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Functional diversity and trait filtering of insectivorous bats relate to forest biogeography and fragmentation in South Africa

Monika Moir[1] | Leigh R. Richards[2] | Ramugondo V. Rambau[1] | Michael I. Cherry[1]

[1]Department of Botany and Zoology, Faculty of Natural Sciences, Stellenbosch University, Stellenbosch, South Africa

[2]Durban Natural Science Museum, PO Box 4085, Durban, South Africa

Correspondence
Monika Moir, Department of Botany and Zoology, Natural Sciences Building, Stellenbosch University, Merriman Ave, Stellenbosch, South Africa.
Email: monikamoir@gmail.com

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Abstract

Aim: Forest fragmentation is a major driver of biodiversity loss causing declines in species richness and functional diversity of biotic communities. Bats are essential components of ecosystems and are useful bio-indicators of habitat disturbance, yet the response and vulnerability of bats to fragmentation have been poorly studied in Africa. We aim to assess the effects of forest biogeographical history and fragmentation on functional diversity of bats and their functional traits.

Location: Eastern Cape and southern KwaZulu-Natal, South Africa.

Taxon: Insectivorous bats.

Methods: We surveyed forest-utilizing bats to derive four functional diversity indices. Generalized linear models were used to assess the response of diversity indices to biogeographical history and fragmentation, represented by forest type and five landscape fragmentation metrics. RLQ and fourth-corner analysis were used to investigate the interaction of traits with fragmentation metrics and forest type.

Results: Pondoland Scarp forests displayed high functional richness, while Eastern Cape Dune forests exhibited high functional divergence yet low functional richness and dispersion. Two fragmentation metrics affected functional diversity dynamically: edge density had a positive effect on functional evenness; and dispersion was negatively affected by river length through forests. Results showed stronger interactions of functional traits with forest type than fragmentation metrics, with filtering effects on body size and wing morphology.

Main conclusions: The large-scale processes related to biogeographical history, and associated forest structure, are important determinants of functional richness, divergence and dispersion of insectivorous bat communities. Scarp forests showed the highest species and functional richness as they experienced less extreme climatic extinction filtering than Mistbelt forests during the Last Glacial Maximum, whereas the low diversity of Eastern Cape Dune forests results from their younger evolutionary history and homogenous vegetation structure. Little is known of the sensitivity of bats to habitat fragmentation in Africa: here, we show larger-sized insectivorous species; and species exhibiting low wing loading may be more vulnerable to fragmentation.

KEYWORDS
Bioacoustics, Chiroptera, clutter-edge guild, edge effects, past climate change, RLQ and fourth-corner analyses, trait–environment relationships

1 | INTRODUCTION

Forest fragmentation is considered one of the major drivers of biodiversity loss with important implications for ecosystem functioning (Fahrig, 2003) in forested regions. Fragmentation effects cause loss of habitat area resulting in increasingly smaller forest patches, reduced structural complexity, decreased resource availability and niche diversity, and increased isolation between fragmented patches (Fahrig, 2003; Tscharntke et al., 2012). Consequently, these fragmentation effects impede dispersal and colonization of fauna between patches, homogenize resources and available niches, and drive declines in abundance, species richness and their associated functional diversity (Filippi-Codaccioni et al., 2010; Fischer & Lindenmayer, 2007; Henle et al., 2004).

Functional diversity is a useful estimator of biodiversity as it links the mechanistic effect of species functional traits with ecosystem processes. Functional traits inform the ecological niches filled by species, and provide insights into the biodiversity sustained in the ecosystem and health of the environment (Filippi-Codaccioni et al., 2010). Functional diversity is an important driver of ecological processes that shape the functionality and resilience of ecosystems (Villéger et al., 2008). It may be used to indicate changes to community structure in response to habitat disturbances (Mouillot et al., 2013), as environmental filters select for specific functional traits (Luck et al., 2012). Habitat disturbances, such as fragmentation, may exert pressure on species with particular functional traits leaving them vulnerable to extinction (Si et al., 2016). Generally, fragmentation negatively affects dispersal-limited, edge-sensitive and sedentary forest specialists that may then be replaced by edge-tolerant generalists (Ehlers Smith et al., 2018; Si et al., 2016), thus altering ecosystem function.

Bats are essential components of ecosystems as they exhibit high diversity, fill multiple niches and provide a myriad of ecosystem services (Kunz et al., 2011). Crop pest suppression by insectivores is considered the most economically valuable ecosystem service bats provide (Boyles et al., 2013). Bats have also been recognized as useful bio-indicators to assess the response of biodiversity to habitat fragmentation (Jones et al., 2009). Considering their ecological and economic importance, the response and vulnerability of bats to fragmentation have been poorly studied in Africa.

Forests in South Africa present an interesting case of fragmentation, in that they occur as naturally small, disjoint patches due to past climatic fluctuations (Eeley et al., 1999). They constitute the smallest biome in the country, covering only 7,177 km^2 of land surface (Low & Rebelo, 1996). There are two main types of forest: Afrotemperate, under which the Mistbelt forests are classed (von Maltitz et al., 2003), are an ancient forest type that has persisted since the Miocene (White, 1981); and the Indian Ocean Coastal belt forests which arose ~8,000 years ago (Macdevette et al., 1989). Located between these two types is a narrow band of Scarp forests, of Afrotemperate origin but younger than Mistbelt forests (Eeley et al., 1999), and comprising both Mistbelt and coastal flora and fauna (Lawes et al., 2007). Historically, Mistbelt forests occurred as extensive tracts across the mid-altitude region, but underwent substantial contractions during cold and dry conditions of glacial periods, with the Last Glacial Maximum (LGM) (~21,000 years ago) being the most recent (Eeley et al., 1999). These climate-induced fragmentation effects caused extinction filtering of forest biota (Lawes et al., 2007). Soon after the southward expansion of the Indian Ocean Coastal belt forests, the warm and wet conditions of the Holocene altitherm (~7,000 years ago) caused forest expansion, with the mixing of Mistbelt and Indian Ocean Coastal belt forests along the current-day Scarp belt (Eeley et al., 1999). This complex biogeographical history, from climate-induced expansions and contractions, has substantially influenced the distributions and diversity patterns of extant forest communities (Lawes et al., 2007). Subsequently, forests have been subjected to anthropogenic fragmentation with unregulated logging continuing through the colonial era (King, 1938) and large-scale clearance for agriculture in KwaZulu-Natal resulting in extensive forest loss (Olivier et al., 2013).

Here, we present a novel approach by investigating functional diversity and functional trait filtering of insectivorous bats in an area characterized by natural fragmentation of continuous forest and anthropogenically fragmented forest patches. We assess the effects of fragmentation on bat functional diversity using five landscape fragmentation metrics. We also consider the effects of forest biogeographical structure, represented by forest type, on functional diversity. Lastly, we investigate the interaction of functional traits with forest type and fragmentation metrics to determine which traits contribute most to species fragmentation sensitivity. We anticipated forest type to be a predominant predictor of functional diversity, as was found for forest birds in the Eastern Cape (Leaver et al., 2019). Also, we hypothesized patch size to positively affect functional richness (García-Morales et al., 2016; Maseko et al., 2020). Lastly, we predicted species with a reduced dispersal capacity, inferred by wing loading, to be more vulnerable to reduced patch size and increased fragmentation as they are less equipped to commute large distances between forests.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in the Eastern Cape and KwaZulu-Natal provinces of South Africa as they hold the highest proportions of indigenous forest in the country: 46% and 29%, respectively (Berliner, 2009), and are located within the Maputaland-Pondoland-Albany global biodiversity hotspot. Seventeen forests were sampled classified into seven forest types within three groupings as per von Maltitz et al. (2003) (Figure 1, Table 1, Appendix S1).

2.2 | Functional traits and diversity indices

The study was approved by the Stellenbosch University Animal Use and Care Research Ethics Committee (protocol #0409) and licensed by Eastern Cape Parks and Tourism Agency (RA0237), Eastern Cape Department of Economic Development, Environmental Affairs and Tourism (CRO 59/17CR, CRO 60/17CR), Department of Agriculture, Forestry and Fisheries (WIFM 04–2016, WIFM 09–2017, WIFM 06–2018), Ezemvelo KZN Wildlife (OP 143/2018, OP 3847/2018) and South African National Parks (CHER-MI/2018-004). We caught bats within forests using ground-level mist nets and harp traps. Body mass and forearm length were recorded from captured individuals (Appendix S2, Table S1). Photographs were taken of the right wing and tail membrane extended. Wing morphology was measured from photographs with ImageJ2 (Rueden et al., 2017). Aspect ratio and wing loading were calculated as described in Norberg and Rayner (1987). Bats were released at the site of capture and release echolocation calls were recorded with a Wildlife Acoustics EchoMeter 3 detector.

Bat communities of each forest were acoustically surveyed for 6–7 nights with six recorders (five Wildlife Acoustics Song Meter SM4BAT and one SM2+BAT). Recorders were set to trigger at 16 kHz and record in full spectrum throughout the night with microphones placed 2–3 m above the ground. Recordings were run through Wildlife Acoustics Kaleidoscope Pro with the species identification filter, Bats of South Africa 5.1.0. All files were then manually vetted for correct identification using a call library developed for forested habitats in the region (Moir, Richards, Rambau, & Cherry, 2020).

Diversity was quantified by species richness and four functional diversity indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al., 2008) and functional dispersion (FDis) (Laliberte & Legendre, 2010). These indices are derived from quantitative values for traits, with species distributed in a multidimensional functional trait space weighted by their relative abundances. FRic is the volume of functional space occupied by the community. FEve quantifies the regularity with which species relative abundances are distributed in the trait space. FDiv quantifies the divergence of species in their distances (weighted by relative abundance) along the range of the trait space (Villéger et al., 2008), whereas FDis measures the mean distance of individual species to the centroid of all species in the trait space (Laliberte & Legendre, 2010).

Species were plotted in a functional space using the following traits: echolocation call type, characteristic frequency, forearm length, aspect ratio, and wing loading (Appendix S2, Table S2). The structure and frequency of bat echolocation calls are adaptations to preferred habitat type and foraging mode (Siemers & Schnitzler, 2004). Forearm length is an indicator of body size, which has been linked to forest fragmentation in the Amazon (Farneda et al., 2015). Wing morphology

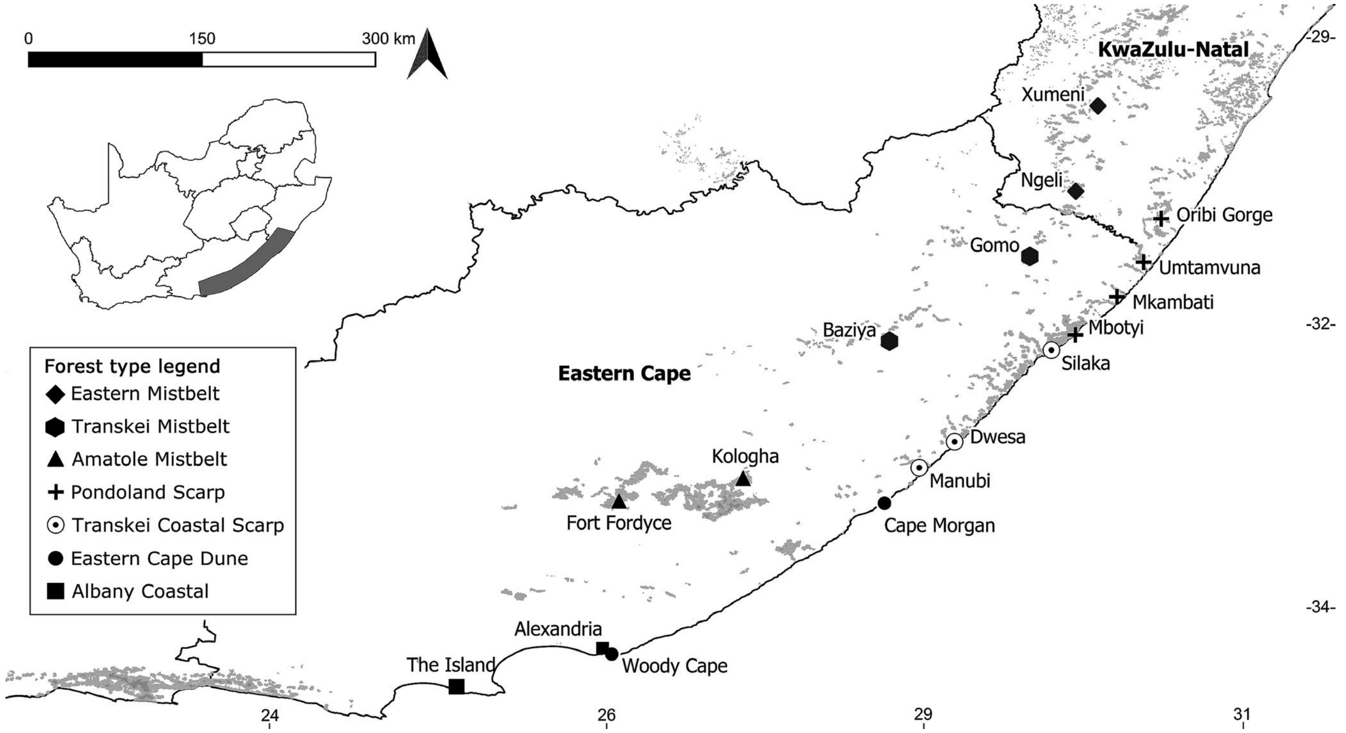

FIGURE 1 Map of indigenous forests in southern KwaZulu-Natal and Eastern Cape provinces of South Africa from which insectivorous bat communities were acoustically surveyed. Forest types (as per von Maltitz et al., 2003) are depicted with different shapes as listed in the legend. Grey shading displays the fragmented nature of forest cover across the country taken from the South African National Land Cover 2018 dataset (Thompson, 2019). Extent of study region is depicted with the grey polygon on the inset map of South Africa

TABLE 1 List of surveyed forests, of seven types (as per von Maltitz et al., 2003), across southern KwaZulu-Natal and Eastern Cape provinces of South Africa. Species richness and mean values of functional diversity indices of bat communities are listed

Forest type	Forest	Species richness	Functional richness	Functional evenness	Functional divergence	Functional dispersion
Eastern Mistbelt	Xumeni	12	0.477	0.575	0.711	0.784
	Ngeli	12	0.334	0.640	0.850	0.977
Transkei Mistbelt	Gomo	12	0.722	0.301	0.574	0.805
	Baziya	12	0.471	0.272	0.711	0.652
Amatole Mistbelt	Kologha	12	0.482	0.351	0.676	0.684
	Fort Fordyce	12	0.482	0.597	0.673	1.061
Pondoland Scarp	Oribi Gorge	15	1.307	0.531	0.779	0.899
	Umtamvuna	13	0.639	0.507	0.804	0.806
	Mbotyi	14	1.229	0.369	0.800	0.861
	Mkambati	11	0.329	0.288	0.758	1.439
Transkei Coastal Scarp	Dwesa	12	0.565	0.479	0.759	0.729
	Manubi	13	1.208	0.253	0.852	0.569
	Silaka	10	0.237	0.261	0.883	0.763
Eastern Cape Dune	Cape Morgan	8	0.101	0.391	0.933	0.523
	Woody Cape	8	0.099	0.281	0.948	0.793
Albany Coastal	The Island	9	0.113	0.535	0.713	1.048
	Alexandria	10	0.197	0.244	0.749	1.053

is a predictor of foraging habitat and strategy, dispersal ability, and size of home range (Norberg & Rayner, 1987). Bats with long, narrow wings are fast, high-flying species that demonstrate high wing loading and high aspect ratio values. Species with short, broad wings (low wing loading and low aspect ratio) demonstrate greater manoeuvrability for flight within cluttered vegetation habitats (Norberg & Rayner, 1987).

When calculating the functional diversity indices, only the acoustic surveys were used for calculating relative abundance data; and species trait values from captured bats were utilized. For species that we recorded acoustically but were not captured, trait values were taken from Monadjem et al. (2010); Norberg and Rayner (1987) and Schoeman and Jacobs (2003, 2008) (Table S2 of Appendix S2). Continuous traits were standardized to a mean of 0 and standard deviation of 1 (Farneda et al., 2015). Relative abundances of mean passes per recording hour were used to account for variation in recording periods between sites (Appendix S3). A pass was defined as one or more echolocation pulses with <1 second between pulses (Fenton, 1970). Functional diversity indices were calculated with the ‘FD’ package (Laliberte et al., 2014) in R (R Core Team, 2019).

2.3 | Fragmentation metrics

We used five landscape metrics to calculate the extent of fragmentation and habitat connectivity (Schumaker, 1996): patch size, edge density, patch cohesion index (PCI) and effective mesh size (EMS). Patch size is the extent of forest cover delineated by abutting open habitats. Edge density is a measure of edge length divided by forest area (McGarigal & Marks, 1995). PCI measures the physical connectedness of forests as perceived by organisms dispersing within the landscape. It is computed using patch area and perimeter and is proportional to the area-weighted mean perimeter-area ratio divided by the area-weighted mean patch shape index (Schumaker, 1996). EMS characterizes anthropogenic penetration and is based on the ability of two animals to find one another within the landscape (Jaeger, 2000). EMS was calculated as the sum of patch area squared, summed across all patches of the corresponding patch type, divided by the total landscape area. The size and connectivity of waterways affect the distribution of bats (Lookingbill et al., 2010). We included the total river length running through the forests as a measure of habitat connectivity (Berliner, 2009) as bats are likely to commute along them. As bats are volant and have a higher dispersal ability relative to non-volant small mammals, we calculated PCI, EMS and total river length within a 5 km-wide buffer around the forests to encompass the home ranges of different-sized African insectivorous bats (Fenton & Rautenbach, 1986; Noer et al., 2012). Fragmentation metrics (Appendix S4) were calculated using the South African National Land Cover 2018 dataset (Thompson, 2019), with the LecoS tool (Jung, 2016) in Quantum GIS (QGIS Development Team, 2014). Total river length per forest was extracted from the 2018 National Biodiversity Assessment rivers dataset (van Deventer et al., 2019).

2.4 | Statistical analyses

We assessed the response of the diversity indices to forest type and fragmentation metrics using generalized linear models

(GLMs). We tested for spatial autocorrelation of species richness and diversity indices between forests using Moran's I test with the 'ape' package (Paradis & Schliep, 2018) in R. The functional diversity metrics were independent of location, but species richness displayed significant autocorrelation (Appendix S2, Table S3), and was removed from further analyses. We tested for correlations between fragmentation metrics and found no significant correlations (Appendix S5). Each diversity index was modelled separately, with the glm function in R, employing additive and interactive models of forest type and fragmentation metrics. Forest type was a categorical variable, with Albany Coastal as the reference site based on alphabetical order. Optimal models were chosen by backward selection of Akaike information criterion values, using the stepAIC function in the 'MASS' package (Venables & Ripley, 2002). Collinearity between predictor variables was tested for with variance inflation factors (VIFs) in the 'car' package (Fox, 2002). Patch size and PCI independently had VIF values greater than five and were removed from the models. We then ran univariate models separately for these two metrics. The coefficient of determination (R^2) was used to assess the goodness of fit for each model with the 'rsq' package (Zhang, 2018).

We analyzed the interaction of the functional traits with forest type and fragmentation metrics using RLQ analysis and the fourth-corner approach (Dray et al., 2014). RLQ utilizes ordination to assign scores to three input datasets: species relative abundances (L), functional traits (Q), and environmental variables (R). Hill-Smith PCA was applied to Q and R (Hill & Smith, 1976), and correspondence analysis to L. We weighted the ordinations of the R and Q matrices with scores from the correspondence analysis. We tested for significance of model 2 (distributions of species with site-independent traits are not influenced by environmental conditions) and model 4 (species composition of sites with fixed environmental conditions is not influenced by species traits) (Dray et al., 2014) with 50,000 permutations. RLQ was performed with 'ade4' R package (Dray & Dufour, 2007). The fourth-corner approach measures and tests the associations between each trait and environmental variable (Dray et al., 2014). We used the 'mvabund' R package (Wang et al., 2012) to construct GLMs for L with additive terms of R and Q, quadratic terms for continuous variables, and interaction terms between traits and environmental variables. We used a LASSO (least absolute shrinkage and selection operator) penalty to perform model selection.

3 | RESULTS

3.1 | Effect of forest type and fragmentation on functional diversity

A total of 21 species was recorded from all forest sites. Oribi Gorge of Pondoland Scarp forest type retrieved the highest species richness (15), while both sites of the Eastern Cape Dune forest type had the lowest species richness (8) (Table 1). The survey completeness is presented in Appendix S6: richness estimates plateaued after 6–7 nights per forest type. Oribi Gorge, of the Pondoland Scarp type, displayed the highest FRic (1.307). FEve was greatest for Ngeli (0.640) and lowest for Alexandria (0.244). The Eastern Cape Dune forests exhibited the highest values of FDiv (0.933 – 0.948) and the lowest FDis (0.523), while Mkambati of the Pondoland Scarp type demonstrated the highest FDis (1.439) (Table 1).

The GLMs found forest type to be the best predictor of FRic, with no fragmentation metrics retained in the top model. GLM estimates showed FRic of the Transkei Mistbelt (β=0.59 ± 0.23, $p = 0.02$), Pondoland Scarp (β=0.71 ± 0.20, $p = 0.006$) and Transkei Coastal Scarp forest type (β=0.56 ± 0.21, $p = 0.02$) differed from Albany Coastal as the reference type (Table 2). FRic per forest type is displayed in Figure 2a with Pondoland Scarp demonstrating a notably higher richness, while Transkei Coastal Scarp shows a wide interquartile range. Forest type was retained in the GLM of FEve, but without significant differences from the reference forest type. Two fragmentation metrics, edge density and river length, were also retained in the model. The effect of river length on FEve was small and non-significant (β=0.04 ± 0.03, $p = 0.18$) while edge density depicted a significant positive effect (β=28.15 ± 10.57, $p = 0.02$) (Table 2). The relationship of edge density with FEve is displayed in Figure 3a, wherein points cluster around the trend-line at lower values of evenness with slightly higher spread as values increase.

Forest type, river length, and effective mesh size were retained in the GLM for FDiv, however, both river length (β=0.01 ± 0.01) and EMS (β=0.04 ± 0.02) showed non-significant effects (Table 2). Eastern Cape Dune forests depicted higher FDiv (β=0.25 ± 0.05, $p = 0.002$) than other forest types (Figure 2b). Forest type, edge density, and river length were the best predictors of FDis, with the Eastern Cape Dune forest type having lower FDis than other types (β=−0.25 ± 0.08, $p = 0.02$; Figure 2b). Edge density exhibited a large negative but non-significant effect (β=−9.60 ± 7.49), while river length demonstrated a significantly negative relationship (β=−0.05 ± 0.02, $p = 0.03$) with FDis. The weak negative relationship of river length with FDis is displayed in Figure 3b, with a relatively wide dispersion of points around the trend-line. Lastly, the univariate models of patch size and PCI with each of the diversity metrics returned no significant relationships.

3.2 | Trait–environment associations

The first axis of the RLQ accounted for 66.5% of total co-inertia between Q and R, with the cumulative projected inertia of the first three axes at 99.66% (Appendix S7). The inertia and co-inertia ratios were high for both R (82% and 75%) and Q (81% and 82%). The permutation test found the inertia was non-significant for model 2 (observation=0.21, $p = 0.16$) and model 4 (observation=0.21, $p = 0.59$). The graphical results of the RLQ show the three main forest groups: Coastal, Mistbelt, and Scarp forests, clustered in separate areas of ordination space (Figure 4a). *Rhinolophus* species were associated with Mistbelt forests, while species with a high wing loading

TABLE 2 Response of bat functional diversity indices to forest type and fragmentation across southern KwaZulu-Natal and Eastern Cape provinces of South Africa. AIC and R^2 values from generalized linear models are shown for best fit models. Significant *p* values are in bold

Functional diversity	Predictor	Estimate	Standard error	T value	*p* value
Functional richness	*Intercept*	−0.83	0.17	−5.00	**<0.01**
AIC =5.79	Eastern Mistbelt	0.43	0.23	1.83	0.09
R^2 = 0.74	Transkei Mistbelt	0.59	0.23	2.53	**0.02**
	Amatole Mistbelt	0.51	0.23	2.18	0.05
	Pondoland Scarp	0.71	0.20	3.50	**<0.01**
	Transkei Coastal Scarp	0.56	0.21	2.64	**0.02**
	Eastern Cape Dune	−0.17	0.23	−0.75	0.47
Functional evenness	*Intercept*	−0.98	0.26	−3.789	**<0.01**
AIC = −18.85	Eastern Mistbelt	0.24	0.11	2.10	0.07
R^2 = 0.71	Transkei Mistbelt	−0.31	0.16	−1.93	0.09
	Amatole Mistbelt	−0.35	0.25	−1.40	0.20
	Pondoland Scarp	−0.14	0.14	−0.99	0.35
	Transkei Coastal Scarp	−0.28	0.15	−1.80	0.11
	Eastern Cape Dune	−0.07	0.12	−0.62	0.55
	Edge density	28.15	10.57	2.66	**0.02**
	River length	0.04	0.03	1.46	0.18
Functional divergence	*Intercept*	0.58	0.08	6.73	**<0.01**
AIC = −46.42	Eastern Mistbelt	0.07	0.05	1.35	0.21
R^2 = 0.87	Transkei Mistbelt	−0.09	0.06	−1.45	0.18
	Amatole Mistbelt	−0.09	0.08	−1.18	0.27
	Pondoland Scarp	0.07	0.06	1.18	0.27
	Transkei Coastal Scarp	0.09	0.06	1.57	0.15
	Eastern Cape Dune	0.25	0.05	4.62	**<0.01**
	River length	0.01	0.01	1.09	0.31
	Effective mesh size	0.04	0.02	1.57	0.16
Functional dispersion	*Intercept*	0.40	0.18	2.17	0.06
AIC = −30.55	Eastern Mistbelt	−0.09	0.08	−1.15	0.28
R^2 = 0.73	Transkei Mistbelt	0.03	0.11	0.31	0.77
	Amatole Mistbelt	0.26	0.18	1.51	0.17
	Pondoland Scarp	0.13	0.10	1.32	0.22
	Transkei Coastal Scarp	0.006	0.11	0.05	0.96
	Eastern Cape Dune	−0.25	0.08	−3.00	**0.02**
	Edge density	−9.60	7.49	−1.28	0.24
	River length	−0.05	0.02	−2.51	**0.03**

and low-duty cycle calls clustered in ordination space aligned with Coastal and Scarp forest types (Figure 4a,c).

The fourth-corner approach showed stronger interactions of traits with forest type than fragmentation metrics (Figure 5). It supported the association of high wing loading with Coastal and Scarp forests seen from the RLQ, with a strong positive effect between wing loading and the Eastern Cape Dune and Pondoland Scarp forests. Mistbelt forests showed a moderate-to-strong negative association with wing loading. Of the fragmentation metrics, patch size displayed the strongest associations with species traits: positively interacting with aspect ratio and forearm length; and negatively with wing loading and characteristic frequency (Figure 5).

4 | DISCUSSION

The large-scale historical processes of forest biogeography and associated structure are important determinants of FRic, FDiv, and FDis of the contemporary insectivorous bat communities. Although we did not find evidence for the effects of fragmentation on FRic, two metrics affected functional diversity dynamically: edge

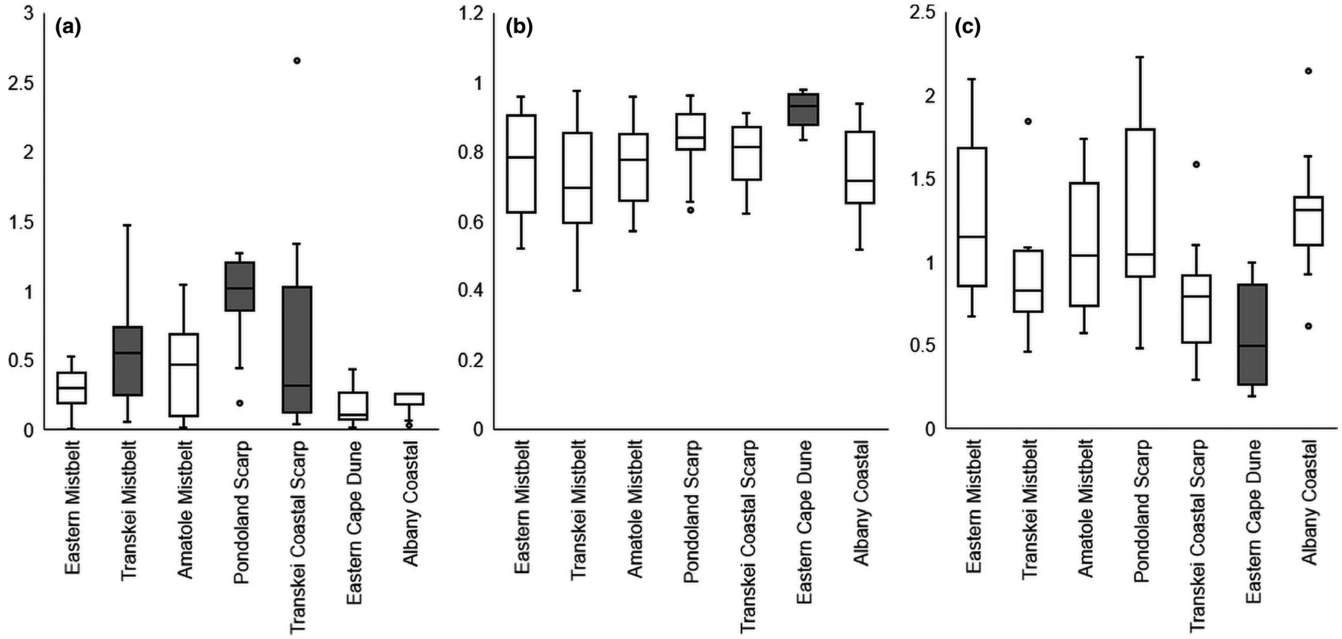

FIGURE 2 Boxplots displaying a) functional richness, b) functional divergence and c) functional dispersion of insectivorous bat communities from forests in southern KwaZulu-Natal and Eastern Cape, South Africa. Results are shown per forest type (as in Figure 1), calculated from six monitoring locations within each forest. Grey shaded plots indicate forest types depicting significant differences from reference forest type as determined with generalized linear models. Small circles depict outliers. Significant variation of functional evenness among forest types was not found

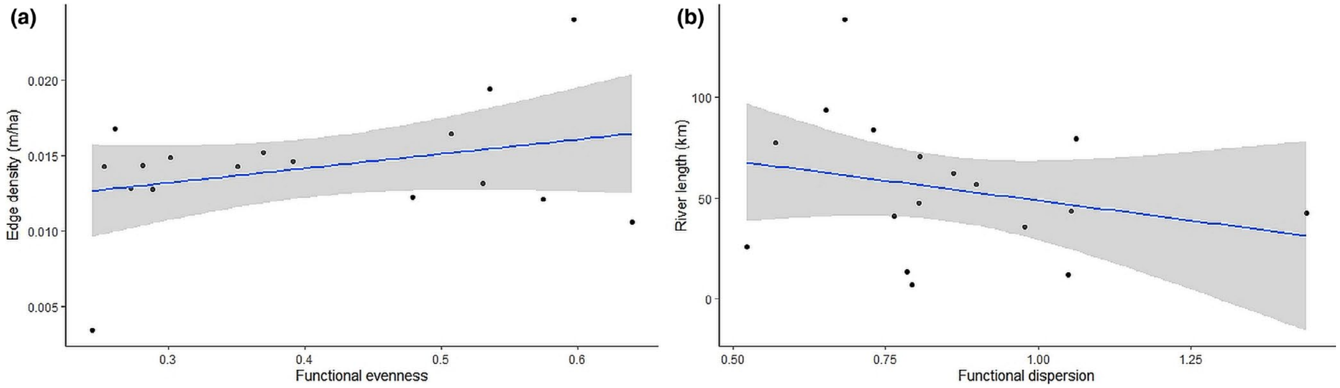

FIGURE 3 Graphical display of generalized linear model effects of a) forest edge density on bat functional evenness; and b) river length through forests on bat functional dispersion (with 95% confidence intervals) for forest sites across southern KwaZulu-Natal and Eastern Cape, South Africa [Colour figure can be viewed at wileyonlinelibrary.com]

density demonstrated a positive relationship with FEve; and FDis was negatively affected by river length. We also found forest type to demonstrate stronger trait filtering than fragmentation metrics. Specifically, Eastern Cape Dune and Pondoland Scarp forests were linked to faster flying species with high wing loading, and Mistbelt forests were associated with slower flying species better able to manoeuvre within forest vegetation. Of the fragmentation metrics, patch size displayed the greatest interaction effect with traits. As we had anticipated, increased patch size filtered for species with slow manoeuvrable flight with a reduced dispersal capacity, indicated by the negative interaction with wing loading. Furthermore, both forest type and fragmentation exhibited greater filtering effects on traits of body size and wing morphology than echolocation characteristics.

4.1 | Historical climate-induced patterns of functional richness

As hypothesized, forest type was the predominant predictor of FRic. Our results align with those found for Eastern Cape forest birds by Leaver et al. (2019). Pondoland Scarp and Transkei Coastal Scarp forests demonstrated the highest bat species richness and FRic.

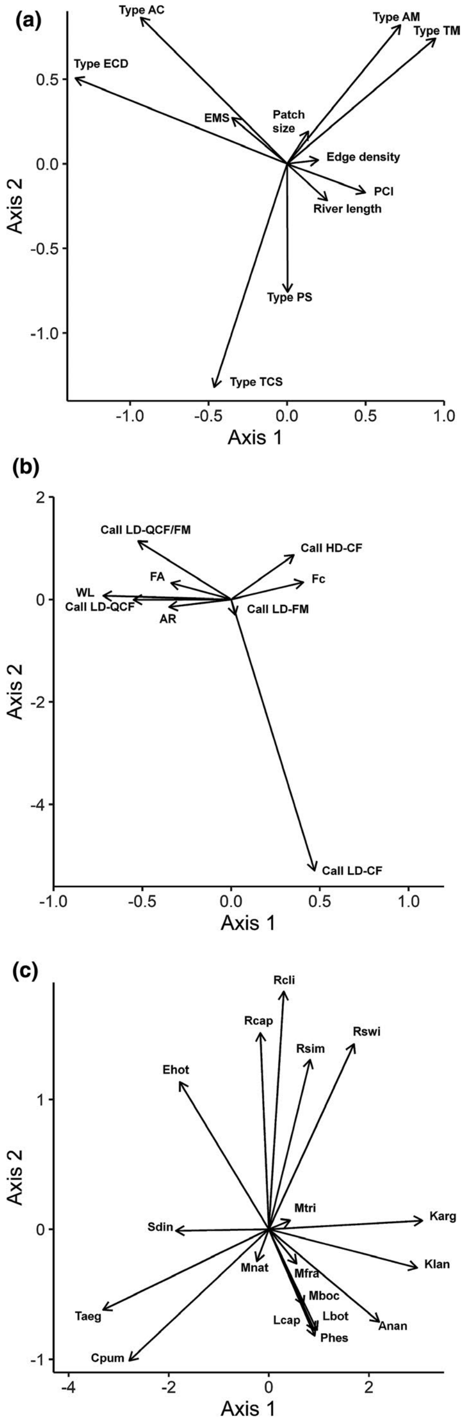

FIGURE 4 RLQ ordination of a) forest type and fragmentation metrics; b) insectivorous bat functional traits and c) insectivorous bat species of forests in southern KwaZulu-Natal and Eastern Cape, South Africa (AC – Albany Coastal; AM – Amatole Mistbelt; ECD – Eastern Cape Dune; EM – Eastern Mistbelt; PS – Pondoland Scarp; TCS – Transkei Coastal Scarp; TM – Transkei Mistbelt; EMS – Effective mesh size; PCI – Patch Cohesion Index; AR – aspect ratio; FA – forearm length; Fc – characteristic frequency; WL – wing loading; HD – high duty-cycle; LD – low duty-cycle; CF – constant frequency; QCF – quasi-constant frequency; FM – frequency modulated; species names abbreviations in Table S2 of Appendix S2)

The closer proximity of Scarp forests than Mistbelt forests to the warm Indian Ocean buffered them from extreme palaeoclimatic events, such as the LGM, that caused extinction filtering of Mistbelt biota. These extinction events likely removed ecologically specialized and sensitive species from Mistbelt communities, while Scarp forests served as refugia for fauna during the LGM (Lawes et al., 2007). With the onset of the Holocene altitherm, Scarp fauna recolonized Mistbelt forests, as well as colonizing the younger Indian Ocean Coastal forests (Lawes et al., 2007). Thus, Scarp forests demonstrate higher richness and more specialized species as they experienced less climatic filtering than Mistbelt forests. This finding is supported by the high genetic diversity of bats from Scarp forests in the study region (Moir, Richards, Cherry, & Rambau, 2020). The Transkei Mistbelt forests also demonstrated high FRic. They are geographically closer to Scarp forests than other Mistbelt forests, likely facilitating post-LGM recolonization of Transkei Mistbelts from Scarp forests by specialized bat species (Figure 1), as for non-volant mammals (Lawes et al., 2007). However, there is noteworthy variability of the diversity indices between forests of the same forest type, pointing to possible local-scale effects on community assembly processes. We recommend future work investigate finer-scale effects on bat functional diversity in the study region.

4.2 | Eastern Cape Dune forests

The Eastern Cape Dune forests present a unique case in that they exhibit the lowest species richness, FRic and FDis, with the highest functional divergence (FDiv). This indicates a low effective number of functionally distinct species, while the most abundant species exhibit traits located at the extremities of the trait range. The RLQ indicates the assemblage to be dominated by common habitat generalists, such as *Tadarida aegyptiaca* and *Eptesicus hottentotus*, with a strong selection for faster flying species demonstrating higher wing loading. The low functional diversity of these forests is likely a result of their younger evolutionary history and homogenous vegetation structure. Generalist bat species dominate the assemblage as Eastern Cape Dune forests have not had as much evolutionary time to develop many ecological niches for specialized species to fill. Also, these forests have short, dense canopies with low plant diversity; and unlike Mistbelt forests that occur as more extensive bands, dune forests are limited to small pockets on a narrow cordon of coastal dunes (von Maltitz et al., 2003). The small patch size and low vegetation diversity present limited roosting potential for foliage or tree roosting bats, while the low and dense canopy limits flight, and therefore foraging opportunities, below or within the canopy for several species. Foraging space is mostly restricted to above the canopy by the open-air foraging guild (bats that forage above the ground over vegetation) and along forest edges by clutter-edge foragers (bats that forage on the edges of dense vegetation). This is evidenced by dominance of species with high wing loading, typical of the open-air guild (Monadjem et al., 2010).

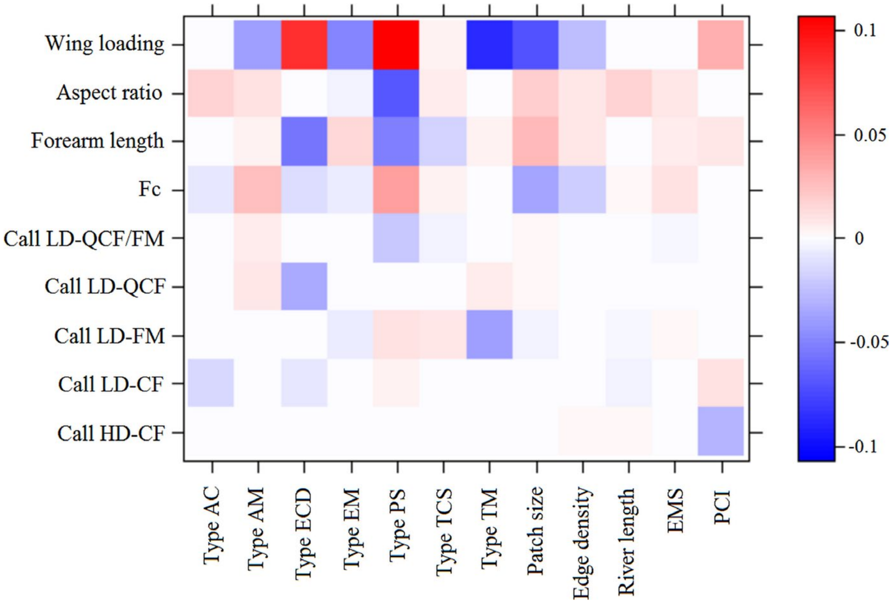

FIGURE 5 Fourth-corner analysis coefficients of interactions of insectivorous bat functional traits with forest type and fragmentation variables for forests in southern KwaZulu-Natal and Eastern Cape, South Africa. Blue shades depict a negative interaction between fragmentation variable and bat functional trait; red indicates a positive effect. Shade of colour displays strength of interaction (see Figure 4 legend for abbreviations) [Colour figure can be viewed at wileyonlinelibrary.com]

4.3 | Edge effects

Contrary to expectations, patch size did not exhibit a significant effect on FRic. Similarly, Ehlers Smith et al. (2020) showed patch size did not influence functional diversity of forest mammals in Coastal and Scarp forests in southern KwaZulu-Natal. By contrast, both Ehlers Smith, Si, Ehlers Smith, Kalle, et al. (2018) and Maseko et al. (2020) found avian functional diversity decreased with decreasing patch size in coastal forests in KwaZulu-Natal. They attributed the response of avian functional diversity to forest specialists being dependent upon large patches, with generalist species unaffected by reductions in patch size (Ehlers Smith, Si, Ehlers Smith, Kalle, et al., 2018). The observed lack of effect on bat functional richness is likely due to the community consisting of a greater proportion of habitat generalist species than in avian communities, with only one species (*Rhinolophus swinnyi*) being forest dependent (Taylor et al., 2018). Also, it is conceivable that the bat community evolved in historically fragmented forests and may thus be adapted to small patch sizes (Ehlers Smith, Si, Ehlers Smith, & Downs, 2018; Olivier et al., 2013). This was evident for the dusky pipistrelle bat (*Pipistrellus hesperidus*) as it depicted high gene flow across the study region despite its dependence on fragmented wooded habitats (Moir, Richards, Rambau, Wannenburgh, & Cherry, 2020).

Rather, we found a positive relationship of edge density with FEve. High FEve is indicative of a robust community with greater regularity of trait abundance distribution in functional space (Mason et al., 2005). In contrast, Meyer et al. (2008) found edge sensitivity as the key trait of vulnerability to forest fragmentation for Neotropical bats, with gleaning animalivorous species showing particular sensitivity to edge effects. Forest fragmentation, through the effects of patch size and edge effect, positively affected avian insectivory and bird FEve in France and New Zealand, as foliage-gleaning avian insectivores forage disproportionately more along edges than in forest interiors (Barbaro et al., 2014). Our finding of increased functional diversity with edge density aligns with other studies of temperate forest insectivores as the assemblage consists of hawking and gleaning insectivores.

Forest edges surrounded by open habitats, as is the case for South African forests, demonstrate high structural heterogeneity and habitat diversity with resources to support different functional groups (Barbaro et al., 2014). Forest edges are thus valuable habitats, often demonstrating high species richness (Caldwell et al., 2019). High bat activity is found along forest edges as insect abundance is typically supported by edge habitats (Heim et al., 2018), and bats preferentially travel along treelines as commuting corridors (Kalcounis-Rueppell et al., 2013).

4.4 | River length and clutter-edge guild

The area and connectedness of waterways are important predictors of activity (Lookingbill et al., 2010) as bats utilize them for drinking; for their high foraging potential (Monadjem & Reside, 2008) and as navigational aids (Cortes & Gillam, 2020). Despite their importance, no studies have assessed how river length affects functional diversity of bat communities. We found the dispersion of species in functional trait space (FDis) decreased with an increase in river length. This implies that the effective number of functionally distinct species decreased as river length increased, with dominance of the assemblage by species of a particular niche. Lloyd et al. (2006) similarly found species-specific utilization of riparian zones in Australian timber landscapes. This study demonstrated the association of miniopterid and vespertilionid bats with river length. These species utilize LD-FM echolocation calls, are relatively small in size with intermediate-to-low aspect ratio and wing loading values, and fall within the clutter-edge foraging guild (Monadjem et al., 2010). Forest interior habitat would typically be dominated by the clutter foraging guild (species that forage within highly cluttered vegetation), with open-air foragers dominating the assemblage above the canopy. Thus, we present the novel findings that increased river length allows for penetration into the forest interior and dominance of the bat community by the clutter-edge guild that might otherwise be occupied by clutter foraging species.

4.5 | Trait selection

Both the RLQ and fourth-corner analyses revealed selection for fast flying species (Figures 4 and 5), with high wing loading, in Eastern Cape Dune and Pondoland Scarp forests. The opposite was found for Mistbelt forests with selection for species with low wing loading. This infers species with slower flight speeds and higher manoeuvrability, useful for navigating through spatially complex environments such as forest interiors, are more prevalent in Mistbelt forests, while open-air species are more dominant in Coastal and Scarp forests. Mistbelt forests are characterized by extensive tracts of forest along the Main Escarpment with tall canopies. Scarp forests also have high canopies but occur as smaller scattered patches; whereas Eastern Cape Dune forests are low-stature, dense-canopied forests occurring in small pockets (von Maltitz et al., 2003). The high canopies and larger tracts of Mistbelt forests may be better suited for slow-hawking or gleaning bats of the clutter and clutter-edge guilds, that typically demonstrate low wing loading, as these species are adapted for flight within and around dense vegetation. While fast-hawking species of the open-air guild may be more predominant in the smaller-sized patches of Scarp and Eastern Cape Dune forests as they can more easily navigate between patches while utilizing neighbouring open biomes.

Of the fragmentation metrics, patch size exhibited the strongest filtering effect on the functional traits of wing morphology and forearm length. Edge density displayed the same interactions with these traits, but the unimodal association of edge density and patch size makes inferences of their relative effects difficult to extricate (Fletcher et al., 2007). As anticipated, increased patch size selected for slow-flying, manoeuvrable species with low wing loading and an inferred reduced dispersal capacity. Avian functional traits are influenced by patch size (Maseko et al., 2020), with sedentary forest specialist insectivores demonstrating the highest extinction risk from fragmentation in KwaZulu-Natal Coastal forests (Ehlers Smith, Si, Ehlers Smith, & Downs, 2018; Olivier & van Aarde, 2017; Peter et al., 2015). Our results further indicated patch size filtered for larger species, with its positive interaction on forearm length. This partly aligns with the trait of body mass, among other traits, as one of the best predictors of extinction vulnerability for forest mammals in a forest mosaic in Durban, South Africa (Zungu et al., 2019). Species of larger body size are typically at higher trophic levels and tend towards higher vulnerability to fragmentation (Henle et al., 2004). Meyer et al. (2008) and Farneda et al. (2015) similarly found fragmentation to filter traits of body size and wing morphology for bats. Several studies have found bats with short, broad wings to be more vulnerable to fragmentation (Farneda et al., 2015), and that wing morphology was a good predictor of extinction risk, both for temperate insectivorous bats (Safi & Kerth, 2004) and on a global scale, based on IUCN threat criteria (Jones et al., 2003). Little is known of the sensitivity of bats to habitat fragmentation in Africa: here, we show larger insectivorous species and species exhibiting low wing loading may be more vulnerable to forest fragmentation.

5 | CONCLUSION

There is a need to understand how climate-mediated biogeographical processes have affected biodiversity within South African forests. This study is the first to show the pervasive role historical processes have had in structuring bat communities of the region. An important implication of our results is that while the Eastern Cape Dune forests displayed the lowest species richness, they exhibited a unique bat community composition and function. Also, Scarp forests demonstrated more specialized species. The unique biogeographic history and bat community composition of these two coastal forest types flag them for conservation priority. Furthermore, we demonstrated how forest edges positively affect bat functional diversity. These results may inform forest management to benefit bat conservation via the maintenance of the integrity, structural heterogeneity, and contrast of forest edges. We show that larger-bodied insectivores and species with a reduced dispersal capacity are potentially vulnerable to habitat fragmentation. These morphological traits should be considered by specialists and practitioners when assessing species conservation statuses and conducting environmental impact assessments. Moreover, future studies should consider exploring the effects of human-mediated disturbances on bat communities given the increasing prevalence and magnitude of forest product harvesting occurring in these forests (Leaver et al., 2019). Lastly, the landscape metrics of patch cohesion index and effective mesh size proved poor ecological indicators of bat functional diversity and functional traits within the study forests. Further work should consider alternative metrics of habitat connectivity and isolation, and on varying geographical scales, to further investigate fragmentation effects on bat communities.

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DATA AVAILABILITY STATEMENT

The data supporting the results reported here are all available in the supporting information files.

ORCID

Monika Moir https://orcid.org/0000-0003-1095-1910

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BIOSKETCH

The Eastern Cape forest research group at Stellenbosch University focus on documenting biodiversity of fauna in Eastern Cape forests to understand the processes affecting faunal communities with focus on habitat fragmentation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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