THE INFLUENCE OF FIRE ON SALTATORIA DIVERSITY IN COASTAL HABITATS NEAR PANGANI, TANZANIA (EAST AFRICA)

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Abstract. In burnt coastal grasslands, fire-disturbed forest remnants, and undisturbed coastal forests of the Pangani area (Tanzania) 61 Saltatoria species were recorded. Comparing open-land habitats with forest and forest edge habitats, diversity rises in open-land habitats, as nearly 60% of the recorded species were found within grasslands. However, the share of endemic and near-endemic species decreases, as only 5% of the species occurring in open-land habitats were endemics, 14% are distributed throughout East Africa, and the majority (81%) are widespread forms. Forest and forest edge habitats, on the other hand, had 60% endemic species, 32% species restricted to East Africa, and only 8% widespread Saltatoria. The majority of the coastal endemics are highly endangered by the ongoing destruction of indigenous forest. Tangana asymmetrica was one of the few coastal endemics that also occurred in fire-influenced forest remnants, while most other forest species were exclusively found in closed undisturbed forest communities of the Gendagenda forest reserve. The new record of Parepistaurus pygmaeus in the Gendagenda reserve offers an explanation of the hitherto disjunct distribution of this flightless species. Accepted 15 June 2005.

Key words: Biodiversity, conservation, endemism, fire influence, indigenous tropical lowland forest, Orthoptera, Saltatoria, Tanzania, tropical coastal grasslands.

INTRODUCTION

The forests along the Kenyan and Tanzanian coast are the remains of a once widespread forest cover. Today this forest has largely gone, leaving around 250 patches of forest, most of which are less than 500 ha in size (Burgess & Clarke 2000). The coastal forests, together with the adjacent forests of the Eastern Arc Mountains, are hotspots of endemism due to a constant climate and long isolation from the Central African forests (Rodgers & Homewood 1982). A stable long-term climate in combination with high rainfall in tropical forest areas are usually associated with a high species diversity (Fjeldså & Lovett 1997). A loss of these forests would result in an enormous loss of biodiversity (Newmark 2002).

In the vicinity of the studied plots lies the coastal town Pangani, which had its greatest importance in the 19th century. Pangani was the starting and destination of caravans coming from or heading for the hinterland, trading with ivory and later with slaves (Glassman 1995). In 1880 about 100 000 people

lived in the area, mostly farmers, cultivating the fields intensively with bananas, maize, sweet potatoes, manihot etc. (Koponen 1994).

Away from the main centers of cultivation around Pangani the coastal area was probably little populated. Most of the coast and hinterland was densely forested. Clearing by fires was practised from the 19th century onwards, reducing the forests especially along the coastal line, mainly for establishing sisal plantations and crop production.

About 20 km inland from Pangani an elevation step of about 50–100 m is apparent. Here at about 300 m a.s.l. stretches dense coastal forest belonging to the Gendagenda reserve. However, in the past 10 years even here the practice of setting fires to reduce tree cover in favor of grassland was observed. It must be feared that also this patch of indigenous lowland forest will disappear in the near future.

The aim of this study was to compare the Saltatoria composition of intact coastal forest within the Gendagenda reserve with fire-influenced patches of forest and grasslands resulting from intensive burning over the last decades near Mwera village, south of Pangani (Fig. 1).

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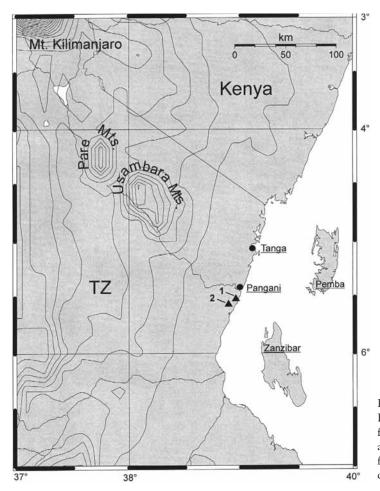


FIG. 1. Map of East Africa. Black triangles: study plots 1: fire-maintained grasslands and fire-influenced coastal forests near Mwera. 2: Gendagenda forest reserve.

RESEARCH AREA

The coastal area of Tanzania receives its precipitation from monsoonal rainfalls from the Indian Ocean coinciding with the northward and southward passages in March to May (long rains with most precipitation) and October to December (short rains). The district city Tanga receives a total of about 1000 mm per year.

The study area is characterized by huge sisal plantations about 5–10 km inland, and wide patches of burnt grasslands intermingled with remnants of forest (East African coastal scrub forest, Burgess & Clarke 2000). Adjacent to the sisal plantations the indigenous forest (East African coastal dry forest, Burgess & Clarke 2000) of the Gendagenda reserve is situated,

some parts of which are already disturbed by infrequent fires (Fig. 2).

Burnt grasslands were investigated directly at the coast near Pangani, about 20 km southward, next to the small village of Mwera (UTM zone 37 04/99/369 east, 93/94/462 south) (Figs. 1, 2). Plant species common in coastal savanna grasslands were the grasses Imperata cylindrica, Digitaria milanjiana, Echinochloa haploclada, Setaria incrassata, Panicum infestum and the herb Kohautia coccinea (A. Hemp unpubl. data). The vegetation cover was 80–100% with a height of about 1m. These grasslands are set on fire nearly every year before the long rains in March.

Remnants of forest are intermingled with the grasslands. After frequent fires the fire-tolerant palmtree *Hyphaene compressa* sprouts. Well adapted to frequent fires, the South American tree Leucaena latisiliqua becomes dominant in the first years after a fire, forming nearly monospecific stands. In the regeneration stage after about 10 to 15 years following a fire indigenous trees like Kigelia africana, Balanites wilsoniana, Lannea schweinfurthii, Xanthoxylum cf. holtzianum, Guettarda speciosa, and Sclerocarya birrea form the tree layer, and shrubs such as Psychotria lauracea, Grewia forbesii, Allophylus rubifolius, Harrisonia abyssinica, Vangueria infausta, Flueggea virosa, Pemphis acidula and Polysphaeria multiflora are found in the undergrowth (A. Hemp unpubl. data). The canopy is usually 10 m high. All investigated forests remnants along the coast in the area belong to regeneration stages after fire. Some central parts of these remnants might be more or less undisturbed by fires, although the patches are mostly not bigger than a few square meters (equivalent to the forest community "coastal scrub forest" in Burgess & Clarke 2000).

Areas of undisturbed indigenous lowland forest mixed with fire-influenced forests were investigated between Kabuko and Mwera at 350 m a.s.l. (Gendagenda forest reserve, Fig. 3). This forest type, which belongs to legume-dominated dry forest, after Burgess & Clarke (2000), was characterized by trees and shrubs such as *Brachystegia spiciformis, Milicia excelsa, Strychnos scheffleri, Hugonia castaneifolia, Polyaltia stuhlmannii, Kraussia kirkii, Polysphaeria parvifolia, Psychotria punctata* and *Pavetta stenosepala* (A. Hemp, unpubl. data). The mean canopy height was 25 m.

METHODS

Saltatoria species composition was recorded for plots of burnt coastal grasslands, for several patches of forest remnants and an adjacent larger forest patch in a regeneration stage (indicated with "1" in Fig. 1), and two plots of dense indigenous forest near the Kabuko-Mwera road (Gendagenda forest reserve, indicated with "2" in Figure 1). All plots were monitored several times (February 1999, January 2000, January and February 2001, December 2004). Four plots were chosen in homogenous grasslands, usually an area of 30 x 30 m. The forest plots had sizes of about 100 x 100 m (two plots within the Gendagenda forest reserve, one plot in regeneration stage, three fire-influenced plots).

In the forest plots it was noted in which microhabitat each species occurred. A differentiation was made between forest edge (clearing or road side) and



FIG. 2. Burnt grassland at the coast near the village Mwera on the Indian Ocean. In the background the fire-tolerant palmtree *Hyphaene compressa*.

closed forest. In the closed forest, whether the species occurred on the forest floor or in the bush or tree layer was registered. In grasslands, Saltatoria species were identified by sight by walking repeatedly on parallel tracks through the plots at distances of about 1–1.5 m. Smaller species and those difficult to identify were caught by net-sweeping. The abundance of gomphocerines was estimated by the male courtship song. In forest habitats all Saltatoria were caught, as the density of individuals was generally low. Bushes and small trees were checked by net-sweeping. The check of one plot lasted in general more than 1 hour, in forest habitats sometimes more than 2 hours. Near



FIG. 3. Coastal forest area at 300 m a.s.l. between Kabuko and Mwera. In the background the Gendagenda Hill. In the foreground fire impact along the road side vegetation.

TABLE 1. List of Saltatoria. Data on habitat and distribution. Gr: grassland species, Fe: forest edge species, F: forest species, Dis: distribution, EA: species restricted to East Africa, C: species restricted to coastal habitats (coastal endemics), remaining species: widespread; Loc: 1: coastal forest remnants and grasslands near Mwera; 2: Gendagenda forest reserve (as shown on Fig. 1).

Species/Family	Habitat	Gr	Fe	F	Dis	loc
Family Tetrigidae						
Paratettix africanus Bolivar, 1908	Open patches in humid grasslands	x				1
Family Eumastacidae						
Plagiotriptus hippiscus (Gerstäcker, 1869)	Forest and forest edge		X		EA	1,2
Euschmidtia sansibarica Karsch, 1889	Bushes at forest edges		X		C	1,2
Family Lentulidae	<u> </u>					
Usambilla sp.*	Undergrowth of coastal forest			X	C	2
Family Acrididae						
Subfamily Hemiacridinae						
Leptacris monteiroi monteiroi (I. Bolivar, 1890)	Burnt grasslands	x				1
Meruana usambarica Karsch, 1896	Burnt grasslands	x			EA	1
Oraistes luridus Karsch, 1896	Shrub layer of coastal forest			X	EA	2
Paraspathosternum pedestris (Miller, 1929)	Undergrowth of coastal forest		X		C	2
Subfamily Oxyinae						
Oxya hyla hyla Serville, 1831	Humid places of burnt grasslands	X				1
Subfamily Coptacridinae						
Parepistaurus pygmaeus (Karny, 1909)	Undergrowth of coastal forest		X		C	2
Subfamily Eyprepocnemidinae						
Cataloipus oberthuri oberthuri (I. Bolivar, 1890)	Burnt grasslands	X				1
Eyprepocnemis plorans ibandana (GigTos,	Burnt grasslands;					
1907)	attracted to light at night	X				1
Heteracris coerulipes (Sjöstedt, 1909)	Undergrowth at forest edges		X		С	2
Metaxymecus gracilipes (Brancsik, 1895)	Burnt grasslands and forest edges	X				1
Taramassus cunctator cunctator (Karsch, 1900)	Burnt grasslands	X			EA	1
Paraprocticus forchhammeri (Johnsen, 1974)	Forest floor and forest edge		X		С	2
Subfamily Catantopinae						
Abisares viridipennis viridipennis (Bur., 1838)	Forests edges		X			2
Catantops momboensis momboensis Sjöstedt,	Burnt grasslands,					
1931	bushland and forest edges		X		EA	1
Diabolocatantops axillaris axillaris (Bur.,	Open sand and coastal grasslands					
1838)	sparse in vegetation	X				1
Eupropacris vana (Karsch, 1896)	On bushes in the understory					
	of coastal forest			X	EA	2
Eupropacris pompalis (Karsch, 1896)	Herb vegetation along forest edges		X		C	1
Tangana asymmetrica Ramme, 1929	Litter of coastal forest			X	C	1,2
Phaeocatantops decoratus (Gerstäcker, 1869)	Coastal bush and forest edges		X		EA	1,2
Pseudophialosphera tectifera (Ramme, 1929)	Undergrowth of coastal forest			X	С	2
Subfamily Cyrtacanthacridinae						
Ornithacris cyanea (Stoll, 1813)	Burnt grasslands	X				1
Subfamily Tropidopolinae						
Tristia marginicosta Karsch, 1896	Burnt grasslands	X				1
Subfamily Oedipodinae						
Ailopus thalassinus (Fabricius, 1781)	Disturbed places	X				1
Gastrimargus africanus africanus (Saussure,						
1888)	Burnt grasslands, disturbed places	X				1
Heteropternis thoracica (Walker, 1870)	Burnt grasslands	X				1

Table 1 continued

Species/Family	Habitat	Gr	Fe	F	Dis	loc
Humbe tenuicornis (Schaum, 1853)	Burnt grasslands	X				1
Jasomenia sansibara (Karsch, 1896)	Burnt grasslands, especially in					
	more humid places; attracted					
	to light at night	X				1
Morphacris fasciata (Thunberg, 1815)	Disturbed places	X				1
Pternoscirtes pallidus (Walker, 1870)	Open sand at the shore	X				1
Subfamily Acridinae						
Acrida bicolor (Thunberg, 1815)	Burnt grasslands, disturbed places	X				1
Acrida sulphuripennis (Gerstäcker, 1869)	Burnt grasslands, disturbed places	X				1
Afrophlaeoba usambarica (Ramme, 1929)	Undergrowth of coastal forest			X	C	2
Comacris semicarinatus (Gerstäcker, 1869)	Burnt grasslands	X			EA	1
Gymnobothrus temporalis flexuosus	Semi-shade on paths					
(Schulthess, 1898)	and forest edges		X		EA	1
Lobopoma mitchelli Popov & Fishpool, 1992					C	1
Machaeridia conspersa I. Bolivar, 1889	Burnt grasslands	X				1
Orthochtha dasycnemis (Gerstäcker 1869)	Burnt grasslands	X				1
Orthochtha dimorpha Miller, 1929	Burnt grasslands	X			EA	1
Subfamily Gomphocerinae						
Minihippus keyi (Uvarov, 1941)	Burnt grasslands	X			C	1
Brachycrotaphus sjostedti Uvarov, 1932	Burnt grasslands	X			EA	1
Mesopsis abbreviatus (Beauvois, 1806)	Burnt grasslands	X				1
Mesopsis laticornis (Krauss, 1877)	Burnt grasslands	X				1
Pnorisa sp.	Burnt grasslands	X				1
Pnorisa squalus squalus (Stål, 1860)	Burnt grasslands	X				1
Family Tettigoniidae						
Subfamily Phaneropterinae						
Catoptropteryx aurita Huxley, 1970	Attracted to light from remnants					
	of coastal forest			X	EA	1,2
Eurycorypha sp.*	Attracted to light from remnants				_	
	of coastal forest			X	С	1,2
Horatosphaga heteromorpha (Karsch, 1888)	Burnt grasslands; attracted to light					
n. n	at night	X			EA	1
Dioncomena ornata Brunner v. Wattenwyl,						
1878	Shrub layer of coastal forest			X	С	2
Ducetia biramosa (Karsch, 1888)	Forest edge in coastal forest		X		С	1,2
Tylopsis rubrescens Kirby, 1900	Burnt grasslands	X				1
Tylopsis irregularis Karsch, 1893	Burnt grasslands	X				1
Subfamily Mecopodinae						
Gymnoscirtus unguiculatus (Karsch, 1888)	Undergrowth of coastal forest			X	С	2
Subfamily Conocephalinae						
Agraecia sansibara Redtenbacher, 1891	Attracted to light near forest			X	С	1,2
Conocephalus (C.) conocephalus (Linné, 1767)	Burnt grasslands	X				1
Megalotheca longiceps (Peringuey, 1916)	Burnt grasslands	X				1
Subfamily Pseudophyllinae	T 1 C 1C				г.	~
Acauloplax exigua Karsch, 1891	Tree layer of coastal forest			X	EA	2
Subfamily Hetrodinae	Dh1 f 1				C	1
Enyaliopsis bloyeti (Lucas, 1885)	Bushes along forest edges		X		С	1

^{*} probably new species, thus it is assumed that these Saltatoria are coastal endemics

TABLE 2. Habitat and distribution pattern of Saltatoria species on Pangani coast. WS: widespread species (whole Africa, tropical Africa), EA: species confined to East Africa, C: coastal endemics, with share of the total number in %, Total: total species number.

Habitat	WS	%	EA	%	С	%	Total
Grasslands	29	81%	5	14%	2	5%	36
Forest edge	2	15%	4	31%	7	54%	13
Forest	0	_	4	33%	8	67%	12
Totals	32	52%	12	20%	17	28%	61

the forest remnants along the coast (indicated with "1" in Fig. 1) light traps were used to register tettigoniids.

RESULTS

A total of 48 Acridoidea (with Tetrigidae) and 13 Tettigonioidea species were recorded from the area (Table 1).

In the grasslands, 36 species were found, most of them (29 species) widespread in Africa (Table 1). Five of the grassland species are restricted to East Africa and only two were coastal forms.

High frequencies of occurrence (80–100% presence during all checks of the plots) were seen in the species Orthochtha dasycnemis, Conocephalus conocephalus, Ornithacris cyanea, Eyprepocnemis plorans and Comacris semicarinatus. Some of these species also reached a high abundance. Especially Orthochtha dasycnemis and Conocephalus conocephalus had population densities of up to 2 individuals per square meter. Comacris semicarinatus were also very conspicuous. Males



FIG. 4. *Heteracris coerulipes* (adult male, Eyprepocnemidinae) is an inhabitant of forest edges.

perform courtship by rising up from high grasses with a flying sound similar to that of the European acridid *Psophus stridulus* (Linné, 1758). In living specimens the color of the alae is bright orange, fading after the insects have been preserved.

The majority of species occurring along forest edges are endemics of coastal habitats (54%) or are restricted to East Africa (31%) (Table 2).

Heteracris coerulipes is conspicuous because of its colorful alae (Fig. 4). This eyprepocnemidine is known from the forests of coastal Tanzania and the Eastern Arc Mountains (Grunshaw 1991). It was found inhabiting patches of grass along forest paths and grassy forest clearings in the forested area between Kabuko and Mwera. Individuals of this species were collected with red or blue alae. The hetrodine Enyaliopsis bloyeti, restricted to coastal Tanzania (Glenn 1991), is a species of forest edge and also bushland. During the day individuals of this species are hardly obtained while during the evening and night hours males, climbing small bushes and trees to a height of 1-2 m, can be located by their loud song. Afrophlaeoba usambarica populated grassy patches on forest clearings and along forest paths. This species was previously known only from the East Usambara Mts. (Jago 1983).

Parepistaurus pygmaeus (Fig. 5) is a coptacridine presently known from the Usambara and Nguru Mts. of the Eastern Arc Range. The records from lowland forest are interesting since Green (1998) discussed its disjunct distribution and possible reasons for it (see Discussion).

In closed forest 12 Saltatoria species were recorded. All of them were either endemics (67%) or restricted to East Africa (33%, Table 2). Eight species occurred only in undisturbed indigenous forest, four species both in the Gendagenda forest reserve and the coastal forest patch in regeneration (Table 1).



FIG. 5. Parepistaurus pygmaeus (Coptacridinae) was previously known from the Usambara and Nguru Mts.

Records of Saltatoria species mentioned below either extend our knowledge (since they were not known from coastal forest), or, for some of them, description data only are available, mostly without any information on habitat or ecology.

Catoptropteryx aurita is the only species of the genus not occurring in West Africa. Nothing has been published on the biology of this or other species of this genus. C. aurita is easily attracted to light during the evening hours. This canopy inhabitant occurred both in forest remnants at the coast near Mwera and in indiginous forest of the Gendagenda forest reserve. On Kilimanjaro it is reported also in the highly anthropogenic Chagga home gardens, where it preferred the tree Margaritaria discoidea (Hemp 2005).

Agraecia sansibara was attracted to light at the coast near Mwera, probably from the surrounding patches of forest. It was known to be present only from Zanzibar (Redtenbacher 1891), this island being not far from the shore of the area investigated. It was also collected from bushes at night in the East Usambara Mts. (Hemp, unpubl. data).

Gymnoscirtus unguiculatus is a lowland species known from localities in the Usambara Mts. (Karsch 1888, Sjöstedt 1909, Hemp 2002). This huge mecopodine occurred in closed forest between Kabuko and Mwera, where it was caught on the forest floor between litter. On the Zigi Trail (450 m a.s.l.) of the East Usambara Mts. it was obtained at night also from the forest floor.

Pseudophialosphera tectifera (Fig. 6) is a catantopine restricted to coastal forests. It was described by Ramme (1929) from the Tanga region and no additional information about this species has been hitherto published. Individuals of this species were found in closed forest of the Gendagenda reserve. Among the litter of the forest floor these flightless yellowish-brownish grasshoppers are well camouflaged. In escaping they showed similar habits as other flightless species e.g., *Tangana asymmetrica* (Fig. 7). In great jumps they tried to escape, landing among the yellowish-brownish leaves of the forest floor and sitting motionless till another disturbance induced them to move on.

DISCUSSION

The Saltatoria diversity of the studied grasslands is higher compared with the species inventory of forests. However the percentage of coastal endemics is by far higher in forest (67%) than in grasslands (5%), where the majority of Saltatoria are widespread forms (81%, Table 2, Fig. 8). Similar observations were made by Cleary & Genner (2004) for butterflies and dragonflies in Borneo. The quality of species changes as endemic species disappear in favor of generalist species in fire-influenced rain forest communities. These authors also found that a recolonization depends largely on the geographical distance between undisturbed habitats. As Saltatoria species are generally bound to certain microclimatic conditions, a recolonization of forest Saltatoria requiring high air humidity seems nearly impossible under present-day conditions, as forest patches are too far apart and are separated by grasslands and agricultural land with low air humidity. Especially the forest remnants investi-



FIG. 6. The well camouflaged *Pseudophialosphera tectifera* (adult female, Catantopinae) is an endemic of coastal forest of Tanzania.

gated along the coast near Mwera, which are fire-influenced, are not close enough to intact forests to guarantee a recolonization by the whole array of forest species, especially flightless forms. This might explain why, even in the relatively large patch of forest near Mwera (in Fig. 1 indicated with 1) which had not been affected by fire for at least 10-15 years and which seemed to offer adequate habitat conditions again for forest species, only few forest species were noted there. Those species found in this forest were either forest edge species, with a wider ecological span, which could have survived here (e.g., Plagiotriptus hippiscus, even occurring in degraded bushland, Euschmidtia sansibara, Ducetia biramosa and Phaeocatantops decoratus) or were fully winged, such as Agraecia sansibara, Eurycorypha sp. and Catoptropteryx aurita. Tangana asymmetrica (Fig. 8) was the only flightless forest species which also occurred in the fireinfluenced forest remnants at the coast near Mwera. Species of the genera Ixalidium and Tangana (the dif-



FIG. 7. Tangana assymetrica (adult male, Catantopinae) is the only forest species which was also found in fire – influenced forest patches.

ferent genus status refers solely to the asymmetric form of the male genitalia in Tangana) seem to be capable of adapting to changing environmental conditions. Ixalidium sjostedti Kevan, 1950 on Mt. Kilimanjaro and at Meru, and I. haematoscelis Gerstäcker, 1869 occurring in the Usambara Mts. and adjacent regions, for example, have obviously adapted to changing environmental conditions in the process of the ongoing destruction of indigenous forest. They were found today to inhabit altitudinally higher areas, often forest edges (I. haematoscelis near Amani, E. Usambara) and even open grassland communities (I. sjostedti, high altitude grasslands, see Hemp & Hemp (2003)). Tangana asymmetrica seems to have the same flexibility as it is able to persist in landscapes where forest cover has been reduced to small patches.

As lowland forests have been fragmented by human influence over the last centuries and even millennia affecting especially the foothills of mountains ranges such as the Usambara, Pare or Uluguru Mts. (Burgess and Clarke 2000) species might have been fragmented in their occurrence as well. In this connection the record of the flightless species Parepistaurus pygmaeus, previously known only from the Usambara and Nguru Mts. (Green 1998), provides an explanation for the hitherto assumed disjunct distribution in the Gendagenda forest reserve. Formerly this species clearly populated the whole area between the Usambara and Nguru Mts, but became extinct in the area between because of loss of adequate habitat. Since it has now been recorded in the Gendagenda reserve, lying somewhat intermediate and also indicating that this species is not restricted to submontane forest communities, it clearly shows that a changing environment was responsible for the retreat of the species. Thus flightless species such as Parepistaurus pygmaeus clearly indicate that forest habitats formerly must have covered huge areas of coastal Tanzania, extending inland even to the ranges of the Eastern Arc complex such as the Nguru, Uluguru and West Usambara Mts., and which are replaced today, due to human influence, by habitat types common to large areas of Africa. Hand in hand with the loss of these forests, goes a loss of species not found elsewhere.

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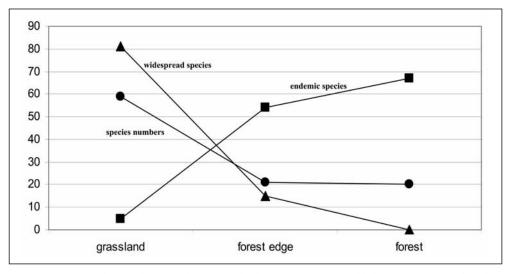


FIG. 8. Species numbers, endemics and widespread Saltatoria in % in coastal habitats near Pangani based on 61 species.

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