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Bark and ambrosia beetle communities (Coleoptera: Curculionidae: Scolytinae: Platypodinae) across five mangrove forests in South Africa

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Abstract

Background Mangrove forests are of fundamental significance that support a diverse array of species, but despite their importance and the benefits they provide, the health of these trees is under constant threat. This is due to a variety of environmental and human factors, which lead to their weakening and susceptibility to colonization by insect pests. Although the diversity of bark and ambrosia beetles has been well documented worldwide, there is limited information available regarding their relationships with mangroves. To investigate the diversity and distribution of ambrosia and bark beetles associated with mangrove habitats in South Africa, extensive field surveys and species sampling across various mangrove sites were carried out, as well as Lindgren and Panel traps were installed along five estuaries in KwaZulu–Natal and one in the Eastern Cape Province, from October to December 2013 and January to February 2014.

Results A total of 8677 individuals comprising 11 genera and 16 species of ambrosia and bark beetles were captured. Of these, the most abundant was *Hypothenemus eruditus* ($n=2178$; 25.10%), followed by *Ambrosiodmus natalensis* ($n=863$; 10.36%), *Xyleborus affinis* ($n=844$; 9.73%) and *Premnobius cavipennis* ($n=833$; 9.60%), respectively. The remaining species registered an incidence lower than 7%. From the analysis of representativeness by rarefaction curves, there was no trend toward an increase in species as the number of trajectories increased.

Conclusions This research contributes to understanding the biodiversity of ambrosia and bark beetle assemblages within South African mangrove ecosystems and underscores the importance of conserving these habitats in the face of environmental and anthropogenic pressures. The findings provide a valuable baseline for future studies and management strategies aimed at preserving mangrove health and monitoring beetle community dynamics in these critical coastal environments.

Keywords *Avicennia marina*, *Bruguiera gymnorhiza*, Coleoptera, *Rhizophora mucronata*, Stress associated insects, wood-boring beetles

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Background

Mangroves are complex ecosystems of fundamental significance, covering approximately 14.79 million hectares of coastlines in 113 tropical and subtropical countries (Food and Agriculture Organization of the United Nations, United Nations Environment Programme (FAO-UN, UNEP) 2020). Mangrove trees have evolved diverse morphological and physiological adaptations to challenge the harsh conditions under which they exist (Spalding 2010; Tomlinson, 2016). Furthermore, they need to cope with a variety of environmental and human disturbances that potentially result in their susceptibility to colonization by a variety of opportunistic pests and microorganisms (Dybas, 2015; Giri et al., 2011; Osorio et al., 2017).

In South Africa, mangroves occur from the Kosi Bay (27° S) in the northern KwaZulu–Natal Province to the southern distributional limit at Nahoon estuary (32° 56' S) in the Eastern Cape Province. *Avicennia marina* (Forssk.) Vierth. (Acanthaceae), and *Bruguiera gymnorhiza* (L.) Savigny (Rhizophoraceae), are the most widely

distributed mangrove species in South Africa, followed by *Rhizophora mucronata* Lam., (Rhizophoraceae), while stands of *Ceriops tagal* (Perr.) C.B Rob., (Rhizophoraceae), *Lumnitzera racemosa* Willd. (Combretaceae) and *Xylocarpus granatum* König, (Meliaceae) have been mostly reported in Kosi Bay (Hoppe-Speer 2013; Naidoo, 2016) (Fig. 1).

Scolytinae (Coleoptera: Scolytidae) commonly known as bark and ambrosia beetles can be classified according to their feeding and colonization biology (Atkinson, 2017; Burgos & Equihua, 2007; Kirkendall et al., 2015; Raffa et al., 2015). Ambrosia beetles have symbiotic relationships with ambrosia fungi which they cultivate as their only food source in gallery systems constructed in the sapwood of trees. Bark beetles typically colonize the phloem and cambial regions below the bark, where they feed primarily on the plant tissues. They are often associated with fungi, but fungal tissue is not the main constituent of the food (Kirkendall et al., 2015; Raffa et al., 2015).

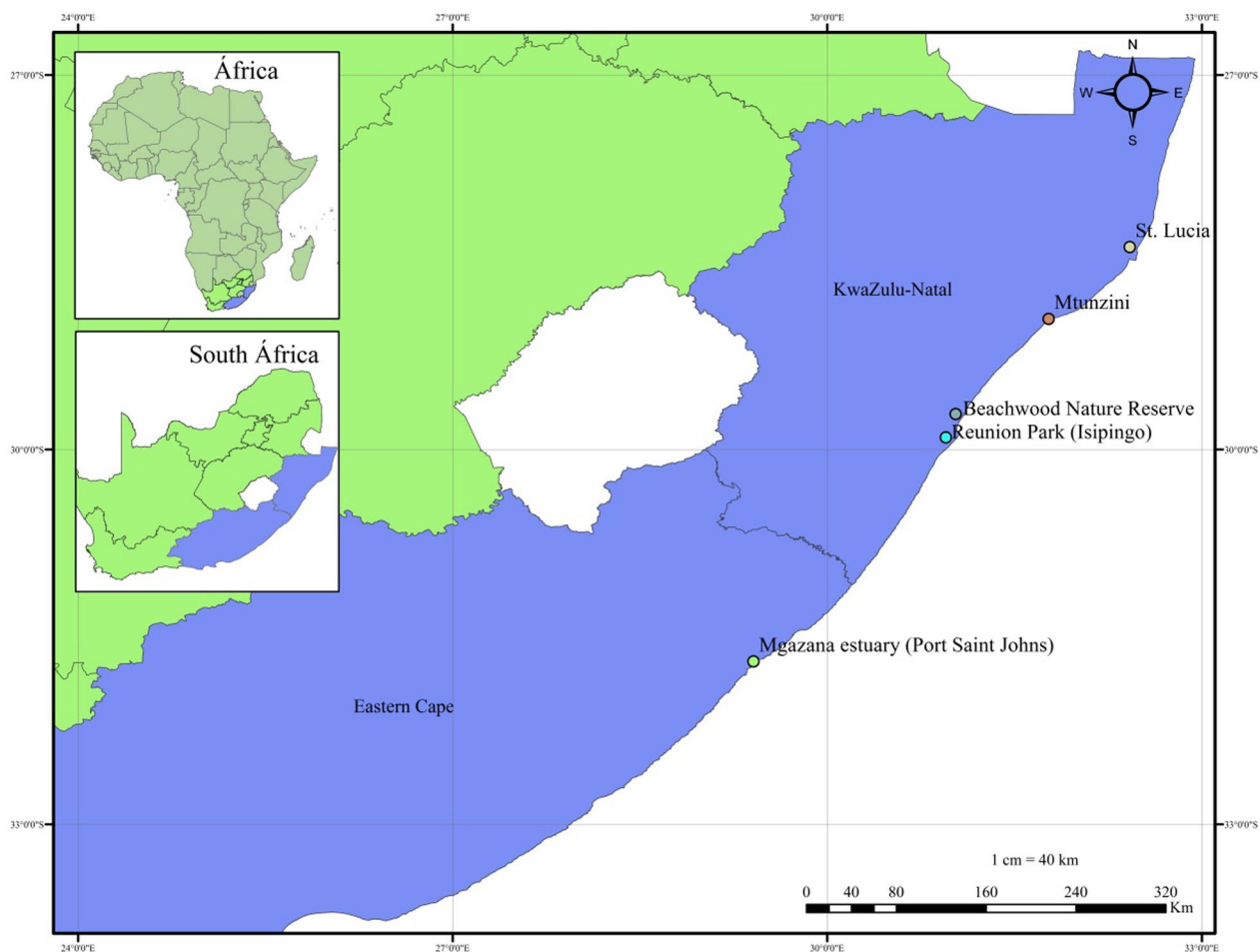


Fig. 1 Sampling sites across the eastern coast of South Africa

Ambrosia and bark beetles are ecologically and biologically important in natural forest ecosystems. However, they can also cause significant damage to ecosystems that are fragile, physically stressed, or where they have been accidentally introduced into new areas (Hulcr & Dunn, 2011; Raffa et al., 2008; Seifert et al., 1993). Very little is known regarding these insects in mangroves but the fact that these trees are commonly subjected to severe stress would make them vulnerable to infestation. In this regard, signs of wood-boring beetles have been reported from mangrove trees, particularly on *Avicennia marina* in South Africa (Osorio et al., 2017). Previous studies have also recorded ambrosia and bark beetles from mangroves in the Americas. For example, *Coccotrypes rhizophorae* (Hopkins) was reported from *Rhizophora mangle* L. in Florida, Ecuador and Peru, and in *Rhizophora harrisonii* Leech. in Panama (Woodruff, 1970; Rabinowitz 1977; Bright & Peck, 1998; Carrillo, 2001). Likewise, several ambrosia and bark beetles have been reported colonizing different mangrove species in Asia and Australia (De Baar & Hockey, 1987; Murphy, 1990; Murphy & Meepol, 1990). However, information is lacking for the African continent. The aim of this study was, therefore, to determine the communities of bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae: Platypodinae) associated with mangrove forests across the geographic distribution of these trees in South Africa.

Methods

Study area

This study was conducted in five estuaries of eastern South Africa, in the provinces of KwaZulu–Natal (KZN) and Eastern Cape (EC). From North East to South West, these estuaries included: 1. St Lucia (28° 22′ 44.87" S, 32° 25′ 22.67" E) commonly dominated by mangrove areas consisting of *Avicennia marina* and *Bruguiera gymnorhiza*; 2. The Mlalazi Nature Reserve located at Mtunzini (28° 57′ 15.39" S, 31° 46′ 23.03" E), with stands of *A. marina* and *B. gymnorhiza*; 3. Beachwood Nature Reserve located at eThekweni/Durban (29° 48′ 19.01" S, 31° 02′ 28.90" E) where trees of *A. marina*, *B. gymnorhiza* and a few individuals of *Rhizophora mucronata* form a small forest; 4. Reunion Park (Isipingo—eThekweni/Durban) (29° 59′ 32.10" S, 30° 56′ 59.72" E) characterized by heavy human impact and pollution, mostly occupied by scattered individuals of *A. marina*, *B. gymnorhiza* and occasionally *R. mucronata*; 5. Mgazana estuary (Port Saint Johns) in the Eastern Cape Province (31° 41′ 44.97" S, 29° 24′ 32.24" E) with the presence of cattle and harvesting of mangrove trees, comprising trees of *A. marina*, *B. gymnorhiza* and *R. mucronata* (Fig. 1).

Insect collection and identification

Fieldwork for ambrosia and bark beetle sampling was conducted between October and December 2013, and again from January to February 2014, across the five study sites. Although the overall field period spanned several months, actual beetle sampling occurred over a continuous four-week period within each seasonal window. Data from both sampling periods were pooled for analysis, as the sampling efforts were conducted over comparable four-week intervals at each site and followed consistent methodological protocols.

The beetles were captured using a total of six traps per site (three Lindgren funnel traps and three panel traps, randomly placed). These two trap types were selected because they complement each other in their effectiveness: Lindgren funnel traps are commonly used to target flying bark and ambrosia beetles attracted to vertical outlines that simulate natural host structures, while panel traps are effective for intercepting beetles flying at lower levels. This combination has been shown to increase sampling efficiency and capture a broader range of species (Miller & Crowe, 2011, 2022). Traps were baited with 96% industrial ethanol and tied to horizontal branches of mangrove trees or anchored high on tree trunks to a maximum of 5 m, to avoid sea tidal fluctuations. After four weeks, the traps were inspected for the presence of beetles and the specimens were transferred in the field into Falcon tubes containing 70% ethanol for transport to the laboratories of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria.

For identification, the captured beetles were separated and sorted into morphogroups using a Nikon SMZ 745 dissection microscope before being sent to Thailand for taxonomic identification. Where possible, at least five individuals per group were preserved in 1.8 ml CryoTubes™ vials with 70% ethanol and sent to Dr. Roger A. Beaver, a leading specialist in ambrosia and bark beetles, for species-level identification. Specimens were subsequently deposited in his private reference collection.

Beetles were identified by with specimens in a reference collection by using an Olympus SZ60 binocular microscope with magnification up to 150X. Specimens for comparison had previously been verified against material housed at the Natural History Museum, London, including type specimens where available. Main morphological structures were examined and documented for diagnosis, including body size, antennal morphology, elytral lateral sides and declivity shape, pronotum and elytral disk morphology, eye shape and size, abdominal shape and mature color.

Analysis of data

Alpha diversity

Nonparametric indicators of species richness (Bootstrap, Jackknife-1, Jackknife-2 and Chao-1) were used to estimate the expected richness and percentage of species represented from the five sites using EstimateS 9.1.0 Software (Colwell 2012). Richness was compared among sites using rarefaction curves at the three orders of diversity at 95% confidence intervals by interpolation and extrapolation methods under the assumption of significant differences at the 5% level between expected diversities if 95% confidence intervals did not overlap.

Beta diversity

To compare the composition of the assemblages among sites, in terms of species richness and abundance, non-hierarchical clustering and ordination analyses were used. A multidimensional nonmetric analysis (NMDS) was implemented by ordering the abundance of each species and trap per site using the Bray–Curtis dissimilarity index. This analysis preserves the order of observations in a reduced number of dimensions and enables the association of extrinsic factors (environmental variables) with the ordination of the species. For clustering (dendrogram), the distance matrix was calculated using the Bray–Curtis index, and *K*-means clustering was applied—a nonhierarchical method that partitions the dataset into *K* nonoverlapping clusters, minimizing the sum of the internal variances. All analyses were performed in R 3.1.2 (RStudio Team 2015) with the Vegan package (Oksanen et al., 2019).

Abundance rank curves were used, standardizing the number of individuals per species at each site by log10, to compare assemblage structure between sites. To evaluate the change in composition among fragments, the complementarity index (Pineda & Halffter, 2004) was implemented and expressed as:

$$C = \frac{Sa + Sb - 2ab}{Sa + Sb - Vab} * 100$$

where *a* and *b* represent the number of species from sites *A*–*B*, respectively, and *Vab* is the number of species common to both sites. Complementarity (*C*) varies from 0 (identical composition) to 100% (completely different composition).

Gamma diversity

Considering the geographic distance between sites and assuming these sites form a spatial gradient, the 30 traps sampled were unified to determine the degree of representativeness by means of rarefaction curves, based on the number of paths and 95% confidence intervals by interpolation and extrapolation methods for a maximum

trap size of 60 (double the number of units implemented). Sample coverage (0–100%) was calculated for the three orders of diversity. These analyses were performed in the R 3.1.2 program (Rstudio Team 2015) with the iNEXT 2.0.12 package (Hsieh et al., 2016).

Results

Insect collection and identification

A total of 8677 beetle individuals belonging to 12 genera and 16 species were captured between October 2013 and February 2014 (Table 1). Of these, *Hypothenemus eruditus* Westwood (sensu Wood & Bright, 1992) was the most abundant, followed by *Ambrosiodmus natalensis* (Schaufuss). The least common species was the single platypodine species found, *Crossotarsus externedentatus* (Fairmaire). Most of the collected beetles are categorized as ambrosia beetles; only two species, *Coccotrypes niger* Eggers and *Hypothenemus eruditus* Westwood are considered as bark beetles. The sites with the largest number of collected individuals were Beachwood (1927) and Isipingo (1924), followed by Mtunzini (1879) and Mgazana (1674); the least number of individuals was recorded in St. Lucia (1273) (Table 1).

Analysis of diversity

Alpha diversity

Beachwood, Isipingo and Mgazana recorded the highest number of species with seven each. Three species were restricted to the Isipingo site (*Eccoptypterus spinosus* (Olivier), *Crossotarsus externedentatus* and *Xylosandrus compactus* (Eichhoff)); two species to the Beachwood site (*Xyleborinus aemulus* (Wollaston) and *Xylosandrus crassiusculus* (Motschulsky)), and one to the Isipingo site (*Xyleborus perforans* (Wollaston)). St. Lucia and Mtunzini recorded six species each, with Mtunzini having two exclusive species, *Ambrosiodmus eichhoffi* (Schreiner) and *Diuncus haberkorni* (Eggers)). A high degree of sampling representativeness (ratio between observed and estimated richness for each of the sites) between 97.24 and 100% was established from the richness estimators (Jackknife-1, Jackknife-2, Chao-1 and Bootstrap) (Table 2).

Beta diversity

From the complementarity values for species richness (average = 70.90%, range 55.56–92.31%), a higher beta diversity was determined between Beachwood and Mgazana (92.31%), followed by Mtunzini and Mgazana (81.82%); Mtunzini–Beachwood, Mtunzini–Isipingo, Isipingo–St. Lucia and St. Lucia–Mgazana; Mtunzini–Beachwood, Mtunzini–Isipingo, Isipingo–St. Lucia and St. Lucia–Mgazana recorded a similar value (70%), while the sites with the highest degree of species similarity (lower complementarity) were St. Lucia and Beachwood

Table 1 Species composition recorded in the sampling events at the five sites in the study area

Species	ST. LUCIA		MTUNZINI		BEACHWOOD		ISIPINGO		MGAZANA		Relative AI	Beetle
	N° I	Fr	N° I	Fr	N° I	Fr	N° I	Fr	N° I	Fr		
<i>Ambrosiodmus eichhoffi</i> (Schreiner)	0	0	390	20.76	0	0	0	0	0	0	4.49	Ambrosia beetle
<i>Ambrosiodmus natalensis</i> (Schaufuss)	93	7.31	340	18.09	0	0	0	0	466	27.84	10.36	Ambrosia beetle
<i>Coccotrypes niger</i> Eggers	114	8.96	0	0	0	0	297	15.4	235	14.04	7.44	Bark beetle
<i>Crossotarsus externedentatus</i> (Fairmaire)	0	0	0	0	0	0	0	0	120	7.17	1.38	Ambrosia beetle
<i>Diuncus haberkorni</i> (Eggers)	0	0	334	17.78	0	0	0	0	0	0	3.85	Ambrosia beetle
<i>Eccoptyrus spinosus</i> (Olivier)	0	0	0	0	0	0	0	0	184	10.99	2.12	Ambrosia beetle
<i>Euwallacea fornicatus</i> (Eichhoff)	79	6.21	79	4.2	61	3.17	141	7.33	0	0	4.15	Ambrosia beetle
<i>Hypothenemus eruditus</i> Westwood s. lat	448	35.19	528	28.1	332	17.23	500	26	370	22.1	25.1	Bark beetle
<i>Premnobius cavipennis</i> Eichhoff	394	30.95	0	0	439	22.78	0	0	0	0	9.6	Ambrosia feeders
<i>Xyleborinus aemulus</i> (Wollaston)	0	0	0	0	245	12.71	0	0	0	0	2.82	Ambrosia beetle
<i>Xyleborus affinis</i> Eichhoff	0	0	208	11.07	302	15.67	334	17.4	0	0	9.73	Ambrosia beetle
<i>Xyleborus ferrugineus</i> (F.)	145	11.39	0	0	270	14.01	172	8.94	0	0	6.77	Ambrosia beetle
<i>Xyleborus perforans</i> (Wollaston)	0	0	0	0	0	0	301	15.6	123	7.35	4.89	Ambrosia beetle
<i>Xyleborus volvulus</i> (F.)	0	0	0	0	0	0	179	9.3	0	0	2.06	Ambrosia beetle
<i>Xylosandrus compactus</i> (Eichhoff)	0	0	0	0	0	0	0	0	176	10.51	2.03	Ambrosia beetle
<i>Xylosandrus crassiusculus</i> (Motschulsky)	0	0	0	0	278	14.43	0	0	0	0	3.2	Ambrosia beetle

N°I: number of individuals; Fr: relative frequency per site; relative AI: index of relative abundance for the area in general

Table 2 Observed and expected species richness for the five sites evaluated

Obs		Bootstrap		Chao-1		Jackknife-1		Jackknife-2	
		R(s)	Repre	R(s)	Repre	R(s)	Repre	R(s)	Repre
ST. Lucia	6	6	100	6	100	6	100	6	100
Mtunzini	6	6.09	98.52	6	100	6.17	97.24	6.17	97.24
Beachwood	7	7	100	7	100	7	100	7	100
Isipingo	7	7	100	7	100	7	100	7	100
Mgazana	7	7	100	7	100	7	100	7	100

Obs: observed richness, R(s): Expected richness, Repr: representativeness (%) in each richness estimator

Table 3 Complementarity index between the five evaluated sites

Sitio	St. Lucia	Mtunzini	Beachwood	Isipingo	Mgazana
St. Lucia		3	4	3	3
Mtunzini	66.67		3	3	2
Beachwood	55.56	70		4	1
Isipingo	70	70	60		3
Mgazana	70	81.82	92.31	72.73	

Upper triangle: number of species shared between pairs of sites; lower triangle: percentage of complementarity between pairs of sites

(55.56%) (Table 3). A similar pattern was shown by the ordination analysis (NMDS) in which differences in species composition were recorded as a function of abundances. In addition, a discernible pattern was presented in the ordination for the Bray–Curtis matrix (stress=0,

139,426). In the two dimensions of the NMDS (Fig. 2), species composition was relatively similar between St. Lucia and Beachwood, and markedly different between this subset and the other sites. Differences were modulated by changes in abundance in 13 of the 16 species recorded, except for *Hypothenemus eruditus*, *Euwallacea fornicatus* (Eichhoff) and *Xyleborus affinis* both with $p > 0.05$ in contribution to the ordination.

Based on the variability in richness-abundance and turnover in species composition, the degree of complementarity and similarity (Bray–Curtis index with average linkage) was established, giving five groupings with a correlation of 88.3. 5% (0.883) (Figs. 3, 4); the highest degree of similarity was between St. Lucia and Beachwood (0.41), followed by Isipingo with St. Lucia (0.52) and Beachwood (0.55). Among these sites, the greatest difference in species composition was recorded between Mtunzini and Mgazana (similarity=0.66) with

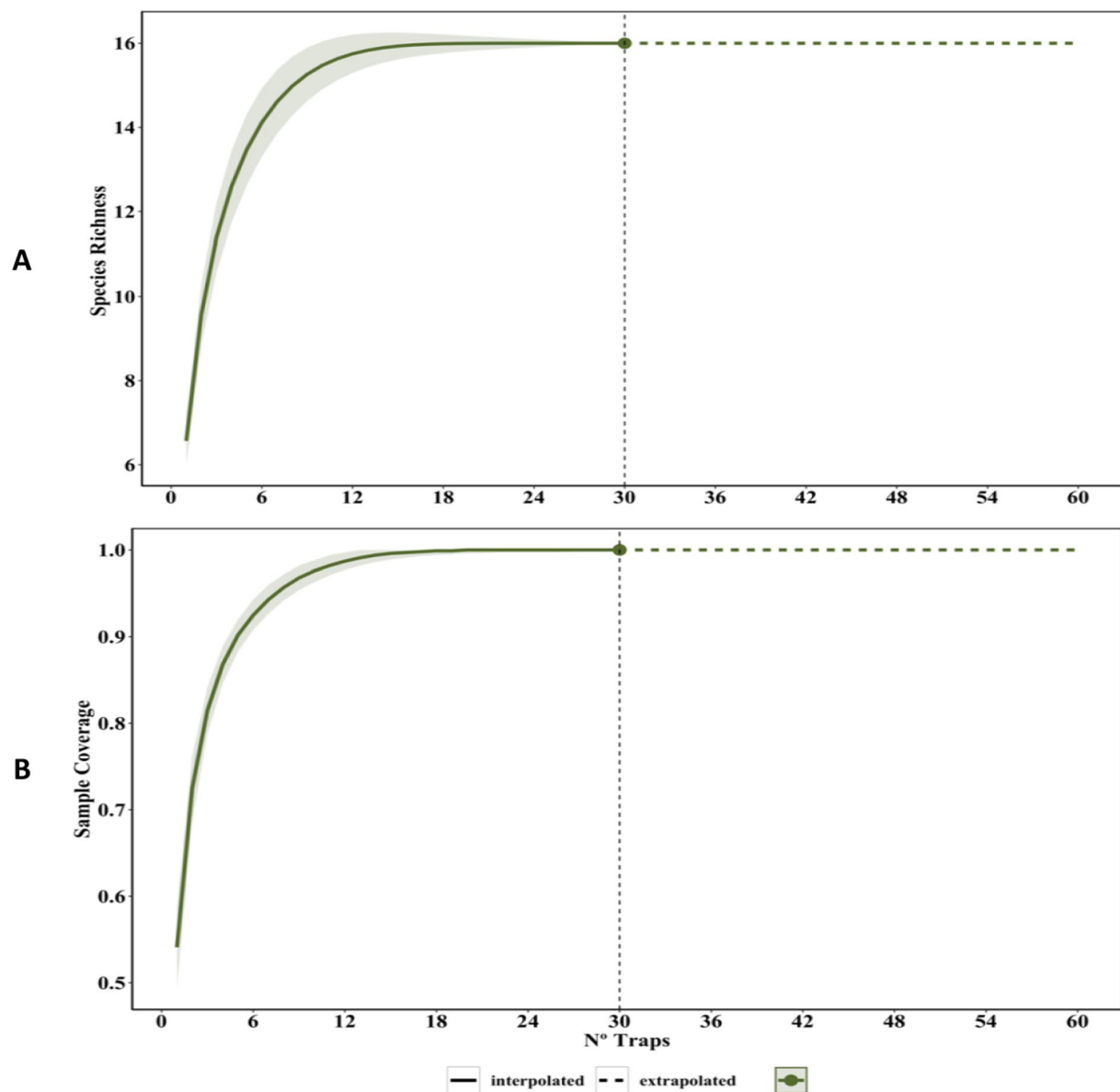


Fig. 2 A-B Extrapolation rarefaction curve for a maximum trap size of 60 (double the number of units deployed) (top **(A)** and sample coverage (bottom **(B)**) for the 30 traps deployed in the study area

the greatest range of difference in composition between Beachwood and Mgazana (0.82).

Gamma diversity

Hypothenemus eruditus presented the highest number of captures with 2178 individuals equivalent to 25.10% of the total, followed by *Ambrosiodmus natalensis* (Schaufuss) ($n=899$, 10.36%), *Xyleborus affinis* Eichhoff and *Premnobius cavipennis* Eichhoff ($n=844$, 9.72%) and ($n=833$, 9.60%), respectively; the remaining

species recorded a capture incidence of less than 7% of the total number of individuals (Table 1). From the analysis of representativeness by rarefaction curves using interpolation and extrapolation methods, there was no trend toward an increase in species as the number of trajectories increased, reaching a maximum of 16 species in 60 potential traps (Fig. 5A, B) and a sample coverage of 100% for the 30 traps and 100% for the hypothetical sample; this suggests that an increase in sampling effort may not imply a greater recording of species (Fig. 6A, B).

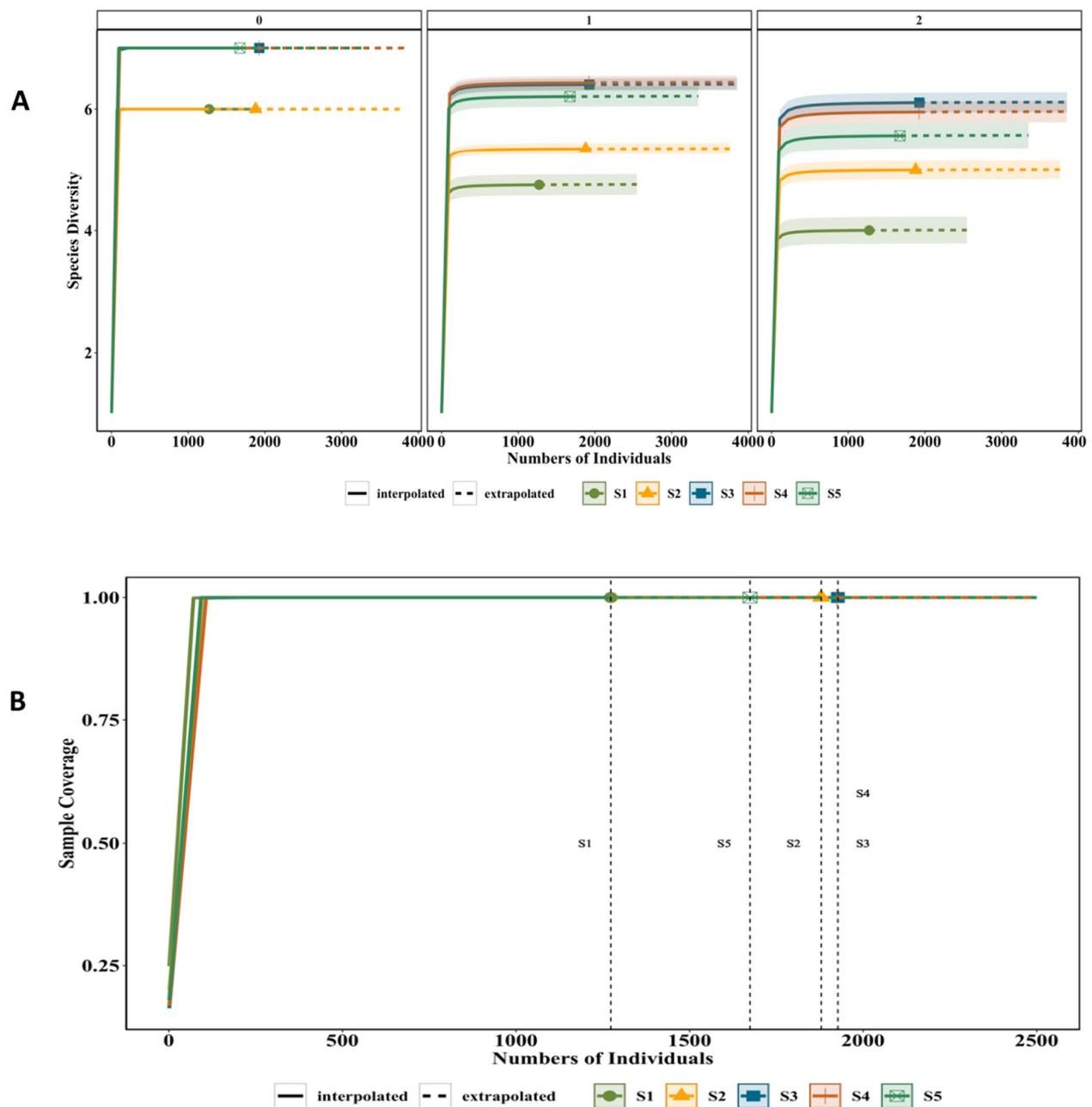


Fig. 3 **A** Rarefaction curves by interpolation and extrapolation of the number of individuals for species richness at the five sites evaluated. S1: St. Lucia; S2: Mtunzini; S3: Beachwood; S4: Isipingo; S5: Mgazana. **B** Rarefaction curves by interpolation and extrapolation of the number of individuals for sample coverage at the five sites evaluated. S1: St. Lucia; S2: Mtunzini; S3: Beachwood; S4: Isipingo; S5: Mgazana

Discussion

In this study, 8677 individuals were collected, comprising 11 genera and 16 species. Of these, *Hypothenemus eruditus* was the most abundant. Although treated here as a single species (following Wood, 2007; Wood & Bright, 1992), this species is in fact a complex of many species, which are very difficult to separate

morphologically, and which have not yet been subjected to detailed molecular analysis (Kambestad et al., 2017).

The difference of mangrove species composition may also explain the greater abundance and diversity represented by ambrosia beetles between the different sampling sites. In this sense, areas such as Beachwood and

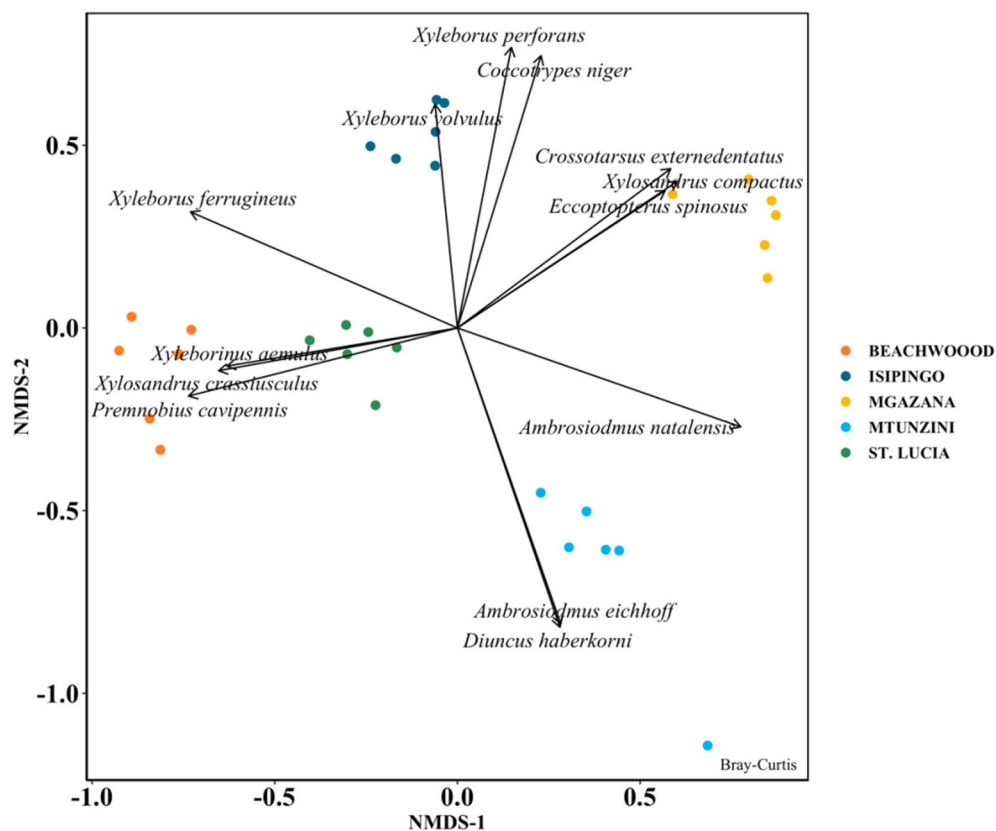


Fig. 4 Nonmetric multidimensional ordination (NMDS) for the Bray–Curtis distance matrix for species composition in the six traps located in each of the five sites sampled

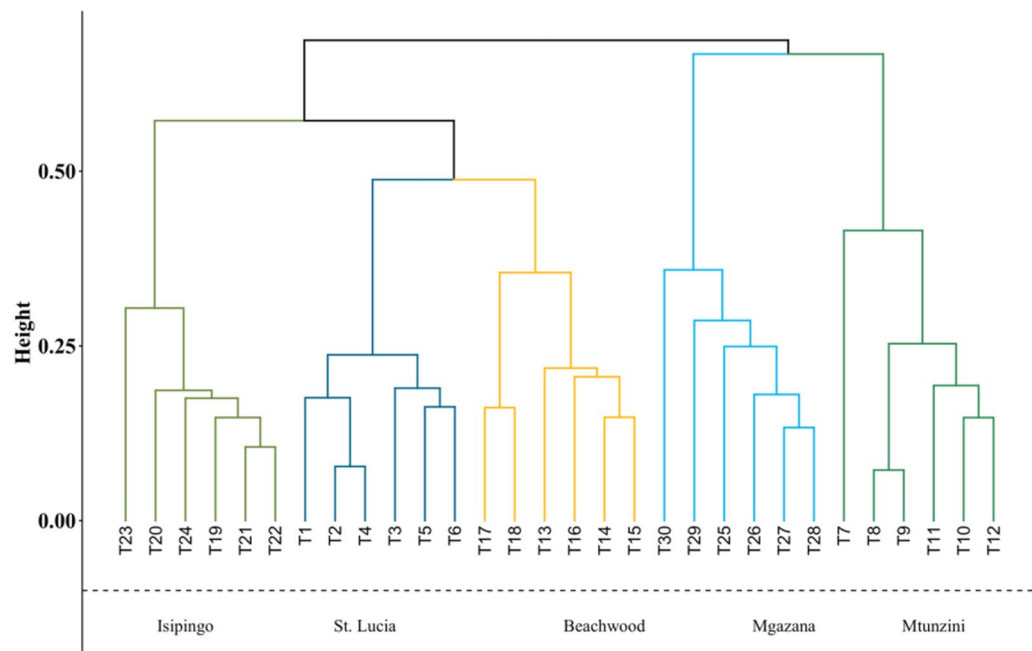


Fig. 5 Bray–Curtis clustering index by average linkage (quantitative similarity) for the composition of species present in the five sites

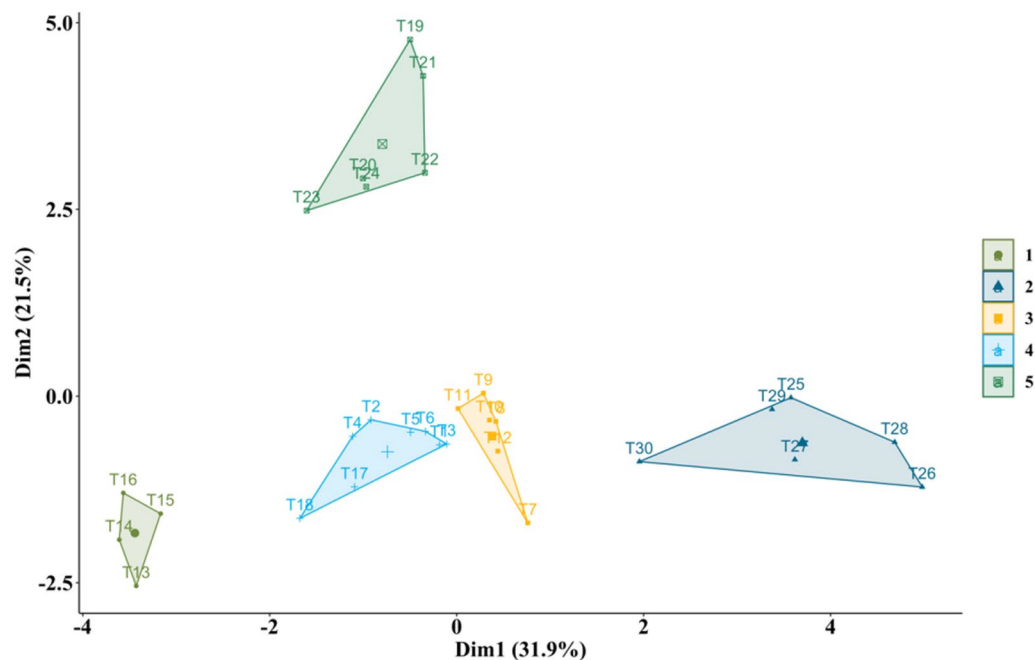


Fig. 6 K-means clustering for the species composition present in the five sites

Isipingo are represented by three species including *Avicennia marina*, *Bruguiera gymnorrhiza* and *Rhizophora mucronata*, hence, greater beetle diversity was found; in contrast, St. Lucia and Mtunzini were only represented by *A. marina* and *B. gymnorrhiza*.

The greatest richness and number of individuals of ambrosia beetle species were found at the Beachwood, Isipingo and Mgazana sites. These areas have been affected and modified by several anthropogenic disturbances causing damage and stress to the mangrove trees (Osorio et al., 2017). These results are consistent with the etiology of ambrosia beetles and other wood-boring insects well known either for been attracted by stressed trees, feed on dead trees or trees that are in the process of decay (Bright & Stark, 1973; Ng & Sivasothi, 1999). On a local scale, mangrove tree health deterioration can be determined and monitored by these beetles' presence.

The sampling carried out in this study is considered efficient in terms of representativeness by rarefaction curves. There was no trend toward an increase in species as the number of trajectories increased, suggesting that an increase in sampling effort may not imply a greater recording of species. This effectiveness can be attributed in part to the ethanol-baited traps strategy used (Fiala et al., 2023; Tobin et al., 2024a, 2024b), since in nature volatile compounds such as alcohols are released by dying, injured, stressed trees and even by fungi, and subsequently detected by several insects including bark and ambrosia beetles (Ranger et al., 2018; Kandasamy 2019).

Ambrosia and bark beetles are well-studied groups of insects, due to their relevance to the health of natural and planted forests worldwide (Ploetz et al., 2013; Wood, 2007). A number of these species are considered stress-associated insects, targeting for instance mangrove trees, which occur under several stressors such as anoxic soils, drought, flooding, high salt levels and mechanical damage by cattle, harvesting and strong winds. Species in *Hypothenemus* and *Xyleborus*, which are widely distributed and with a greater species richness in tropical regions (Wood, 1982), can be considered as occasionally aggressive to mangroves since they can damage or keep damaging any part of both healthy and injured trees.

In the present study, two *Ambrosiodmus* species were caught (*A. eichhoffi* and *A. natalensis*); however, only *A. natalensis* represented a higher Index of relative abundance between both species. This is a widespread genus that mostly colonize decayed wood, which is why it has been considered with minimal economic importance and therefore might be associated to nutrient cycling (You et al., 2015). In South Africa, *A. natalensis* has been reported colonizing dying *Euphorbia ingens* (Van der Linde et al., 2018); however, no clear association between the beetles and the injured *Euphorbia* trees was established. In line with the foregoing, the high abundance of *A. natalensis* caught in the mangrove areas might be considered as an indication of the high number of decline trees.

A study assessing beetle diversity, community composition and potential threats to forestry using ethanol-baited kairomone traps was conducted in South Africa (Olivier et al., 2017). Among the 436 beetles morphologically identified, *Coccotrypes niger* and *Xyleborus perforans* were captured in low abundances and reported for the first time in South Africa. Contrary to the previous study, the number of *C. niger* and *X. perforans* individuals captured at the mangrove areas of Isipingo and Mgazana (SA) was relatively high. Likewise, it should also be noted that Olivier et al., 2017 placed the traps inside or nearby *Pinus elliottii* and *Pinus patula* plantations, reflecting low host specificity patterns by *C. niger* *X. perforans*.

On the contrary, species, such as *Crossotarsus externedentatus* (Fairmaire), are important forestry pests worldwide distributed, also well known for causing significant harm to tree plantations (Bickerstaff et al., 2020). Although *C. externedentatus* individuals captured were relatively low at the mangrove sampling sites, it is also true that despite their unique economic and ecological role, this a species that have received little research attention particularly in mangroves areas. However, a greater concern arises when the hostile and the harsh environmental pressures that mangroves regularly face can lead to an outbreak, favoring the pest or disadvantaging its natural enemies (Berryman, 2008).

In a recent study on the disease assessment of mangroves in South Africa, *Hypothenemus eruditus* was collected from the bark of dead and living trees of the mangroves *A. marina*, *B. gymnorhiza* and *R. mucronata* in different areas of the KwaZulu–Natal (KZN) and Eastern Cape (EC) Provinces, confirming its broad host spectrum and its highly polyphagous habit (Osorio et al., 2017). *Hypothenemus eruditus* is a worldwide distributed species, and it has been considered the most common bark beetle collected from numerous host plants. (Kambestad et al., 2017; Wood, 2007). Likewise *Hypothenemus* nor *Coccotrypes* are known to be highly aggressive, its wide distribution does not necessarily indicate a risk to a given host or ecosystem (Turner & Beaver, 2015), due in part to the fact that these beetles normally colonize dead or dying plants; however, it is also true that their highly polyphagous habit may lead to the attack of branches, fruits, petioles, stems of different diameters, among other plant parts (Brockerhoff et al., 2014).

The polyphagous ambrosia beetle *Euwallacea fornicatus* is native to Asia, it has also been reported in other countries including USA and Israel; likewise, it is already considered as a widely invasive pest, becoming increasingly common also in South Africa, where these have been documented infesting plane trees (Paap et al., 2018), and other hosts of economic importance including avocado, citrus, and macadamia (Eskalen et al., 2013).

Interestingly, although *E. fornicatus* was previously reported from mangroves in South Africa (Osorio et al., 2017), no evidence of any interaction between beetles and fungal symbionts was found.

A common tribe collected in this study was *Xyleborini*, represented by four species *Xyleborus affinis*, *X. ferrugineus* (F.), *X. perforans* and *X. volvulus* (F). Members in this group are known for their polyphagous—generalist habits, hence their success in the colonization of a wide variety of plants particularly in tropical and subtropical areas (Schedl, 1963; Wood, 1982). Moreover, species of *Xyleborus* have also shown specificity in areas of disturbed and non-disturbed forests (Zambrano, 2016).

Furthermore, a study conducted in the mangroves of Tabasco (Mexico), resulted in a high number of individuals of *Xyleborus* (Gerónimo et al., 2015). *Xyleborus affinis*, *X. ferrugineus* and *X. volvulus*, collected in the present study, are well known as potential pests and invaders (Gohli et al., 2016), and for being involved in the death of different groups of plants in tropical countries; therefore, it should be treated as potential quarantine pest (Haack et al., 2013). Many species of *Xyleborus*, like *X. volvulus*, may become of pathological interest either because of their high activity in stressed or living trees or the ability to occupy a vast number of host species in disturbed areas (CABI compendium., 2022). Individuals of *Xyleborus affinis* and *Xylosandrus crassiusculus* were collected from plant material in different locations at Tzaneen, Limpopo Province, South Africa; however, no evidence of host was provided (Nel et al., 2021). Likewise, other species of *Xyleborus* including *X. perforans* and *X. volvulus* have been reported as introduced insects from different hosts in at least 27 African countries including South Africa (Wood & Bright, 1992), and *X. perforans* reported for first time in 2017 (Olivier et al., 2017).

Ambrosia and bark beetle species maintain a close interaction in nature with the plant resources available in an area (Biedermann et al. 2009; Kirkendall et al., 2015), in many cases preserving a relationship with symbiotic fungi as a source of food (Huang et al., 2019; 2020). The impact of such interactions can be considered a factor contributing to mangrove weakening and decline, since many of the fungi vectored by these beetles are important economic pathogens (Boland & Woodward, 2019; Stephenson et al., 2019). However, the presence of fungi, particularly those in the Ophiostomatales vectored by ambrosia and bark beetles in saline mangrove ecosystems, is still unknown (Osorio et al., 2016). Further investigations are therefore necessary in these ecosystems to test this hypothesis.

This study represents an important foundation for future research on ambrosia and bark beetles in South Africa and worldwide. Given the overlapping

morphological features of these beetles, upcoming work should include detailed molecular analyses of the species associated with ambrosia and bark beetles in mangrove ecosystems. Additionally, studies focusing on the fungal associates of these beetles would provide deeper insights into their ecological role and enable more detailed investigations of their potential contribution to mangroves decline.

Conclusion

The interaction between ambrosia and bark beetles and mangrove ecosystems reveals a complex ecological relationship that emphasizes the importance of biodiversity in coastal environments. Although often regarded as pests, ambrosia beetles may fulfill a dual role in mangrove habitats by contributing to nutrient cycling through their associations with wood-decaying fungi. This interaction facilitates the decomposition of dead and dying mangrove trees and supports a wide range of species that rely on these ecosystems for survival. However, the introduction and spread of non-native beetle species pose a significant threat to mangrove health and resilience, potentially disrupting these critical ecological processes. A comprehensive understanding of these dynamics is essential for effective conservation strategies aimed at safeguarding mangrove ecosystems and mitigating the impacts of biological invasions. Continued research into the relationships among ambrosia beetles, their fungal symbionts and mangrove trees will be vital for developing sustainable management approaches to protect these valuable coastal resources in the face of climate change and ongoing ecological disruption.

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Author contributions

JAO conceptualized the study and conducted field sampling contributing to this study. JAO conducted laboratory and data analysis. JCh contributed to data analyses. Both authors contributed to the interpretation of data and writing of the manuscript and approved it for publication.

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Declarations

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Consent for publication

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Competing interests

There is not any potential conflict of interest.

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