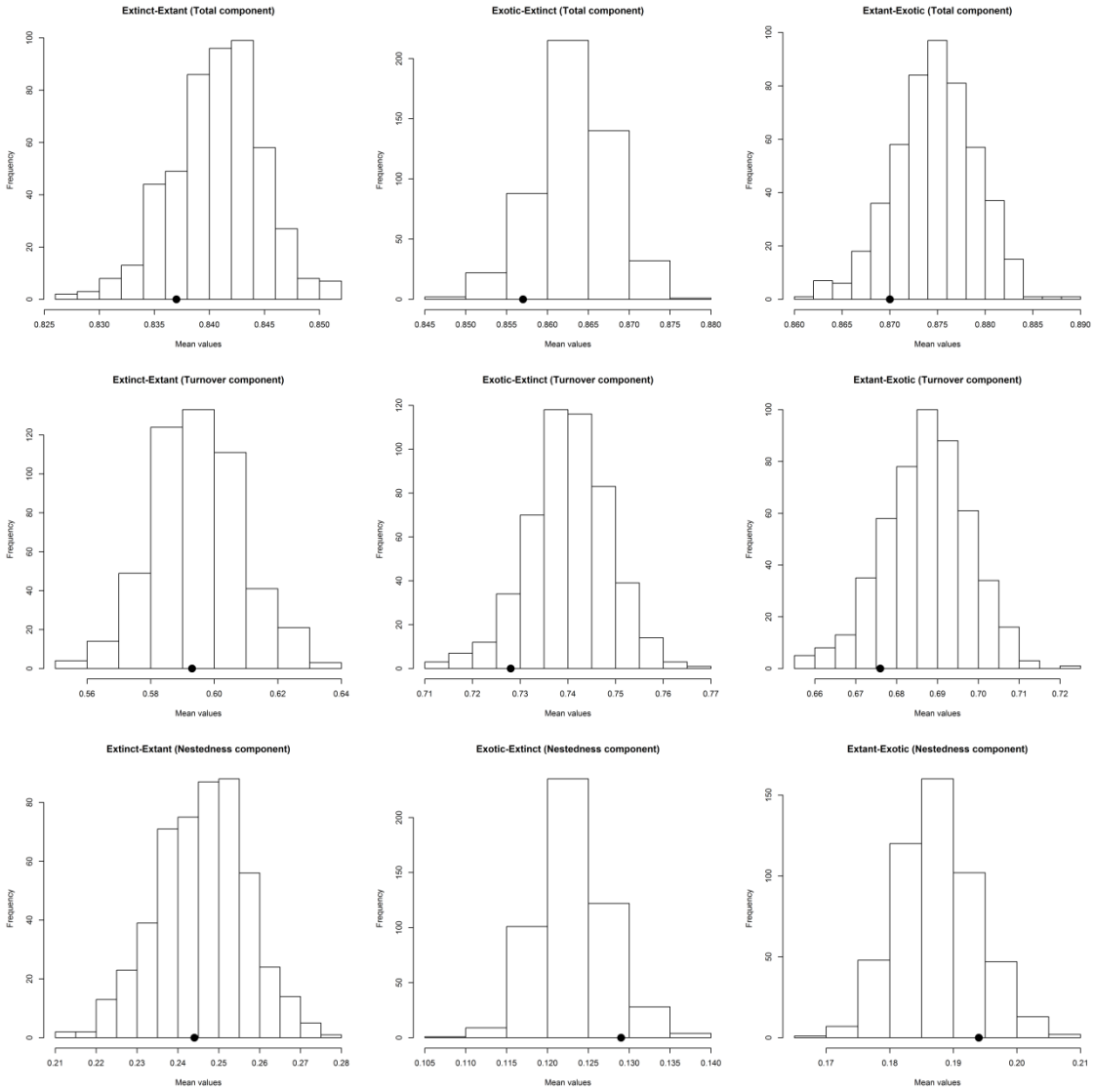


Table 2 – Standardized effect sizes (z) and coefficients of variation (cv) of each phylogenetic diversity measure (PRic, PDis, MPD_{PD} and $MNTD_{PD}$) and the respective scenarios for islands with only species introductions. In general, the z-values were close to zero and the cv-values were low, indicating that our analyses were not affected by phylogenetic uncertainty.

Measure	Island	Past		Present	
		z	cv (%)	Z	cv (%)
PRic	Azores	0.81	29.76	0.77	29.23
	Bermuda	NA	NA	NA	NA
	Canary	0.77	32.49	-0.24	33.37
	Cape Verde	0.40	16.56	0.40	16.56
	Christmas	0.33	11.27	0.46	11.17
	Comoros	0.38	29.36	0.38	29.36
	Europa	NA	NA	NA	NA
	Falkland	0.52	30.52	0.52	30.52
	Fernando de Noronha	-0.89	12.57	0.33	10.41
	Galápagos	0.19	22.23	0.19	22.23
	Juan Fernández	0.34	10.63	0.29	10.72
	Maldives	NA	NA	NA	NA
	Nauru	NA	NA	NA	NA
	Palau	0.37	15.77	0.37	15.77
	Snares	2.56	96.79	1.13	18.47
	Socotra	-0.25	44.56	-0.25	44.56
PDis	Azores	0.38	5.06	0.33	5.09
	Bermuda	0.49	5.01	0.49	5.00
	Canary	0.49	5.03	0.47	5.01
	Cape Verde	0.73	5.05	0.72	5.06
	Christmas	0.45	5.04	0.46	5.00
	Comoros	0.56	4.99	0.55	4.98
	Europa	0.42	5.02	0.62	5.00
	Falkland	0.29	5.10	0.22	5.13
	Fernando de Noronha	0.35	5.07	0.29	5.14
	Galápagos	0.43	5.09	0.43	5.03
	Juan Fernández	0.35	5.10	0.34	5.08
	Maldives	0.43	5.06	0.46	4.97
	Nauru	0.43	5.06	0.15	5.05
	Palau	0.56	5.02	0.56	5.00
	Snares	1.10	6.05	0.66	5.89
	Socotra	0.59	5.02	0.56	5.01

MPD_{PD}	Azores	0.31	5.07	0.27	5.10
	Bermuda	0.48	4.99	0.46	5.00
	Canary	0.45	5.03	0.43	5.00
	Cape Verde	0.71	5.06	0.69	5.06
	Christmas	0.43	5.01	0.44	4.99
	Comoros	0.56	4.98	0.55	4.97
	Europa	0.42	5.02	0.65	5.01
	Falkland	0.27	5.10	0.19	5.13
	Fernando de Noronha	0.35	5.07	0.18	5.15
	Galápagos	0.31	5.08	0.33	5.02
	Juan Fernández	0.33	5.10	0.31	5.07
	Maldives	0.43	5.06	0.44	4.96
	Nauru	0.43	5.06	-0.01	5.10
	Palau	0.56	5.01	0.56	4.99
	Snares	1.10	6.15	0.60	5.88
	Socotra	0.54	5.01	0.52	4.99
$MNTD_{PD}$	Azores	-0.36	6.15	-0.43	6.14
	Bermuda	0.19	5.28	-0.30	5.41
	Canary	0.23	5.77	0.49	5.56
	Cape Verde	0.52	6.08	0.40	6.00
	Christmas	0.31	5.10	0.01	5.12
	Comoros	0.04	5.66	0.17	5.83
	Europa	0.42	5.02	0.90	5.24
	Falkland	-0.12	6.98	-0.26	6.87
	Fernando de Noronha	0.24	5.25	-0.44	5.70
	Galápagos	-0.56	6.54	-0.19	6.51
	Juan Fernández	-0.34	6.37	-0.37	5.76
	Maldives	0.43	5.06	0.11	5.18
	Nauru	0.43	5.06	-0.62	6.05
	Palau	0.17	6.13	0.24	5.82
	Snares	0.78	8.69	-0.24	7.21
	Socotra	-0.41	5.54	-0.29	5.53

Figure 3 – Distribution of mean values for each phylogenetic beta diversity component (total, turnover and nestedness) from 500 random trees. Black dots indicate the mean values for each component quantified using MCC tree (Table 3 in the manuscript). Results from the MCC tree overlap with the results from the 500 random trees, indicating that our analyses were not affected by phylogenetic uncertainty.



Supporting Information 4

Generalized linear mixed models (GLMM) quantifying for the relative influence of island type (islands or archipelagos) and category (continental or oceanic) on functional and phylogenetic structure across scenarios (past, native and present). The models included the functional and phylogenetic diversity measures as a fixed effect, and island type, category and identity as random effects.

Table 1 – Contribution of the random variables to the functional and phylogenetic diversity variability across 32 islands included in the study.

Diversity	Measure	Variable			
		Type	Category	Island	Residual
Functional	FRic	< 0.001	< 0.001	0.886	0.113
	FDis	0.013	< 0.001	0.666	0.320
	$MPD_{(FD)}$	0.213	< 0.001	0.641	0.145
	$MNTD_{(FD)}$	0.150	< 0.001	0.759	0.090
Phylogenetic	PRic	< 0.001	0.057	0.628	0.314
	PDis	0.030	< 0.001	0.697	0.272
	$MPD_{(PD)}$	0.074	< 0.001	0.685	0.240
	$MNTD_{(PD)}$	0.084	< 0.001	0.705	0.210

Table 2 – Contribution of the random variables to the functional and phylogenetic diversity variability across 16 islands with records of species extinction and introduction.

Diversity	Measure	Variable			
		Type	Category	Island	Residual
Functional	FRic	< 0.001	< 0.001	0.857	0.142
	FDis	< 0.001	< 0.001	0.557	0.442
	$MPD_{(FD)}$	< 0.001	0.143	0.533	0.323
	$MNTD_{(FD)}$	< 0.001	< 0.001	0.838	0.161
Phylogenetic	PRic	< 0.001	< 0.001	0.517	0.482
	PDis	0.056	< 0.001	0.674	0.269
	$MPD_{(PD)}$	0.128	< 0.001	0.648	0.223
	$MNTD_{(PD)}$	0.187	< 0.001	0.561	0.251

Table 3 – Contribution of the random variables to the functional and phylogenetic diversity variability across 16 islands with only species introduction.

Diversity	Measure	Variable			
		Type	Category	Island	Residual
Functional	FRic	< 0.001	< 0.001	0.892	0.107
	FDis	0.179	< 0.001	0.621	0.199
	$MPD_{(FD)}$	0.257	< 0.001	0.602	0.140
	$MNTD_{(FD)}$	0.258	< 0.001	0.635	0.106
Phylogenetic	PRic	< 0.001	< 0.001	0.999	< 0.001
	PDis	< 0.001	< 0.001	0.878	0.121
	$MPD_{(PD)}$	0.120	< 0.001	0.629	0.250
	$MNTD_{(PD)}$	0.139	< 0.001	0.588	0.272

Supporting Information 5

Changes in the functional and phylogenetic diversity across the 32 island bird assemblages included in this study following the species extinction and introduction.

Figure 1 – Functional diversity across the 16 bird assemblages recording extinctions and introductions. The 'past scenario' involves extinct + extant native species; the 'native scenario' extant native species, and the 'present scenario' is comprised of extant native + introduced species. Statistics for the ANOVA tests are also presented. For some islands FRic could not be calculated due to the lack of more than 3 unique species (Villéger et al. 2008). Some islands showed FRic values very similar and are overlapping in figure (Seychelles, Barbados, Chatham, Fiji, Guadalupe, Madeira, Mauritius and Réunion).

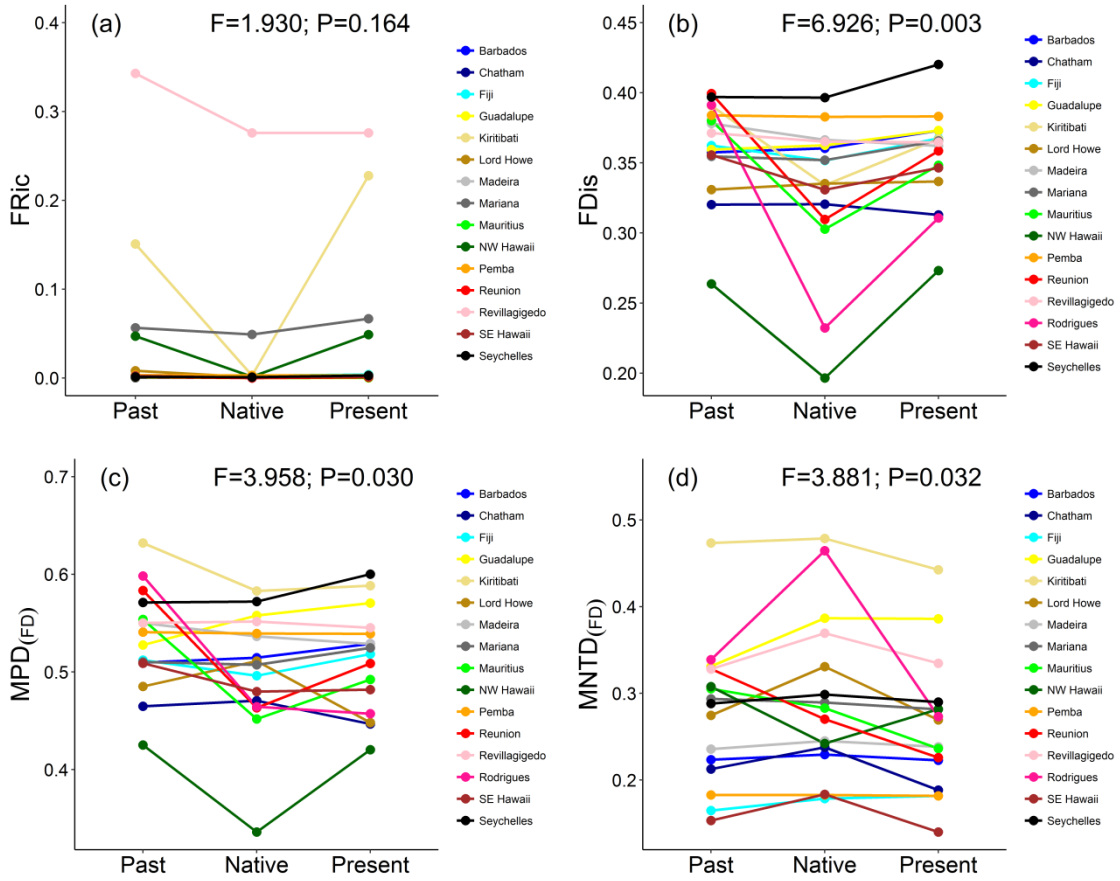


Figure 2 – Changes in the phylogenetic diversity across the 16 bird assemblages recording extinctions and introductions. The 'past scenario' involves extinct + extant native species; the 'native scenario' extant native species, and the 'present scenario' is comprised of extant native + introduced species. Statistics for the ANOVA tests are also presented. For some islands PRic could not be calculated due to the lack of more than 3 unique species (Villéger et al. 2008). Some islands showed PRic values very similar and are overlapping in figure (Revillagigedo, Kiribati and Mariana).

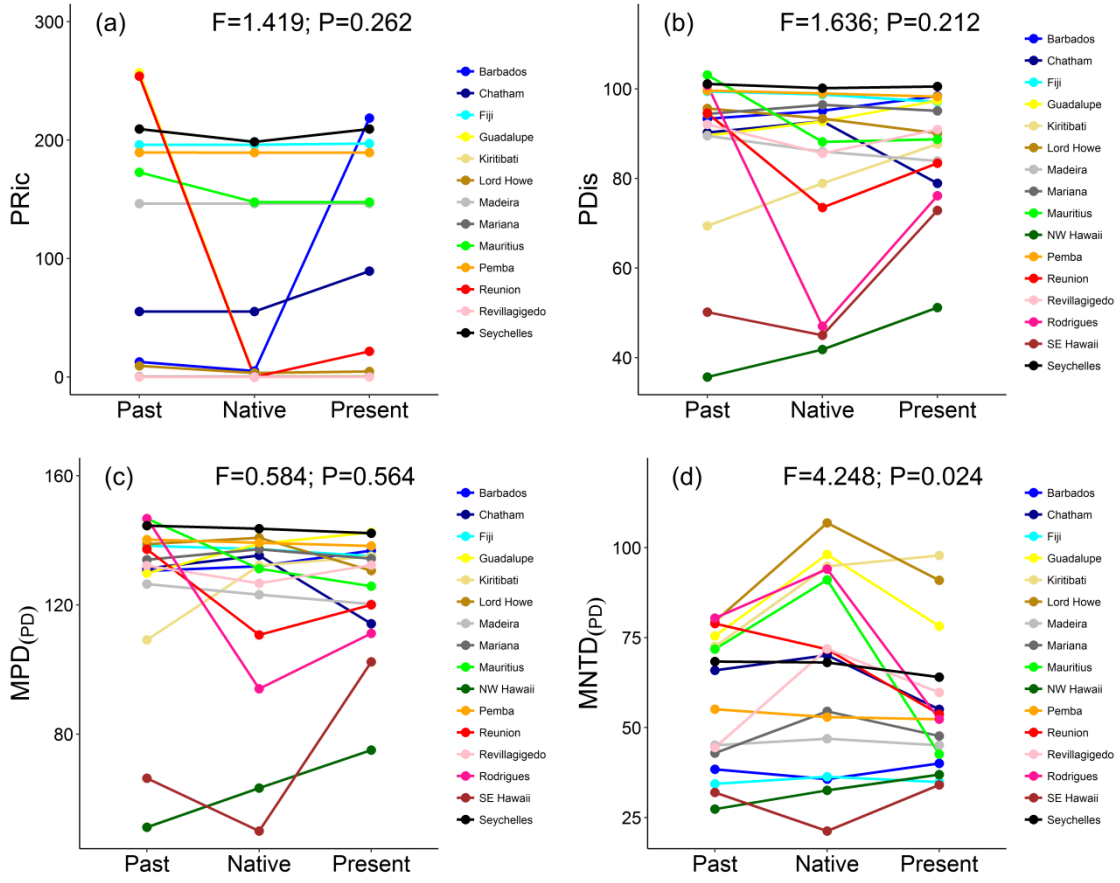


Figure 3 – Changes in the functional diversity across the 16 bird assemblages recording only introductions. The 'past scenario' involves extinct + extant native species, and the 'present scenario' is comprised of extant native + introduced species. For some islands FRic could not be calculated due to the lack of more than 3 unique species (Villéger et al. 2008). Some islands showed FRic values very similar and are overlapping in figure (Socotra, Azores, Bermuda, Comoros and Falkland).

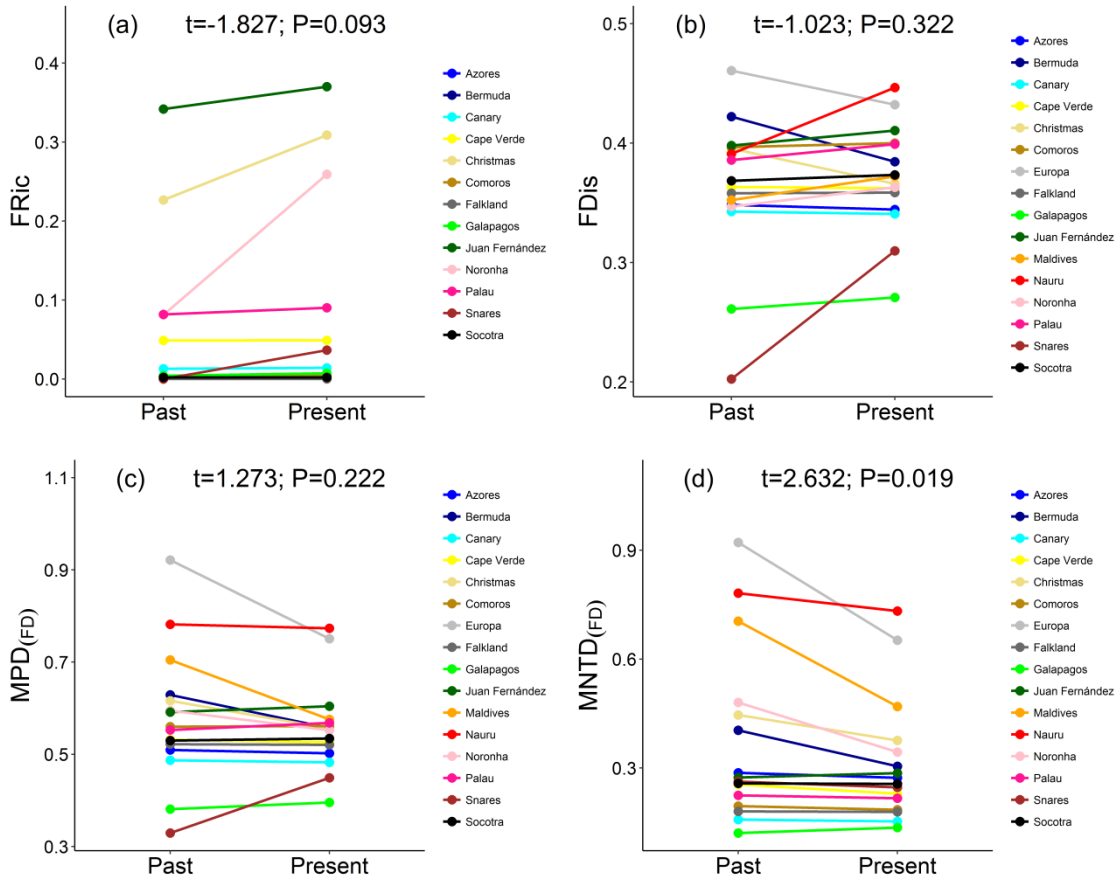
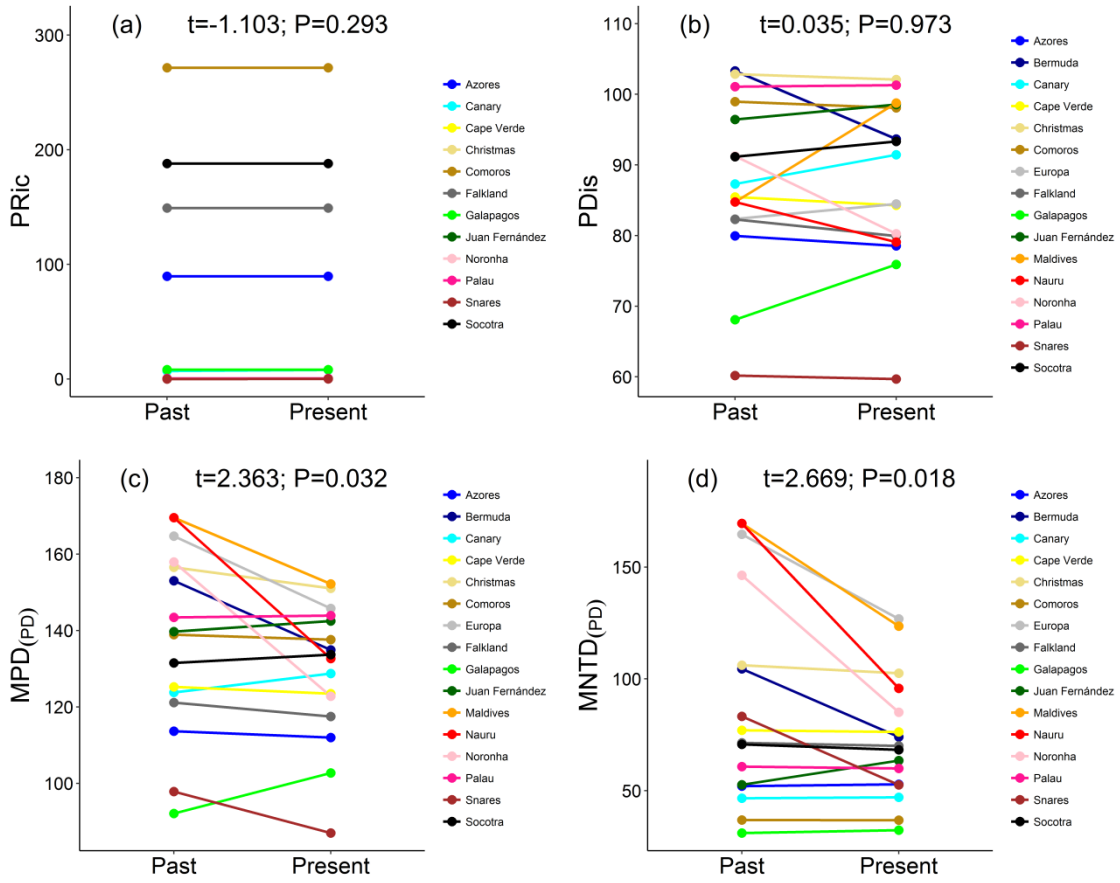


Figure 4 – Changes in the phylogenetic diversity across the 16 bird assemblages recording only introductions. The 'past scenario' involves extinct + extant native species, and the 'present scenario' is comprised of extant native + introduced species. For some islands PRic could not be calculated due to the lack of more than 3 unique species (Villéger et al. 2008). Some islands showed PRic values very similar and are overlapping in figure (Snares, Cape Verde, Christmas, Noronha, Juan Fernández and Palau; Galápagos and Canary).



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CAPÍTULO II

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Species introductions associated with erosion of the functional but not phylogenetic diversity of insular bird assemblages

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Abstract

The introduction of non-native species has a pervasive impact on the richness and composition of native species assemblages. These changes have the potential to profoundly affect the natural mechanisms responsible for generating and maintaining species diversity over time and hence the functional and phylogenetic diversity of biological assemblages. Using path analysis, we investigated how biogeographic, environmental and anthropogenic factors shape the proportion of introduced bird species on oceanic and continental islands, and the impact of these introductions on the functional and phylogenetic diversity of assemblages. We found that the functional diversity of assemblages is positively associated with temperature and negatively associated with the proportion of introduced bird species, whilst phylogenetic diversity is not clearly associated with any variable. On the other hand, the proportion of introduced bird species is strongly negatively associated with native species richness and positively associated with local human population size. These results suggest that species introductions have accompanied a decrease in functional diversity, but not the phylogenetic diversity of insular bird assemblages. Successful introduced species tend to be ecologically similar, leading to a decrease in the functional distance among species in insular systems. This may lead to ecological homogenization of insular bird assemblages over time. Our results also indicate that native species richness and diversity may act to restrict the establishment of introduced species, potentially through competition and agonistic interactions.

Keywords: ecological traits, evolutionary history, functional homogenization, human activities, introduced species, island biogeography, path analysis.

Introduction

The re-moulding of biotas by human agency via the twin processes of species extinctions and introductions is a defining facet of the Anthropocene (Thomas, 2013) and has been particularly pervasive in insular environments (Sax et al., 2002; Helmus et al., 2014; Whittaker et al., 2014). Humans have transported and introduced thousands of non-native species to islands (Blackburn et al., 2008, 2015; Dyer et al., 2017) overcoming physiological and geographical barriers to long-range dispersal that are naturally insurmountable for these species (Duncan et al., 2003; Blackburn et al., 2011). This has profoundly altered natural ecosystems, resulting in a decrease or maintenance of species richness in some locations (due to species extinctions), and an increase in species richness in others (Sax et al., 2002). These changes have impacted the functional and phylogenetic diversity of insular assemblages over time from a pre-human impact baseline (Winter et al., 2009; Sobral et al., 2016). The introduction, establishment and spread of non-native species is therefore a major threat to biodiversity worldwide (Duncan et al., 2003; Blackburn et al., 2011).

Human activities directly or indirectly influence the establishment and enhance the persistence probability of species introduced on islands through multiple pathways. For example, shipping traffic (dictated by volume of trade and level of tourism) is a strong determinant of the transport and exchange of species (e.g. Helmus *et al.*, 2014). In turn, anthropogenic habitat modification (e.g. habitat loss, fragmentation and degradation) can result in changes to land cover which prejudice native species and favor the establishment of introduced species. Local human population size is a good proxy for the magnitude of effect of anthropogenic activities on the richness and proportion of introduced species (Kummu & Varis, 2011). However, there is also ample evidence for the role of natural pre-existing abiotic and biotic factors such as island

area, isolation and productivity, as well as the interaction with other locally co-occurring species in determining introduction success (Blackburn et al., 2008, 2015). The interplay of abiotic and biotic factors affecting the richness and composition of native and introduced species across islands, will shape the functional and phylogenetic diversity of insular assemblages over space and time (Winter et al., 2009; Helmus et al., 2014; Whittaker et al., 2014).

Classical assumptions of the theory of island biogeography (MacArthur & Wilson, 1967) such as the effects of island size and degree of isolation are expected not only to influence the richness of native and introduced species but also the functional and phylogenetic diversity of insular assemblages. Larger islands typically have higher habitat diversity (and hence more ecological niches), which offer more opportunities for allopatric divergence of native species (Kisel & Barraclough, 2010) and more opportunities for establishment of introduced species. Larger island size is also associated with lower extinction probability for both native and introduced species as larger populations are less affected by stochastic demographic and environmental factors (Blackburn et al., 2008, 2015). Distance from island to the nearest continent can be negatively associated with the richness of both native and introduced species because propagule pressure is lower on more-isolated islands (MacArthur & Wilson, 1967; Lees & Gilroy, 2014). Alternatively, the number of introduced species may be primarily independent on the distance from the island to the nearest continent. Many historical island introductions represented deliberate introductions of exotic species during the European colonial expansion to 'acclimatize' the new human residents, while recent introductions are largely unplanned and associated with increasing levels of economic activity at insular locations (Dyer et al., 2016). Although island isolation should not directly impact introduced species richness independent of other factors, larger and less-

isolated islands are expected to harbor more species with more diverse natural histories and trait distributions from different lineages than smaller and more isolated islands and hence assemblages concomitantly higher functional and phylogenetic diversity.

Ecosystem productivity in response to latitudinal, altitudinal and pluvial gradients also has the potential to mediate richness of both native and introduced species richness because given greater resource available in more productive systems which facilitates higher species packing (Wright, 1983; Kalmar & Currie, 2006). High local alpha diversity results in strong abiotic and biotic interactions, which promotes character displacement and ecological speciation among species (Schluter, 1988) leading to higher functional and phylogenetic diversity. Native species richness can have negative or positive associations with the richness and proportion of introduced species. On the one hand, islands with high native species richness present a barrier to establishment of introduced species because of negative competitive and antagonistic interactions (Elton, 1958). On the other hand, islands with higher native species richness are usually benign and productive and may offer a wider-range of conditions that suit more introduced species (Stohlgren et al., 2003a; Blackburn et al., 2015; Dyer et al., 2017). The proportion of introduced species can potentially have a negative effect on the diversity of biological assemblages. Introduced species tend to be distributed in only a few lineages and hail from a limited number of biogeographical regions, resulting in non-random distributions of their ecological and life-history traits (Newsome & Noble, 1986; Cassey, 2001; Duncan et al., 2003; Cassey et al., 2004). The introduction and proliferation of species which are ecologically and evolutionarily similar to each other, at typically species-poor locations such as islands can lead to decreases in the mean functional and phylogenetic distance among species over time (Sobral et al., 2016). Therefore, it is expected that the functional and phylogenetic diversity of insular

assemblages will be higher in islands which are: (1) larger, (2) less-isolated, (3) more-productive, (4) richer in native species, and (5) poorer in introduced species.

Here we quantified the proportion of introduced bird species across different islands worldwide and quantified the functional and phylogenetic diversity of bird assemblages to test: (i) whether different biogeographic, environmental and anthropic factors can explain the differences in the degree of introduction of birds in islands; and (ii) the impact of these introductions on the functional and phylogenetic diversity of insular bird assemblages. We focused on birds given the ready availability of high quality data (on occurrence, introductions, life history and phylogenetic position) for island locations.

Material and methods

We investigated the effect of species introductions on functional and phylogenetic diversity of bird assemblages across 32 island locations around the world. Some of these locations are single islands (15) whereas others are close-knit archipelagos (17), and all are situated at least 100 km to the nearest continental mainland. We included in the study all species (extant native and introduced) of terrestrial and aquatic birds that are resident on these islands and which use resources in terrestrial, aquatic or coastal habitats. Thus, we excluded all species that are fully pelagic (e.g. Procellariiformes) which only visit the islands to breed. Data on the composition of native and introduced bird species from each island were extracted from various sources, mainly annotated checklists in ornithological journals, technical reports, books and websites maintained by regional authorities and committees (see Supporting Information 1).

The role of birds in ecological processes and ecosystem services is directly related to life history traits (Sekercioglu, 2006). Therefore, to quantify the functional diversity of assemblages, we used the following avian traits: diet, treated as the estimated percentage of each diet item (invertebrates, vertebrates, scavenger, fruits, nectar, seeds and plants); foraging niche, treated as the estimated percentage of time spent in each strata (ground, understory, mid high, canopy and air), foraging period, treated as a binary categorical variable (diurnal and nocturnal); and body mass, as a continuous variable. We extracted all the data from Wilman *et al.* (2014). To quantify the phylogenetic diversity of assemblages, we used the phylogenetic hypothesis proposed by Jetz *et al.* (2012). From 9999 random, complete and dated phylogenetic trees, we constructed a maximum clade credibility tree that was used in all analyzes of phylogenetic diversity (see Sobral *et al.*, 2016 for more details).

To quantify the functional diversity of assemblages, we constructed a functional distance matrix for each island, including only the bird species present in each of them (native + introduced species). We have chosen to construct individual functional distance matrices, because islands distributed in different regions of the world have particular abiotic and biotic conditions. They thus vary in the number and type of available niches. This can be observed by the low number of species shared between different islands (for example, about 73% of all species included in our database occur on only one unique island). Considering that a functional distance matrix is a way to represent the distribution of species within the niche space, building a functional distance matrix for each island is a more straightforward way of representing the niche (island) that each species occupies.

To calculate the functional distance matrices, we used a modification of the Gower distance that assigns the same weight to different types of categorical and

continuous traits. Then, from the resulting distance matrices we quantified the mean pairwise distance (MPD) of assemblages, a measure independent of species richness (Webb, 2000). When used as a measure of functional diversity, the mean pairwise distance quantifies the mean distance between all pairs of co-occurring species in the functional space (Webb, 2000; Webb et al., 2002; de Bello et al., 2016). To quantify the phylogenetic diversity of assemblages, we used the maximum clade credibility tree to produce the cophenetic distance matrix for each island, taking into account only the species present in each of them (native + introduced species). Then, from the cophenetic distance matrices we quantified the phylogenetic diversity of each island. All the analyses were carried out in R v.3.3.1 using the *picante* package (Kembel et al., 2008).

In addition to the functional and phylogenetic diversity, we also obtained the following data for all the islands included in our study: area (km^2), distance from the nearest continental mainland (km), precipitation (mm), latitude (degrees from the Equator), temperature (°C), current estimated human population size, native bird richness and proportion of introduced bird species. Here, we used the temperature and precipitation as surrogate variables for productivity of islands. We used the natural logarithm of island area, human population size and native bird richness, and the absolute values of latitude for all statistical analyses. We extracted all these data (excluding native bird richness and proportion of introduced bird species) for 29 islands from Blackburn *et al.* (2015). For the other three islands we compiled data from institutional websites (see Supporting Information 2).

We used path analysis to investigate the direct and indirect effects of island area, distance from island to the nearest continental mainland, precipitation, latitude, temperature and human population size on the degree of introduction of non-native bird species on islands. Furthermore, we also used path analysis to assess the effect of these

biogeographic, environmental and anthropogenic factors on the functional and phylogenetic diversity of current insular bird assemblages. In the path analyses, the direct effect expresses how much a response variable changes in response to changes in the explanatory variable while controlling for the effect of the other explanatory variables. Therefore, the direct effect corresponds to the standardized partial regression coefficient in a multiple regression. The indirect effect expresses the influence of an explanatory variable on a response variable that is mediated by one or more variables through a causal relation presented in the model. The total effect represents how much a response variable changes in response to the direct and or indirect effects from an explanatory variable (Grace, 2006).

The path analysis for the functional diversity of insular bird assemblages was based on the following rationale: (1) island area, distance from the island to the continent, precipitation and latitude were our explanatory variables of interest, and were included in the model as exogenous variables; (2) temperature was included as an exogenous and endogenous variable because it is expected to be influenced by latitude and to influence human population size, native birds species richness, proportion of introduced bird species and functional diversity of insular bird assemblages; (3) human population size was included as an exogenous and endogenous variable because it is expected to be influenced by island area, distance from the island to the continent, precipitation, latitude and temperature and to influence the native bird species richness, the proportion of introduced bird species and the functional diversity of insular bird assemblages; (4) native bird species richness was included as an exogenous and endogenous variable because it is expected to be influenced by the island area, distance from the island to the continent, precipitation, latitude, temperature and human population size and to influence the proportion of bird species introduced and the

functional diversity of island bird assemblages; and (5) proportion of introduced bird species was also included as an exogenous and endogenous variable because it is expected to be influenced by island area, distance from the island to the continent, precipitation, latitude, temperature, human population size and native bird species richness and to influence the functional diversity of insular bird assemblages. We used an identical model to test the potential effect of these biogeographic, environmental and anthropic factors on the phylogenetic diversity of insular bird assemblages.

We developed the path analysis using a model selection approach according to the Akaike Information Criterion (AIC) (Grace, 2006). We initiated the analyses starting with the models that have all causal interrelations hypothesized between the variables. And so, step-by-step we removed the non-significant relationships until we reached the model with the lowest AIC. We assessed model fit through Chi squared tests and by examining the Tucker-Lewis Fit Index (TLI), the Comparative Fit Index (CFI), and the Root Mean Square Error of Approximation (RMSEA). To verify whether the path models had adequate statistical power, we used the approach introduced by MacCallum *et al.* (1996). We checked the normality using the Mardia test (Mardia, 1970), and inspected the outliers using the Mahalanobis distance (Mahalanobis, 1936). To meet normality requirements, we applied the logarithmic transformation to island area, human population size and native bird species richness. In addition, we used the absolute values for latitude. We constructed and analyzed the path models using AMOS 5.0 (Arbuckle, 2003). We calculated the statistical power of the path models using RMSEA with the R code developed by Preacher & Coffman (2006).

Results

The AIC selected path model for the functional diversity of insular bird assemblages (AIC = 70.440) showed a good fit between the model and the observed data (X^2 = 10.440, df = 15, p = 0.791, CFI = 1.000, TLI = 1.060: RMSEA = 0, p-value for the test of close fit = 0.839) and an adequate statistical power (0.999). In general, this model accounted for 67% of variation in observed values of functional diversity (Figure 1). Similarly, the AIC selected path model for the phylogenetic diversity of insular bird assemblages (AIC = 70.667) also showed a good fit between the model and the observed data (X^2 = 10.667, df = 15, p = 0.776; CFI = 1.000; TLI = 1.068: RMSEA = 0, p-value for the test of close fit = 0.827), and an adequate statistical power (0.999). However, this path model accounted for only 16% of variation in observed values of phylogenetic diversity (Figure 2). In addition, both models also accounted for 70% of variation in the proportion of introduced species, 65% of variation in native species richness, 68% of variation in human population size, and 81% of variation in temperature (Figures 1 and 2).

Temperature had a strong positive direct effect and a weak negative indirect effect on the functional diversity of assemblages, resulting in a positive total effect for this variable (Figure 1, Table 1). In contrast, the proportion of introduced species had a strong negative direct effect on functional diversity (Figure 1, Table 1). Latitude had both a strong positive direct and negative indirect effects on functional diversity, resulting in a weak negative total effect for this variable (Figure 1, Table 1). Native species richness, human population size, island area, precipitation, and distance from island to the nearest continent did not have significant direct effects on functional diversity (Figure 1, Table 1). Conversely, none of the variables included in the path analysis had a significant direct effect on phylogenetic diversity (Figure 2 and Table 1).

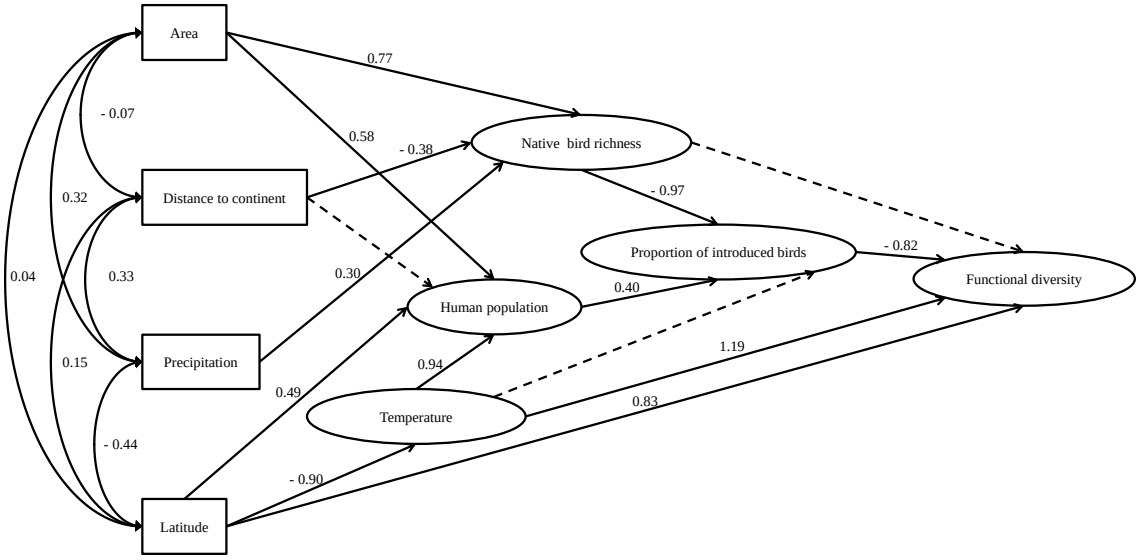

Figure 1. Path analysis for the functional diversity of insular bird assemblages explained by island area, distance from island to the nearest continent, precipitation, latitude, temperature, human population size, native bird species richness and proportion of introduced bird species. The explanatory variables (exogenous) are shown in rectangles while the response variables (endogenous) are shown in ellipses. The R^2 values of the path analysis for each response variable are as follows: temperature = 0.81, human population size = 0.68, native bird richness = 0.65, proportion of introduced bird species = 0.70, and functional diversity = 0.67. The numbers associated with paths between the variables are path coefficients presented as standardized values (scaled by the standard deviations of the variables). Continuous lines represent significant effects ($p < 0.05$), whereas dashed lines represent non-significant effects ($p > 0.05$).

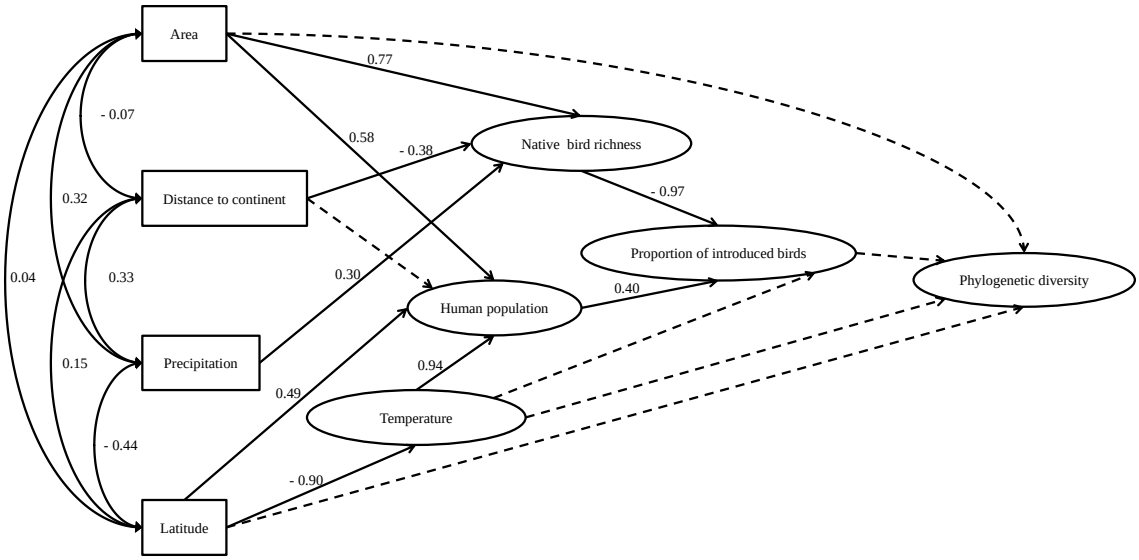

Figure 2. Path analysis for the phylogenetic diversity of insular bird assemblages explained by island area, distance from island to the nearest continent, precipitation, latitude, temperature, human population size, native bird species richness and proportion of introduced bird species. The explanatory variables (exogenous) are shown in rectangles while the response variables (endogenous) are shown in ellipses. The R^2 values of the path analysis for each response variable are as follows: temperature = 0.81, human population size = 0.68, native bird richness = 0.65, proportion of introduced bird species = 0.70, and phylogenetic diversity = 0.16. The numbers associated with paths between the variables are path coefficients presented as standardized values (scaled by the standard deviations of the variables). Continuous lines represent significant effects ($p < 0.05$), whereas dashed lines represent non-significant effects ($p > 0.05$).

Table 1. Explanatory models for the response variables (endogenous) included in the path analyses for both functional and phylogenetic diversity of insular bird assemblages following Figures 1 and 2. Significant direct effects ($p < 0.05$) are shown in bold.

Response variables	Explanatory variables	Effect		
		Direct	Indirect	Total
Functional diversity	Area	---	0.18	0.18
	Precipitation	---	0.15	0.15
	Distance to continent	---	-0.12	-0.12
	Latitude	**0.83**	-1.08	-0.25
	Temperature	**1.19**	-0.17	1.02
	Human population	---	-0.33	-0.33
	Native bird richness	-0.31	0.79	0.48
	Proportion of introduced birds	**-0.82**	---	-0.82
Phylogenetic diversity	Area	-0.26	0.13	-0.13
	Precipitation	---	0.08	0.08
	Distance to continent	---	-0.09	-0.09
	Latitude	0.64	-0.63	0.01
	Temperature	0.70	-0.05	0.65
	Human population size	---	-0.10	-0.10
	Native bird richness	---	0.25	0.25
	Proportion of introduced birds	-0.26	---	-0.26
Proportion of introduced birds	Area	---	-0.51	-0.51
	Precipitation	---	-0.29	-0.29
	Distance to continent	---	0.30	0.30
	Latitude	---	0.01	0.01
	Temperature	-0.17	0.38	0.21
	Human population	**0.40**	---	0.40
	Native bird richness	**-0.97**	---	-0.97
Native bird richness	Area	**0.77**	---	0.77
	Precipitation	**0.30**	---	0.30
	Distance to continent	**-0.38**	---	-0.38
	Latitude	---	---	---
	Temperature	---	---	---
	Human population	---	---	---
Human population	Area	**0.58**	---	0.58
	Precipitation	---	---	---
	Distance to continent	-0.18	---	-0.18
	Latitude	**0.49**	-0.85	-0.36
	Temperature	**0.94**	---	0.94
Temperature	Area	---	---	---
	Precipitation	---	---	---
	Distance to continent	---	---	---
	Latitude	**-0.90**	---	-0.90

Native species richness had a strong negative direct effect on the proportion of introduced species. In contrast, human population size had a positive direct effect on the proportion of introduced species (Figures 1 and 2, Table 1). Temperature, island area, distance from island to the nearest continent, precipitation and latitude did not have significant direct effects on the proportion of introduced species (Figures 1 and 2, Table 1). On the other hand, island area and precipitation had a positive direct effect on the native species richness, while distance from island to the nearest continent had a negative direct effect on this variable (Figures 1 and 2, Table 1). Human population size, temperature and latitude did not have significant direct effects on native species richness. Temperature and island area had a positive direct effect on human population size. Latitude also had positive direct and negative indirect effects on human population size, resulting in a negative total effect for this variable. Precipitation and distance from island to the nearest continent did not have significant direct effects on human population size. Finally, only latitude had a significant direct effect (negative) on temperature (Figures 1 and 2, Table 1).

Discussion

We found that the functional and phylogenetic diversity of insular bird assemblages has been shaped by a complex interplay of biogeographic, environmental, and anthropogenic determinants. We found that temperature had a strong positive direct effect on functional diversity, whilst latitude had positive direct and negative indirect effects via temperature, resulting in a weak total effect on this variable. This means that, all else being equal, islands at lower latitudes with higher temperatures harbor bird

assemblages with higher functional diversity. Classic niche-based theory posits that local species diversity is directly related to the variety and abundance of available resources (MacArthur & Levins, 1967; Ricklefs & O'Rourke, 1975). Accordingly, tropical species should exhibit a higher diversity of ecological traits molded by their multi-faceted interactions with the regionally-abundant resources, competitors and antagonists (MacArthur & Levins, 1967; Ricklefs & O'Rourke, 1975). Strong interactions are expected to cause character displacement and ecological speciation over evolutionary time (Schluter, 1988), potentially resulting in assemblages with high functional diversity. Indeed, along with continental systems, islands also follow a productivity and energy gradient (Wright, 1983; Kalmar & Currie, 2006), in which tropical locations support bird species that occupy niches and utilize resources not available at temperate locations, potentially reflecting in the functional diversity patterns shown by assemblages.

Our models also show that the proportion of introduced species had a strong negative direct effect on functional diversity, but no effect on phylogenetic diversity. However, this decrease in assemblage functional diversity of the assemblages should not be attributable to extinctions (since we did not include extinct species) and should reflect the contribution of introductions to the current functional and phylogenetic diversity of assemblages. Therefore, such a decrease in functional diversity could indicate that introduced species are functionally similar to native species, resulting in a decrease in the mean functional distance among all species. This result is commonly reported for plants communities, in which local co-occurrence of non-native species sharing similar functional traits with the native species results in a decrease in the mean functional distance among the species (Duncan & Williams, 2002; Diez et al., 2009; Lososová et al., 2015). However, there is evidence that introduced bird species are

functionally distinct from native bird species in insular locations (Sobral et al., 2016). Our result reinforces the evidence that introduced bird species are functionally similar to each other, which can also result in a decrease in the mean functional distance between all species currently occurring in insular assemblages (Sobral et al., 2016).

Birds chosen for introduction are nonrandom with relation to their taxonomy, biogeographic regions of origin and ecological and life-history traits (Lockwood, 1999; Blackburn & Duncan, 2001; Duncan et al., 2003; Cassey et al., 2004). For example, the highest proportion of introduced species belong to the major families of game birds (e.g. Anatidae, Phasianidae and Columbidae) and cage birds (e.g. Psittacidae, Estrildidae and Sturnidae) (Dyer et al., 2017). Given that ecological traits of species are not randomly distributed across taxa and regions (Cardillo, 2002), introduced species also tend to exhibit selectivity in their life-history traits, such as, body size, diet , and habitat use (Newsome & Noble, 1986; Cassey, 2001; Duncan et al., 2003; Cassey et al., 2004). A high proportion of ecologically proximate species, introduced into assemblages that are naturally poor in species, such as on islands, certainly results in a decrease in local functional diversity. Despite this striking taxonomic selectivity for exotics, introduced species have not precipitated changes in the phylogenetic diversity of the assemblages included in our study. On average, the number of introduced clades is lower than the number of native clades occurring across assemblages. In addition, many of the introduced clades are already represented by native species. This incongruence between phylogenetic and functional patterns, once again reinforces the notion that we cannot unquestioningly use evolutionary distances as surrogates for ecological distances (see Gerhold *et al.*, 2015).

We found a strong negative direct effect of native bird species richness on the proportion of introduced bird species, supporting the hypothesis that introduction

success can also be mediated by natural factors (Blackburn et al., 2016; Dyer et al., 2017). This negative association suggests that islands richer in native species potentially have higher biotic resistance, restricting the establishment and spread of introduced species through negative competitive and antagonistic interactions (Elton, 1958). However, this hypothesis should be viewed with caution given the low bird species richness currently observed in some islands included in our study, and the low levels of ecological similarity observed among insular native and introduced bird species (Sobral et al. 2016). Thus, this potential biotic resistance should not be a process observed fully on all islands. In addition, this result is also surprising given the strong positive association consistently found between native and introduced bird species at insular, continental, and even global scales (Stohlgren et al., 2006; Fridley et al., 2007; Blackburn et al., 2015; Dyer et al., 2017). This widely-reported pattern maintains that locations with high native species richness typically also support more introduced species the "the rich get richer" result (Stohlgren *et al.*, 2003).

Conversely, human population size had an expected positive effect on the proportion of introduced bird species and areas with larger human populations offer more opportunities for exchange and introduction of new species (Pysek et al., 2010). Introduction is a process primarily anthropic activities-mediated, in which species are intentionally or accidentally transported to areas beyond their natural ranges (Blackburn et al., 2011). Historically, the introductions were largely planned and linked to acclimatization events in locations newly colonized by Europeans, especially British. In this period, the introductions had as aim to establish populations of species considered beneficial or ornamental, such as game birds. Currently, however, introductions are largely unplanned, linked to the increased economic activity and dictated by the cage bird trade (Duncan et al., 2003; Dyer et al., 2017).

We found positive direct effects of island area and precipitation (a surrogate variable for productivity) and direct negative effect of distance from the island to nearest continent on the native bird species richness. These results corroborate the classical species-area and species-isolation relationships, and productivity gradient in species richness (MacArthur & Wilson, 1967; Wright, 1983; Kalmar & Currie, 2006). In addition, temperature and area had positive direct effects on human population size, while latitude had a total negative effect on this variable. This only shows that biogeographic and environmental factors also influence human population size at insular locations.

Here we showed that avian introductions have negatively impacted the functional but not the phylogenetic diversity of insular bird assemblages. An increasingly number of studies have shown that species introductions not only result in the extinction of native species but also lead to changes (e.g. decrease and homogenization) in the functional and phylogenetic diversity of biological assemblages over time (Winter et al., 2009; Helmus et al., 2014; Whittaker et al., 2014). These changes are a threat to biodiversity and biodiversity services, since introduced species tend to play ecological and evolutionary roles distinct from species lost from insular systems, and their addition does not compensate for the ecological functions and evolutionary histories losses following extinctions (Sobral et al., 2016). This despite an apparent softening in attitudes towards introduced species from some quarters (Russell & Blackburn, 2017). Thus, avoiding the transport and introduction of species to new locations and considering the removal of established exotics is still critical to guarantee the processes that generate biodiversity and maintain the ecosystem services and functions in a world increasingly threatened by human activities.

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Supporting Information 1

Sources used to collect data on the occurrence of birds across different islands

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Supporting Information 2

Sources used to collect data on the biogeographic, environmental and anthropogenic variables from islands

Barbados island

https://en.wikipedia.org/wiki/Barbados

Niue island

https://en.wikipedia.org/wiki/Niue

Socotra island

https://en.wikipedia.org/wiki/Socotra

CAPÍTULO III

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Darwin's naturalization conundrum: visitors are functionally distant from residents in insular systems

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Abstract

The functional distance among potential colonizers and resident species is hypothesized to play an important role in species colonization success. It has been suggested that the functional similarity of potential colonists to resident species may increase colonization success given shared pre-adaptations to local environmental conditions among species. Alternatively, high functional similarity may reduce colonization success due to high niche overlap between potential colonizers and residents. Here, we tested whether the functional distance between transient visitor and resident native bird species may predict occupancy of insular locations. We quantified the functional distance to the nearest resident species of species occurring both as visitors and as residents on different islands. We found that when bird species occur as transitory visitors across insular locations they show a higher functional distance to the nearest resident species than when they occur as residents. This indicates that the colonization failure of visitor bird species increases with the functional distance to the nearest resident species, which supports the hypothesis of pre-adaptation to local environmental conditions. This suggests that failure to colonize new locations may be linked to the absence or low local availability of suitable habitat for visitor species. Future studies quantifying habitat availability across islands are needed to falsify this hypothesis of pre-adaptation to insular environments.

Keywords: bird species, colonization failure, ecological similarity, functional traits, islands, natural colonization, pre-adaptation hypothesis.

Introduction

Species diversity at insular locations is the product of the balance between colonization, speciation and extinction. Understanding how and when immigration leads to colonization is a crucial aspect of island biogeography (MacArthur and Wilson 1967, Losos and Ricklefs 2010). Successful immigration and establishment of viable populations in new locations is driven by species-specific traits directly related to (i) dispersal ability, (ii) capacity to adapt to novel environments, and (iii) capacity to avoid strong competition for shared resources (Darwin 1859, Diamond 1974, Simberloff 1978, Thuiller et al. 2010, Lees and Gilroy 2014). Therefore, the life-history traits of potential colonists are expected to play a key role in colonization success and, hence, in the local diversity of insular assemblages (e.g. Blackburn et al., 2009).

Dispersal is the first step in the colonization process. The 'supertramp hypothesis' posits that species with better dispersal abilities are more likely to successfully colonize new locations (Diamond 1974). This is expected as species with traits associated with long-distance dispersal capability should show higher propagule pressure and to arrive at more different locations. However, empirical support for this hypothesis has been varied. While some have supported the supertramp hypothesis (Diamond et al. 1976, Mayr and Diamond 2001), more recent studies have not found a strong relationship between dispersal ability and colonization success (Lees and Gilroy 2014). For example, transient visitation of insular locations is expected to precede the process of natural colonization and expansion of species' ranges. For birds, Lees and Gilroy (2014) accessed the relationship among transient visitor species immigration and colonization success, and found that dispersal ability is a poor predictor of species establishment across islands. This result suggests that other factors, such as the

ecological and evolutionary relationship between potential colonizers and resident species, may play an important role in the colonization success of species.

Accordingly, functional similarity and phylogenetic relatedness among potential colonizers and resident species are also expected to play an important role in colonization success (Thuiller et al. 2010, Ma et al. 2016). Darwin (1859) was the first to propose that potential colonists might be more successful if they were closely related to resident species. According to this hypothesis (the pre-adaptation hypothesis), these potential colonizers may show high colonization success because they are expected to share pre-adaptations to environmental conditions with resident species. Conversely, Darwin (1859) also pointed out that potential colonizers are less likely to colonize local assemblages when they are closely related to resident species. This hypothesis (Darwin's naturalization hypothesis) states that potential colonizers may have low colonization success because they are expected to exhibit high niche overlap with resident species and, hence, should compete more strongly with them for resources (Rejmánek 1996).

These two contrasting hypotheses are together viewed as 'Darwin's naturalization conundrum' (Diez et al. 2008), and they have motivated a large number of studies to investigate how ecological and evolutionary relationships between potential colonists and resident species can influence colonization success (e.g. Ferreira et al., 2012; Lososová et al., 2015; Strecker and Olden, 2014; Tingley et al., 2011). These studies have come to often conflicting conclusions, perhaps unsurprisingly given the multitude of factors expected to affect the testing of both hypotheses (Procheş et al. 2007, Diez et al. 2008). For example, the relationship between the functional and phylogenetic distance among potential colonizers and resident species and colonization success may also depend on the spatial scale. The relationships predicted by pre-

adaptation hypothesis may only emerge at regional scales, when environmental filtering is expected to select species with pre-adaptations to similar environmental conditions. Conversely, the relationships predicted by Darwin's naturalization hypothesis should act at local scales, where interspecific interactions take place (Thuiller et al. 2010, Ma et al. 2016).

The majority of tests on the Darwin's naturalization conundrum have centered on invasion ecology studies (Ma et al. 2016). To our knowledge, no study has investigated the functional similarity or phylogenetic relatedness among naturally-arriving potential colonists on islands and the resident species already occurring at those locations. In addition, most of these studies have investigated Darwin's naturalization conundrum only through evolutionary relatedness among species (but see, for example, Marx et al., 2016; Skóra et al., 2015). These studies assume that there is phylogenetic conservatism on the functional traits of species (Wiens and Graham 2005). However, the evidence shows that phylogenetic similarity does not always reflect functional similarity (Gerhold et al. 2015), including for birds (Sobral and Cianciaruso 2016). Here, for the first time, we assessed the functional distance between transient visitor bird species and resident native bird species to investigate colonization success at insular locations. We hypothesize that transient visitor bird species fail to naturally colonize continental and oceanic islands when they are functionally distant from resident species. This would be possible because: (i) the pre-adaptation hypothesis is expected to emerge at the island scale (i.e. regional) (Thuiller et al. 2010, Ma et al. 2016); (ii) introduced birds show high colonization success in islands when they are ecologically close to resident species (Maitner et al. 2012); and (iii) establishment success in introduced birds depends on the suitability to the abiotic environment at the introduction location (Blackburn and Duncan 2001).

Material and methods

We collected data for 49 insular locations distributed in nine biogeographic realms (Afrotropical, Antarctic, Australian, Madagascan, Nearctic, Neotropical, Oceanian, Oriental and Palearctic). The locations included in the study represent single islands and close-knit archipelagos, all with a minimum distance of 100 km to the nearest continental mainland. We have included in the study all terrestrial, coastal and pelagic bird species currently occurring in each island (native and introduced). Therefore, we considered all species that are non-breeding visitors to the islands (here treated as visitors, many nominally 'vagrants' but some are annual passage migrants or winter visitors) and all species that reproduce in the islands (here treated as residents, despite the only seasonal presence of some species). We extracted data on the bird species occurrences across islands from a variety of sources, mainly annotated checklists in ornithological journals, technical reports, books and websites maintained by regional authorities and committees (see Supporting Information 1).

To carry out the analyses, we first separated species into two groups. In the first, we included those species that are dependent on terrestrial or coastal food webs. In the second, we included pelagic seabirds; those species that obtain resources predominantly from the open ocean beyond the Continental Shelf, and which use terrestrial habitat only for reproduction. We separated these species with the aim of grouping birds that in general potentially interact with each other and that are relatively homogeneous with respect to their life-histories and use of local habitats.

To quantify the functional distance among visitor and resident bird species we used the following life-history traits: diet, treated as the estimated percentage of each

diet item (invertebrates, vertebrates, scavenger, fruits, nectar, seeds and plants); foraging niche, treated as the estimated percentage of time spent in each strata (ground, understory, mid high, canopy and air); foraging period, treated as a binary categorical variable (diurnal and nocturnal); and body mass, as a continuous variable. These ecological traits mediate the effects and responses of species interactions with the environment and other locally co-occurring species. Therefore, they are expected to govern the multiple interactions of bird species with their resources, competitors and antagonists (Sekercioglu 2006). We extracted trait data from Wilman et al., (2014).

To quantify the functional distance among the visitor and resident species, we constructed a functional distance matrix for each of the nine biogeographic realms considered in the study, including only the bird species currently occurring in each of them. To produce the distance matrices, we used a modification of the Gower Distance that assigns the same weight to different types of categorical and continuous traits (Pavoine et al. 2009). For each biogeographic realm, we selected those species that occur concomitantly as visitor to at least one island and also as resident to at least one other island. Here, it is important to note that a species does not occur as both visitor and resident within the same island. Then, only for these species we quantified the functional distance to the nearest resident species (DNRS) in each island where it occurs as visitor and as resident (equivalent to DNNS in Thuiller et al., 2010). When one of these species occurs as visitor or resident in more than one island located in the same biogeographic realm, we used the mean of DNRS values. Finally, to test for potential differences in functional distances when such species occur as visitor or resident we conducted paired t-tests. We ran all analyses in R using the 'dist.ktab' function to produce the functional distance matrices and the 't.test' function to quantify the paired t-tests.

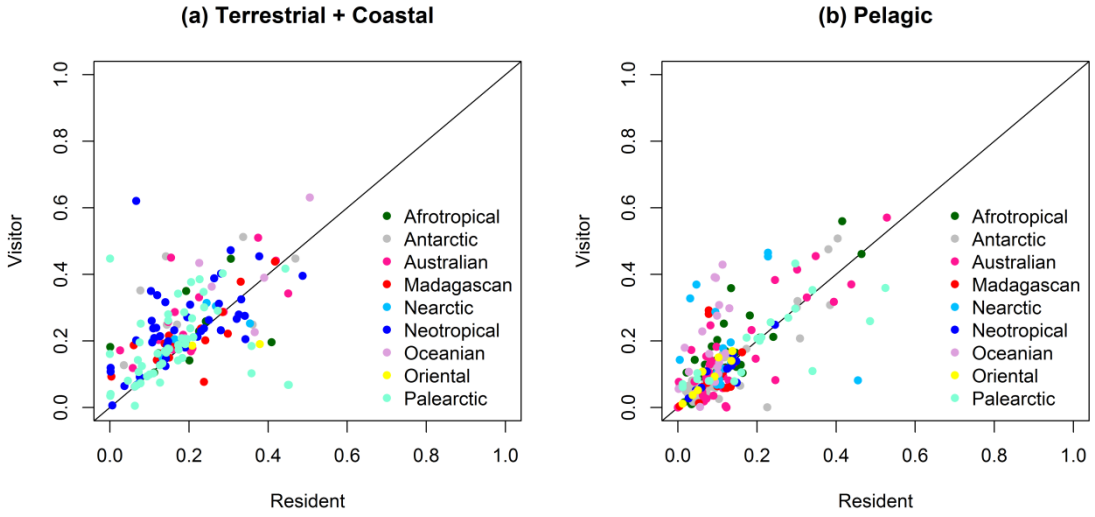
Results

Across the 49 insular locations included in the study, we collated 4909 records of visitor species and 1891 records of resident species. Of these, 3459 are records of terrestrial and coastal visitor species, 1450 of pelagic visitor species, 1236 are records of terrestrial and coastal resident species, and 655 of pelagic resident species. In total, we amassed 163 records of terrestrial and coastal species and 213 records of pelagic species from birds that occur concomitantly as visitor in at least one island and as resident in at least other island within the same biogeographic realm. Regardless of the group considered (terrestrial + coastal birds or pelagic birds) we found a higher functional distance to the nearest resident species when the species occurred as visitor than when they occurred as residents across islands (Table 1, Figure 1).

Table 1. Mean functional distances to the nearest resident species (DNRS) when species occur concomitantly as residents in at least one island and also as visitors in at least other island within the same biogeographic realm. The DNRS values and their respective standard deviations (in parentheses) are presented for the two bird species groups included in the study. The degrees of freedom (d. f.), t and p-values for paired t-tests testing for potential differences in the DNRS values are also presented.

Species group	Resident	Visitor	d. f.	t	p-value
Terrestrial + Costal	0.188 (0.115)	0.229 (0.119)	162	- 4.534	< 0.001
Pelagic	0.123 (0.103)	0.144 (0.118)	212	- 3.313	0.001

Figure 1. Mean functional distances to the nearest resident species (DNRS) when species occur concomitantly as residents in at least one island and also as visitors in at least other island within the same biogeographic realm. (a) Distribution of DNRS using terrestrial and coastal bird species. (b) Distribution of DNRS using pelagic bird species. Each point in graphics represents a particular species, and their respective color represents their biogeographic realm of origin. Points above the line indicate higher DNRS values when species occur as visitors across the islands.



Discussion

We found that when bird species occur as visitor across insular locations, they show a higher functional distance to the nearest resident species than when they occur as residents. This pattern was consistent across terrestrial, coastal and pelagic species. These results suggest that the failure of visitor bird species to become established increases with functional distance to the nearest resident species. In addition, it provides further support for the pre-adaptation hypothesis, which proposes that potential colonizers which are ecologically dissimilar to resident species should exhibit lower colonization success at new locations because they are not expected to be pre-adapted to local environmental conditions (Darwin 1859).

The observed functional distance between visitors and residents provides some clues about environmental filtering that may potentially be restricting the establishment of these species. For example, colonization failure may be related to the absence or low availability of suitable habitat types on the islands. Even within the same biogeographic realm, different islands can vary in relation to the area and the geographic isolation from the continents. Smaller and more-isolated islands are expected to have lower habitat diversity and resource availability than larger and less-isolated islands, which could explain the success in the colonization of only some locations within the same region. For example the Striated Heron *Butorides striata* is a Pantropical inhabitant of mangroves and wetlands, in Oceania it occurs as visitor to Palau (466 km^2), Guam (540 km^2) and Tonga (748 km^2), but only breeds on the far larger island of Fiji (18,274 km^2).

The capacity to adapt to novel environments seems to play an important role in the colonization process, especially for bird species. For example, Blackburn and Duncan (2001) showed that establishment success in introduced birds depends on the suitability of the abiotic environment at the introduction location. In addition, traits of introduced species that enable them to cope with novel environments (i.e. habitat breadth, diet breadth, and geographical range size) tend to increase colonization success (Blackburn et al. 2009). Maitner et al., (2012) found that being closely related to members of the resident avifauna was positively associated with introduction success for birds at insular locations. They argue that close relatedness to resident species may indicate that introduced species must possess ecological traits necessary to persist in new locations, potentially under particular biotic and abiotic conditions, such as temperature, precipitation, seasonality, predators, parasites and pathogens (Maitner et al. 2012). The pre-adaptation hypothesis have also been corroborated in other studies using different taxonomic groups, such as plants, reptiles, amphibians and fish (e.g. Ferreira et

al., 2012; Lososová et al., 2015; Strecker and Olden, 2014; Tingley et al., 2011). Conversely, these studies have investigated the relationships between potential colonizers and resident species using only evolutionary information about taxa (but see, for example, Marx et al., 2016; Skóra et al., 2015). For this, they assume phylogenetic conservatism of ecological adaptations (Wiens and Graham 2005). However, the evidence shows that phylogenetic similarity between species does not always reflect functional similarity (Gerhold et al. 2015), including for birds (Sobral and Cianciaruso 2016). In contrast to these studies, we used the ecological traits of species to quantify the functional distance between visitor and resident birds. This allowed us to infer in a more direct way than though phylogenies that the adaptation to the environment can be an advantage in the colonization of new locations.

In this study, we showed that the functional distance among potential colonizers and resident native species can underpin failure of establishment of bird species at insular locations. We found that bird species fail to colonize continental and oceanic islands when they are functionally distant from resident species. These results do not corroborate Darwin's naturalization hypothesis, instead, they add evidence that the bird species most likely to naturally colonize insular locations are those that are pre-adapted to local environmental conditions (Darwin 1859, Blackburn and Duncan 2001, Maitner et al. 2012). This suggests that habitat availability for visitor species at novel locations is a key determinant of colonization success. Future studies investigating ecological similarity between potential colonizers and resident species including information on habitat available across islands, would be valuable to empirically validate the pre-adaptation hypothesis.

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Supporting Information 1

Sources used to collect data on the occurrence of birds across different islands

Amsterdam

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Conclusão geral

Ao final dessa tese, nós chegamos às seguintes conclusões:

- As introduções não compensam pelas extinções. No primeiro capítulo, nós corroboramos a hipótese de falsa compensação funcional e filogenética. Isso significa que as introduções compensam pela quantidade de funções ecológicas e histórias evolutivas perdidas por meio das extinções (diversidade alfa). Entretanto, as espécies introduzidas possuem atributos funcionais e parentesco filogenético distintos das espécies nativas (substituição funcional e filogenética);

- A introdução de espécies causa erosão na diversidade funcional, mas não na diversidade filogenética das assembleias. No segundo capítulo, nós mostramos que a seletividade ecológica e taxonômica no processo de introdução reduz a distância funcional média, mas não a distância filogenética média, entre as espécies ocorrentes nas assembleias locais. Essa é mais uma evidência de que os padrões ecológicos nem sempre são congruentes com os padrões evolutivos mostrados pelas espécies;

- As espécies visitantes são funcionalmente distantes das espécies residentes. No terceiro capítulo, nós mostramos que as espécies são funcionalmente mais distantes das espécies residentes mais próximas quando elas ocorrem como visitantes ao longo das ilhas. Isso indica que a falha no processo de colonização parece aumentar com o aumento na distância funcional para a espécie residente mais próxima, o que corrobora a hipótese de pré-adaptação ao ambiente local.