

Research

Disentangling phylogenetic from non-phylogenetic functional structure of bird assemblages in a tropical dry forest

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Understanding the factors driving assembling structure of ecological communities remains a fundamental problem in ecology, especially when focusing on ecological and evolutionary relatedness among species rather than on their taxonomic identity. It remains critical though to separate the patterns and drivers of phylogenetic and functional structures, because traits are phylogenetically constrained, but phylogeny alone does not fully reflect trait variability among species. Using birds from the Brazilian dry forest as a study case, we employed two different approaches to decompose functional structure into its components that are shared and non-shared with the phylogenetic structure. We investigated the spatial pattern and environmental hypotheses for these phylogenetically constrained and unconstrained aspects of functional structure, including climate-induced physiological constraints, historical climatic stability, resource availability and habitat partitioning. We found only partial congruence between the two methods of structure decomposition. Still, we found a differential effect of factors on specific components of functional structure of bird assemblages. While climate affects phylogenetically constrained traits through endurance, habitat partitioning (especially forest cover) affects the functional structure that is independent of phylogeny. With this strategy, we were able to decompose the patterns and drivers of the functional structure of birds along a semiarid gradient and showed that the decomposition of the functional structure into its phylogenetic and non-phylogenetic counterparts can offer a more complete portrait of the assembling rules in ecological communities. We claim for a further development and use of this sort of strategy to investigate assembling rules in ecological communities.

Key words: Caatinga, functional traits, community phylogenetics

Introduction

Along with the central question in ecology of why species richness varies in space lays the one of which species are involved and how they are pulled together in local species pools (Hutchinson 1959, MacArthur and Levins 1967). These species pools are



referred to as “ecological assemblages”, whereas the processes underlying the coexistence patterns are called “assembling rules”, and these resulting patterns comprise the assemblage structure (Weiher and Keddy 1995, Webb 2000, Pausas and Verdú 2010). The rules structuring assembling patterns include ecological factors, such as environment and interactions, historical factors, including isolation and dispersal, and evolutionary forces, such as local origination and extinction of species (Ricklefs and Schluter 1993, Webb 2000, Weber et al. 2017). All these factors interact intricately with each other and across spatial scales, hindering a clear picture of the drivers of particular assemblages and the establishment of a general theory of species assembling (Webb et al. 2002, Emerson and Gillespie 2008, Pausas and Verdú 2010).

A central aspect of the debate on the determinants of species coexistence is the balance between niche similarities/dissimilarities and the evolutionary pattern underlying this balance among coexisting species (Webb et al. 2002, Cadotte et al. 2017). That is, because species traits are constrained by the phylogenetic history (Wiens and Donoghue 2004), phylogenetic relatedness among species has been adopted as representative of ecological similarity (Webb et al. 2002, Cavender-Bares et al. 2004). Nevertheless, the variability in these traits among species may depart substantially from phylogenetic relationships, and the resulting assemblage structure involving ecological and phylogenetic aspects can be either partially or not at all inter-related (Swenson and Enquist 2009, Saito et al. 2016, de Bello et al. 2017). In summary, while on the one hand, ecological relationships among species cannot ignore phylogenetic structure, on the other hand, phylogenetic relatedness cannot fully describe ecological (i.e. functional) similarities among species.

Accordingly, using both phylogenetic and functional information would be desirable to investigate the overlapping and the independent contributions of both evolutionary and ecological factors on species assembling patterns, especially if their contributions could be separated (Cadotte et al. 2013, de Bello et al. 2017). While phylogenetic relatedness describes deeper evolutionary and biogeographical constraints on regional species distribution through local diversification, isolation and past interactions (Gerhold et al. 2015), functional similarities and differences can express fine-grained, environmental factors affecting coexistence through fitness and ecosystem roles (Violle et al. 2007). Therefore, by decomposing species phylogenetic from functional (dis)similarities among coexisting species, we may be able to distinguish the patterns and the likely drivers of both evolutionary from ecological components of species assemblages (Swenson and Enquist 2009, de Bello et al. 2017). A particularly informative case study for this sorting out of phylogenetic and functional components of assemblage structure should be species-rich assemblages that are distributed at acute environmental gradients, as the constraints imposed by evolutionary history, environmental features and ecological interactions are especially pervasive.

Bird assemblages in semiarid regions, such as the Brazilian Caatinga, fit closely in the above portrait. The Caatinga is among the richest semiarid biome worldwide, with over 500 species of birds (Silva et al. 2003), and one of the main centres of bird endemism in South America, which has long been alleged to result from the interplay between evolutionary and ecological factors, including environment and interactions (Cracraft 1985). Climatically, the Caatinga is marked by high temperatures (averaging between 25 and 29°C) and low and unpredictable annual rainfall (< 750 mm year⁻¹). These conditions account for a mosaic of xerophytic, dry forests, composed of a variety of more open to more dense vegetal formations (Ab’Saber 2003). Furthermore, the Caatinga has experienced elevated levels of human-induced degradations, which reduced and simplified its forest cover (Alves et al. 2009), with expected consequences for the structure of bird assemblages.

In this regard, our study aims to investigate the patterns of the phylogenetic and functional structure of bird assemblages in the Caatinga. We partitioned the functional structure into its phylogenetic and non-phylogenetic components and assessed the effect of climatic and habitat drivers on these components. The environmental drivers represented four particular hypotheses attributable to the phylogenetically-constrained and phylogenetically-independent counterparts of functional structure. These hypotheses included 1) physiological constraints along existing climatic gradients in the biome; 2) historical stability of climate, which reflects climatic changes from the last glacial maximum (LGM, ~21 ky) to the present; 3) resource availability, which can be described by environmental productivity; and 4) local niche availability as described habitat heterogeneity. Any of the above explanations can be relevant for both phylogenetic and non-phylogenetic components of functional structure. We expect, however, that long-term climatic factors, such as climate and its historical stability, play a more prominent role in deeper (i.e. phylogenetically-constrained) aspects of functional structure. In contrast, factors related to resource availability and habitat heterogeneity should account for more recent (i.e. phylogenetically-independent) counterparts of functional structure.

Material and methods

Study area and data

Our study encompassed 123 surveyed localities within the Caatinga dominion, including localities at transition zones. These areas encompassed a variety of vegetal formations, including typical dry forests, enclaves of high-elevation and wetter formations, and savanna transitions. To characterise the bird assemblages across the study region, we conducted a literature survey of studies and theses on bird assemblages and species lists published up to 2015 (Supplementary material Appendix 1 Table A1). All these surveys are typical,

local-scale inventories, usually smaller than 70 km². We then constructed an incidence matrix of species per assemblage, according to their geographic location. We also took note on information on the sampling effort of each study.

Phylogenetic relationships among species were determined by the phylogeny of Jetz et al. (2012), using Hackett et al.'s (2008) backbone. This phylogenetic tree has a well-supported crown topology (i.e. the backbone), which was generated by combining relaxed clock molecular trees with fossil data. Species without genetic information and undefined position in the tree were assigned to it according to consensus trees (based on the relaxed-clock trees) and taxonomy. Still, this procedure results in uncertain in species' placements. Because of this inherent uncertainty at its tips, we randomly selected 100 different trees for analyses. We then ran all following analyses with all 100 trees, hence accommodating phylogenetic uncertainty in the results. Results are thus presented as the average of phylogenetic structure obtained from all 100 trees.

Functional traits were compiled from Wilman et al. (2014) and Birdlife (for similar applications, see Petchey et al. 2007, Sobral and Cianciaruso 2016). We summarised information on four fundamental aspects of the birds' ecology: (1) diet, divided into (i) invertebrates, (ii) mammals and birds, (iii) reptiles and amphibians, (iv) fishes, (v) detritus, (vi) fruits, (vii) seeds, (viii) nectar, (ix) other plant structures, (x) unknown; (2) foraging microhabitat, divided into (i) forest-dependent, (ii) aquatic submerged, (iii) aquatic superficial, (iv) ground, (v) forest understory lower than 2 m, (vi) understory higher than 2 m, (vii) forest canopy, (viii) above canopy; (3) body mass (in g); and (4) migratory status, divided into (i) altitudinal migrant, (ii) highly migrant, (iii) nomad, (iv) non-migrant (for further details see Wilman et al. 2014). Data on diet and foraging microhabitat are given as proportion of each item used. To reduce data dimensionality and cross-correlation among variables, we used principal components analysis (PCA) to summarise each of these traits in a set of informative principal components (PC) axes. To select PC axes, we selected axes with eigenvalues higher than a broken-stick model (Legendre and Legendre 1998). This procedure rendered four axes for diet and three for microhabitat, which accounted for 54.8% and 58% of the variation in data, respectively. Diet axes (from 1st to 3th) were descriptive of invertebrates, plant parts and vertebrates, and nectar, respectively. Habitat axes (from 1st to 4th) described forest dependency and mid-high strata, understory and canopy, aquatic habitat, and aerial strata, respectively. The other variables (migratory status and body mass) were kept as raw data.

Finally, we obtained environmental descriptors that are representative of the four different hypotheses addressed. They included 1) climatic constraint, represented by (i) mean annual temperature, (ii) annual precipitation and (iii) precipitation seasonality; 2) past climate, described by the (i) temperature and (iii) precipitation of the last glacial maximum (LGM, ~21 ky bp), and (iii) the magnitude of temperature change (measured as difference) between the LGM and the present; 3) environmental productivity, as given by

the actual evapotranspiration (AET); and 4) environmental heterogeneity, described by the (i) proportion of vegetation cover, (ii) number of vegetation cover types, (iii) altitudinal range (in meters). We estimated the proportion of vegetation cover at each locality from a 5-km buffer around its coordinate. Number of forest cover types refers to the number of height forest strata within the buffer area. We obtained data on current and past climates from Hijmans et al. (2005), AET from CGIAR-CSI global soil-water balance (Trabucco and Zomer 2010) and forest cover data from Hansen et al. (2013).

Phylogenetic and functional structures

To describe the phylogenetic structure of bird assemblages with different sampling efforts, we used the phylogenetic species variability (PSV) metric (Helmus et al. 2007), which is independent of the assemblage's species richness. Still, in order to obtain a standardised measure of PSV that is comparable to the functional structure (below) and from which we can test the significance of the observed pattern, we performed a 999-times randomisation procedure of the species composition over the tree topology for each local assemblage (Webb et al. 2008), according to the formula

$$SPSV = -1 \times \frac{(X_{obs} - X_{null})}{sd.X_{null}}$$

where *SPSV* is the standardised PSV, X_{obs} is the observed PSV, X_{null} is the PSV expected under the null model and $sd.X_{null}$ is the standard deviation from the 999 null models of PSV. Positive *SPSV* values stand for over-dispersed phylogenetic structure, i.e. with species more phylogenetically distant than expected by chance, whereas negative *SPSV* values reflect phylogenetically clustered assemblages, i.e. species closer than expected by chance. Values of *SPSV* not significantly different from zero are indicative of assemblages formed by phylogenetically random species pools (Webb et al. 2002). To circumvent phylogenetic uncertainty, we calculated *SPSV* as the average of all *SPSV* values obtained from all 100 phylogenetic trees.

The functional structure of the bird assemblages was calculated with the same metric as for phylogenetic structure, but by replacing the phylogenetic distance with a functional distance between species within each assemblage (Best and Stachowicz 2014). We performed this procedure by creating a functional distance matrix of all species using the Gower's (1971) distance, which is suitable for different data types (i.e. continuous and categorical).

Disentangling functional from phylogenetic structures

Because of the expected partial association between functional and phylogenetic relationships among co-existing species, we aimed at disentangling the function-phylogeny interaction in order to take advantage of their similarities (i.e. concordances) and differences (i.e. departures). For this

end, we adopted two different approaches to decompose the phylogenetic and the functional components of the structure of ecological assemblages.

The first approach (hereafter referred to as ‘partitioning’) consisted of a simple partitioning procedure through linear regression analysis (Safi et al. 2011). In this procedure, we regressed the variation of functional structure against the phylogenetic structure. The functional structure that is related to the phylogenetic structure is given by the model fit, whereas the counterpart of the functional structure that is not predicted by phylogenetic relationships among is the model residual. The former can be interpreted as the phylogenetically constrained functional structure, whereas the latter represents the phylogenetically non-constrained functional structure or the assemblage-level adaptive deviation of functional structure. Accordingly, a high positive residual indicates that a particular assemblage has a functional variability higher than that expected based on its phylogenetic variability, whereas a low, negative residual characterises an assemblage with a functional variability lower (functionally clustered or convergent) than that expected by its phylogenetic variability. In summary, these metrics reflect an emerging, assemblage-level property of the species’ departures of functional structure from a purely phylogenetic structure.

A second approach to decompose dependent and independent counterparts of functional and phylogenetic structure (hereafter referred to as ‘decoupling’) followed the decoupling framework proposed by de Bello et al. (2017). Rather than separating functional from phylogenetic structure at the assemblage level (as described above), the authors propose a species-level decomposition of the joint functional–phylogenetic components of the species from the exclusive components of both functional and phylogenetic structures through eigen-analyses (based on partitioning of functional and phylogenetic eigenvectors of a principal coordinate analysis – PCoA; Diniz-Filho et al. 1998). Then, these separate components can be attributed to the assemblages and describe patterns of joint and independent functional and phylogenetic diversity or structure (de Bello et al. 2017). The selection of eigenvectors followed that proposed by de Bello et al. (2017) through retaining all eigenvectors that were significantly related to at least one trait.

The main difference between the partitioning and the decoupling procedures is that the former describes overlaps and departures of functional and phylogenetic relationships directly from the assemblage level, whereas the latter describes these factors from the species level, which is posteriorly aggregated in the assemblage level. In addition, the decoupling approach allows a measure of phylogenetic structure that is independent on the functional structure, which can be viewed as the phylogenetic relationships among species that are related to other traits not accounted for by the functional traits used. Still, we expect the phylogenetically-constrained functional structure obtained from the partitioning (i.e. model fit) to be correlated with the community structure obtained from joint dissimilarity between trait

and phylogeny derived from the decoupling approach. Both should describe the fraction of functional variation that is constrained by the phylogenetic relationships among the co-existing species. Analogously, we expect our phylogenetically-independent functional structure (i.e. the model residual) to be correlated with the assemblage structure calculated from the decoupled traits. Because the partitioning yields no measure comparable to the decoupled phylogeny, we focused here on the shared contribution between functional and phylogenetic and the independent component of functional structure, as derived from the two approaches.

Statistical tests

We tested the effect of each set of predictors that represents the individual hypothesis on the response variables (phylogenetically-constrained and non-constrained functional structures from both the partitioning and the decoupling processes) in a linear regression framework. However, because spatially patterned observations are often affected by spatial autocorrelation (Legendre 1993), we first assessed, through inspection of spatial Moran’s I correlograms, the presence of this effect on the four response variables.

As all four variables were indeed spatially autocorrelated (Supplementary material Appendix 1 Fig. A1), we resorted to the simultaneous autoregressive regression (SAR) models (Crassie 1993), which account for spatial autocorrelation in data by incorporating the variables’ spatial structure through a weighed neighbourhood matrix. SAR incorporates spatial structure according as a weighing function of distance with exponent α ($\alpha = 1.0$ results in a linear function) and a spatial correlation parameter ρ (estimated from data by maximum likelihood). We evaluated model performance through their SAR standard coefficients (R^2 ; for predictor variables only) and compared them through the Akaike information criterion for small sample sizes (AICc; Burnham and Anderson 2004). The relationship between the partitioning (i.e. model residual) and the decoupled phylogenetically non-constrained functional structure was accessed through Pearson’s correlation while accounting for spatial autocorrelation through Dutilleul et al.’s (1993) correction of degrees of freedom. Analyses were run in SAM ver. 4.0 (spatial analysis in macroecology; Rangel et al. 2006) and R environment (www.r-project.org), with the packages *Picante* (Kembel et al. 2010) and *SDMTools* (VanDerWal et al. 2014). We adopted a significance level of 5% in all statistical analyses.

Results

Species richness ranged from 21 to 254 species (Fig. 1), totaling 532 species belonging to 67 families. For the assemblage structure calculated for phylogenetic and functional distances without decomposing their shares with either partitioning or decoupling, ca half (54.4%) of the assemblages had positive

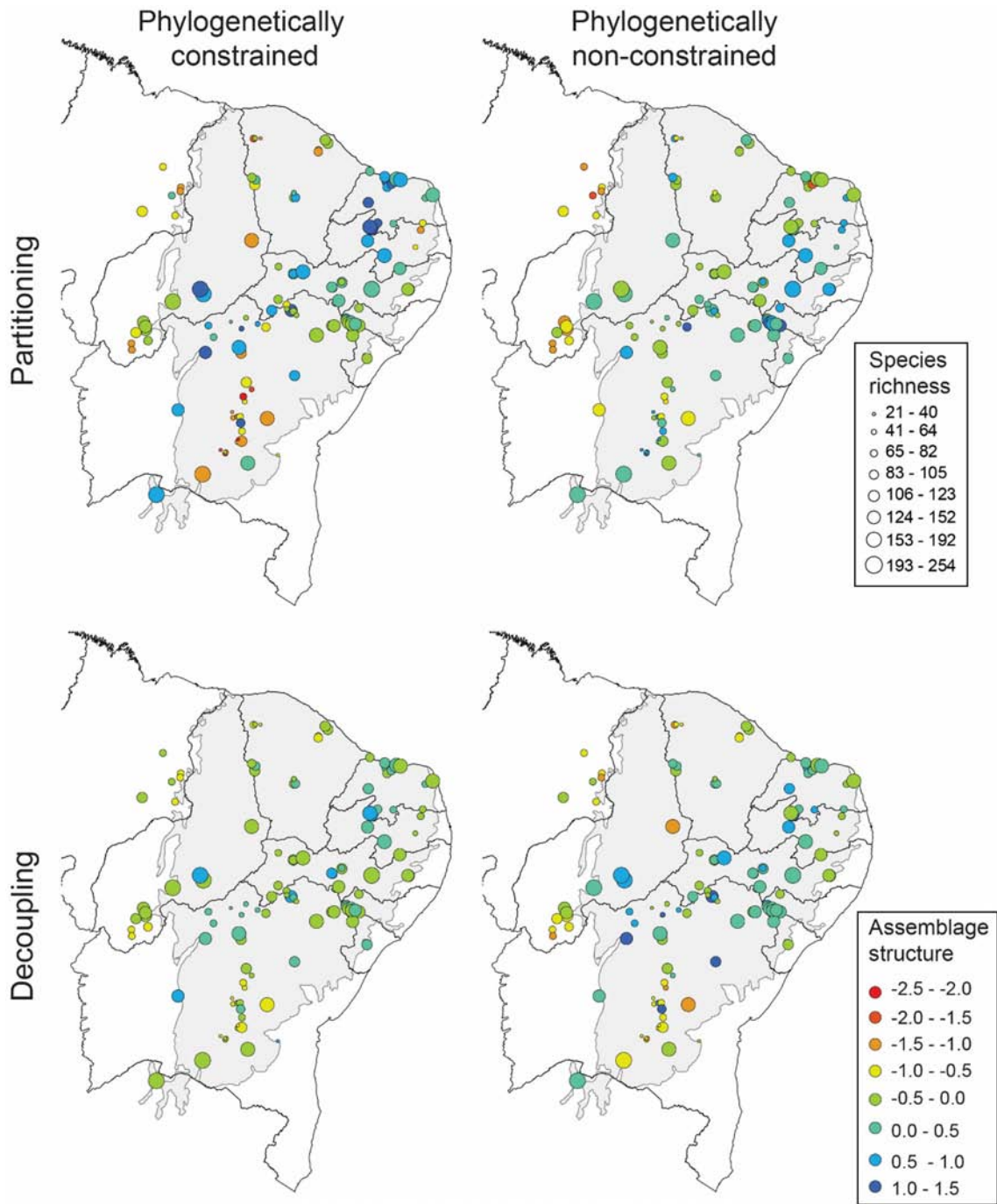


Figure 1. Distribution and assembling pattern of phylogenetic constrained and non-constrained functional structure of birds' assemblages from the Caatinga. Circle size is proportional to the species recorded in each location. Color ramp describes the assembling structure, in which negative values reflect assemblages with a tendency for clustering and positive for overdispersal.

SPSV values, indicating a tendency to phylogenetic dispersal, although none of them was significantly different from chance. The other half (45.6%) had negative SPSV values, with five assemblages (8.9%) being significantly different from chance (Fig. 2). Regarding functional structure, half of the assemblages were positive (i.e. towards dispersal), with 10 assemblages (8%) being significantly different from chance.

The other half of the functional structure was negative (i.e. towards clustering), with seven (5%) assemblages significantly different from chance.

Regarding the partitioning of the functional structure into its phylogenetic and non-phylogenetic components, the linear regression between functional and phylogenetic structures was positive, strong and significant, ($R^2=0.652$,

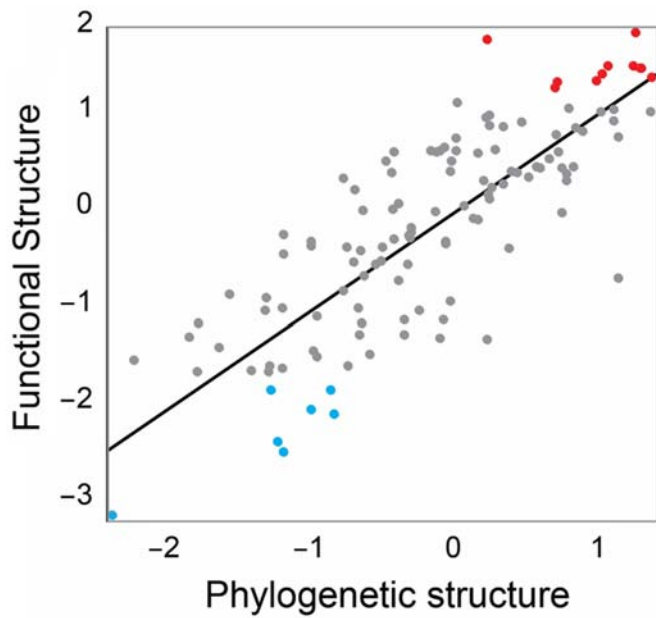


Figure 2. Linear relationship ($R^2=0.652$, $p=0$) between functional structure and phylogenetic structure of birds' assemblages from the Caatinga as obtained from the partitioning procedure. Phylogenetically constrained functional structure is given by the model's fit and the phylogenetically non-constrained functional structures by the model's residual. Blue and red dots are significantly clustered and overdispersed, respectively.

$p \approx 0$; Fig. 2), although the model residual contained relevant information (~35%) on the departure of the functional structure relative to the pure phylogenetic structure. The output of the decoupling procedure consisted of a set of distance matrices, including phylogenetic, functional, decoupled phylogenetic, decoupled functional, joint phylogenetic–functional and the sum of functional and phylogenetic distances.

As expected, the shared variation between functional and phylogenetic structures obtained from the partitioning

procedure (i.e. the model fit) was highly correlated with the joint functional–phylogenetic component of the decoupling procedure (Pearson's $r=0.84$, $p < 0.001$). On the other hand, the phylogenetically non-constrained functional structure from the partitioning (i.e. model residual) was weakly related to the decoupled functional structure from the decoupling process ($r=0.26$, $p=0.057$), after accounting for spatial autocorrelation in data.

When testing the effects of the predictors on the phylogenetic component of functional structure from the partitioning procedure, we found that the climate constraint was the best predictor of the phylogenetically constrained functional structure ($R^2=0.465$, $p=0$), with past climate showing a comparable predictive power (Table 1). This result was congruent with that found for the joint functional–phylogenetic structure from the decoupling procedure, as expected.

For the phylogenetically non-constrained functional structure, which we interpret as functional structure independent on the phylogenetic structure, we found habitat heterogeneity as the best predictor ($R^2=0.271$, $p < 0.001$). However, for the decoupled functional structure, climatic constraint was also the best predictor ($R^2=0.375$, $p < 0.001$; Table 2). In fact, and unexpectedly, the decoupled functional structure was strongly correlated with the joint functional–phylogenetic structure ($r=0.706$, $p=0$), both derived from the decoupling process.

Discussion

The variety of patterns in the phylogenetic and functional structures suggests that mixed processes drive bird assemblage patterns at the Caatinga and transition zones. These structures included clustered, over-dispersed and random patterns in species composition regarding both their evolutionary and ecological relatedness. These patterns have been attributed to ecological filtering, limiting similarity driving species exclusion and neutral processes of random dispersal

Table 1. Spatial autoregressive model's statistics ($\alpha=1.0$; $\rho=0.999$) of the effects of predictors representing individual hypotheses of environmental drivers of phylogenetically constrained functional structure (from partitioning) and the joint functional–phylogenetic structure (from decoupling) of birds' assemblages in the Caatinga dry forest. Temp. = temperature; CN is for the condition number, which measure the degree of multicollinearity; Prec. = precipitation; Prec. Season = Precipitation seasonality; 21k temp. = Temperature of the last glacial maximum (LGM, 21 ky bp); Precipitation of the LGM; 21k–0 temp. = Temperature change (i.e. difference) from the LGM to the present; Veg. cover = proportion of vegetation cover; #Veg. types = no. of vegetation cover types; Alt. range = altitudinal range; AET = actual evapotranspiration. * p -value < 0.001 .

Hypothesis	Predictor	CN	Partitioning			Decoupling		
			Slope (β)	R^2	AICc	Slope (β)	R^2	AICc
Climatic constraint	Temp.	1.848	0.485	0.465*	242.760	0.381	0.386	72.646
	Prec.		–0.375			–0.400		
	Prec. Season.		0.072			–0.017		
Past climate	21k temp.	1.654	0.540	0.452*	245.867	0.386	0.378	74.340
	21k prec.		–0.349			–0.372		
	21k–0 temp.		0.089			0.072		
Environmental heterogeneity	Veg. cover	1.362	–0.276	0.279*	279.545	0.349	0.267	94.616
	#Veg. types		–0.047			–0.141		
	Alt. range		–0.234			–0.022		
Environmental productivity	AET	–	–0.272	0.147*	295.793	–0.309	0.208	99.704

Table 2. Spatial autoregressive model's statistics ($\alpha=1.0$; $\rho=0.999$) of the effects of predictors representing individual hypotheses of environmental drivers of phylogenetically non-constrained and decoupled functional structures of birds' assemblages in the Caatinga dry forest. Coded as Table 1.

Hypothesis	Predictor	CN	Partitioning			Decoupling		
			Slope (β)	R ²	AICc	Slope (β)	R ²	AICc
Climatic constraint	Temp.	1.848	-0.210	0.213*	212.927	0.273	0.375	185.433
	Prec.		-0.293			-0.462		
	Prec. Season.		0.037			0.020		
Past climate	21k temp.	1.654	-0.220	0.233*	209.760	0.297	0.362	188.040
	21k prec.		-0.312			-0.416		
	21k-0 temp.		0.014			-0.032		
Environmental heterogeneity	Veg. cover	1.362	-0.259	0.271*	203.400	-0.267	0.192	217.155
	#Veg. types		0.160			-0.060		
	Alt. range		0.323			-0.057		
Environmental productivity	AET	-	-0.331	0.152*	217.606	-0.412	0.269	200.373

and extinction, respectively (Webb et al. 2002, Cavender-Bares et al. 2004, Cadotte et al. 2017). However, attributing any of these processes based on the observed pattern locally should take into account the regional species pool of which the local assemblages are composed. That is, this species pool may undertake some of these abiotic or biotic filters at a regional scale through biotic interchange and biome expansion–retraction dynamics, for example. Thereby, the observed pattern among local assemblages will be constrained at the biome level (Sobral and Cianciaruso 2016). The Caatinga is unique when compared to adjacent biomes in terms of climatic and vegetation composition and configurations. It is thus likely that this condition has modulated to patterns of species interchange between the Caatinga and other formations along their biogeographic history (Cracraft 1985, de Albuquerque et al. 2012), which may have determined the range of possible structures at the assemblage level currently observed.

In the Brazilian dry forest, phylogenetic and functional structures of bird assemblages – without decomposing their shared and independent components – are strongly interrelated, hence, phylogenetic could inform functional structure, at least to some extent. However, they are not interchangeable; either divergences or convergences in the functional structure unrelated to the pattern of phylogenetic (dis)similarities exist, which can reflect processes within and beyond evolutionary history (Gerhold et al. 2015, de Bello et al. 2017). After decomposing functional and phylogenetic structures – through both partitioning and decoupling procedures – we find that their shared variation is better explained by the climatic gradient across the biome, which has persisted throughout the post-glacial period (Behling et al. 2000). This shared component is interpreted as the functional structure that can be predicted by the species phylogenetic relatedness, i.e. the phylogenetically conserved variation of traits among species. Therefore, drier and warmer areas in the Caatinga contain more over-dispersed assemblages of phylogenetically conserved traits (see also Stevens and Gavilanez 2015).

The above scenario is consistent with a process of convergence of adaptive traits linked to the endurance of high

temperature and aridity, affecting bird communities assembling through physiological constraints (Stager et al. 2016). In fact, Graham et al. (2009) found that hummingbird assemblages tend to be clustered at higher and colder regions, whereas in the Caatinga, there is a tendency for over-dispersion into warmer and drier areas. As climatic drivers operates at broad spatial scales, and it involves ecological aspects that are more phylogenetic structured, we can argue that macroscale climatic gradients act by arranging bird assemblage structure towards clustering at increasingly cold and dry environments. This pattern is consistent, for instance, with the finding that bird assemblages at higher latitudes are more recent and phylogenetically related across New World (Hawkins et al. 2006). In addition, the minor effect of environmental productivity argues against the competition for resources as a driver of the phylogenetically constrained functional structure, as traditionally conjectured to drive over-dispersed patterns of community assembling (Webb et al. 2002).

Regarding the functional structure after discounting the phylogenetic constraint, the resulting functional structure differed substantially between the partitioning and the decoupling procedures. The best predictor of the partitioned functional structure was environmental heterogeneity, whereas the decoupled functional structure was better explained by climate, similarly to that found for the joint functional–phylogenetic structure. In fact, the decoupled functional and the joint structures were strongly inter-correlated, suggesting that the decoupling procedure did not properly decompose the variation between functional and phylogenetic dissimilarities. This issue could result from an overestimation of the contribution of phylogeny through selecting more eigenvectors than required (de Bello et al. 2017). According to the authors, this may occur when traits are inter-correlated, which could generate redundancy in eigenvector selection. Apparently, this is not the case in our study, as we described functional dissimilarities among species through unrelated PCA axes. Alternatively, this liberal selection of eigenvectors may be related to the inherent problem of filter selection in eigen-analyses of phylogenetic structure (Rohlf 2001,

Diniz-Filho et al. 2012). As we employed the filter selection strategy referred to by authors as the more appropriate (de Bello et al. 2017), we averted from exploring other filter selection alternatives.

Because of the likely failure of the decoupling procedure to separate the functional from the phylogenetic structure, and because the independent functional structure from the partitioning was better explained by habitat heterogeneity, as predicted, we focus here on the result from the partitioning procedure. As vegetation cover decreases and the number of vegetation strata and topographical complexity increases, the species composition becomes more functionally over-dispersed, a pattern consistent with previous findings at different neotropical regions. For instance, functional over-dispersion increase towards more disturbed areas in the Amazon region (Hidasi-Neto et al. 2012), and clustering reduces towards more open formations in a savanna biome (Sobral and Cianciaruso 2016). Altogether, these findings suggest that functional clustering in Neotropical bird assemblages increase with forest structure. A direct consequence of this relationship is the predictable effect of forest reduction and fragmentation on bird assembling structure at the Caatinga, either through the loss of closely related species or the entry of more opportunistic ones, resulting in more functionally over-dispersed assemblages. Either way, forest cover loss can be linked to a low functional redundancy in the bird assemblages in this dry forest, contrary to richer regions, such as the Amazon forest (Hidasi-Neto et al. 2012).

Altogether, these results lend support to the idea that climatic gradients and habitat heterogeneity are critical components driving the structure of bird assemblages in the Neotropics. Nevertheless, our conclusion is based on dependent and independent components of functional structure. In this regard, our findings demonstrate that this structuring of bird assemblages operates on different traits that are subject to different selective pathways. While climate appears to affect phylogenetically constrained adaptations linked to climatic endurance, local environmental aspects tend to select traits linked to local habitat occupancy, such as habitat preferences. Owing to this improvement in discriminating ecological drivers of assemblage structure, we emphasise that decomposing the shared and independent components of phylogenetic and functional structures in ecological assemblages constitutes an important strategy to deconstruct the drivers of the observed patterns at different time scales. More broadly, this approach can enlighten future syntheses on the rules of ecological assembling regarding the contribution of phylogenetically constrained and non-constrained ecological processes (Gerhold et al. 2015, de Bello et al. 2017).

In summary, we have shown that environmental drivers acting on two different spatial and temporal scales drive the functional structure of bird assemblages in the Brazilian dry forest Caatinga. Climate determines phylogenetically constrained traits at deeper time scales, whereas local environmental heterogeneity drives phylogenetically independent traits. We point out that the method of decoupling functional

and phylogenetic structure is still constrained by the selection of filters (i.e. eigenvectors), although we acknowledge that – when a proper filter selection is conceivable – it should be promising in describing different aspects of the species similarities within assemblages, including unaccounted functional traits (de Bello et al. 2017). In any case, by using regression-based partitioning, we could portray a more complete picture of the geographical pattern and its likely environmental drivers in bird assemblages from the Caatinga. Finally, we stress the relevance of further developing and employing such trait decomposition into evolutionary constrained and non-constrained counterparts in order to unveil a more complete portrait of the assembling rules in ecological communities.

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Supplementary material (available online as Appendix oik-04910 at <www.oikosjournal.org/appendix/oik-04910>). Appendix 1.