

**Environmentally and behaviourally mediated co-occurrence of functional traits in bird communities of tropical forest fragments**

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(Abstract)

Two major theories of community assembly—based on the assumption of ‘limiting similarity’ or ‘habitat filtering’, respectively—predict contrasting patterns in the spatial arrangement of functional traits.

Previous analyses have made progress in testing these predictions and identifying underlying processes, but have also pointed to theoretical as well as methodological shortcomings. Here we applied a recently developed methodology for spatially explicit analysis of phylogenetic meta-community structure to study the pattern of co-occurrence of functional traits in Afrotropical and Neotropical bird species inhabiting forest fragments. Focusing separately on locomotory, dietary, and dispersal traits, we tested whether environmental filtering causes spatial clustering, or competition leads to spatial segregation as predicted by limiting similarity theory. We detected significant segregation of species co-occurrences in African fragments, but not in the Neotropical ones. Interspecific competition had a higher impact on trait co-occurrence than filter effects, yet no single functional trait was able to explain the observed degree of spatial segregation among species. Despite high regional variability spanning from spatial segregation to aggregation, we found a consistent tendency for a clustered spatial patterning of functional traits among communities in fragmented landscapes, particularly in non-territorial species. Overall, we show that behavioural effects, such as territoriality, and environmental effects, such as the area of forest remnants or properties of the landscape matrix in which they are embedded, can strongly affect the pattern of trait co-occurrence. Our findings suggest that trait-based analyses of community structure should include behavioural and environmental covariates, and we here provide an appropriate method for linking functional traits, species ecology and environmental conditions to clarify the drivers underlying spatial patterns of species co-occurrence.

## Introduction

Since Diamond (1975) proposed a framework for assessing the rules governing community assembly, the spatial patterning of species occurrences has been a core theme of ecological research (Weiher et al. 2011, Götzenberger et al. 2012, Lyons et al. 2016). Although most of the debate about ‘assembly rules’ has centred around whether closely related species are spatially segregated or clustered (Presley et al. 2010, Ulrich and Gotelli 2013), it has been noted that patterns of species co-occurrence might not directly translate into equivalent patterns in functional traits. In particular, species with similar morphology, resource use or key aspects of life history might compete more intensely than species that differ in these functional traits, regardless of habitat characteristics and evolutionary history (Darwin 1859, Elton 1946). This suggests that studies investigating assembly rules should look beyond the spatial distribution of species, and instead consider how communities are spatially structured with regard to their functional and life history traits (Ulrich et al. 2012, Cadotte et al. 2015).

One view of community assembly is that species from the regional pool pass multiple abiotic and biotic filters favouring particular traits before entering a local community (Wiens and Graham, 2005). Ecological communities should therefore contain species with traits that are more similar to each other than would be expected if species were drawn at random from the respective species pool (Velázquez et al. 2015). An alternative view founded on the competitive exclusion principle applies the concept of limiting similarity (Hutchinson 1959, MacArthur and Levins 1967) to predict that coexisting species should instead differ more than expected in ecologically relevant traits (Abrams 1983), producing a pattern of trait over-dispersion rather than clustering. However, most support for these hypotheses comes from theoretical models and simulation studies (e.g. Schilck and Ackerly 2005, Abrams and Rueffler 2009, van Leeuwen and Etienne 2013) while empirical evidence comes mostly from plant communities and remains inconsistent (Soliveres et al. 2015). In birds, Ricklefs (2012) and Pigot et al. (2016) found variation in dispersal ability and niche packing to be more important drivers of community assembly than competitive interactions, whereas Price et al. (2014) considered competitive exclusion and limiting similarity to be the main driver underlying community structure.

However, the spatial distribution of species traits in communities has mainly been studied within a phylogenetic framework to account for niche conservatism (Wiens et al. 2010, Barnagaud et al. 2014). To better understand which species traits drive the assembly of avian communities in heterogeneous landscapes, we conducted a trait analysis of bird communities from three Neotropical (Atlantic Rainforest) and three Afrotropical (Eastern Arc Mountains) fragmented landscapes and study the spatial arrangement (co-occurrence) of dispersal, dietary and locomotory traits (hereafter, functional traits), which are often linked to competitive performance. Tropical birds provide an excellent case study of vertebrate community assembly. They can be efficiently surveyed and many species hold territories year-round and defend them against heterospecifics (Robinson and Terborgh 1995), suggesting that competitive exclusion may play a major role in structuring tropical bird communities (Jankowski et al. 2012). Our approach goes beyond common comparisons of total trait spaces among habitats (Swenson 2013) or pairwise comparisons of co-occurring species (Velázquez et al. 2015) by explicitly including the spatial co-occurrence (i.e. spatial arrangement) of traits among study sites.

By exploring the spatial co-occurrence of bird functional traits, we test whether, and to what extent, similar functional traits show stronger levels of clustering (indicating environmental filtering) or

segregation (implying competition-driven divergence in habitat use and corroborating the concept of limiting similarity) than expected by chance. We also incorporate the degree of territoriality in each species as a behavioural measure linked to levels of competition. Traditionally, spatial segregation in avian beak shape, beak size and body mass are thought to arise through ongoing or past competitive effects. We further predict the greatest segregation should occur between permanently territorial species, lowest segregation in non-territorial ones, and intermediate values of segregation in weakly territorial ones. Conversely, high dispersal ability has been assumed to dilute patterns of trait co-occurrence by masking species interactions (e.g. Moulton and Pimm 1987, Ricklefs 2012, Jønsson et al. 2015). Consequently, we predict a low degree of spatial trait patterning in highly dispersive species.

## Methods

### *Study sites and environmental data*

Data were collected in the Atlantic Plateau of the State of Sao Paulo (23°67' - 24°25'S, 46°92' - 48°40'W; Brazil), the East and West Usambara Mountains (EUM 38°35' - 38°38'S, 5°1' - 5°7'E, WUM 38°22' - 38°28'S, 5°3' - 5°7'E; Tanzania), and the Taita Hills (38°17' - 38°38'S, 3°18' - 3°30'E; Kenya). Sampling in Brazil was conducted in three fragmented 10,000 ha landscapes within the same biogeographical region (Banks-Leite et al. 2014). All three landscapes are located within an elevational range of 700-1100 m but vary in total amount of forest cover (11%, 31%, and 49%, respectively). A total of 53 forest patches were sampled, i.e. 17 patches each in the 11% and 31% landscapes, and 19 patches in the 49% landscape. Forest patches were selected to have the same range of patch size in each of the three fragmented landscapes: seven small patches ranging from 2 to 9 ha, seven to eight medium-sized patches from 12 to 40 ha, and three or four large patches of 45 to 150 ha. In Tanzania, the EUM and WUM landscapes cover ca. 7,000 ha and 6,500 ha respectively, and are separated by a 17.5 km wide, non-forested valley 290 m in elevation. No individual birds have ever been recorded in over 30 years moving between the EUM and WUM study sites based on >27,400 captures and  $2.96 \times 10^6$  mistnet<sup>-m-hrs</sup>. Indeed the mean observed distance of movement is <150 m assuming 'leap-frogging' across the landscape. We sampled 15 forest patches within the range of 0.2 to 908 ha across elevational ranges of 972-1,150 m (EUM) and 1,171-1,300 m (WUM). The Taita forest archipelago (Kenya) is located ca. 150 km N of the Usambara Mountains and hosts a partially overlapping forest understory bird community which we sampled in 12 forest fragments ranging in size from 1 to 179 ha. These fragments were scattered across a 31,200 ha landscape within an elevational range of 1,200-2,208 m.

For each of our 79 sampling sites, the following four fragment characteristics were extracted from Google/DigitalGlobe and Landsat Satellite Images and worldwide treecover data (Global Land Cover Facility, landsat Treecover available at <http://glcf.umd.edu/data>) using Fragstats v. 3.3 (McGarigal et al. 2012) and ArcView 3.2: (i) Patch size; (ii) Percentage of closed-canopy forest cover within 100 m and (iii) 800 m around each fragment; and (iv) Fragment proximity, a distance-weighted and area-based isolation index (PPI, Tischendorf et al. 2003).

### *Bird sampling*

The understory bird community in each of the six forest landscapes was sampled using comparable mist netting protocols, albeit implemented over different time intervals. In the Atlantic Forest, mist net

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surveys between 2001 and 2007 captured 117 species (Banks-Leite et al. 2014); in EUM and WUM, surveys between 1987 and 2014 captured 86 species; and in Taita Hills, surveys between 1996 and 2010 captured 67 species (raw data for the present study in Ulrich et al. 2017). Full details on trapping procedures can be found in Banks-Leite *et al.* (2012, 2014), Korfanta et al. (2012), and Callens et al. (2011). While mist nets are widely regarded as the best technique for assessing the relative abundance of tropical understorey birds (Karr 1981, Newmark 1991), capture rates may be misleading if habitat modifications such as removal of canopy trees or understory vegetation alters the flight heights of species, thereby changing their susceptibility to mist net capture without changing their relative abundance (Remsen and Good 1996). To minimize these potential biases, we sampled only in mature forests with low variation in forest structure, and restricted our analyses to the understorey bird community, i.e. species that are reliably caught in mist nets.

#### *Functional traits*

For each Neotropical and Afrotropical bird species, we assembled a dataset of functional traits (raw data in Ulrich et al. 2017). These included a suite of biometric traits: beak shape, wing shape, tarsus, tail and wing length, and body mass, all of which are related to the functional roles of birds in ecosystems (Luck et al. 2012, Trisos et al. 2014, Bregman et al. 2016), potentially linked to competitive performance (cf. Mayfield and Levine 2010). In these cases, we focused on continuous traits as these can be objectively measured and often provide more information than discrete traits about species differences and functional roles (McGill et al. 2006). Beak shape, wing shape, and tarsus, tail and wing length were quantified from biometric measurements obtained from skins in museum collections (mainly Natural History Museum, Tring, UK) following standardized protocols (Tobias et al. 2014, Trisos et al. 2014, Bregman et al. 2016). Species averages for each trait were calculated from a minimum sample of four individuals of each species, where possible.

Beak shape was assessed as the dominant principal component (based on the variance co-variance matrix) of each species' average beak length, depth and width (mm). We note that prior work used the second principle component as a proxy of beak size variability (Trisos et al. 2014). However, in our data this second axis explained less than 10% of variability. As bird size is allometrically related to shape we used the first eigenvector as a joined measure. We calculated the difference between wing length and secondary length (cm) to quantify the hand wing index, a standard measure of wing loading related to flight power and dispersal ability in birds (Claramunt et al. 2012). Locomotory traits were quantified as the respective dominant eigenvector of tarsus length, tail length and wing length (cm). Dispersal ability and locomotion were weakly correlated (OLS:  $r^2 = 0.23$ ). Data for body mass (g) were compiled from Wilman et al. (2014). All biometric data were spot-checked for accuracy and examined for outliers.

Diet for each species was obtained from Wilman et al. (2014), who provide the percent use of food resources from each of following the ten categories: invertebrates, vertebrates (endothermic), vertebrates (ectothermic), vertebrates (fish), vertebrates (unknown), scavengers, fruit, nectar, seeds, other plant matter. This classification was used to assign each species to one of four feeding guilds: (i) insectivores, (ii) granivores, (iii) frugivores and nectarivores, and (iv) omnivores. Foraging stratum for each species was also obtained from Wilman et al. (2014), who provide the percentage of foraging on each of the following substrates: ground, understory, mid-canopy, canopy, and aerial. The percent values of stratum and diet were also used to calculate the dominant eigenvectors of the associated variance – covariance

matrices. Categories of foraging stratum were summarised in the same way as diet. We focused on understory bird species which were primarily assigned to ‘ground’ and ‘understory’ categories, but many of these species use the other foraging strata to some extent. Territoriality scores were compiled from a global dataset (Tobias et al. 2016) which quantified territorial behaviour as a categorical variable with three levels: year-round territorial, seasonally or weakly territorial, and non-territorial.

#### *Co-occurrence analysis*

We organised the data in three types of matrix: species  $\times$  traits matrices **T** (one for Afrotropical and one for Neotropical species); environmental variables  $\times$  sites matrices **V** (one for each continent); and species  $\times$  sites presence-absence matrices **M** (one for each of the four feeding guilds in each of the six landscapes, as well as one for all Afrotropical and one for all Neotropical species together).

We first studied differences in the particular pattern of the spatial arrangement of species or traits between the six landscapes. For this task, we identified all pairs of species within each trophic guild that were distributed in either a checkerboard or clumped pattern, using the species by site matrix **M**. We used two commonly applied metrics (Gotelli 2000, Ulrich and Gotelli 2013) to assess the degree of species spatial patterning within the **M** matrices. The C-score is a normalized count of the number of checkerboard submatrices of the form  $\{1,0\},\{0,1\}$  and quantifies the degree of spatial species segregation (Stone and Roberts 1990). A checkerboard pattern might either stem from competitive effects or habitat variability both resulting in an associated segregated distribution of species functional traits. Accordingly, the clumping score (Ulrich and Gotelli 2013) is a count of  $\{1,1\},\{1,1\}$  submatrices and quantifies species spatial clumping, and thus indicates habitat filter effects (Ulrich et al. 2012).

To reduce the influence of the variation in fragment sizes and numbers of fragments across study areas, and to obtain approximate estimates of standard errors for each metric for the whole matrix, we used a sliding window (width of six sites) approach moved across the **M** matrices in steps of two sites, resulting in three to six windows for each measurement, respectively. Such an approach makes it possible to correlate the pattern of co-occurrence with the environmental conditions of the respective window. To minimise the variability of fragment size in each window the **M** matrices were sorted according to fragment size. We calculated the C-score and the clumping score on each of the 26 species by sites matrices (**M**).

We then studied the pattern of co-occurrence of traits using an approach introduced by Ulrich et al. (2012) for the analysis of phylogenetic diversity (Fig. 1). We first produced for each trait a species  $\times$  species distance matrix by calculating the Euclidean distance of the species traits from the trait matrix **T** (containing for each species raw scores of body size and hand-wing index, and the above mentioned eigenvector for beak shape, diet, and stratum). Then we produced for each environmental variable a similar sites  $\times$  sites distance matrix by calculating the Euclidean distance of the environmental variables from the environmental matrix **V** (containing for each patch area and isolation, and the percentage forest cover at 100 and 800 m buffers). We then calculated the average trait distances and site distances for all species pairs engaged in a checkerboard or clumped pattern (Fig. 1). With respect to clumping, large average distances in the traits matrix combined with small distances in the environmental matrix indicate trait segregation in environmentally similar habitats, and hence, possible effects of competition. Joint low distances in traits and environment, in turn, point to trait filtering (Ulrich et al. 2012). This approach allowed us to identify traits associated with either co-existence or mutual exclusion (Fig. 1). To link the

degree of territoriality to the pattern of co-occurrence, we calculated the C-score for the 52 submatrices from **M** combining in each fragment species with identical degree of territoriality.

Raw scores of species co-occurrence metrics depend on species richness, matrix size and matrix fill. Metrics of the spatial distribution of traits are additionally biased by the variability in species composition among sites and possibly by spatial non-independence. To be ecologically meaningful these metrics need to be compared to a standard that is typically derived from an ecological null model. This standard has to account for the influence of constraining factors not related to the pattern of interest. Here we had to account for differences in species composition and richness among fragments and different abundances among species. We took advantage of the quantitative structure of our data to apply the abundance fixed null model of Ulrich and Gotelli (2010), and resampled the **M** matrices with placement probabilities proportional to observed row and column abundance totals until for each row and column observed abundances are reached. This null model retains observed species abundance differences and the number of occurrences, and has the advantage of accounting for unequal a priori colonization probabilities due to mass effects while effectively randomizing the pattern of interest (Ulrich and Gotelli 2010). It is equivalent to a random island colonisation of equidistant islands, with immigration probabilities proportional to island area and mainland abundance (MacArthur and Wilson 1963). Note that this randomization leaves trait and environmental matrices unchanged.

We compared observed clumping and C-scores of each sliding window with those obtained from 1000 randomizations of the respective **M** matrices. To compare scores among guilds and traits, we calculated standardized effect sizes (SES) = (observed score – expected score)/standard deviation of expectation. We ran all species co-occurrence analyses with the software applications Niche (Ulrich et al. 2012) and Turnover (Ulrich and Gotelli 2013), both available online (<https://www.biol.umk.pl/keib/>).

Co-occurrence analysis allows us to identify spatial patterns but does not quantify the strength of this pattern relative to the overall arrangement of species in the matrix. To quantify this effect size, we used general linear fixed effects modelling (GLM) with linear link functions and normal error structures (calculated with Statistica 12). For each metric, we compared the effect of trait, environmental variable, and feeding guild. We provide effect sizes of single predictors by partial  $\eta^2$  values that quantify the proportion of variance explained by each predictor in a similar way as does the coefficient of determination  $r^2$  for the whole model. To eliminate the influence of sample size (the numbers of 2x2 submatrices), we used this number as metric covariate. Statistical significance of GLM parameters and comparisons of means are always based on the F distribution.

## Results

### *Species co-occurrences*

Our study is based on a total of 108 Afrotropical and 115 Neotropical bird species (Tab. 1, Ulrich et al. 2017). The Neotropical study sites generally supported more species of insectivores and fewer granivores than the Afrotropical sites (Tab. 1). Irrespective of feeding guild, we found significant differences in the spatial patterning of species occurrences between continents: Afrotropical communities tended to be significantly segregated (SES of C-score > 2, Fig. 2 a-c) while Neotropical communities were either aggregated or randomly distributed (Fig. 2 d-f).

Territorial species tended to be spatially segregated (Fig. 3). Thirty-six of the 52 data points in Fig. 3 pointed to segregation, indicating that species with similar territorial strategies occurred in different

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fragments more often than expected from our null model. Territorial species (coded 2 and 3) were spatially more segregated than non-territorial ones (coded 1) (Fig. 3). Five of the 12 sub-communities consisting of permanently territorial species were significantly segregated ( $P < 0.05$ ) while none of the 14 non-territorial sub-communities showed a significant tendency towards segregation.

#### *Co-occurrence of traits*

We found weak, albeit consistent, support for an aggregated spatial patterning of traits (Fig. 4), i.e. smaller distance in trait expression of co-occurring species than expected from the null model, which indicates that co-occurring species possess more similar traits. Except for insectivores ( $P(F) < 0.01$ ), there were no significant differences between Afrotropical and Neotropical feeding guilds (Fig. 4).

Spatial co-occurrences of functional traits varied among fragments, traits, and feeding guilds (Fig. 5, Supplementary material: Figs. S1, S2), as evident from the significant two-factor interaction terms in the GLM analysis (Tab. 2). Patterns were on average stronger (higher absolute SES scores) in Afrotropical than Neotropical landscapes (Figs. 5, S1, S2), and two-factor interaction terms explained more than 30% of variability in the co-occurrence metrics in the former, but less than 20% in the latter (Tab. 2). In contrast, species richness, matrix fill and sample sizes only weakly explained variation in trait co-occurrence (Tab. 2).

For the Afrotropical, but not for the Neotropical fragments, co-occurring bird species tended to be similar in stratum use and the degree of territoriality (Figs. 5, S1), particularly in the case of frugivores/nectarivores and insectivores (Fig. S1). There were no consistent trends in the spatial patterning of traits related to locomotion, neither among feeding guilds nor among landscapes (Figs. 5, S1, S2). The only exception being the highly significant ( $P < 0.001$ ) tendency in omnivores and granivores to be spatially segregated in stratum use in the WUM landscape (Figs. S1b, S2b). Traits related to dispersal ability, particularly of insectivores (Fig. S1a), were spatially clustered (Fig. 5).

There were no consistent spatial trends in diet, body size, and beak shape among the different feeding guilds (Figs. S1, S2) but rather marked landscape-specific patterns, particularly so in the Afrotropical landscapes. After averaging across landscapes, patterns in the co-occurrence of body weight and diet tended to be segregated in Afrotropical landscapes, while aggregated in Neotropical ones (Fig. 5).

In the species pair approach (Tab. 3), standardized effect sizes of the clumping and C-scores calculated for all species pairs within each feeding guild did not significantly differ from random expectation. Likewise, in none of the comparisons did the number of significant SES scores exceed 2%, whereas 2.5% is expected at the two-sided 95% confidence interval (not shown). Hence, our results did not allow to unequivocally identify any species pair showing significant positive or negative associations of functional traits.

#### *Environmental effects on the co-occurrence of species traits*

The strength of spatial co-variation of traits and environmental variables as a signal of environmental filtering strongly varied between Afrotropical and Neotropical landscapes (Tab. 4), again being stronger in the former. Tukey Post hoc comparisons for clumped occurrences revealed the strongest differences to occur in beak shape and stratum. With respect to beak shape a significant positive covariation in trait and environmental distances occurred in the Afrotropics ( $SES = 1.58 \pm 0.12$ ,  $P(F) < 0.001$ ), while this



covariation was random among the Neotropical sites ( $SES = 0.19 \pm 0.11$ ,  $P(F) > 0.1$ ). With respect to stratum both covariations were significantly positive (Afrotropics:  $SES = 0.98 \pm 0.19$ ,  $P(F) < 0.001$ ; Neotropics:  $SES = 0.45 \pm 0.09$ ,  $P(F) < 0.001$ ). When averaged over all traits, the Afrotropical trait and environmental differences were positively correlated ( $SES = 0.49 \pm 0.21$ ,  $P(F) < 0.05$ ), while the respective Neotropical differences were not significantly correlated ( $SES = 0.03 \pm 0.12$ , n.s.). Likewise, the degree of environmentally mediated trait patterning in species engaged in checkerboards significantly differed among traits in the Afrotropical landscapes, but only weakly so in the Neotropical ones (Tab. 4). These results indicate that species with similar trait expression occupy habitats with similar environmental conditions in the Afrotropical sites but less so in the Neotropical sites. We did not observe the opposite pattern in any of the traits.

## Discussion

In line with standard theories of community assembly (Diamond 1975) and limiting similarity (MacArthur and Levins 1967), we hypothesized that competitive effects are mirrored by negative associations of species functional traits. We aimed to identify those traits that determine the co-occurrences of species and to detect common patterns of trait assembly irrespective of differences in habitat and functional guild. Based on our analyses, we found a strong tendency for species segregation, particularly among the African fragments (Fig. 2), and an overall tendency for trait aggregation in co-occurring species (Figs. 4, 5). The first finding is in accordance with recent meta-analyses on predominant species segregation (equivalent to high spatial species turnover) among various plant and animal taxa and habitat types (Gotelli and Ulrich 2010).

Previous analyses of trait space and functional diversity have focused on comparing community structure using standard metrics (reviewed in Pausas and Verdú 2010, Pavoine 2016), where links between trait and environmental characteristics are assessed either by ordination (Legendre and Legendre 1998) or by variations of fourth corner techniques (Legendre et al. 1997). Some studies go further in integrating data on traits, phylogenetic relationships, environmental conditions, and species co-occurrence (e.g. Cavender-Bares et al. 2004, Ives and Helmus 2011, Baraloto et al. 2012, Bregman et al. 2015). However, none of these techniques are able to uncover the precise pattern of spatial arrangement of traits among communities and to link them to environmental variables and the pattern of species co-occurrences. To achieve this, we adapted a methodology developed for the study of phylogenetic patterning (Ulrich et al. 2012) which allows us to directly compare patterns of trait and species co-occurrence, and to link them to the distribution of environmental variables.

We identified weak but highly significant correlations between the segregation of species traits and important environmental drivers (Tab. 4). For example, species segregation was particularly evident for territorial species with low dispersal among fragments (Fig. 3), supporting the hypothesis that aggressive competitive interactions and reduced movement among fragments contribute to negative species co-occurrences. Although such effects are marginal, we note that they may have strong impact on the co-occurrence of species when acting over several generations.

In apparent support of limiting similarity, recent meta-analyses have documented an excess of segregated species pairs in modern communities, i.e. most closely related species pairs co-occur less frequently than would be expected by chance (Ulrich and Gotelli 2013). At large spatial scales, this

pattern has been explained by the spatial turnover of species across habitats (Soininen 2010) or by signatures of allopatric speciation (Tobias et al. 2014). At smaller scales, such as among habitat patches within heterogeneous landscapes, it has been interpreted as evidence of interspecific competition (Bregman et al. 2015). Ulrich et al. (2016) found this type of filter in local plant communities just above the individual interactions horizons, i.e. among plots at a distance of at most a few meters. In the present study, these effects were weak and explained on average less than 10% of variance in trait occurrence (Tab. 2).

Our analyses included an array of functional traits, representing several major niche axes, and revealed that no single trait is responsible for the observed negative species co-occurrences. Recently, Mayfield and Levine (2010) argued that traits related to ecological niche and those related to competitive ability might have different effects on phylogenetic community structure, and might also influence the spatial pattern of co-occurrence. Our results do not corroborate such a conclusion. In particular, it seems difficult to unequivocally distinguish between both types of traits. Rather, the high habitat-specific variability in the co-occurrences of traits (Figs. S1, S2) expressed by the highly significant GLM results of region  $\times$  trait interaction terms (Tab. 2) was unexpected. Thus, our study suggests that environmental differences, including fragment area and total species richness, can heavily influence the co-occurrence of traits. As these quantifications regard absolute differences in metric scores, this result is independent of the underlying null model used for statistical inference. These results suggest caution when generalizing patterns of trait or species co-occurrences stemming from single meta-communities or samples.

In addition to region-specific differences in trait co-occurrence, we found other significant differences between the Neotropical and African sites (Tabs. 2, 4, Figs. 2, S1). For example, average SES scores for species co-occurrence (Fig. 2) and for stratum and territoriality (Fig. 5) were strongest for the African sites indicating a stronger spatial patterning of species occurrences and traits. This result is most likely explained by the higher variability in habitat characteristics between the fragments of the three African regions, which should theoretically lead to more pronounced species turnover among sites. In addition, according to Ricklefs (2012), the Afrotropical avifauna has lower morphological variation compared to Neotropical passerines, raising the possibility that competition for resources is stronger in Afrotropical communities because species are on average more similar in their traits.

According to our starting hypotheses, we expected to see differences in the pattern of co-occurrence between dietary guilds with a general tendency towards stronger competitively driven trait segregation within local communities of insectivores (Bregman et al. 2015). This was not the case. With the exception of Afrotropical insectivores (Fig. 4) we did not detect significant differences in the pattern of co-occurrence among the dietary guilds neither at the level of species (Fig. 2) nor at the trait level (diet preferences and morphology: Fig. 4, Figs. S1, S2). If present, the degree of feeding specialisation explains at most a minor part of the variability in occurrences and is apparently subordinate to other factors, including territoriality, dispersal dynamics, and environmental effects.

When drawing inferences from these results it is worth bearing in mind some possible pitfalls. For example, in common with previous methods, our approach is based on average measured trait values, and thus ignores individual and population wide variability in trait expression. Further, trait and environmental variable selection is partly subjective and important factors might have been ignored. However, the traits and environmental variables used here have previously been shown to influence bird community assembly (Trisos et al. 2014, De Coster et al. 2015) and species interactions (Ulrich et al.

2016), suggesting that they may also influence the pattern of species co-occurrence. Another shortcoming of all approaches available at present is the use of static (or snapshot) data, which potentially overlook the role of evolutionary adaptation. This relates particularly to ‘soft’ traits like stratum or dietary preferences that can undergo fast local adaptations (Sih et al. 2011). These limitations may weaken the statistical power of trait-based analyses of community structure and assembly.

In conclusion, we have shown how a methodology that directly links the spatial arrangement of species functional traits and species occurrences with environmental characteristics can uncover patterns of bird community assembly. Importantly, we found a consistent tendency for a clustered spatial patterning of functional traits among communities in fragmented landscapes. Our results extend previous findings (e.g. Bregman et al. 2015, 2016), and highlight the complex interplay of processes governing the assembly and disassembly of bird communities in fragmented or degraded tropical forests. Particularly, the observed differences in assembly between Neo- and Afrotropical regions call for caution when generalizing findings about bird community structure. Further work should focus on explaining why these processes vary across scales and regions, clarifying how they are mediated by the size, isolation, and degradation of forest fragments.

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### Table Legends

**Table 1.** Landscape and avian community characteristics of the three Afrotropical and Neotropical study areas.

| Continent    | Landscape        | No. fragments | % forest cover | Individuals trapped | Species richness    |              |            |           |       |
|--------------|------------------|---------------|----------------|---------------------|---------------------|--------------|------------|-----------|-------|
|              |                  |               |                |                     | Frugi-/Nectarivores | Insectivores | Granivores | Omnivores | Total |
| Afrotropical | Eastern Usambara | 10            | 24.0           | 12767               | 10                  | 38           | 7          | 8         | 63    |
|              | Western Usambara | 5             | 30.3           | 11566               | 8                   | 34           | 5          | 8         | 55    |
|              | Taita Hills      | 12            | 17.8           | 17531               | 12                  | 36           | 10         | 11        | 69    |
| Neotropical  | Caucaia          | 17            | 35.1           | 1289                | 7                   | 45           | 3          | 7         | 62    |
|              | Ribeirao         | 17            | 42.0           | 1946                | 9                   | 42           | 4          | 11        | 66    |
|              | Tapirai          | 19            | 17.4           | 1569                | 16                  | 57           | 5          | 7         | 85    |



**Table 2.** General linear models identified significant (\*: parametric  $P(F) < 0.05$ , \*\*:  $P(F) < 0.01$ , \*\*\*:  $P(F) < 0.001$ ) differences in the co-occurrence of species (SES scores of the proportional null model of the clumping and C- score) between feeding guilds, landscapes, and trait categories. Regional species richness, matrix fill, and the total number of  $2 \times 2$  submatrices on which score calculations were based (Sample size) served as metric covariates to exclude the possible effect of matrix structure.

| Variables           | Afrotropical |                  |                  | Neotropical |                  |                  |
|---------------------|--------------|------------------|------------------|-------------|------------------|------------------|
|                     | df           | Clumping         | C-score          | df          | Clumping         | C-score          |
|                     |              | partial $\eta^2$ | partial $\eta^2$ |             | partial $\eta^2$ | partial $\eta^2$ |
| Feeding guild       | 3            | 0.10**           | 0.03             | 3           | 0.04***          | <0.01            |
| Landscape           | 2            | 0.04             | 0.02             | 2           | 0.01             | <0.01            |
| Trait               | 6            | 0.15**           | 0.11*            | 6           | 0.06***          | <0.01            |
| Guild*Landscape     | 6            | 0.26***          | 0.13**           | 6           | 0.11***          | 0.09***          |
| Guild*Trait         | 18           | 0.20*            | 0.14             | 18          | 0.12***          | 0.08***          |
| Trait*Landscape     | 12           | 0.19*            | 0.23**           | 12          | 0.09***          | 0.05*            |
| Richness            | 1            | <0.01            | <0.01            | 1           | <0.01            | 0.02*            |
| Matrix fill         | 1            | 0.04*            | <0.01            | 1           | 0.03**           | <0.01            |
| Sample size         | 1            | 0.04*            | <0.01            | 1           | 0.02**           | 0.02**           |
| Error               | 115          |                  |                  | 456         |                  |                  |
| $r^2$ (whole model) |              | 0.54***          | 0.53***          |             | 0.36***          | 0.28***          |

**Table 3.** General linear models (main effects) did not reveal detectable differences in spatial patterning of species traits (SES scores of the proportional null model as dependent variable) in pairwise species comparisons. Regional species richness, matrix fill, and the total number of 2×2 submatrices on which score calculations were based (Sample size) served as metric covariates to exclude the possible effect of matrix structure. \*\*\*: Parametric  $P(F) < 0.001$ .

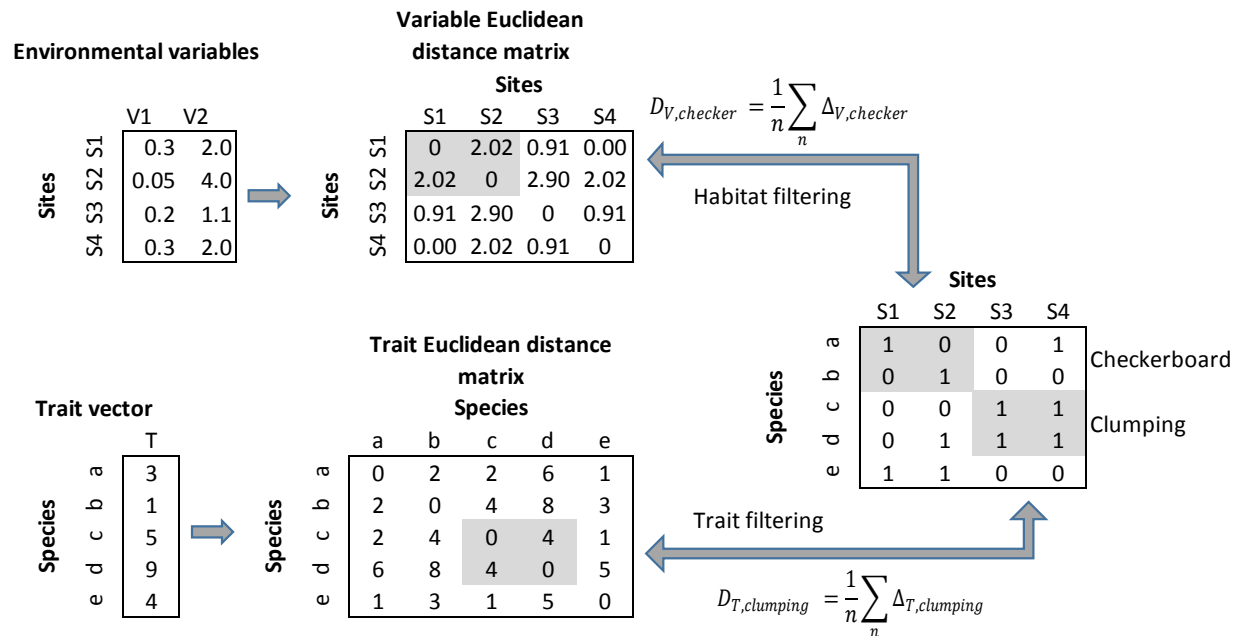
|                     |      | Clumping         | C-score          |
|---------------------|------|------------------|------------------|
|                     | Df   | partial $\eta^2$ | partial $\eta^2$ |
| Continent           | 1    | <0.01            | <0.01            |
| Feeding guild       | 3    | <0.01            | <0.01            |
| Trait               | 6    | <0.01            | <0.01            |
| Landscape           | 5    | <0.01            | <0.01            |
| Richness            | 1    | <0.01            | <0.01            |
| Matrix fill         | 1    | <0.01            | <0.01            |
| Sample size         | 1    | 0.06***          | 0.03***          |
| Error               | 8669 |                  |                  |
| $r^2$ (whole model) |      | 0.11***          | 0.08***          |

**Table 4.** General linear modelling identified significant (\*: parametric  $P(F) < 0.05$ , \*\*:  $P(F) < 0.01$ , \*\*\*:  $P(F) < 0.001$ ) although weak differences in environmental mediated trait filtering (Fig. 1) (SES scores of the proportional null model as dependent variable). Regional species richness, matrix fill, and the total number of  $2 \times 2$  submatrices on which score calculations were based (Sample size) served as metric covariates to exclude the possible effect of matrix structure.

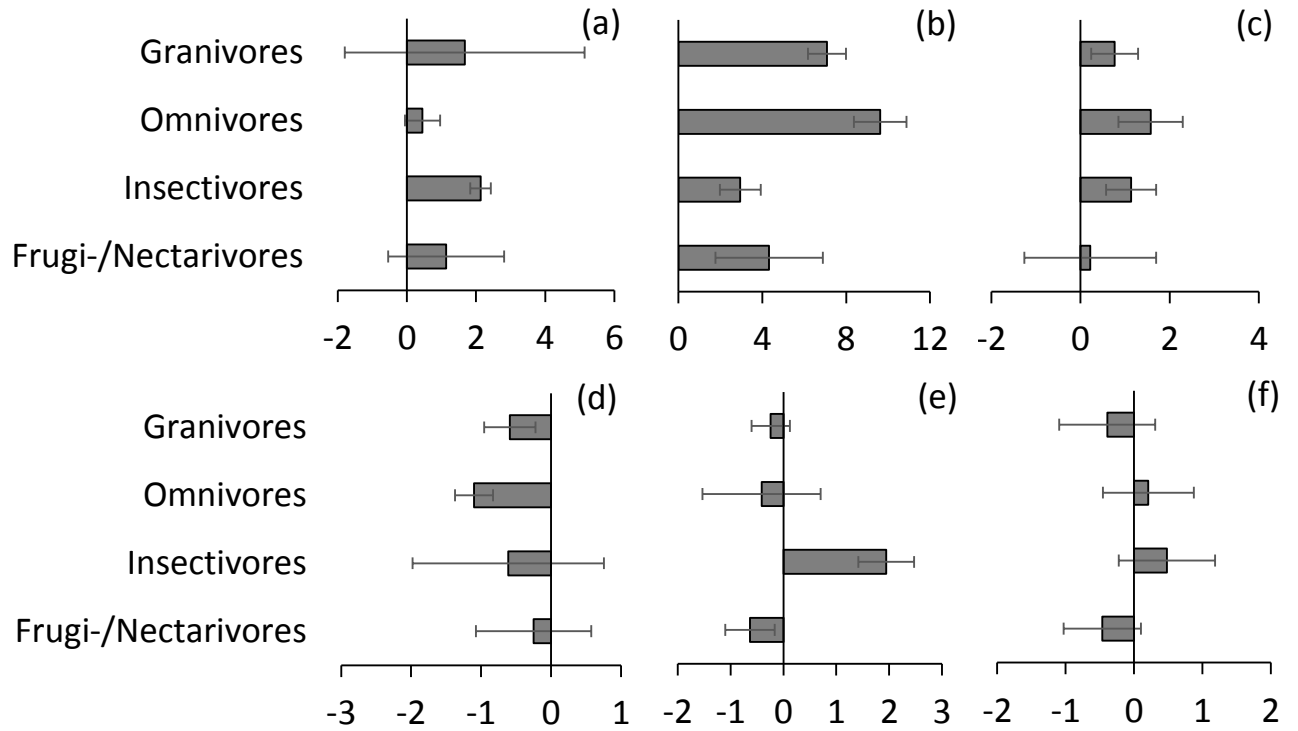
| Variables           | Afrotropical |                  |                  | Neotropical |                  |                  |
|---------------------|--------------|------------------|------------------|-------------|------------------|------------------|
|                     |              | Clumping         | C-score          |             | Clumping         | C-score          |
|                     | df           | partial $\eta^2$ | partial $\eta^2$ | df          | partial $\eta^2$ | partial $\eta^2$ |
| Trait               | 6            | 0.17***          | 0.30***          | 6           | 0.05***          | 0.01*            |
| Environment         | 4            | <0.01            | 0.03             | 4           | <0.01            | <0.01            |
| Trait*Environment   | 24           | 0.02             | 0.06             | 24          | <0.01            | <0.01            |
| Richness            | 1            | <0.01            | 0.02             | 1           | 0.01*            | <0.01            |
| Matrix fill         | 1            | 0.01             | <0.01            | 1           | <0.01            | <0.01            |
| Sample size         | 1            | 0.09***          | 0.03**           | 1           | <0.01            | <0.01            |
| Error               | 244          |                  |                  | 1371        |                  |                  |
| $r^2$ (whole model) |              | 0.42***          | 0.41***          |             | 0.14***          | 0.04***          |

**Figure Legends**

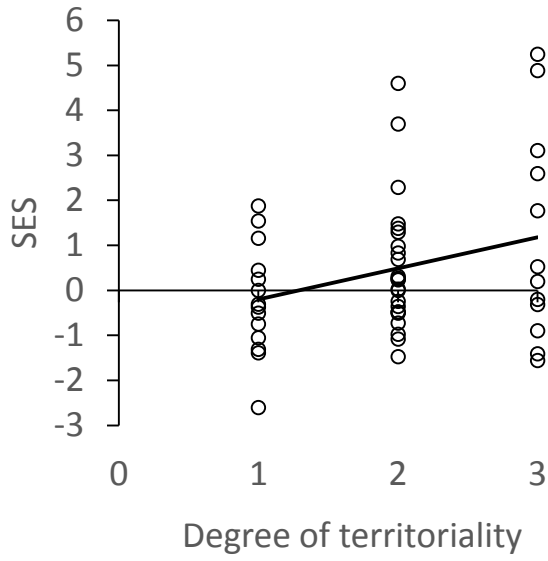
**Figure 1.** Co-occurrence analysis of numerical traits. The environmental and trait matrixes (or vectors) are translated into sites × sites and species × species Euclidean distance matrixes, respectively. The average sums  $D_V$  and  $D_T$  of all distances  $\Delta_V$  or  $\Delta_T$  of all species pairs showing a checkerboard or a clumping pattern are compared to the expected average sums of 1000 randomized species occurrences matrixes. Lower distances  $D_{V,clumping}$  and  $D_{T,clumping}$  than expected by chance point to spatial aggregation of traits (trait filtering) and similar environmental characteristics in co-occurring species (habitat filtering). Relatively high distances  $D_{V,clumping}$  and  $D_{T,clumping}$  of co-occurring species can be linked to competitive effects (limiting similarity). In the case of checkerboard species co-occurrences, lower distances  $D_{V,checker}$  and  $D_{T,checker}$  than expected by chance indicate that species pairs that reciprocally exclude each other are relatively close in trait expression or environmental conditions, again pointing to filter effects.



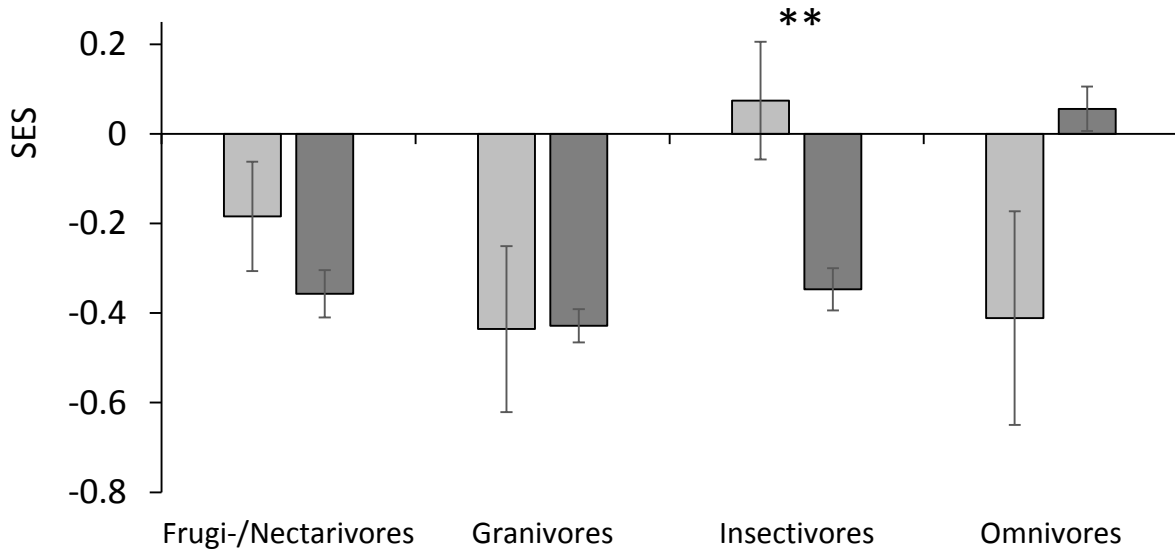
**Figure 2.** Average standardized effect sizes (SES  $\pm$  standard error) of the C-score in Afrotropical (a: Eastern Usambara, b: Western Usambara, c: Taita) and Neotropical (d: Caucaia, e: Ribeirao, f: Tapirai) fragmented landscapes. Positive C-scores show that species co-occur less often than expected by chance, which suggested segregation. Negative C-scores suggest aggregation.



**Figure 3.** The degree of species spatial segregation (C-score) increases with increasing degree of territoriality ( $r^2 = 0.08$ ,  $P(F_{2,49}) = 0.04$ ).



**Figure 4.** SES clumping scores ( $\pm$  standard error) of Afrotropical (light grey) and Neotropical (dark grey) traits averaged across landscapes and trait categories indicate a trend of similar trait expression in co-occurring species pairs. Negative clumping scores reveal that traits of species with pair-wise co-occurrence [(1,1),(1,1)] are more similar than expected by chance. Unequal variances t-test significances: \*\*:  $p(t) < 0.01$ .



**Figure 5.** SES clumping scores ( $\pm$  standard error) of Afrotropical (light grey) and Neotropical (dark grey) traits averaged over all landscapes and feeding guilds indicate contrasting patterns of trait co-occurrence between both continents. Unequal variances t-test significances: \*\*:  $p(t) < 0.01$ , \*\*\*:  $P(t) < 0.001$ .

