





Precipitation mediates termite functional diversity and dominance in southern Africa

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Background: Termites are important ecosystem engineers in the tropics and sub-tropics, so understanding their diversity, particularly their functional diversity, across biogeographical scales is important for understanding where they alter the environment and deliver ecological services. Feeding groups combine phylogenetic and dietary information about termites into ecologically significant functional categories.

Objectives: To characterise termite feeding group prevalence, distribution and diversity in southern Africa and assess the effect of precipitation on termite diversity and assemblage composition.

Method: Termite genus and species-level occurrence data were acquired from the South African Termite Database and classified into one of five feeding groups. We evaluated the prevalence of each feeding group and assessed species and feeding group richness and dominance. Linear regressions were performed to determine the relationship between 1) species richness and precipitation; and 2) feeding group richness and precipitation.

Results: We find that southern Africa 1) is dominated by FG-IIw (feeding group – II, wood feeding) termites; 2) is occupied by multiple feeding groups across the entirety of the rainfall gradient; and that precipitation 3) influences feeding group species diversity variably; and 4) causes notable shifts in termite community structure.

Conclusion: Our results indicate that termites likely make substantial contributions to plant material decomposition across southern Africa and that while shifts in feeding group dominance are associated with rainfall gradients, the services unique to individual feeding groups are not isolated to certain regions, but rather are widespread regardless of the amount of precipitation received.

Introduction

Termites are important ecosystem engineers (Lee & Wood 1971; Jones et al. 1994; Sileshi et al. 2010; Jouquet et al. 2011; Ashton et al. 2019), so understanding the species and functional diversity across biogeographic scales is important for understanding how and where they alter the environment and deliver services. Although all termites alter soil properties and facilitate nutrient cycling, their specific impacts vary with species composition and the functional traits (or feeding groups (Donovan et al. 2001; Jouquet et al. 2011)) that are most prevalent at a location.

Globally, termites have previously been organised into functional or feeding groups (FG-I, FG-II, FG-III, FG-IV) based on phylogenetic information and diet (Donovan et al. 2001). Divergence in food preference across feeding groups provides insight into services rendered. For example, FG-I mostly consumes wood and FG-II has broad diet preferences (including wood, leaves and grass),

suggesting that in areas where these feeding groups are present, decomposition of larger plant material will be enhanced. In contrast, FG-III termites consume partially decayed organic matter and FG-IV termites consume compounds stabilised in soils (Jouquet et al. 2011), indicating that in areas where these feeding groups are found, soil organic matter dynamics will be influenced. Scaling up these insights helps to clarify the presence or absence of broad scale processes across large geographical areas.

Several studies have explored how termite diversity shifts along climate and productivity gradients. Davies et al. (2003) showed that termites are most functionally diverse in lowland closed canopy tropical forests. Local (Buxton 1981; Davies et al. 2012) and inter-biome comparison studies (Eggleton 1994; Bignell & Eggleton 2000; Davies et al. 2003; Jones & Eggleton 2011; Dahlsjö et al. 2014) have documented an increased number of feeding groups, and a general shift from FG-I and FG-II termites to FG-III and FG-IV termites with increasing mean annual rainfall. Similarly, in Namibia, Vohland and Deckert (2005) found that termite species richness increased with increased rainfall. To our knowledge, no studies have assessed how feeding group diversity and assemblage composition shifts across a continuous and geographically extensive (multi-country) rainfall gradient.

Here we capitalise on a relatively comprehensive termite occurrence dataset in southern Africa to advance our understanding of termite biogeography and to assess the effect of precipitation on termite functional diversity and assemblage composition. Southern Africa contains roughly 54 genera and 165 species of termites,

which represents nearly 20% of 280 termite genera known globally (Uys 2002). In this study, we aim to 1) characterise termite functional prevalence, distribution and diversity across the bioclimatic and elevation gradients of southern Africa; and 2) assess the effect of precipitation on termite functional diversity and assemblage composition.

Methods

Data description

Termite species data and study area

Termite presence–absence data were acquired from the South African Termite Database (SATD) maintained by the Biosystematics Division of the Plant Protection Research Institute at the Agricultural Research Council in Pretoria, South Africa. The SATD contains >35 000 occurrence records, mostly a product of the South African National Survey of Isoptera (NSI) led by Dr W.H.G. Coaton and co-workers (Coaton & Sheasby 1972); some records were also gleaned from Mitchell (1980). The original survey was initially intended to include every quarter degree square ($0.25^\circ \times 0.25^\circ$, or 50×50 km) of South Africa, but was later expanded to include surveys from Namibia, Zimbabwe and Eswatini. Unfortunately, no termite survey data is available from Botswana or Lesotho (Uys 2002; Figure 1).

The National Survey of Isoptera was conducted over two decades (~1960–1980). Termites were sampled mostly during the wet season (when they are most active),

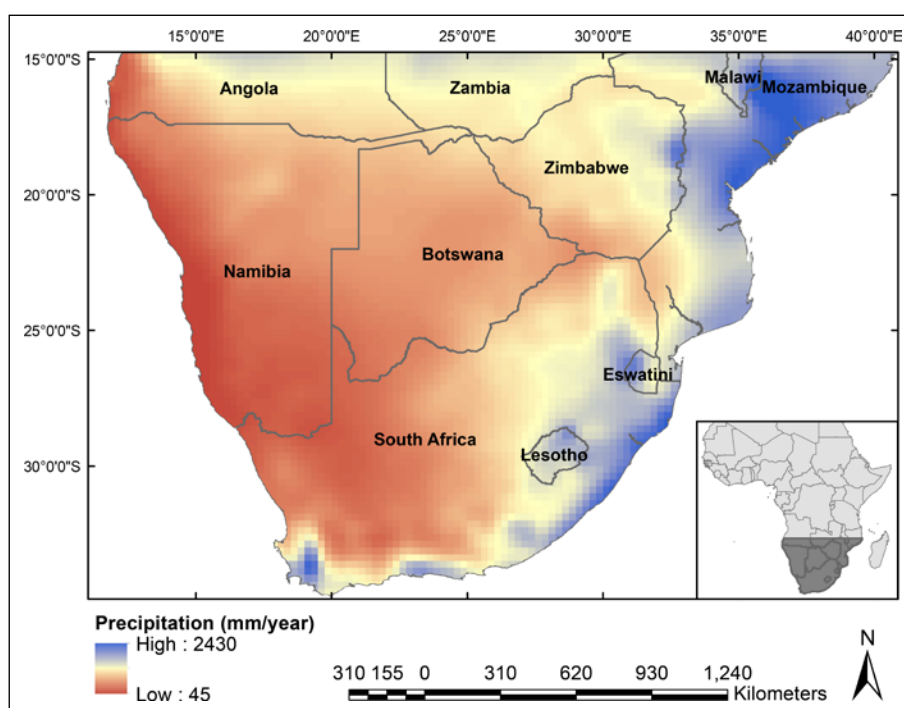


Figure 1. Regional 100-year average cumulative annual precipitation (mm/year; Harris & Jones 2015) in southern Africa. Inset: Continental Africa, showing extent of the study region in dark grey and the rest of the continent in light grey.

through active searching by trained termitologists at one or more locations within each sample area (Coaton & Sheasby 1972; Uys 2002). Multiple sample locations falling within the same quarter degree square were aggregated to reduce bias and location error and maintain consistent resolution. All termite specimens were identified by an expert taxonomist (Coaton and colleagues engaged by the NSI) to genus level and, time permitting, to species level. As many database entries were recorded only to genus, overall species-richness estimates likely underestimate true diversity (Meredith et al. 2019). We re-examined the SATD to correct minor spelling mistakes and antiquated species names. Ambiguous georeferences (e.g., points where latitude–longitude did not correspond with additional locality information on nearby towns or country name) were corrected where possible or removed. In so doing, the database was ultimately reduced to 26 968 reliable presence records that cover 1 952 grid cells) and includes 52 genera and 121 species (Supplementary Table S1).

Feeding group classification

Termites were classified into five feeding groups (FGs) based on their phylogeny and the level of decomposition of feeding substrate in their gut (Donovan et al. 2001). FG-I species are primitive termites belonging to families Kalotermitidae, Termopsidae, Hodotermitidae, Rhinotermitidae) and feed on non- or lightly decayed material including dead wood and grass, whereas FG-II through FG-IV species belong to the family Termitidae and feed on more decayed materials (Donovan et al. 2001). FG-II termites include species of the conspicuous mound-building genera (*Macrotermes*, *Odontotermes*), which have broad diet preferences including dead wood, grass, leaf litter and micro-epiphytes, and can be separated into fungus-feeders (FG-II_f) and wood-feeders (FG-II_w) (Jones & Eggleton 2011). FG-III termites feed on visible organic material in the soil, while FG-IV termites are known as ‘true soil feeders’ and feed on clay-bound proteins and peptides (Donovan et al. 2001; Ji & Brune 2005).

Precipitation Data

Annual cumulative precipitation data at a 0.5° × 0.5° resolution were acquired from the Climate Research Unit at the University of East Anglia, UK (Harris & Jones 2015), averaged for 1901–2014 into 0.5° × 0.5° and disaggregated to a 0.25° × 0.25° grid using bilinear resampling in ArcGIS 10.7.1. to match the resolution of the South African Termite Database (Figure 1, ESRI, 2020). Mean annual precipitation in the study region ranges from 50 to 2 100 mm/year, encompassing a wide range of biomes including deserts and semi-deserts, fynbos, temperate Afromontane forests, grasslands, savannas, and moist broad leaf forests (Olson et al. 2001).

Mapping and analysis

Termite feeding group distribution maps were generated in ArcGIS 10.7.1 (ESRI 2020). The maps depict the geographical extent of feeding groups in the nearly two thousand (n=1 952) 50 × 50 km areas sampled as part of the SATD. Darker shades indicate higher numbers of species present in a sampled area (Figure 2, Figure 3). We calculated the prevalence of each feeding group as the percentage of sampled locations that had a positive occurrence record, where prevalence = (no. positive samples / 1952) × 100. We also assessed species richness, or the number of species present in a single 50 × 50 km sampled location, and feeding group richness, or the number of feeding groups present in a sampled location. While the SATD is composed of acquisitions identified to both the genus and species levels, we combined all acquisitions to a ‘species richness’ value by conservatively assuming that species richness equals one when only genus-level acquisition is present and otherwise using the number of species-level acquisitions.

Simple linear regressions were performed to assess the relationship between 1) species richness and precipitation; and 2) feeding group richness and precipitation. We define feeding group richness as the number of species present at a sample location belonging to the same feeding group. To interrogate the relationship between feeding groups and precipitation further, we first organised the data into eight precipitation bins, each representing roughly 200 sampling locations and a 150–250 mm increase in precipitation between bin categories, and then calculated feeding group dominance by summing occurrence records for each individual feeding group and then dividing by the total number of occurrences in that bin. This provided the relative percentage that each feeding group contributed to the entire assemblage across the precipitation gradient. Statistical analyses were performed in base R version 4.0.3. (R Core Team 2020).

Results

Feeding group distribution and prevalence

Termite feeding groups are not distributed evenly in space or species number across southern Africa. While most feeding groups occur in more than half of sampled locations, FG-II_w are by far the most widely distributed, occurring in over 80% of sampled locations. FG-IV termites are the least prevalent and occur in less than 40% of sampled locations, and mostly in the wetter northeast (Figure 2). Individual maps reveal trends in diversity and geographic preferences. Fungus-growing FG-II termites (FG-II_f) have the highest maximum diversity, often with

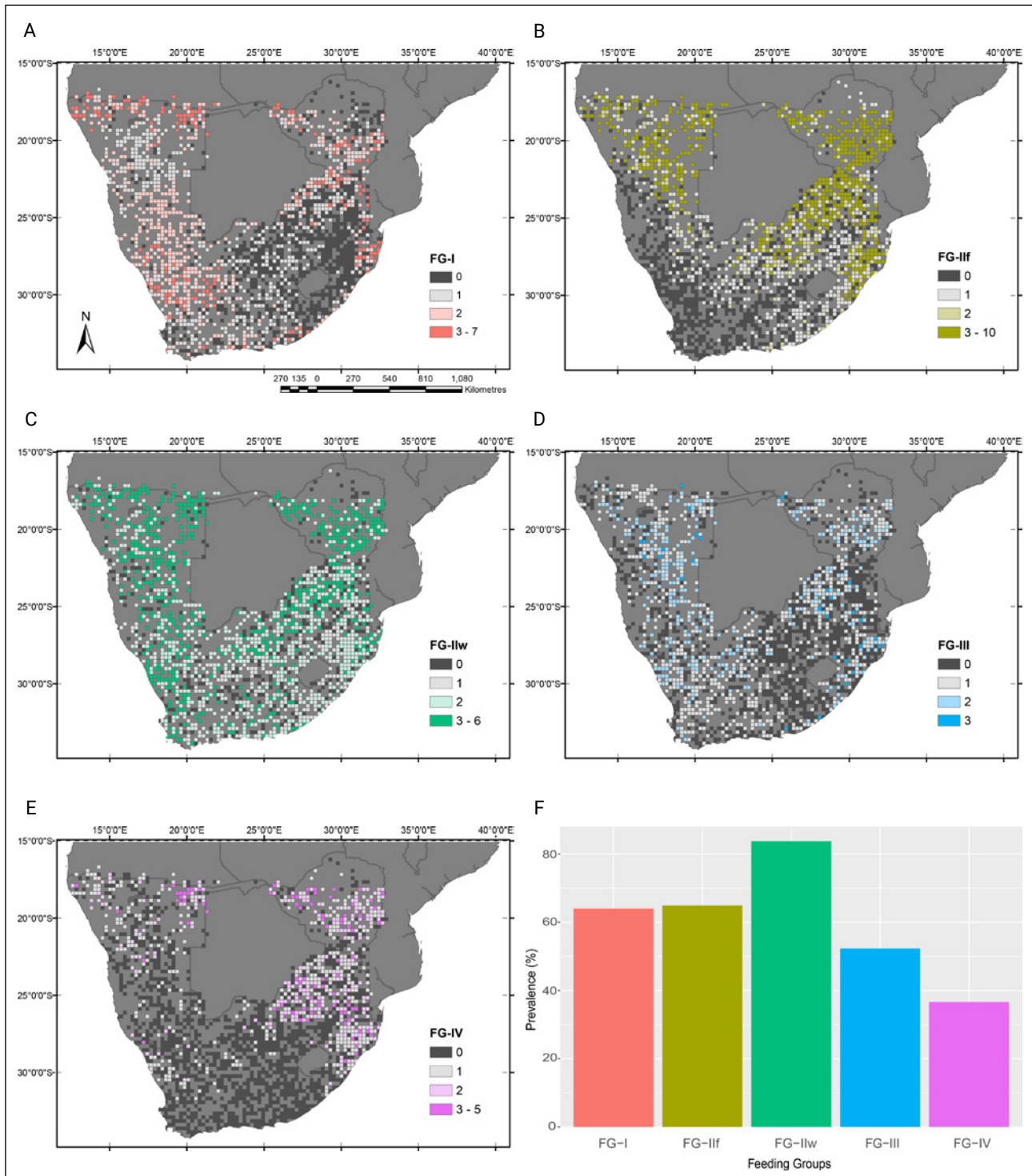


Figure 2. A–F, termite feeding group distribution maps for termites in quarter degree sample cells (n=1952) across southern Africa, showing species richness (number of species present in a pixel) for each feeding group. Colour schemes in A–E correspond to the feeding group prevalence diagram (F).

eight to ten different species in the same location. In contrast, FG-III termites exhibit the lowest diversity; a maximum of three different species rarely occurring in the same location. FG-I exhibits high diversity in western Namibia, whereas FG-II-f are rare in western Namibia and the western Cape, but widely distributed elsewhere. Feeding groups I, III and IV have low diversity and prevalence to the north, south and east of Lesotho (Figure 2).

Taxonomic and feeding group species richness

Species richness ranged from 1 to 25 and at least one termite was found at all sampled locations. Areas of highest overall species richness generally occurred to the north of the study area in regions with higher rainfall (Figure 3A and 4A). Feeding group richness ranged from 1 to 5 and

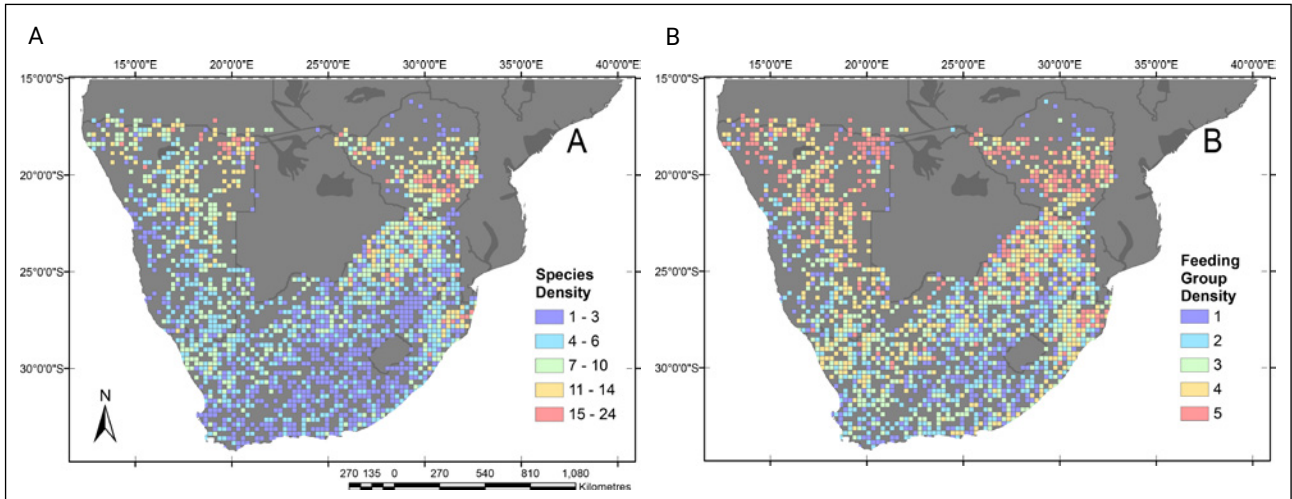


Figure 3. A, species richness for termites in quarter degree sample cells (1952 locations) across southern Africa; B, feeding group richness. One feeding group is present in 353 cells, two are present in 356 cells, three are present in 454 cells, four are present in 485 cells, and five are present in 304 cells.

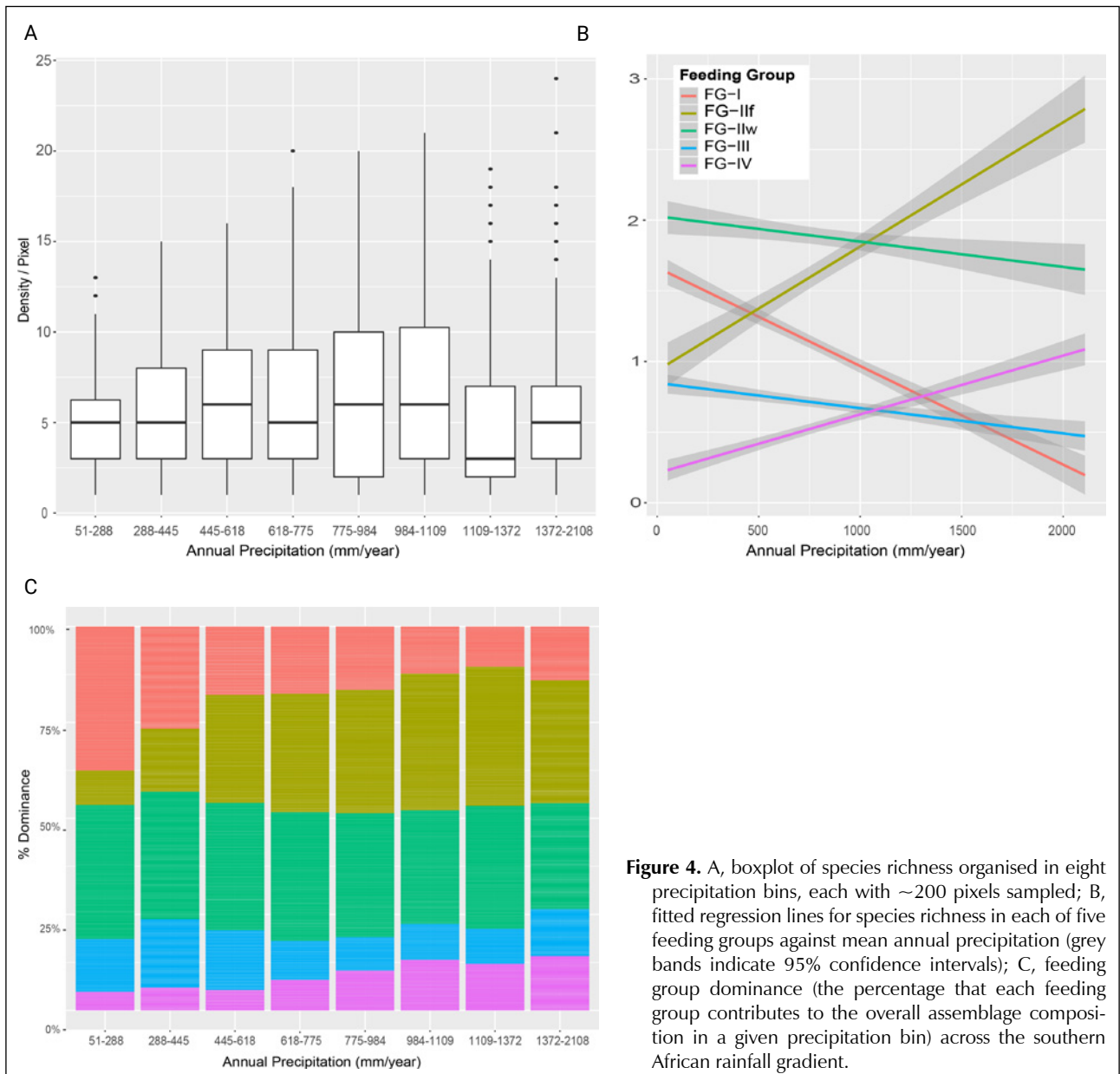


Figure 4. A, boxplot of species richness organised in eight precipitation bins, each with ~200 pixels sampled; B, fitted regression lines for species richness in each of five feeding groups against mean annual precipitation (grey bands indicate 95% confidence intervals); C, feeding group dominance (the percentage that each feeding group contributes to the overall assemblage composition in a given precipitation bin) across the southern African rainfall gradient.

while the majority of sampled locations (64%) contain at least three or more feeding groups, the regions to the north of the study area are generally more functionally rich (i.e., more FGs are present) than in the south.

Relationship to precipitation

Although the relationship between overall species richness and rainfall is not significant (Figure 4A, Table 1), we find distinct, significant and contrasting relationships between precipitation and species richness within each of the five feeding groups (Figure 4B and Table 1). More specifically, the diversity of FG-II_f and FG-IV is positively related with rainfall, while the remaining feeding groups (FG-I, FG-II_w and FG-III) show a negative relationship in this regard (Figure 4B, Table 1).

Feeding group dominance also varies with precipitation. Whereas FG-I is the most dominant in arid landscapes (50–200 mm rainfall bin), its dominance decreases as precipitation increases. This decrease in FG-I dominance is mirrored by a nearly four times increase in FG-II_f. FG-II_w maintains a near constant ~25% of assemblage composition across the entire precipitation gradient, but in the wettest landscapes (> 950 mm precipitation), FG-II_f and FG-II_w combined constitute nearly 65% of the termite assemblage (Figure 4C).

Discussion

The Southern African Termite Database provides an unprecedented opportunity to examine termite feeding group distributions at broad spatial scales across southern Africa. The major findings of this study are that southern Africa: 1) is dominated by FG-II_w termites; and 2) is occupied by multiple FGs across the entire rainfall gradient; and that 3) precipitation influences feeding group richness variably, with some FGs increasing with rainfall, while others decrease in prevalence; and 4) patterns in FG variability with rainfall cause notable shifts in assemblage with possible implications for the role of termites in carbon and nutrient cycles.

We find that FG-II_w termites have a nearly ubiquitous presence across southern Africa, covering over 80% of sampled locations. The broad diet of FG-II_w termites allows them to thrive in climatically diverse environments ranging from semi-deserts to tropical rainforests (Jones & Eggleton 2011). This indicates that wood and litter decomposition is a geographically consistent ecosystem service provided by FG-II_w termites in southern Africa.

Our research further suggests that despite southern Africa's aridity, multiple feeding groups occupy the region across the entire rainfall gradient. While previous studies have suggested that the number of FGs, and therefore the range of termite mediated services, are often greater in wetter environments (Bignell & Eggleton 2000; Davies et al. 2012), we find that most sampled locations, regardless of precipitation, contain between three and the maximum of five termite feeding groups. Similarly, even in areas of low species diversity, feeding group diversity (i.e., functional diversity) remains relatively high (>=3), broadly suggesting that despite low overall species richness, there is still the opportunity for termites to process organic material across a nearly complete humification gradient.

Linear regressions suggest that there is no significant relationship between overall species diversity and precipitation, but that significant relationships for individual feeding groups exist. In general, species diversity within FG-II_f and FG-IV increases with increasing precipitation and tends to decrease in the remaining feeding groups, either strongly (FG-I) or slightly (FG-II_w, FG-III), with increasing precipitation. Feeding group dominance varies similarly with precipitation. Whereas FG-I, which feed on lightly decayed materials, are the most dominant feeding group in arid landscapes (50–200 mm precipitation bin), as precipitation increases the fungus cultivating termites (FG-II_f) become most dominant. There is a particularly strong positive trend with rainfall for FG-II_f termites, which, given the water-limited nature of southern Africa, may suggest a preference for resource-rich environments where there is more readily available plant biomass for consumption. Because FG-II_f termites are thought to have evolved in African

Table 1. Regression statistics of annual precipitation on termite diversity

Feeding group	F-Value	Slope	P-Value	Significance
I	(1, 1950) = 182.9	-6.97E-02	2.20E-16	***
II _w	(1, 1950) = 7.129	-1.79E-04	0.007649	**
II _f	(1, 1950) = 98.35	8.78E-04	2.20E-16	***
III	(1, 1950) = 21.06	-1.79E-04	0.00000474	***
IV	(1, 1950) = 97.22	4.16E-04	2.20E-16	***
All FGs Combined	(1, 1950) = 1.359	2.29E-04	0.244	not significant

rainforests (Aanen & Eggleton 2005; Bourguignon et al. 2014), they may have a natural preference for wetter environments that facilitate maintenance of optimal mound humidity and temperature conditions for fungus cultivation. This may be related to the high energy costs of growing and consuming fungus and associated with the indirect benefits of the greater availability of trees (providing shade) and rainfall (maintaining humidity) to facilitate maintenance of the physiological conditions required for fungus garden maintenance within mounds (Korb 2003; Turner et al. 2006).

Regardless of this shift, we find that plant material consumers (FG-I, FG-IIw, FG-IIf) dominate the assemblage composition across the entire precipitation gradient, consistently representing roughly 75% of termites sampled. As seen in the linear regressions, we find an increase in FG-IV diversity with precipitation, from barely 5% of the assemblage in the driest regions, to 12.5% in the wettest areas. While this represents over a doubling in assemblage representation, the relatively low overall contribution is lower than expected, based on previously documented shifts from litter feeders to soil feeders with increasing precipitation (Buxton 1981; Eggleton 1994; Bignell & Eggleton 2000; Davies et al. 2003; Jones & Eggleton 2010; Davies et al. 2012; Dahlsjö et al. 2014). This lack of representation of soil feeders in wetter regions is intensified by the consistently minor presence of FG-III termites. However, in the case of FG-III, the taxonomic difficulty in identification of soldierless Apicotermitinae may be a cause of under-sampling in the SATD. The lack of an anticipated transition point, where soil feeders comprise the majority of the assemblage over litter feeders, may be related to the character of the precipitation gradient. To allow species richness comparison across the full precipitation gradient, we chose to maintain a relatively equal number of samples per precipitation interval (i.e., bin, 200 grid cells per rainfall interval), and therefore sacrificed the consistency of our rainfall interval sizes. While all the rainfall intervals are between 150 and 250 mm along the rainfall gradient from 50 to 1 400 mm/year, the final precipitation interval covers nearly 700 mm (roughly 1 400–2 100 mm/year). This suggests that the range where we have the most reliable and comparable sampling power is closer to 50 to 1 400 mm/year, which may be too arid to observe large increases in soil feeding termites.

Conclusion

Interpreting termite distribution data through a Feeding Group lens provides a spatially explicit framework for interpreting how individual FGs partition and contribute to the processing and recycling of primary production in the tropics at large biogeographical scales. While the SATD represents one of the most geographically

extensive and continuous survey efforts of termites globally, our analysis is restricted in the sense that it excludes a notable portion of southern Africa (Botswana and Mozambique) and the areas of highest precipitation in southern Africa (Mozambique). Thus, we are capturing a large, but abbreviated portion of the documented precipitation gradient, where termite feeding group diversity has been reported to increase into the moist tropical forests (Bignell & Eggleton 2000). In our analysis of arid and semi-arid systems across southern Africa, we find that multiple termite FGs occupy the majority of the landscape, suggesting that ecosystem services related to individual FGs are likely widely distributed regardless of the amount of precipitation received. We also find that plant material feeders (FG-I, FG-IIw, FG-IIf) dominate in distribution, diversity and assemblage composition across the entire precipitation gradient. The dominance of litter feeders suggests that termites make substantial contributions to plant material decomposition across southern Africa. Quantifying these contributions more systematically is an important next step in understanding how termite feeding groups contribute to ecosystem function in arid, semi-arid and moist environments. Specifically, contextualising the role of termites as consumers in relation to other well-known consumers like fire and mammalian herbivory (Archibald & Hempson 2016) is of high priority.

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Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Authors' contributions

B.M.L. (New Mexico State University) and N.P.H. (New Mexico State University) designed the study, V.M.U. (Agricultural Research Council, Pretoria) provided the data, B.M.L. analysed the data, and B.M.L., N.P.H., V.M.U., and P.E. (The Natural History Museum, London) wrote the manuscript.

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

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Data availability statement

Upon acceptance of this manuscript, species density, feeding group density and precipitation data used to conduct the study will be made publicly available on www.datadryad.com.

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Supplementary Material

Supplementary Table 1: List of termite species included in study

Family	Subfamily	Feeding Group	Genus	Species
Kalotermitidae		I	<i>Bifiditermes</i> (Krishna, 1961)	<i>durbanensis</i> (Haviland, 1898)
				<i>sibayiensis</i> (Coaton, 1949)
		I	<i>Cryptotermes</i> (Banks, 1906)	<i>brevis</i> (Walker, 1853)
				<i>havilandi</i> (Sjöstedt, 1900)
				<i>merwei</i> (Fuller, 1921)
				<i>naudei</i> (Coaton, 1950)
		I	<i>Epicalotermes</i> (Silvestri, 1918)	spp.
				<i>mkuzii</i> (Coaton, 1949)
				<i>munroi</i> (Coaton, 1949)
		I	<i>Kalotermes</i> (Hagen, 1858)	spp.
				<i>umtatae</i> (Coaton, 1949)
		I	<i>Neotermes</i> (Holmgren, 1911)	spp.
			<i>zuluensis</i> (Coaton, 1949)	
	I	<i>Postelectrotermes</i> (1961)	spp.	
Stolotermitidae	Porotermitinae	I	<i>Porotermes</i> (Hagen, 1858)	<i>planiceps</i> (Sjöstedt, 1904)
	Stolotermitinae	I	<i>Stolotermes</i> (Hagen, 1858)	<i>africanus</i> (Emerson, 1942)
Hodotermitidae		I	<i>Hodotermes</i> (Hagen, 1858)	spp.
				<i>mossambicus</i> (Hagen, 1853)
	I	<i>Microhodotermes</i> (Sjöstedt, 1926)	<i>viator</i> (Latreille, 1804)	
Rhinotermitidae	Coptotermitinae	I	<i>Coptotermes</i> (Wasmann, 1896)	spp.
				<i>amanii</i> (Sjöstedt, 1911)
				<i>formosanus</i> (Shiraki, 1909)
	Psammotermitinae	I	<i>Psammotermes</i> (Desnux, 1902)	<i>allocerus</i> (Silvestri, 1908)
	Rhinotermitinae	I	<i>Schedorhinotermes</i> (Silvestri, 1909)	<i>lamanianus</i> (Sjöstedt, 1911)
Termitidae	Macrotermitinae	IIff	<i>Allodontermes</i> (Silvestri, 1914)	spp.
				<i>rhodesiensis</i> (Sjöstedt, 1914)
				<i>schultzei</i> (Silvestri, 1908)
				<i>tenax</i> (Silvestri, 1912)
		IIff	<i>Ancistrotermes</i> (Silvestri, 1912)	<i>latinotus</i> (Holmgren, 1912)
		IIff	<i>Macrotermes</i> (Holmgren, 1909)	<i>falciger</i> (Gerstäcker, 1891)
				<i>michaelseni</i> (Sjöstedt, 1914)
				<i>natalensis</i> (Haviland, 1898)
				<i>subhyalinus</i> (Rambur, 1842)
				<i>ukuzii</i> (Fuller, 1922)
			<i>vitrialatus</i> (Sjöstedt, 1899)	

Supplementary Table 1: List of termite species included in study (continued)

Family	Subfamily	Feeding Group	Genus	Species	
Termitidae	Macrotermitinae	Ilf	<i>Microtermes</i> (Wasmann, 1896)	spp.	
				<i>albopartitus</i> (Sjöstedt, 1911)	
				<i>etiolatus</i> (Fuller, 1922)	
				<i>haviglandi</i> (Holmgren, 1913)	
				<i>lounsburyi</i> (Fuller, 1922)	
		<i>occidentalis</i> (Fuller, 1922)			
		Ilf	<i>Odontotermes</i> (Holmgren, 1912)	spp.	
				<i>angustatus</i> (Rambur, 1842)	
				<i>badius</i> (Haviland, 1898)	
				<i>cafrariae</i> (Sjöstedt, 1897)	
				<i>capensis</i> (De Geer, 1778)	
				<i>lacustris</i> (Harris, 1960)	
				<i>latericius</i> (Haviland, 1898)	
				<i>monodon</i> (Gerstäcker, 1891)	
				<i>okahandjae</i> (Fuller, 1922)	
	<i>tragardhi</i> (Holmgren, 1913)				
	<i>transvaalensis</i> (Sjöstedt, 1902)				
	<i>vulgaris</i> (Haviland, 1898)				
	Ilf	<i>Pseudacanthotermes</i> (Holmgren, 1912)	<i>militaris</i> (Hagen, 1858)		
	Apicotermitinae	III	<i>Adaiphrotermes</i> (Sands, 1972)	<i>choanensis</i> (Fuller, 1925)	
				<i>moretelae</i> (Fuller, 1925)	
				<i>oryctes</i> (Sands, 1972)	
		III	<i>Alyscotermes</i> (Sands, 1972)	<i>kilimandjaricus</i> (Sjöstedt, 1907)	
				<i>Anoplotermes</i> (Mueller, 1873)	spp.
				IV	<i>Apicotermes</i> (Holmgren, 1912)
		<i>tragardhi</i> (Holmgren, 1912)			
		III	<i>Astalotermes</i> (Sands, 1972)		
<i>brevior</i> (Holmgren, 1913)					
<i>comis</i> (Sands, 1972)					
IV		<i>Ateuchotermes</i> (Sands, 1972)	<i>empodius</i> (Sands, 1972)		
			<i>muricatus</i> (Sands, 1972)		
	III		<i>Skatitermes</i> (Coaton, 1971)	<i>psammophilus</i> (Coaton, 1971)	
<i>watti</i> (Coaton, 1971)					
Cubitermitinae	IV	<i>Basidentitermes</i> (Holmgren, 1912)	spp.		
			<i>Batillitermes</i> (Uys, 1994)	<i>monachus</i> (Uys, 1994)	
			<i>Crenetermes</i> (Silvestri, 1912)	spp.	
			<i>Cubitermes</i> (Wasmann, 1906)	spp.	

Supplementary Table 1: List of termite species included in study (continued)

Family	Subfamily	Feeding Group	Genus	Species		
Termitidae	Cubitermitinae			<i>anatruncatus</i> (Fuller, 1925)		
				<i>bilobatus</i> (Haviland, 1898)		
				<i>conjenii</i> (Fuller, 1925)		
				<i>duplex</i> (Holmgren, 1913)		
				<i>microduplex</i> (Fuller, 1925)		
				<i>pallidiceps</i> (Sjöstedt, 1913)		
				<i>pretorianus</i> (Silvestri, 1914)		
				<i>sanctaeluciae</i> (Fuller, 1925)		
				<i>transvaalensis</i> (Fuller, 1925)		
				<i>truncatoides</i> (Fuller, 1925)		
				<i>undulatus</i> (Fuller, 1925)		
			IV	<i>Euchilotermes</i> (Silvestri, 1914)	spp.	
			IV	<i>Lepidotermes</i> (Sjöstedt, 1924)	spp.	
					<i>amydrus</i> (Uys, 1994)	
					<i>goliathi</i> (Williams, 1954)	
					<i>lounsburyi</i> (Silvestri, 1914)	
					<i>mtwalumi</i> (Fuller, 1925)	
					<i>planifacies</i> (Williams, 1954)	
					<i>pretoriensis</i> (Sjöstedt, 1914)	
					<i>scalenus</i> (Uys, 1994)	
					<i>simplex</i> (Holmgren, 1913)	
					<i>vastus</i> (Uys, 1994)	
			IV	<i>Noditermes</i> (Sjöstedt, 1924)	spp.	
			IV	<i>Okavangotermes</i> (Coaton, 1971)	<i>giessi</i> (Coaton, 1971)	
			IV	<i>Ovambotermes</i> (Coaton, 1971)	spp.	
					<i>sylvaticus</i> (Coaton, 1971)	
			IV	<i>Unguitermes</i> (Sjöstedt, 1924)	spp.	
					<i>unidentatus</i> (Ruelle, 1973)	
			IV	<i>Unicornitermes</i> (Coaton, 1971)	<i>gaerdesi</i> (Coaton, 1971)	
			Termitinae	llw	<i>Amitermes</i> (Silvestri, 1901)	spp.
					<i>braunsi</i> (Fuller, 1922)	
					<i>hastatus</i> (Haviland, 1898)	
			<i>messinae</i> (Fuller, 1922)			
			<i>obtusidens</i> (Mjöberg, 1920)			
		III	<i>Angulitermes</i> (Sjöstedt, 1924)	spp.		
			<i>braunsi</i> (Wasmann, 1908)			
			<i>elsenburgi</i> (Fuller, 1925)			
		llw	<i>Microcerotermes</i> (Silvestri, 1901)	spp.		

Supplementary Table 1: List of termite species included in study (continued)

Family	Subfamily	Feeding Group	Genus	Species		
Termitidae	Termitinae			<i>apricitatis</i> (Fuller, 1925)		
				<i>choanensis</i> (Fuller, 1925)		
				<i>collinsi</i> (Fuller, 1925)		
				<i>dumisae</i> (Fuller, 1925)		
				<i>hypaenicus</i> (Fuller, 1925)		
				<i>ilalazonatus</i> (Fuller, 1925)		
				<i>limpopoensis</i> (Fuller, 1925)		
				<i>malmesburyi</i> (Fuller, 1925)		
				<i>mzilikazi</i> (Fuller, 1925)		
				<i>parvus</i> (Haviland, 1898)		
				<i>pondweniensis</i> (Fuller, 1925)		
				<i>psammophilus</i> (Fuller, 1925)		
				<i>sanctaeluciae</i> (Fuller, 1925)		
				<i>thermarum</i> (Fuller, 1925)		
				<i>zuluensis</i> (Holmgren, 1913)		
				III	<i>Pericapritermes</i> (Silvestri, 1914)	spp.
				III	<i>Promirotermes</i> (Silvestri, 1914)	spp.
						<i>bechuana</i> (Fuller, 1922)
						<i>dumisae</i> (Fuller, 1925)
						<i>rotundifrons</i> (Silvestri, 1914)
				III	<i>Termes</i> (Lineé, 1758)	<i>boultoni</i> (Coaton & Sheasby, 1978)
			Nasutitermitinae	IIw	<i>Baucaliotermes</i> (Sands, 1965)	<i>hainesi</i> (Fuller, 1922)
				IIw	<i>Fulleritermes</i> (Coaton, 1963)	spp.
						<i>coatoni</i> (Sands, 1965)
						<i>contractus</i> (Sjöstedt, 1913)
						<i>mallyi</i> (Fuller, 1922)
				IV	<i>Mimeutermes</i> (Silvestri, 1914)	spp.
				IIw	<i>Nasutitermes</i> (Dudley, 1890)	<i>infuscatus</i> (Sjöstedt, 1902)
						<i>kempae</i> (Harris, 1954)
				IIw	<i>Rhadinotermes</i> (Sands, 1965)	<i>coarctatus</i> (Sjöstedt, 1902)
				IV	<i>Spatulitermes</i> (Coaton, 1971)	spp.
						<i>coolingi</i> (Coaton, 1971)
		IIw	<i>Trinervitermes</i> (Holmgren, 1912)	spp.		
				<i>dispar</i> (Sjöstedt, 1902)		
				<i>rapulum</i> (Sjöstedt, 1904)		
				<i>rhodesiensis</i> (Sjöstedt, 1911)		
				<i>trinervius</i> (Rambur, 1842)		
				<i>trinervoides</i> (Sjöstedt, 1911)		