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# On Bird Functional Diversity: Species Richness and Functional Differentiation Show Contrasting Responses to Rainfall and Vegetation Structure in an Arid Landscape

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## ABSTRACT

Biodiversity affects ecosystem function through species' functional traits. Although it is possible to predict species richness (SR) patterns along environmental gradients, whether functional diversity (FD) changes in predictable ways is not known. In arid environments, SR typically increases with rainfall. Aridity may limit functional differentiation by allowing only certain traits, but could also be associated with diverse traits associated with various strategies for coping with spatial and temporal variation in resources. Rare species may have unique traits, making them particularly important to continued ecosystem function. We investigated SR, FD, and functional differentiation in bird assemblages along an aridity gradient, with attention to functional uniqueness of rare species. We surveyed bird

communities in open savanna, bush-thickened, and riparian habitats at five sites of increasing aridity (~150–400 mm rainfall year<sup>-1</sup>) in wet and dry seasons for 3 years in Namibia. We calculated the standardized effect size of FD (sesFD) as a measure of functional differentiation and used mixed models to ascertain how SR, FD, and sesFD relate to rainfall, season, and habitat type. SR and FD increased with increasing rainfall. Conversely, sesFD declined with increasing rainfall and was lower in woody habitats, suggesting habitat filtering and greater niche overlap. Rare species were more functionally unique than common species, in all three habitats, so loss of rare species could degrade ecosystem function. Our results are consistent with a linear diversity–productivity relationship maintained by regular disturbance (drought) preventing strong competitors from excluding weaker competitors in higher productivity environments.

**Key words:** aridity gradient; bush encroachment; bush thickening; environmental gradients; environmental filtering; functional uniqueness; null models; rare species; shrub encroachment; standardized effect size.

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**Author contributions** The ideas behind this research were conceived by CS, RS, and JS, data collection was carried out by RS. CS, JS, and GJ analyzed the data; CS and JS led the writing which was shared by all authors.

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## INTRODUCTION

Species richness (SR) and functional diversity (FD) profoundly influence ecosystem function (Cardinale and others 2012) and can provide insurance against sudden environmental change (MacDougall and others 2013). FD, the range of species and organismal traits that impact ecosystem functioning (Tilman 2001), usually embodies the diversity of species' niches or functions (Petchey and others 2004). Species abundance is also important, and there is a growing body of evidence that rare species can contribute disproportionately to FD (Mouillot and others 2013; Bracken and Low 2012; Jain and others 2014). Given that FD reflects ecosystem pattern and process better than species-based measures of diversity (Díaz and Cabido 2001), there is a growing interest in assessing FD, its role in ecosystem processes, how it varies along environmental gradients (Mace and others 2014), and the relative importance of rare species to FD (Jain and others 2014).

Despite a fair understanding of general patterns in SR at various scales and along environmental gradients (for example, latitude, altitude, productivity, and aridity; Gaston 2000; Field and others 2009), little is known of how FD changes along these gradients, or even if consistent patterns exist. Understanding how SR and FD relate to gradients can help predict how SR and FD may vary as environments are altered by global change (Chapin and others 1996). The relationship between SR and FD in natural systems is unclear (Naeem 2002). As SR increases, so too should FD, because more species present more opportunities for different traits to occur (Petchey and Gaston 2006). Yet this relationship can be complicated by biotic and abiotic factors, and the span of the gradient considered (Cadotte and others 2011). For a given SR, FD will be low if species within an assemblage have similar traits, but high if their traits are very different. Various factors can affect trait variance within a community. For example, abiotic factors can limit FD by selecting for species with traits able to survive certain environmental conditions, constraining the range of traits present within an assemblage ("environmental filtering"; Weiher and others 1998). Conversely, biotic factors such as competition can have the opposite effect, preventing species that are too similar from co-occurring ("limiting similarity"; MacArthur and Levins 1967). The relative influence of these factors affects both SR and FD because they limit membership of a community to species with appropriate traits for the given environment, and only allow co-occurrence of species that are sufficiently functionally differentiated to minimize competition.

Environmental filtering should be strongest at extreme ends of gradients, such as arid, dystrophic, or highly saline environments where one or more resources are either extremely limiting or in such overabundance as to be toxic (Díaz and others 1998; Joseph and others 2014). Communities in these environments should be composed only of species with traits that allow them to survive. For example, aridity is associated with fewer species, particularly in the tropics (Hawkins and others 2003). Yet while aridity should be associated with low species diversity, and environmental filtering should be strong, biota may evolve various strategies for coping with water scarcity, so aridity could also be associated with diverse life history traits (Stubbs and Wilson 2004; de Bello and others 2006). Global change effects could be particularly strong in arid environments, given expected increases in drought and overall drying (Dai 2013; Sherwood and Fu 2014). Arid systems are sensitive to land-use impacts and recover slowly from disturbance (Valone and others 2002; Seymour and others 2010). There is therefore a need to understand patterns, drivers, and constraints of functional diversity if we are to predict or mitigate global change impacts in these environments.

Birds fill various roles in ecosystems and can contribute to ecosystem services (Sekercioglu 2006). Loss of bird species and their functional diversity could have unanticipated effects on ecosystem function (Anderson and others 2011), although more studies are needed to confirm the links between functional diversity and ecosystem functioning. Furthermore, birds might be particularly sensitive to gradients: with agricultural intensification, bird FD declined faster than species diversity, suggesting that functionally distinct species were lost first (Flynn and others 2009). Additionally, rare species often have attributes that make them prone to extinction risk, for example, they frequently have narrow geographical ranges, few populations that are often small and lack genetic variability, and may require specialized niches (Isik 2011).

Despite their susceptibility to extinction, rare species may be functionally pivotal to the system in which they occur (Mouillot and others 2013), so their loss can have cascading effects (Bracken and Low 2012). Roughly half of the fish and tree species supporting vulnerable functions in tropical reefs and forests, respectively, were found to be represented by only a single individual per sample (Mouillot and others 2013), and declines in consumer biomass of over 40% were observed after experimental removal of about 10% of biomass

represented by rare species, compared to no losses associated with removal of similar biomass of common species (Bracken and Low 2012). Rare species may either support unique functions or act as important contributors to functional redundancy, and are likely to be particularly important if the abundance of rare species increases in response to future environmental change (Jain and others 2014).

Bush thickening (“encroachment”) occurs in savannas worldwide (Brown and Archer 1989; Murphy and others 2014; O’Connor and others 2014), and arises when woody plant density increases to the point that herbaceous plants are suppressed. Bush thickening, estimated to affect 17.5 million ha in Namibia (Bester 1999), where this study was conducted, threatens biodiversity and farmland productivity (Bester 1999; Meik and others 2002; Blaum and others 2006). Bush thickening changes habitat structure, affecting representation of species life history traits among birds (Seymour and Dean 2010; Ehlers Smith and others 2015), and so should affect FD. Riparian habitats in arid areas are often under threat of transformation (Belsky and others 1999; Seymour and Simmons 2008), so we also focused on their importance to bird SR and FD.

We assessed bird SR and FD in wet and dry seasons for 3 years along an aridity gradient in Namibia, in three habitats: (i) “open savanna”, primarily grassland with scattered large trees [mostly *Acacia* (*Senegalia*) *erioloba*], of which woody cover was 5–20%; (ii) “bush thickened” sites with 70–90% woody plant cover below 2 m in height, usually *Acacia mellifera* and *Catophractes alexandri*; and (iii) “riparian” vegetation along ephemeral rivers, composed of mature, relatively tall trees of *Acacia*, *Ziziphus*, and *Boscia* spp. constituting 30–60% cover. The aridity gradient spans about 250 km and there is an increasing need for research into biodiversity patterns and process at larger scales (Heffernan and others 2014). We used line transects to survey the bird communities and asked the following:

1. How do bird SR and FD change along the aridity gradient, and is there variation among habitats and with season?
2. Are rare species functionally similar to common species, or do they contribute disproportionately to FD?

## METHODS

### Study Area

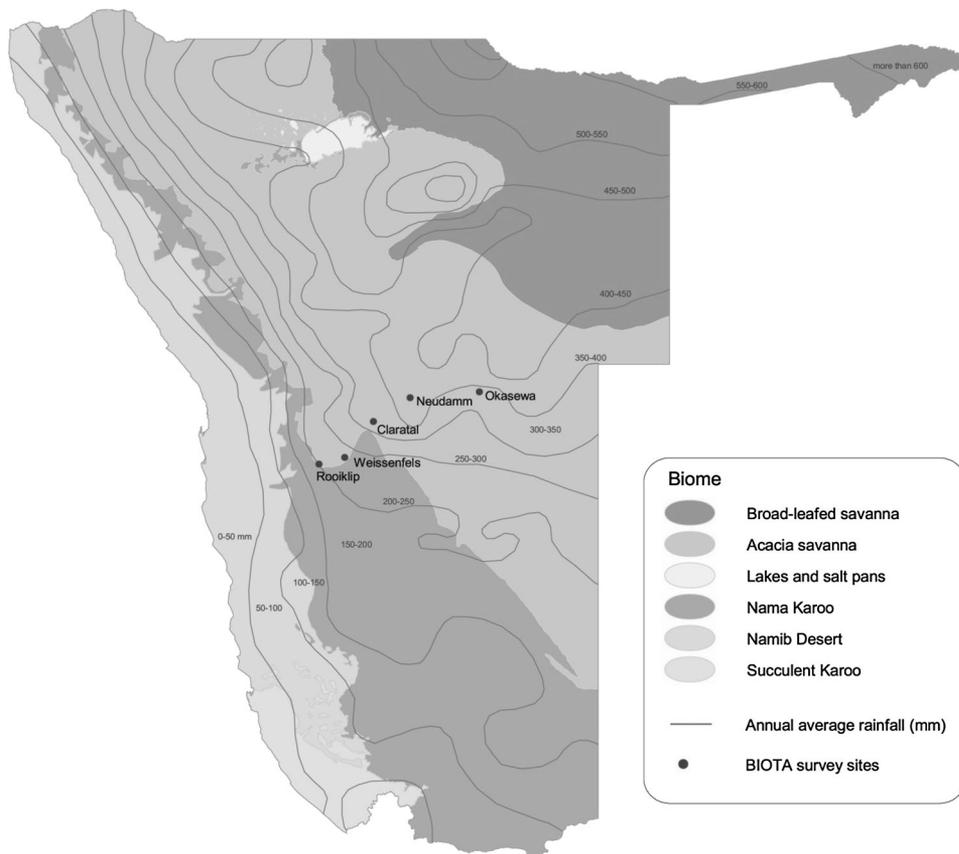
Sites were situated in the central Namibian Savanna Woodland (Burgess and others 2004) (Figure 1;

Table 1). The area is primarily livestock or game rangeland. We selected five sites of increasing aridity from east (Mean Annual Precipitation, MAP: 405 mm year<sup>-1</sup>) to west (MAP: 157 mm year<sup>-1</sup>), with similar mean temperatures (19°C daily annual temperature). All sites were larger than 1000 ha and at least 40 km apart. Within each site, we sampled areas representative of the three habitats (open savanna, bush thickened, and riparian). We measured woody plant height and density to confirm that the three different habitat types conformed to our habitat definitions in terms of woody species density and did not differ significantly between sites (see Supporting Information, Appendix S1).

### Sampling Design

Within each habitat at each site, bird assemblages were surveyed along three fixed 1 km line transects, at least 500 m apart. Surveys were carried out in the dry winter and wet summer (bird breeding) season, for three years, that is, on six occasions (August 2007, 2008, and 2009, and February 2008, 2009, and 2010). Daily rainfall records are kept for each site by landowners (Table 1) and the Desert Research Foundation of Namibia. Records extend back decades, allowing calculation of MAP. We used three measures of rainfall (MAP and precipitation 6 and 12 months prior to our surveys) to determine whether birds respond to average site aridity, the medium-term flush of grasses/seeds provided by the previous year’s rains, or the immediate flush in primary productivity provided by recent rains. A number of migratory species arrive for summer.

Transects were sampled within 3 h of sunrise. All small birds (< 30 cm in length) seen or heard within 120 m of each transect were counted, as were larger scavenging and game birds (> 30 cm in length) up to 350 m. We paced the perpendicular distances from the transect at regular intervals for all birds and also checked these distances using a GPS. We compared observed species richness in each habitat with eight estimators for both abundance and incidence data (ACE, ICE, Chao 1 and 2, Jackknife 1 and 2, Michaelis–Menten, and bootstrap), which we calculated using EstimateS (Colwell 2013). These indices estimate the number of undetected species (Gotelli and Colwell 2011). We calculated the proportion of species observed in each habitat based on these “true” species richness estimators to enable comparisons of bird detectability in the three different habitats. Our species accumulation curves indicated that our sampling was sufficient in each habitat (Appendix S2). Birds identified by calls were assumed to be single individuals unless duetting or



**Figure 1.** Biomes and mean annual precipitation (MAP) isohyets for Namibia, in relation to study sites. Map by T. Robertson.

calling from different directions simultaneously. Similarly, if there was uncertainty as to whether an individual had already been counted, it was ignored. Birds flying over transects were excluded, as were aquatic bird species (associated with farm dams, and thus not necessarily responding to habitat structure or recent rainfall).

The five sites are large areas ranging from 20,000 to 50,000 ha in size. Transects were chosen that best represented the three habitats. The transects were 1 km long and three separate transects were carried out in different areas of the sites for each habitat, giving nine (three each of the three habitat types) fixed transects altogether at each site. Thus, about 210 ha (three transects of 1 km by 700 m) of each habitat was sampled at each site. Riparian habitat constituted between 3 and 7%, open habitats between 10 and 20%, and thickened habitats between 30 and 55% of the area of the various sites. The remaining non-riparian habitat did not meet our criteria for “open” or “thickened” habitats.

### Relationship Between SR and Aridity, Habitat, and Season

Since we used repeat sampling, we used generalized linear mixed models (GLMM, Poisson distri-

bution, R package lme4; Bates and others 2013) with random intercepts to ascertain how species richness changed with habitat type, rainfall (that is, MAP, and rainfall over the previous 6 and 12 months), season (wet or dry, pooled over years), and any interactions between these. Thus, the 45 transects were sampled six times over the study period. We first constructed “beyond optimal” models where the fixed component contained as many independent explanatory variables as possible, and discarded variables that had no significant effect on the response variable (Zuur and others 2009). We assessed model fit to ensure that the model assumptions were obeyed, by plotting residuals against both fitted values and explanatory variables, and checking explanatory variables for collinearity (Zuur and others 2009, 2010). We used SR as our dependent variable, environmental variables (that is, habitat type, season, and rainfall) were fixed effects, with transect as a random effect. We used AIC and Akaike weights to evaluate degree of support for each model (Burnham and Anderson 2002). Akaike weights fall between 0 and 1, representing the probability that a given model is the best approximating model of those tested (Symonds and Moussalli 2011). We calculated

**Table 1.** Sites Used in This Study, with Rainfall Given in mm

Sites	MAP	Location	Rainfall		Rainfall		Rainfall		Rainfall		Rainfall	
			Feb 2007– Aug 2007	Feb 2008– Feb 2008	Feb 2008– Aug 2008	Feb 2008– Feb 2009	Feb 2009– Aug 2008	Feb 2009– Feb 2010	Feb 2009– Aug 2008	Feb 2009– Feb 2010		
<i>Neudamm</i>	405.4	S 22°28.18'; E 17°21.68'	265.5	456	241	521	272	497				
<i>Okasewa</i>	387	S 22°28.18'; E 17°21.68'	357	367	200	382	262	504				
<i>Claratal</i>	355.3	S 22°48.5'; E 16°51.05'	215	265	208	555	337	349				
<i>Weissenfels</i>	214	S 23°19.18'; E 16°26.96'	54	58	110	110	142	142				
<i>Rooiklip</i>	157.4	S 23°19.18'; E 16°26.96'	40	96	147	147	104	171				

MAP denotes mean annual precipitation, based on site data spanning 10–90 years.

variance explained by fixed (marginal  $R^2$ ), and fixed and random effects (conditional  $R^2$ ) (Nakagawa and Schielzeth 2013).

## Functional Diversity

To assess FD, we constructed a trait matrix for bird species encountered based on Hockey and others (2005). We included traits related to food requirements, movements, and nesting habits (Table 2). We chose these traits because they yield information about which resources (type and amount) the various bird species require and how they secure them. Information on movement (migratory/resident/nomadic) was included as it can also reflect species' strategies to deal with aridity and/or drought (Dean and others 2009). To ensure variation within each trait was treated equally, we standardized trait data so that the mean of each trait was zero with a standard deviation of one (Petchey and Gaston 2006). Categorical traits were treated as binary and weighted. For example, there were nine different food types that are not mutually exclusive, so species were allocated a "1" for those items in their diets, or a "0" for those that are not (Table 2). Having nine variables would artificially inflate the importance of this trait, so we weighted "food type" by 1/9 (Laliberté and Legendre 2010). Species and traits allocated to them are listed in Supporting Information, Appendix S3.

We converted the species-by-trait matrix into a distance matrix using Gower distances, which allows individual traits to be weighted differently (Podani 1999), and use of quantitative and qualitative traits together (Podani and Schmera 2006). We used the unweighted pair-group method with arithmetic mean (UPGMA) to cluster the matrix, because UPGMA gave the highest cophenetic correlation (0.67) between original and estimated distances resulting from the dendrogram. We calculated FD by summing the branch lengths of the dendrogram corresponding to the species assemblage for each transect to calculate FD (Petchey and Gaston 2002, 2006).

FD should increase as number of species increases, because each new species raises the probability of sampling a new trait value (Petchey and Gaston 2002). This correlation with species richness is a characteristic of a number of indices of functional diversity (Mouchet and others 2010). Petchey and Gaston's (2002, 2006) measure of FD has been used in a number of studies on spatial and temporal changes in bird functional diversity (for example, Petchey and others 2007; Flynn and others 2009; Mendez and others 2012; Luck and others 2013; Boyer and Jetz 2014), so its use allows comparison

**Table 2.** Traits Used to Ascertain Functional Diversity of Bird Communities, Based on Hockey and others (2005)

Trait types	Traits	Scale
Resource quantity required	Weight	Continuous
	Average clutch size	Continuous
Feeding strategy	Aerial	Binary
	Perch and swoop	Binary
	Hovers	Binary
	Aquatic	Binary
	Canopy gleaner	Binary
	Ground surface feeding	Binary
	Digs in ground	Binary
	Shrub gleaner	Binary
Food types	Carrion	Binary
	Bulbs, rhizomes, corms	Binary
	Foliage	Binary
	Freshwater fish & invertebrates	Binary
	Fruit	Binary
	Nectar and Pollen	Binary
	Seeds	Binary
	Terrestrial invertebrates	Binary
	Terrestrial vertebrates	Binary
	Nest types	Burrow
Ground		Binary
Hanging		Binary
Cavity		Binary
Supported nest		Binary
Movements	Non-breeding migrant	Binary
	Breeding migrant	Binary
	Nomadic	Binary
	Resident	Binary

with other studies. Furthermore, FD is able to efficiently identify assembly rules (Mouchet and others 2010). Therefore, to correct for increases in FD with added species, that is, to ascertain the degree of functional differentiation among taxa, we used simulation models to compare observed FDs against a null distribution of FD values, to calculate standardized effect size (sesFD). Assessing standardized effect size and comparing the results after taking species prevalence into account versus ignoring species prevalence also gives some insight into the relative functional importance of rare species.

For each site, with  $n$  species, the simulation models randomly selected  $n$  species from the total species pool without replacement, yielding an expected FD for that group of species. We repeated the models 999 times, creating a distribution of 1000 null values for each observed value. The mean of the null distribution was then subtracted from the observed FD value and divided by the

standard deviation of the null distribution, to yield sesFD. Thus, sesFD reflects the number of standard deviations that the observed community is above or below the mean (0) of the simulated communities from the null model (Gotelli and Rohde 2002).

There is uncertainty on how best to generate null models (de Bello 2012), so we used four alternative models to ask different questions, as recommended by Gotelli (2000). All null models maintained species number within each sample. First, species were drawn from the total species pool, but the prevalence of each species in the samples, that is, the number of sites each species occurred in, was kept constant. In this way, rare species were only included in simulations rarely, while common species were chosen more often, in proportion to their incidence in the dataset. This tests whether functional differentiation is structured based on the position of species along the rainfall gradient and/or between habitats. The second model was similar, but the prevalence of each species across samples was not constrained and each species had an equal chance of occurring at any site. This tests whether functional differentiation is structured by either position of species along the rainfall gradient and between habitats or by relative prevalence of the different trait combinations (species) in the total dataset, and allows exploration of effects of rare species. If rare species are functionally different to others within the assemblage, then null models that ignore their relative prevalence will yield lower values. We then repeated these two null models (prevalence-constrained or not), but partitioned them such that species were only drawn from the species pool for the habitat to which each transect belonged. This tests whether FD is structured based purely on the position of species along the rainfall gradient, and excludes effects of structuring between habitats.

To test the sensitivity of our analyses to the chosen functional diversity metric, we also performed all analyses using convex hull volumes (FRic) of Cornwell and others (2006), and the standardized effect size of Fric (sesFric), following Trisos and others (2015). Results of mixed models using FRic and sesFRic were qualitatively similar to those produced for FD and sesFD (see below), and are reported in Appendix S4.

## Variation in FD with Aridity and Habitat Type

To determine relationships between FD and sesFD with habitat, rainfall, and season, we fit generalized linear mixed effects models with random intercepts

(R package lme4; Bates and others 2013). FD and sesFD were response variables, transect was a random effect, and habitat, season, and one of the three measures of rainfall were fixed effects. As sesFD values are standardized effect sizes and should center on zero in the absence of strong environmental filtering or competition, we set the intercept to zero to test for deviations from the zero null expectation. Consistent deviations from zero across multiple communities can indicate community structuring processes (that is, competition or environmental filtering; Kraft and Ackerly 2010). We used AIC and Akaike weights to assess model support and fit, and calculated variance explained by fixed and random effects.

### Assessing the Contribution of Rare Species to FD

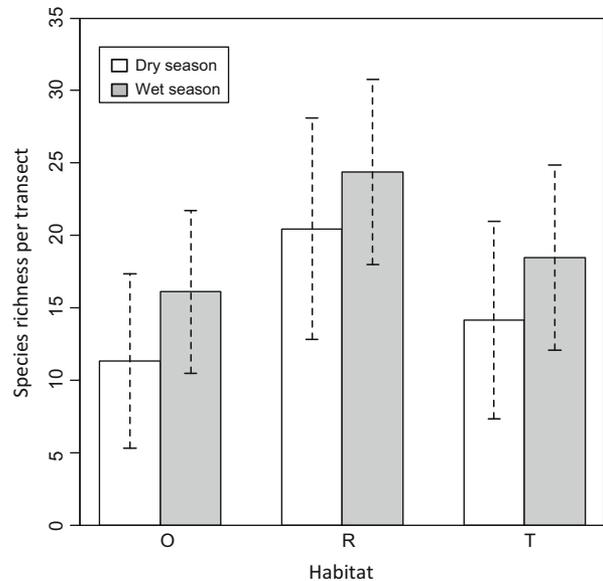
We calculated functional uniqueness, the functional equivalent of phylogenetic uniqueness for each species (Pavoine and others 2005) using a functional dendrogram (see, for example, Thompson and others 2010). We split species into “rare” or “common” by lumping the rarest species until we reached a set that represented 10% of total abundance (134 of 201 species) and compared their functional uniqueness to that of the remaining 90% (67 species) using a Wilcoxon rank sum test.

## RESULTS

### Bird Species Richness Along the Aridity Gradient and Among Habitats

The eight estimators for “true” species richness, found the three habitats to be comparable in the proportion of species detected (mean  $S_{obs}/S_{est}$  by index: thickened:  $83.4 \pm 8.5\%$ ; open:  $83.5 \pm 7.3\%$ ; riparian:  $84.5 \pm 6.7\%$ ), thus we could compare observed SR between the three habitats. We also assessed species richness patterns using Chao1 estimators to account for any bias in detectability but the results obtained were near identical so analyses based only on raw species richness data are reported.

The best models assessing variation in SR identified by AIC and Akaike weightings had 63 and 35% of support for all models considered; variance explained was 12 and 39% for fixed and both fixed and random variables, respectively, (Figure 2; Table 3). Riparian habitats, followed by thickened habitats, had significantly more species per unit area (that is, per transect) than open habitats. SR was greater in the wet season, although this seasonal increase was significantly less marked in riparian habitats. SR also



**Figure 2.** Species richness per transect in each habitat, in the dry and wet seasons. *Error bars* indicate standard deviations from the mean. O, R, and T indicate open, riparian, and thickened habitats, respectively.

increased with rainfall over the previous year, that is, SR decreased with aridity of sites, and varied within sites over different years.

### Variation of FD

The best model for variation of FD with rainfall, habitat, and season had 98% of support for all models considered; fixed effects explained 20.3% and fixed and random effects together explained 51.3% of the variance. FD followed similar patterns to species richness, being greater in riparian habitat, increasing with rainfall over the previous year and being greater in the wet season (Table 3).

Functional differentiation (sesFD) behaved differently to FD. Simulation models run on the complete dataset and those partitioned by habitat were virtually identical, so only results of the simulation models partitioned by habitat are presented (Table 4).

When the simulation model was constrained by species prevalence, sesFD in open habitats was significantly greater than the null expectation (0), although riparian and thickened areas were no different from zero. Functional differentiation decreased with increasing rainfall over the previous 6 months and was generally lower in the wet season in open and thickened habitats (Table 4; Figure 2). The best model had 36%, the second and third best models, 21% of the support. Fixed effects

**Table 3.** Variation in (a) Species Richness and (b) Functional Diversity with Habitat, Rainfall, and Season

	Habitat (R)	Habitat (T)	Rainfall over prev. 6 months	Rainfall over prev. year	Season	Habitat (R) × Season	Habitat (T) × Season	d.f.	AIC	Akaike weighting
<b>(a) Species richness</b>										
Model 1 (Best model)	$p < 0.001$	$p < 0.01$	–	$p < 0.001$	$p < 0.001$	$p = 0.02$	n.s.	8	1818.2	0.63
Model 2	$p < 0.001$	$p < 0.001$	–	$p < 0.001$	$p < 0.001$	–	–	6	1819.4	0.35
Model 3	$p < 0.001$	$p = 0.014$	$p < 0.001$	–	$p < 0.001$	$p = 0.043$	n.s.	8	1826.7	0.0009
Null model	–	–	–	–	–	–	–	2	2030.6	< 0.0001
<b>(b) Functional diversity</b>										
Model 1 (Best model)	$p < 0.001$	n.s.	–	$p < 0.001$	$p < 0.001$	–	–	7	333.7	0.98
Model 2	$p < 0.001$	n.s.	$p < 0.001$	–	$p < 0.001$	–	–	7	341.7	0.017
Model 3	$p < 0.001$	n.s.	$p < 0.001$	–	$p < 0.001$	n.s.	n.s.	9	350.9	0.00007
Null model	–	–	–	–	–	–	–	2	435.3	< 0.00001

(a) Best model (Model 1):  $SR = e^{2.04 \pm 0.07 + 0.56 (\pm 0.08) \times \text{riparian} + 0.17 (\pm 0.07) \times \text{thickend} + 0.0013 (\pm 0.0001) \times \text{rain over previous year} + 0.31 (\pm 0.05) \times \text{wet season} - 0.15 (\pm 0.07) \times \text{wet season} \times \text{riparian}$ , Model 2:  $SR = e^{2.09 \pm 0.06 + 0.48 (\pm 0.07) \times \text{riparian} + 0.14 (\pm 0.07) \times \text{thickend} + 0.0013 (\pm 0.0001) \times \text{rain over previous year} + 0.22 (\pm 0.03) \times \text{wet season}$

(b) Best model:  $FD = 0.63 (\pm 0.11) + 0.81 (\pm 0.17) \text{ riparian} + 0.36 (\pm 0.14) \text{ wet season} + 0.0019 (\pm 0.0003) \text{ rainfall over previous year (mm)}$ . MAP represents mean annual precipitation and all rainfall measures are in mm. Significant differences to open habitats (O) are reported, with R and T representing riparian and thickened habitats, respectively. Models are listed according to their AICs and Akaike weightings. The model with the smallest AIC value is considered the best model, and models that differ by  $AIC < 2$  are considered to fit equally well. Akaike weightings are values between 0 and 1 representing the probability that the model is the best approximating model of those considered. Given p values indicate the significance of each variable, n.s. indicates non-significance, and a dash (–) indicates that the variable was not included in that model.

**Table 4.** Variation of FD, Measured as Standardized Effect Size (SES), with Habitat, Various Measures of Rainfall and Season

	Habitat (O)	Habitat (R)	Habitat (T)	Rainfall over prev. 6 months	Rainfall over prev. year	Habitat (R) × Season	Habitat (T) × Season	Season	d.f.	AIC	Akaike weighting
(a) Based on SES calculated assuming chance of each species occurring in random assemblages is linked to its abundance in the dataset (that is, constrained)											
Model 1	$p < 0.05$	n.s.	n.s.	$p < 0.05$	–	$p < 0.001$	n.s.	$p < 0.01$	9	376.8	0.73
Model 2	$p < 0.05$	$p < 0.001$	n.s.	–	$p < 0.05$	$p < 0.001$	n.s.	$p < 0.05$	9	380.2	0.13
Model 3	–	–	–	$p < 0.01$	–	–	–	$p < 0.1$	5	381.4	0.07
Null model	–	–	–	–	–	–	–	–	2	388.2	<0.0001
(b) Based on sesFD calculated assuming equal chance of each species occurring in random assemblages:											
Model 1 (Best model)	n.s.	$p < 0.001$	$p < 0.001$	$p < 0.001$	–	$p < 0.001$	n.s.	$p < 0.01$	9	844.0	0.97
Model 2	n.s.	$p < 0.001$	$p < 0.001$	$p < 0.001$	–	–	–	$p < 0.01$	7	852.9	0.017
Model 3	n.s.	$p < 0.001$	$p < 0.001$	–	$p < 0.01$	–	–	$p < 0.01$	7	854.2	0.009
Null model	–	–	–	–	–	–	–	–	2	912.5	<0.0001

(a) Best model equations: sesFD = 0.31 ( $\pm 0.09$ ) × open habitat – 0.27 ( $\pm 0.08$ ) × wet season – 0.0008 ( $\pm 0.0002$ ) × rainfall over previous 6 months + 0.36 ( $\pm 0.12$ ) × riparian  $\phi$  wet season; Model 2: SES = 0.30 ( $\pm 0.12$ ) open – 0.45 ( $\pm 0.17$ ) riparian – 0.34 ( $\pm 0.14$ ) wet season – 0.0007 ( $\pm 0.00036$ ) × rainfall over previous year + 0.81 ( $\pm 0.26$ ) riparian  $\phi$  wet season; Model 3: SES = –0.001 ( $\pm 0.0004$ ) × rainfall over previous 6 months – 0.16 ( $\pm 0.09$ ) wet season.

(b) Best model equation: sesFD = –1.07 ( $\pm 0.22$ ) × Riparian – 0.88 ( $\pm 0.23$ ) × Thickened – 0.0017 ( $\pm 0.0005$ ) × rainfall over previous 6 months – 0.67 ( $\pm 0.20$ ) × Wet Season + 0.99 ( $\pm 0.28$ ) Riparian  $\phi$  Wet Season. MAP represents mean annual precipitation; O, R, and T, open, riparian, and thickened habitats, respectively. These are compared to the zero null expectation. Rainfall is measured in mm. The best model was identified using AICs and Akaike weights. The model with the smallest AIC value is considered the best model, and models that differ by AIC < 2 are considered to fit equally well. Akaike weightings are values between 0 and 1 representing the probability that the model is the best approximating model of those considered. The p values listed indicate the significance of each variable, n.s. indicates non-significance, and a dash (–) indicates that the variable was not included.

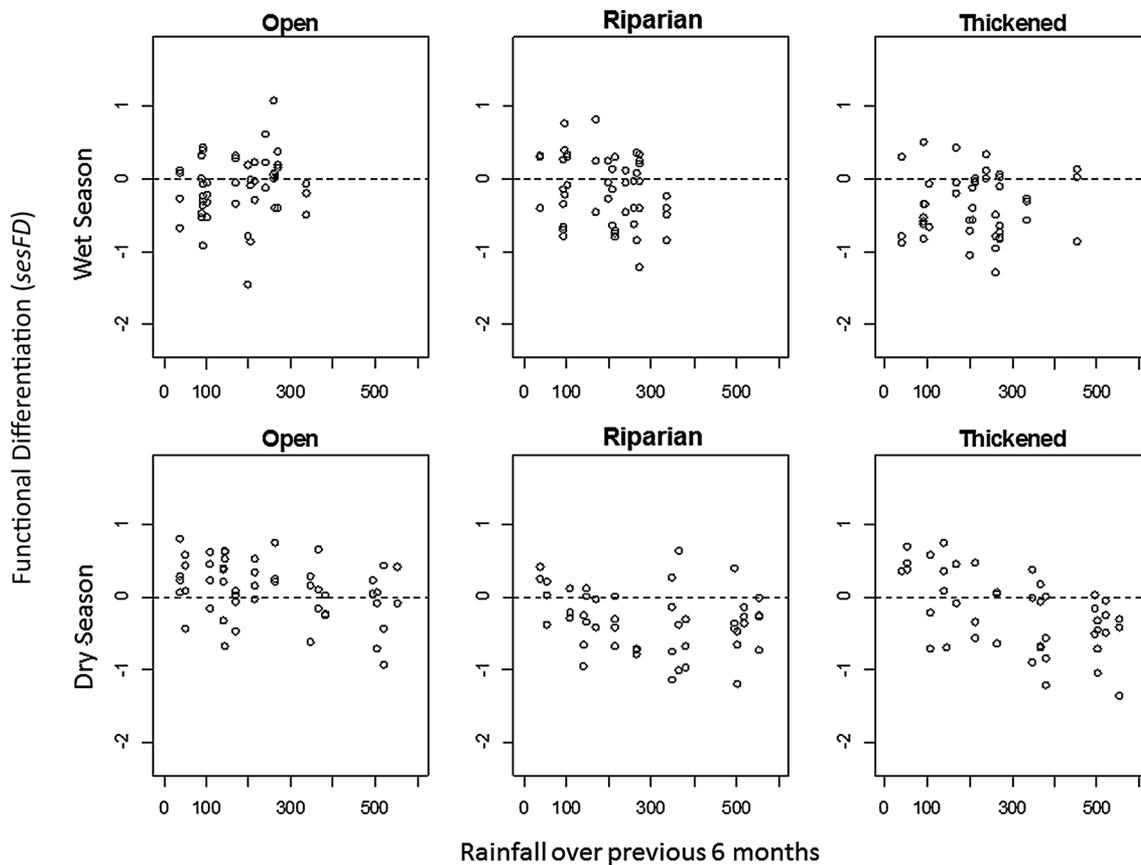


Figure 3. Measures of sesFD when corrected for species prevalence along the aridity gradient, separated by habitat [open (O), riparian (R), and thickened (T)], and season (models presented in Table 4).

explained 14% and both fixed and random effects explained 34% of the variance.

When species' prevalence was not constrained (that is, all species assumed to have an equal chance of occurring, irrespective of rarity), sesFD was significantly lower than zero in riparian and thickened areas, decreased with increasing rainfall over the previous 6 months, and was lower in the wet season (Table 4). The decrease in sesFD in the wet season was not as marked in riparian areas. The best model had 96% probability of being the best model, with 21.6 and 52.7% of the variance explained by fixed and both fixed and random effects, respectively.

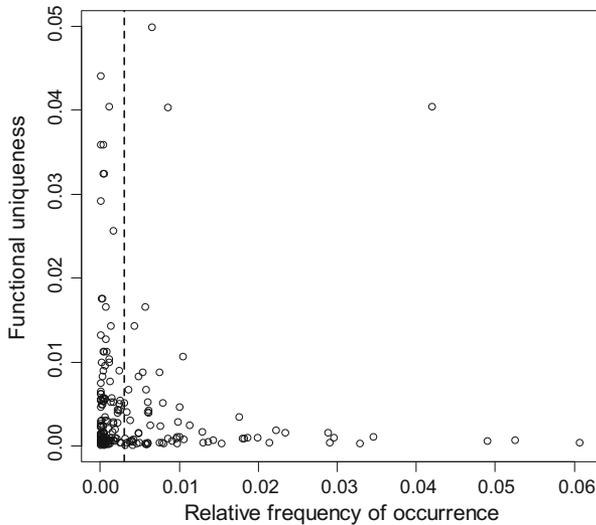
### The Contribution of Rare Species to FD

The median functional uniqueness value for the 134 rare species (10% of individuals) was significantly higher (2.3 times) than that of common species representing the remaining 90% (67 species) of individuals (median: first 10% = 0.046, median: remaining 90% = 0.020;  $W = 5402.5$ ,  $p = 0.0188$ ) (Figure 3).

## DISCUSSION

### Patterns in Bird SR, FD, and Functional Differentiation

Patterns in bird SR followed classical expectations for a tropical arid area: richness increased with increasing rainfall (a measure of productivity: Hawkins and others 2003) and vegetation structure (Tews and others 2004; Culbert and others 2013), and was greater in the wet season (when migratory species arrive). FD followed a similar pattern, but functional differentiation among species (that is, FD corrected for species richness, sesFD), showed the opposite trend. Functional differentiation decreased with increased rainfall and was lower in the wet season irrespective of the simulation model used to calculate sesFD. In short, bird assemblages in less arid sites and in the wet season were more functionally diverse, because they are more species rich, but species in these assemblages are less functionally differentiated. These findings are congruent with classical niche theory (MacArthur and Levins 1967) because wetter sites and wetter



**Figure 4.** Relationship between functional uniqueness and relative frequency of occurrence, based on functional uniqueness calculated using all traits considered in this study. The *vertical dashed line* indicates the cut-off between two-thirds of the rarer species to the left and the remaining third of more common species, to the right.

times of year offer more potential niches and resources for species to exploit, reducing competition among functionally similar species (Figure 3).

### Functional Differentiation in Open, Riparian, and Bush-Thickened Habitats

We note that different sets of traits could have produced different results (Luck and others 2013), but those we used were based on species' resource and habitat requirements and the ability of some bird species to respond to the vicissitudes of arid environments by relocating (Dean and others 2009). Furthermore, the traits we used to calculate FD were similar to those used in previous investigations of FD and bird resource use (Bailey and others 2004; Petchey and others 2007), which allows comparisons between studies.

The analyses of sesFD based on simulation models run on the complete dataset and those partitioned by habitat were virtually identical, suggesting that there is no evidence of environmental filtering structuring the functional composition of communities between habitats. Notwithstanding, bird assemblages in open habitats were marginally, but significantly, more functionally differentiated than expected when species prevalence was constrained, while the woodier habitats did not deviate from null expectation. This indicates that communities within open habitats were more functionally differentiated than would

be expected and suggests that there is a competition for resources and/or specialization to divergent niches within this habitat. There are typically fewer breeding and feeding niches in open habitats, because woody plant structure allows for a number of different nest types and foraging strategies, potentially increasing competition for these limiting resources.

### The Contribution of Rare Species to FD

If rare species are more functionally unique (that is, rare species have "unusual" traits), then community sesFD values should appear lower when prevalence is not constrained (Thompson and others 2010). Indeed, when species prevalence was allowed to vary, community sesFD values were lower for all habitat types such that open habitats did not deviate from null expectation, while riparian and thickened habitats showed significantly lower functional differentiation. Interestingly, this suggests that rare species are functionally unique even in bush encroached habitats, which are considered degraded (Millenium Ecosystem Assessment 2005).

Although there is considerable evidence that the majority of ecosystem function is carried out by more common species (Schwartz and others 2000), the role of rare species, through aggregate effects (Lyons and Schwartz 2001), specific traits (Theodose and others 1996), and via temporal and spatial variability in species abundance (Lyons and others 2005) means that their loss can have unanticipated cascading effects (Bracken and Low 2012). Over a decade ago, Gaston and others (2003) estimated that global bird abundance had declined by 20–25%. Approximately one-eighth of bird species face extinction, and another eighth inhabit small ranges where habitat destruction is likely (Pimm and others 2006), and the steady progression of global change increases the likelihood of loss of rare species.

### Patterns in FD Along Gradients

Studies are starting to find trends in FD along various natural or anthropogenic gradients, but patterns are not yet clear (Stevens and others 2003; de Bello and others 2006; Flynn and others 2009; Bihn and others 2010; Niu and others 2014). Our data are consistent with a pattern of increasing species and functional diversity in areas of greater productivity (higher rainfall and vegetation structure). Although our results may appear to contradict the hump-shaped diversity–productivity relationship expected by many studies, Kondoh

(2001) argues that the diversity–productivity relationship should appear linear in systems subject to high disturbance, such as extreme seasonal drought. High productivity favors stronger competitors, but high disturbance creates gaps for weaker competitors and/or prevents competitive interactions from running their course and leading to competitive exclusion. This is further supported by the common co-occurrence of functionally similar birds in the less arid sites and wetter seasons, and suggests the utility of functional diversity approaches in dissecting the mechanisms behind diversity–productivity relationships. Similarly, rainfalls over the previous 6 or 12 months were better predictors of SR, FD, and sesFD than mean annual precipitation, suggesting that birds are rapidly responding to fluctuating moisture availability in this highly variable environment.

Finally, it is notable that rare species in all three habitats tended to be functionally unique. This study emphasizes the functional importance of rare species (Bihn and others 2010; Mouillot and others 2013), the loss of which could have serious consequences for ecosystems (Bracken and Low 2012).

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