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

First published: 28 June 2016 DOI: 10.1111/ele.12646 Volume 19, Issue 9, September 2016, Pages 1091–1100

Fernando L. Sobral[1], Alexander C. Lees[2] & Marcus V. Cianciaruso[3*]

[1]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, CP 131, 74001-970, Goiânia, Goiás, Brazil, fernandolsobral@gmail.com

[2]Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Rd, Ithaca, NY 14850, USA, alexanderlees@btopenworld.com

[3]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, CP 131, 74001-970, Goiânia, Goiás, Brazil, cianciaruso@gmail.com

[*]Correspondence: Marcus Vinicius Cianciaruso, Telephone: +55(062)3521-1474, E-mail: cianciaruso@gmail.com

Statement of authorship: FLS, ACL and MVC designed the study. ACL and FLS collected the data. FLS and MVC performed the analysis. FLS wrote the first draft of the manuscript and MVC and ACL contributed substantially to revisions.

Short running title: Introductions do not compensate for extinctions

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

Type of article: Letters

Number of words: Abstract: 150, Main text: 4536

Number of references: 54

Number of figures and tables: 3 figures and 3 tables

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.

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).

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).

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 ($\mathrm{MPD_{FD}}$) 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 ($\mathrm{MNTD_{FD}}$) 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).

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).

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).

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.

ACKNOWLEDGEMENTS

We thank Lucas Jardim and Leonardo Bergamini for helping us with the phylogenetic analyses. We also thank Boris Leroy and two anonymous reviewers for suggestions that improved this manuscript. Fernando L. Sobral thanks CAPES for support. Marcus V.

Cianciaruso has a productivity grant awarded by CNPq (grants 306843/2012-9, 307796/2015-9).

REFERENCES

Baker, J., Harvey, K.J. & French, K. (2014). Threats from introduced birds to native birds. *Emu*, 114, 1–12.

Blackburn, T.M. & Cassey, P. (2007). Patterns of non-randomness in the exotic avifauna of Florida. *Divers. Distrib.*, 13, 519–526.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science*, 305, 1955–1958.

Blackburn, T.M. & Duncan, R.P. (2001). Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *J. Biogeogr.*, 28, 927–939.

Boyer, A.G. (2010). Consistent ecological selectivity through time in pacific island avian extinctions. *Conserv. Biol.*, 24, 511–519.

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

Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P. & Lockwood, J.L. (2004). Global patterns of introduction effort and establishment success in birds. *Proc. R. Soc. London. Ser. B Biol. Sci.*, 271, S405–S408.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. & Couvet, D. (2008). Functional biotic homogenization of bird communities in disturbed landscapes. *Glob. Ecol. Biogeogr.*, 17, 252–261.

Drummond, A.J., Suchard, M. a., Xie, D. & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.*, 29, 1969–1973.

Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Mendenhall, C.D., Zook, J., Kremen, C., *et al.* (2014). Loss of avian phylogenetic diversity in neotropical agricultural systems. *Science (80-.).*, 345, 1343–1346.

García, D., Martínez, D., Herrera, J.M. & Morales, J.M. (2013). Functional heterogeneity in a plant – frugivore assemblage enhances seed dispersal resilience to habitat loss. *Ecography (Cop.).*, 36, 197–208.

García, D., Martínez, D., Stouffer, D.B. & Tylianakis, J.M. (2014). Exotic birds increase generalization and compensate for native bird decline in plant – frugivore assemblages. *J. Anim. Ecol.*, 83, 1441–1450.

Gerhold, P., Cahill, J.F., Winter, M., Bartish, I. V & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct. Ecol.*, 29, 600–614.

Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014). Island biogeography of the Anthropocene. *Nature*, 513, 543–546.

Jackson, H., Jones, C.G., Agapow, P., Tatayah, V. & Groombridge, J.J. (2015). Micro-evolutionary diversification among Indian Ocean parrots : temporal and spatial changes in phylogenetic diversity as a consequence of extinction and invasion. *Ibis (Lond. 1859).*, 157, 496–510.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444–448.

Kembel, S., Ackerly, D.D., Blomberg, S.P., Cowan, P., Helmus, M.R. & Webb, C.O. (2008). picante: Tools for Integrating Phylogenies and Ecology.

Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.

Laliberté, E. & Shipley, B. (2011). FD: measuring functional diversity from multiple traits, and other tools for functional ecology.

Lees, A.C. & Bell, D.J. (2008). A conservation paradox for the 21st century: the European wild rabbit Oryctolagus cuniculus, an invasive alien and an endangered native species. *Mamm. Rev.*, 38, 304–320.

Lees, A.C. & Gilroy, J.J. (2014). Vagrancy fails to predict colonization of oceanic islands. *Glob. Ecol. Biogeogr.*, 23, 405–413.

Leprieur, F., Albouy, C., De Bortoli, J., Cowman, P.F., Bellwood, D.R. & Mouillot, D. (2012). Quantifying Phylogenetic Beta Diversity: Distinguishing between “True” Turnover of Lineages and Phylogenetic Diversity Gradients. *PLoS One*, 7, e42760.

Lockwood, J.L. (1999). Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. *Conserv. Biol.*, 13, 560–567.

Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.*, 11, 995–1003.

Lozupone, C. & Knight, R. (2005). UniFrac : a new phylogenetic method for comparing microbial communities. *Appl. Environ. Microbiol.*, 71, 8228–8235.

Maire, E., Grenouillet, G., Brosse, S. & Villéger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Glob. Ecol. Biogeogr.*, 24, 728–740.

Maron, J.L., Estes, J. a., Croll, D. a., Danner, E.M., Elmendorf, S.C. & Buckelew, S.L. (2006). An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. *Ecol. Monogr.*, 76, 3–24.

Matsuzaki, S.S., Sasaki, T. & Akasaka, M. (2013). Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Glob. Ecol. Biogeogr.*, 22, 1071–1082.

Pavoine, S. & Bonsall, M.B. (2011). Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.*, 86, 792–812.

Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S. & Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos*, 118, 391–402.

Podani, J. & Schmera, D. (2006). On dendrogram based measures of functional diversity. *Oikos*, 1, 179–185.

Sax, D.F. & Gaines, S.D. (2008). Species invasions and extinction: The future of native biodiversity on islands. *Proc. Natl. Acad. Sci.*, 105, 11490–11497.

Sax, D.F., Gaines, S.D. & Brown, J.H. (2002). Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.*, 160, 766–783.

Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., *et al.* (2007). Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.*, 22, 465–471.

Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *Trends Ecol. Evol.*, 21, 464–471.

Sobral, F.L., Jardim, L., Lemes, P., Machado, N., Loyola, R. & Cianciaruso, M. V. (2014). Spatial conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic and functional diversity. *Nat. Conserv.*, 12, 150–155.

Sol, D., Maspons, J., Vall-llosera, M., Bartomeus, I., García-Peña, G.E., Piñol, J., *et al.* (2012). Unraveling the life history of successful invaders. *Science (80-.).*, 337, 580–583.

Steadman, D.W. (1995). Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science (80-.).*, 267, 1123–1131.

Steadman, D.W. (2006). *Extinction and Biogeography of Tropical Pacific Birds*. University of Chicago Press, Chicago.

Strauss, S.Y., Lau, J. a. & Carroll, S.P. (2006). Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol. Lett.*, 9, 357–374.

Sullivan, M.J.P., Davies, R.G., Mossman, H.L. & Franco, A.M.A. (2015). An anthropogenic habitat facilitates the establishment of non-native birds by providing underexploited resources. *PLoS One*, 10, 1–19.

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B. & Araujo, M.B. (2011). Consequences of climate change on the tree of life in Europe. *Nature*, 470, 531–534.

Triantis, K.A., Borges, P.A. V, Ladle, R.J., Cardoso, P., Gaspar, C., Dinis, F., *et al.* (2010). Extinction debt on oceanic islands. *Ecography (Cop.).*, 33, 285–294.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010). Conservation of species interaction networks. *Biol. Conserv.*, 143, 2270–2279.

Vamosi, J.C. & Wilson, J.R.U. (2008). Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecol. Lett.*, 11, 1047–1053.

Villéger, S., Grenouillet, G. & Brosse, S. (2013). Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Glob. Ecol. Biogeogr.*, 22, 671–681.

Villéger, S., Grenouillet, G. & Brosse, S. (2014). Functional homogenization exceeds taxonomic homogenization among European fish assemblages. *Glob. Ecol. Biogeogr.*, 23, 1450–1460.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–301.

Webb, C.O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.*, 156, 145–155.

Webb, T.J., Kershaw, M. & Gaston, K.J. (2001). Rarity and phylogeny in birds. In: *Biotic Homogenization* (eds. Lockwood, J.L. & McKinney, M.L.). Springer Science + Business Media, New York, pp. 57–80.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 366, 2403–2413.

Whittaker, R.J., Rigal, F., Borges, P. a V, Cardoso, P., Terzopoulou, S., Casanoves, F., *et al.* (2014). Functional biogeography of oceanic islands: scaling of functional diversity in the Azores. *Proc. Natl. Acad. Sci. U. S. A.*, 111.

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

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., *et al.* (2009). Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc. Natl. Acad. Sci. U. S. A.*, 106, 21721–21725.

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; $\mathrm{MPD_{FD}}$ = Mean functional distance; $\mathrm{MNTD_{FD}}$ = Mean functional distance to the nearest species; PRic = Phylogenetic richness; PDis = Phylogenetic dispersion; $\mathrm{MPD_{PD}}$ = Mean phylogenetic distance; $\mathrm{MNTD_{PD}}$ = Mean phylogenetic distance to the nearest species.

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; $\mathrm{MPD_{FD}}$ = Mean functional distance; $\mathrm{MNTD_{FD}}$ = Mean functional distance to the nearest species; PRic = Phylogenetic richness; PDis = Phylogenetic dispersion; $\mathrm{MPD_{PD}}$ = Mean phylogenetic distance; $\mathrm{MNTD_{PD}}$ = Mean phylogenetic distance to the nearest species.

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.

Table 1 –

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 –

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**

Table 3 -

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)

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.

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.

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.