

# Habitat creation and biodiversity maintenance in mangrove forests: Teredinid bivalves as ecosystem engineers

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# Habitat creation and biodiversity maintenance in mangrove forests: Teredinid bivalves as ecosystem engineers

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## Abstract

Substantial amounts of dead wood in the intertidal zone of mature mangrove forests are tunnelled by teredinid bivalves. When the tunnels are exposed, animals are able to use tunnels as refuges. In this study, the effect of teredinid tunnelling upon mangrove forest faunal diversity was investigated. Mangrove wood not containing teredinid-tunnels had very few species and abundance of animals. However, with a greater cross-sectional surface area of teredinid tunnels, the numbers of species and abundance of animals was significantly higher. Temperatures within teredinid-attacked wood were significantly cooler compared with air temperatures, and the animals in tunnels inside the wood may avoid desiccation by escaping the higher temperatures. Animals co-existing in teredinid tunnelled wood ranged from animals found in terrestrial ecosystems including centipedes, crickets and spiders, and animals found in sub-tidal marine ecosystems such as fish, octopods and polychaetes. There was also evidence of breeding within teredinid-attacked wood, as many juvenile individuals were found, and they may also benefit from the cooler wood temperatures. Teredinid-tunnelled wood is a key low-tide refuge for cryptic animals, which would otherwise be exposed to piscivorous fishes and birds, and higher external temperatures. This study provides evidence that teredinids are ecosystem engineers and also provides an example of a mechanism whereby mangrove forests support intertidal biodiversity and nurseries through the wood-boring activity of teredinids.

## Introduction

Mangrove ecosystems have long been considered as low bio-diverse habitats (Duke et al. 1998; Alongi 2002), especially when compared with other tropical marine ecosystems, for example, coral reefs (Connell 1978; Knowlton et al. 2010). However, mangrove forests provide a variety of niches to creatures that depend upon these coastal ecosystems (Nagelkerken et al. 2008). Animals commonly described from mangrove forests are found in a broad range of different biomes, such as aquatic sesarmid crabs, which break down and recycle much of the leaf litter (Robertson 1990), and terrestrial beetles that processes large woody debris (LWD) in the high- to mid-intertidal areas of the forests (Feller 2002). Thus, mangrove forests host organisms commonly found in terrestrial and aquatic habitats (Nagelkerken et al. 2008). Principally, within the mangrove environment, there are three main substrata that fauna are able to exploit; sediments (Kristensen 2007), root structures (Ellison and Farnsworth 1990; Ellison et al. 1996) and LWD (Cragg and Hendy 2010; Hendy et al. 2013).

~~Studies in to the assessments of~~ tropical habitat structure have shown that the structural complexity maintains the greatest level of biodiversity (Gratwicke and Speight 2005; Fuchs 2013). Mangrove forests provide a wide number of niches that maintain a high level of biodiversity, maintained by substrata such as mangrove roots (Gratwicke and Speight 2005). The complexity of root structures provides cover and protection for small and juvenile fish communities (Ronnback et al. 1999; Correa and Uieda 2008; Wang et al. 2009) that decrease their risk of becoming predated upon (Verweij et al. 2006; Tse et al. 2008; MacDonald et al. 2009). ~~Thus,~~ the structural heterogeneity provided by the roots may either impede the movement of hunting predatory fish or the prey-fish are able to reduce their visibility by using the roots to hide behind (Laegdsgaard and Johnson 2001; Kruitwagen et al. 2010) – therefore the diversity of animals and the abundance of individuals are largely

considered to be attributed by deterministic factors such as habitat complexity (Syms and Jones 2000).

Although the mangrove roots ~~have been studied for their role~~ as a nursery habitat, little is known about the mangrove faunal communities relying upon fallen wood as a habitat; in particular wood that has been attacked by teredinid bivalves. Terebinids create many tunnels in LWD (Filho et al. 2008). When ~~the terebinids~~ die, the tunnels ~~may support biodiversity when vacant~~, for animals to exploit (Cragg and Hendy 2010, Hendy et al. 2013). This means that LWD may provide an important ecosystem service as a bio-diverse micro-habitat within intertidal areas (Storry et al. 2006). It is known that when trees fall in to freshwater ecosystems they attract a high level of biodiversity (Roth et al. 2007). The riparian zone is important as this habitat sustains many aquatic animals. Thus, LWD serves as an important link between terrestrial and aquatic ecosystems (Roth et al. 2007), ~~such as important predation refugia (Hendy et al. 2013).~~

This study aims to investigate the ecological role of teredinid bivalves in creating niches for fauna within LWD ~~from Indonesian mangrove ecosystems. The complexity of the mangrove forest determines the habitat for many fauna (Gratwicke and Speight 2005; Nagelkerken et al. 2010).~~ Thus, the engineered internal structural complexities within dead wood created by teredinid tunnels was quantified and measured, and then correlated with counts of animal abundance and number of species - to determine if increases of habitat complexity created by teredinids can enhance ecosystem-level animal abundance and numbers of species.

To increase biodiversity at ecosystem level the *engineering species*, in this case, teredinids must create conditions not present elsewhere in the landscape, and other animals must be able to live only in the engineer-created patches (Wright et al. 2002). Thus, this study tested the hypotheses that;

1. the tunnels created by teredinids, when vacant are exploited by other fauna
2. with a greater number of teredinid tunnels there will be a greater level of animal diversity within fallen wood
3. fallen wood provides a biodiversity mechanism for mangrove fauna, from environmental buffering due to cooler internal temperatures

## Materials and methods

### *Assessing the effect of teredinid tunnelling on LWD in mangrove forests*

The abundance of animals and ~~counts of species~~ within teredinid tunnels was estimated from five mangrove forests Langira, Kaluku, Loho, One Onitu and the Gili forest in East Sulawesi, Indonesia (05° 12' - 06° 10' S, 123° 20' - 124° 39' E). Within each forest, LWD samples were collected from five transects extending from the strandline out to the seaward edge. Each transect was 4m wide, and between 50 and 100m apart. For details of transect lengths and numbers of LWD samples collected, see Table 1. All wood was measured and a sample from every piece of wood within the transects that fitted the criteria for LWD (> 20 mm diameter) was ~~removed from the forest~~ for examination, and measured. The proportion of sampled wood from the total volume of fallen wood in each of the transects from each mangrove forest ranged from 1.4 to 5.5% of the total volume (Table 2B). Counts of animals removed from within the tunnels in each sample of wood was estimated to 1 litre.

The LWD samples were carefully broken apart and all animals were collected and identified. The percent of teredinid tunnels was used ~~within the samples of LWD~~ to categorise the level of teredinid attack, by measuring the percentage of the surface occupied by teredinid tunnels across the longitudinal section of each LWD sample using the digital

analysis package, Image Tool Version 3.00 (The University of Texas Health Science Centre at San Antonio).

Within each mangrove forest, the substratum type that each LWD sample was collected from was noted. Ground water salinities were measured using a Bellingham and Stanley E-Line Aquatic hand-held refractometer, and the distance from the land (strandline) of each LWD sample was recorded.

### ***In situ internal wood and ambient air temperature measurements***

A calibrated thermocouple thermometer (Oakton WD-35427-00 Temp 10 Type J) was used to measure internal temperatures of 27 *in situ* teredinid-attacked logs and outside air temperatures in the Langira mangrove forest. The thermometer had 2 temperature probes: one probe was placed upon the wood surface and the other placed in the centre of the wood. The wood was very quickly split open and the probe placed in to the centre before closing the split section. After 5 minutes of placing both probes in position, the temperature was recorded. A sample of wood from each piece of wood that temperatures were recorded from was taken back to the lab, and all animals within the vacant teredinid tunnels within the wood sample were removed and counted. ~~Temperatures were then matched with counts of animals removed from the LWD samples.~~

### ***Statistical data analysis***

The univariate and non-parametric multivariate techniques of the distance-based linear modelling package (DistLM) contained in PRIMER 6.1 (PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research) were used to explore the animal abundance and number of species removed from vacant teredinid tunnels in wood from five mangrove

forests, and tested against environmental variables: salinity, substrate type (mud, sand, and calcareous mud), distance from land (D.F.L), % surface area of teredinid attack, mangrove area and size of wood sample. Similarities of animal abundance and species between mangrove forest sites were examined using PERMANOVA, based on square-root transformed data in Bray-Curtis similarity matrices. DistLM was employed to verify relationships between the abundance of fauna and number of species removed from teredinid tunnels from each site with the environmental variables. DistLM produces a sequential test, which assesses the variation each predictor (environmental variable) has on its own, and a marginal test, assessing the variation of all the environmental variables (McArdle and Anderson 2001). The most parsimonious model was identified using the selection criterion  $R^2$ . Distance-based redundancy analyses (dbRDA) were used for visualizing the results as an ordination, constrained to linear combinations of the environmental variables. The DistLM was based on abundance and environmental data, with 4999 permutations.

To test for differences of abundances of animals and numbers of species between the sites, a General Linear Model was used. A 1-way ANOVA was used to test for site-specific variations of the percent surface area of teredinid tunnels, counts of animals removed from wood and the numbers of species removed from wood. Regression analyses were used to test for relationships of animal abundance and numbers of species within vacant teredinid tunnels with environmental factors: distance from the land, volume of LWD, surface area of teredinid tunnels and ambient air- and within wood- temperatures. A Pearson Correlation was used to test for relationships with internal wood cooling and the abundance of fauna within wood. A Paired t-test was used to determine temperature differences within wood and ambient air temperatures. Tukey's *post-hoc* pairwise comparison tests separated values into statistically distinct subsets for ANOVA. All data were checked for normality, residuals were inspected to ensure that assumptions for ANOVA were not compromised. Count data were square root

transformed and all percentage data were arcsin transformed. Statistical analyses were performed using MINITAB (MINITAB Inc, version 13.20).

## Results

In total, 44 species, amounting to 1636 individuals were found in vacant teredinid tunnels inside wood, which consisted of 9 phyla across the 5 mangrove forest localities (Table 2A and B).

The kinds of animals found inhabiting teredinid tunnels in LWD samples were diverse, and ranged from terrestrial species, such as coleopteran larvae and crickets (Insecta), intertidal species including reef spiders, *Desis martensi* (Arachnida) and mussels (Bivalvia) and aquatic species including moray eels, *Gymnothorax richardsonii* (Actinopterygii) and octopods (Cephalopoda). In addition, different stages of animal development were found — as many juvenile species were also found in the teredinid tunnels (Fig. 1).

A broad similarity between mangrove sites with the abundance of animals and numbers of species removed from LWD samples was made responsible by one variable, principally % surface area of teredinid attack explaining, 28% of the similarity between sites (Fig. 2A, B and C, DistLM sequential test,  $F = 74.2$ ,  $p = <0.001$ ). The remaining variables substrate type, LWD sample volume (L vol), site area, distance from land (D.F.L) and salinity were each non-significant (Fig. 2B, sequential test,  $p = >0.05$ ). The most parsimonious model for the five sites explained 31% of the variation, with % surface area of teredinid attack, again explaining 28% of the similarity between sites (DistLM marginal test,  $F = 74.2$ ,  $p = <0.001$ ). Site area, substrate type and D.F.L each explained a negligible similarity (DistLM marginal test,  $F = 3-8$ ,  $p = <0.05$ ).

No difference was found with the abundance of animals in wood when tested with salinity, increasing distance from the land and with the total area of the mangrove forest (Multi-regression,  $p = >0.05$ ). However, a significant difference was found with greater

volumes of LWD when correlated with greater numbers of species and abundances ( $F_{1, 193} = 8.12$ ,  $p = <0.01$ ), nonetheless a low relationship was found,  $R^2$  (adj) = 4%. The strongest relationship with best fit and significance for the numbers of species and abundance of animals in LWD was the percentage surface area of teredinid tunnels (Fig. 3A,  $F_{1, 193} = 159.34$ ,  $p = <0.001$ ,  $R^2$  (adj) = 45% and Fig. 3B,  $F_{1, 193} = 93.3$ ,  $p = <0.001$ ,  $R^2$  (adj) = 32% respectively). Also corroborated by a General Linear Model ( $p = < 0.001$ ), with site and percent surface area of teredinid attack as factors.

Distributions of the abundance and number of species removed from teredinid-attacked LWD samples varied between each site (PERMANOVA,  $F_{4, 190} = 3.5$ ,  $p = <0.01$ ). These differences were found with the degree of teredinid-tunnelling in LWD samples between the sites. Four of the mangrove forests were statistically indistinguishable, while the % surface area of teredinid attack in the Gili forest was significantly lower than Langira, Loho and Kaluku,  $12.9\% \pm 3.6\%$ ,  $28.1\% \pm 2.7\%$ ,  $28.4\% \pm 3.2\%$  and  $32.3\% \pm 5.6\%$  respectively. The greatest degree of teredinid-tunnelling was found in LWD samples from the Kaluku mangrove forest (Fig. 4A, 1-way ANOVA,  $F_{4, 190} = 5.29$ ,  $p = <0.001$ , mean  $\pm$  SE).

The Gili forest had the least abundance ( $9.2 \pm 2$ ) and number of species ( $4 \pm 0.8$ ) removed from the LWD samples, but Kaluku had significantly the greatest abundance ( $44.7 \pm 16.4$ ) and number of species ( $11.8 \pm 3.6$ ) within teredinid-attacked LWD (Fig. 4B and C, 1-way ANOVA,  $F_{4, 190} = 6$ ,  $p = < 0.001$  and  $F_{4, 190} = 3.3$ ,  $p = < 0.05$ , mean  $\pm$  SE respectively).

Temperature measurements within wood was significantly cooler compared with the ambient air temperature outside of the wood (Paired t-test,  $p = <0.001$ ). As ambient air temperature increased, internal wood temperatures were significantly cooler, with the greatest difference being  $-9.5^\circ\text{C}$  (Fig. 5, Regression analysis  $R^2 = 82\%$ ,  $F_{1, 25} = 116$ ,  $p = < 0.001$ ) and the abundance of animals within wood increased with cooler temperatures (Regression analysis  $R^2 = 19\%$ ,  $F_{1, 25} = 5.9$ ,  $p = < 0.05$ ). The cooler the internal temperature within wood

relative to ambient air temperature, the greater the abundance of animals were found within teredinid-attacked wood (Pearson Correlation,  $-0.5$ ,  $p = <0.01$ ).

## Discussion

We support our hypotheses that vacant teredinid tunnels benefit many species in Indonesian mangrove forests, and a greater surface area of tunnels will maintain a greater number of species and abundance of fauna. Animal diversity is positively correlated with increasing habitat complexity (Petren and Case 1998; Gratwicke and Speight 2005; Saha et al. 2009). If it was not for the tunnels created by teredinids, LWD would have significantly fewer animals due to the lack of niches, and a reduced nursery function, important for species such as octopods, and dartfish (Hendy et al. 2013). Thus, the fauna collected from the teredinid-attacked LWD in the mangrove forests from this study are maintained by a habitat-specific structure – teredinid tunnels inside LWD.

Large woody debris within aquatic ecosystems are important constituents in the structure and complexity of water ways and will probably become colonised by a wide variety of animals (Hilderbrand et al. 1997; Storry et al. 2006; Hendy et al. 2013). Fallen wood represents a vital resource providing a spatial subsidy for many animals within the aquatic ecosystem (McClain and Barry 2014). Wood enhances habitat complexity (Shirvell 1990; Brooks et al. 2004), the deposition of sediments, and the retention of organic matter (Bilby and Likens 1980; Smock et al. 1989). With the removal of wood however, sediment discharge will increase and a reduction of ecosystem-level habitat structural complexity will occur (Larson et al. 2001; Brooks et al. 2004). Large woody debris is therefore an important component within aquatic ecosystems (Shields et al. 2006). Thus, a major threat to mangrove ecosystems is wood harvesting (Valiela et al. 2001; Duke et al. 2007; Sanchirico and Mumby 2009), which could reduce ecosystem-level mangrove faunal diversity due to the reduced

wood volume (Benke et al. 1985; Wright and Flecker 2004; Hendy et al. 2013) and lack of niches otherwise created by teredinids.

Indeed, the results from this study corroborate previous research that LWD does increase animal diversity (Everett and Ruiz 1993; Wright and Flecker 2004). However, this study is the first to link the association of the Teredinidae with enhancing ecosystem-level biodiversity. Teredinids create niches as they consume LWD, by creating tunnels for a wide range of animals – but only when those tunnels become vacant. As the number of teredinid tunnels increase within LWD, the abundance and diversity of animals will become greater. The great amounts of animal abundance and number of species found within increasing numbers of teredinid tunnels may likely be due to a higher proportion of refuges from predation (Willis et al. 2005; Hendy et al. 2013). For example, the refuge provided by woody detritus is exploited by grass shrimp, as LWD significantly reduces their risk of predation from predatory fish (Everett and Ruiz 1993). Vulnerable species have more options for avoiding and escaping potential predation in habitats containing a greater number of niches. Structurally complex habitats may also reduce visual contact, encounter rates and aggressive behaviour between competitors (Jones et al. 2001; Willis et al. 2005).

Cryptic niches are typically exploited by animals to avoid predation (Ruxton et al. 2004), and animals may also exploit LWD to avoid extreme air temperatures. Many areas of the mangrove environment may be affected by rapid fluctuations in temperature (Taylor et al. 2005; Bennett 2010). Yet, as air temperatures increased, the temperatures measured within LWD became cooler creating a more desirable environment, and the numbers of animals in cooler samples of LWD increased, which may also reduce their risks from desiccation.

Juvenile dartfish, *Parioglossus interruptus*, although able to tolerate high temperatures, reside in the cooler teredinid tunnels during low tide (Hendy et al. 2013). Under laboratory conditions, emerged LWD has an evaporative cooling process (Hendy et al.

2013). The fauna from this study may also benefit from a lower metabolic rate due to the significantly lower temperatures within teredinid-attacked wood. Evidence of breeding within the tunnels was found, and the cooler internal temperatures in LWD may provide a key refuge for juveniles to escape high temperatures, as well as seeking relative safety from predation.

Temperature is the primary factor affecting development of invertebrates (Smith et al. 2013). Previous studies have shown that survival rates of developing veliger gastropods decrease with increasing temperatures due to higher energetic demands of development at higher temperatures (Smith et al. 2013). In this study, we found many octopods with egg sacs lining the vacant teredinid tunnels. Octopods in Indonesian mangrove forests may benefit by residing inside cooler teredinid tunnels, as metabolic processes may be slower in cooler temperatures, which may prolong octopod embryonic development – producing stronger hatchlings (Robison et al. 2014).

The contribution of teredinid-attacked LWD, and the evaporative cooling within wood (Hendy et al. 2013) to mangrove biodiversity maintenance is significant and remarkable. Mangrove forest biodiversity is significantly enhanced by a large volume of teredinid attacked LWD and the cooler temperatures in LWD may also enhance the development of eggs and juveniles found in the teredinid tunnels. Non-tunnelled LWD has a limited number of species and abundance of individuals due to the reduced niche availability. A lack of teredinid tunnels within LWD maintains a reduced habitat complexity that may likely increase predator-prey encounters. Differences of spatial structure will influence the frequency of interactions such as predation or niche exploitation for animals (Warfe and Barmuta 2004; Nurminen et al. 2007). This may also be the case for the spatial structure teredinid tunnels provide in LWD, which explains the sharp change in animal assemblages and diversity of animals in LWD without tunnels when compared to LWD with tunnels.

Biodiversity is dependent on the substratum sample size (Magurran 2004), as larger samples are likely to contain additional resources and therefore greater numbers of species.

To effectively rule out the factor of sample size from this study all LWD samples were standardised to the same volume. Even so, a greater amount of teredinid tunnels significantly enhance the animal abundance and numbers of species within LWD samples of the same volume.

Teredinid tunnelling will also influence faunal diversity at the whole ecosystem level in Indonesian mangrove forests. The lowest overall level of teredinid attacked LWD was recorded in the Gili forest, which also had the lowest counts of animal abundance and number of species when compared with the other four mangrove localities. This is more apparent when compared with Kaluku, which had the highest degree of teredinid tunnelling in LWD combined with the greatest abundance of animals and number of species. Although LWD is essential for the biodiversity of both the specialist and more generalist animals (Hilderbrand et al. 1997; Kappes et al. 2009; Hendy et al. 2013); teredinid tunnels will increase the internal structural complexity within LWD and the tunnels significantly enhance ecosystem-level biodiversity.

Teredinid tunnels are home to many vulnerable animals (juveniles and adults), which cannot bore into the very hard, un-decayed wood. Thus, the large numbers of animals that rely on teredinid tunnels for predation refugia, or environmental buffering, or both, would not be as abundant, or may not even be present in the mangrove ecosystem. With the data presented here, it is this reason we classify teredinids as *ecosystem engineers*. Vacant teredinid tunnels within LWD in mangrove forests provide many niches and the high complexity of tunnels lead to a broad range of co-existing animals within LWD. Notwithstanding, the considerable turnover of large volumes of fallen wood by teredinids in mangrove habitats – as the processed wood coupled with teredinid tissue and faecal matter

may significantly contribute to mangrove out-welling of nitrogen and carbon, improving the productivity of near-shore adjacent ecosystems.

Spatial heterogeneity is a fundamental property of the natural world (Kostylev et al. 2005) and heterogeneity within an ecosystem is a vital component for the interaction of co-existing animals (Petren and Case 1998; Gratwicke and Speight 2005). By comparison structurally simple habitats are not able to support the same levels of biodiversity when compared with habitats consisting of high levels of complexity and rugosity (Levin 1992). If mangrove harvesting and wood removal persists, then Indonesian mangrove faunal abundance and diversity will be significantly reduced at whole ecosystem levels.

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Table 1, The range of lengths (metres) of five transects extending from the strandline, and out to the fringing edge from each mangrove forest locality, combined with the total number of wood samples collected from the five transects in each mangrove forest.

Site	Transect length (m)	Number of LWD samples
Langira	340 to 440	70
Kahuku	25 to 60	20
Loho	60 to 160	44
One Onitu	80 to 110	32
Gili	70 to 100	30

Table 2 A, the Phyla and Class of animals removed from teredinid tunnels in wood from the five mangrove forest sites. \* = present in that mangrove forest. B, details of the five mangrove forest sites, with the total area of each forest (hectares), the total area surveyed of the combined five transects (hectares), the total volume of fallen wood found in the five transects (metre<sup>3</sup>), the % of wood used to quantify animals and teredinid attack from the total volume of wood within the five transects, and the total number of species and abundance of animals removed from the wood samples, combined with the abundance of animals per sample within each mangrove forest locality.

**A**

Phylum	Class	Langira	kaluku	Site Loho	One Onitu	Gili
Porifera	Homoscleromorpha	*	*	*		
Platyhelminthes	Rhabditophora	*	*	*		
Nemertea	Enopla	*	*	*		
Mollusca	Bivalvia	*	*	*		
	Gastropoda	*	*	*	*	*
	Polyplacophora	*		*		
	Cephalopoda	*		*		
Sipuncula	Sipunculidea	*	*	*	*	
Annelida	Polychaeta	*	*	*	*	*
Arthropoda	Arachnida	*	*	*	*	
	Chilopoda		*	*		*
	Insecta	*	*	*	*	*
	Malacostraca	*	*	*	*	*
Chordata	Actinopterygii	*	*	*	*	*
	Ascidiacea				*	
Echinodermata	Echinoidea	*				
	Ophiuroidea	*				

**B**

Site	Mangrove area (ha)	Mangrove area surveyed (ha)	LWD volume in transects (m <sup>3</sup> )	% of LWD analysed	Total species	Total abundance	Abundance per sample
Langira	60	1	3.5	1.6	32	608	9
Kaluku	0.5	0.1	0.22	5	25	354	18
Loho	3.1	0.2	0.75	5.5	27	412	9
One Onitu	1	0.2	1.5	1.4	21	118	4
Gili	1	0.1	1	1.6	13	126	4



Figure 1, a range of animals each removed from teredinid tunnels in wood. Images: A, a developing baby octopus. B, The Reef Spider, *Desis martensi*, removed from within its tunnel. Further evidence of the teredinid tunnel nursery-function: the desid has an egg-sac below its abdomen. C, The exposed tentacles of an octopus with egg-sacs. D, The dorsal view of a cirolanid isopod. Note the large egg-sac almost covering the pereopods. E, Richardson's Moray eel found within a teredinid tunnel. F, a megalopa (juvenile) spider crab.

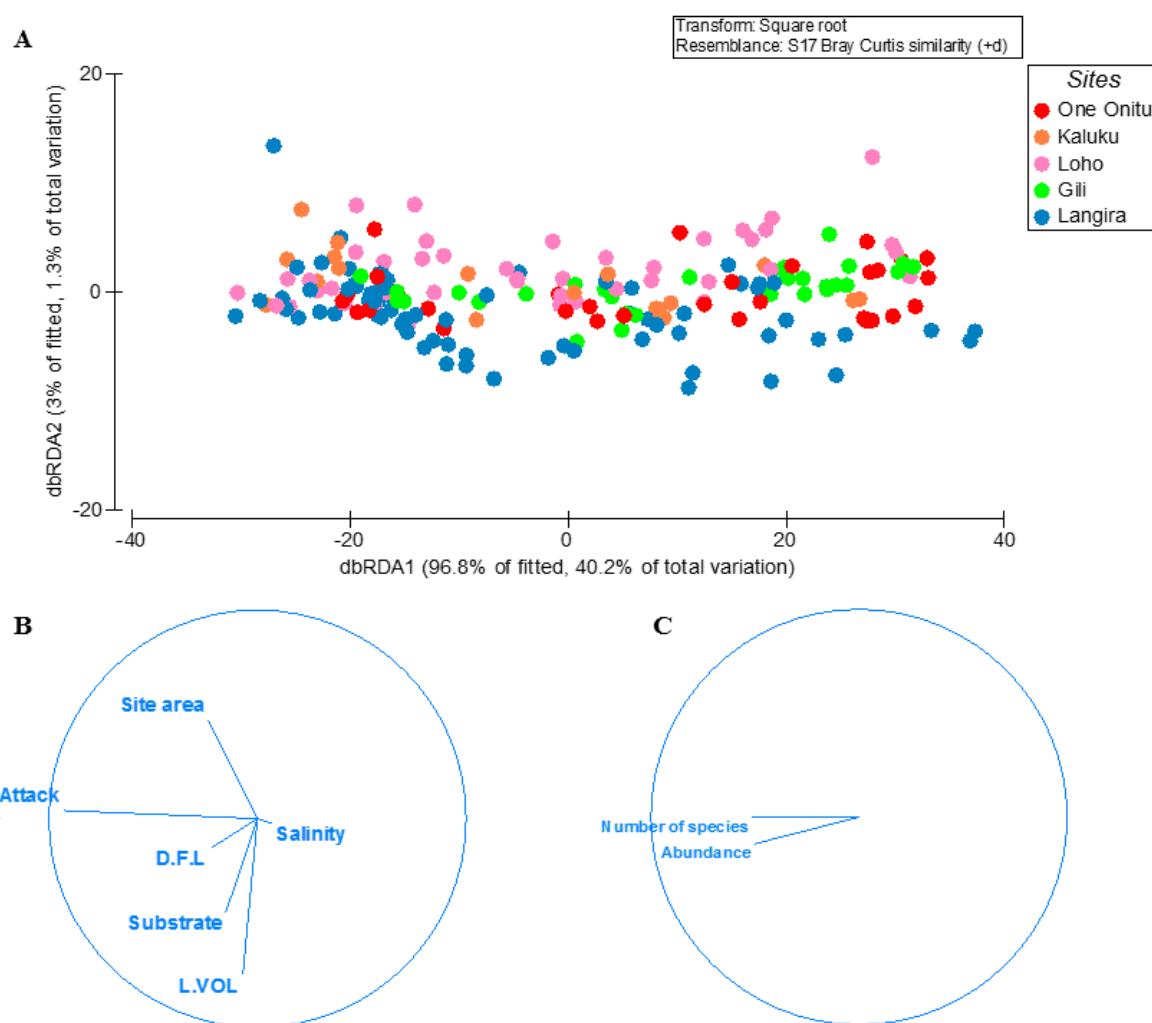


Figure 2, Distance-based redundancy analysis (dbRDA) expressed as ordinations. A, the variation of teredinid-attacked wood samples analysed from five mangrove sites in, relation to; B, measured environmental variables: teredinid-attack (attack), site area, distance from land (D.F.L), substrate type, volume of wood sample (L vol) and salinity. The strongest relationship explaining the scatter of wood samples is correlated with teredinid attack, and C, a strong relationship is found with the number of species and abundance of animals found in the wood samples with teredinid attack.

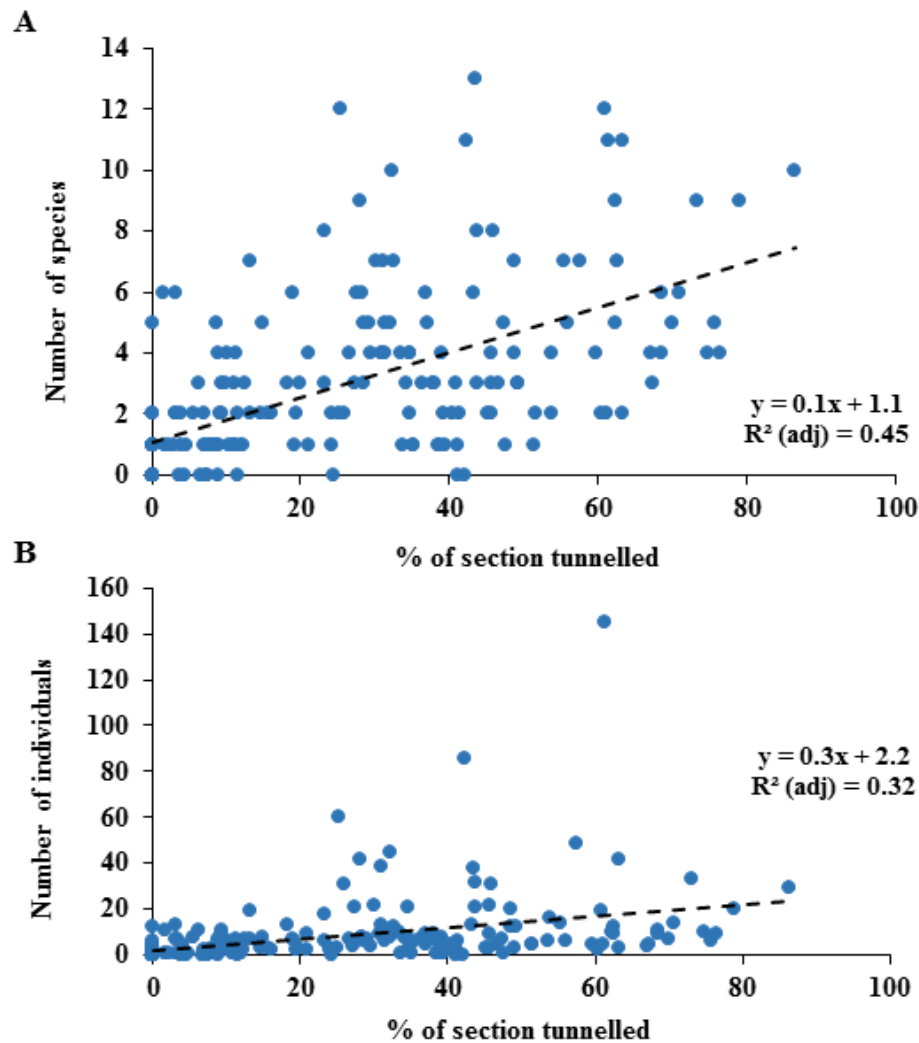
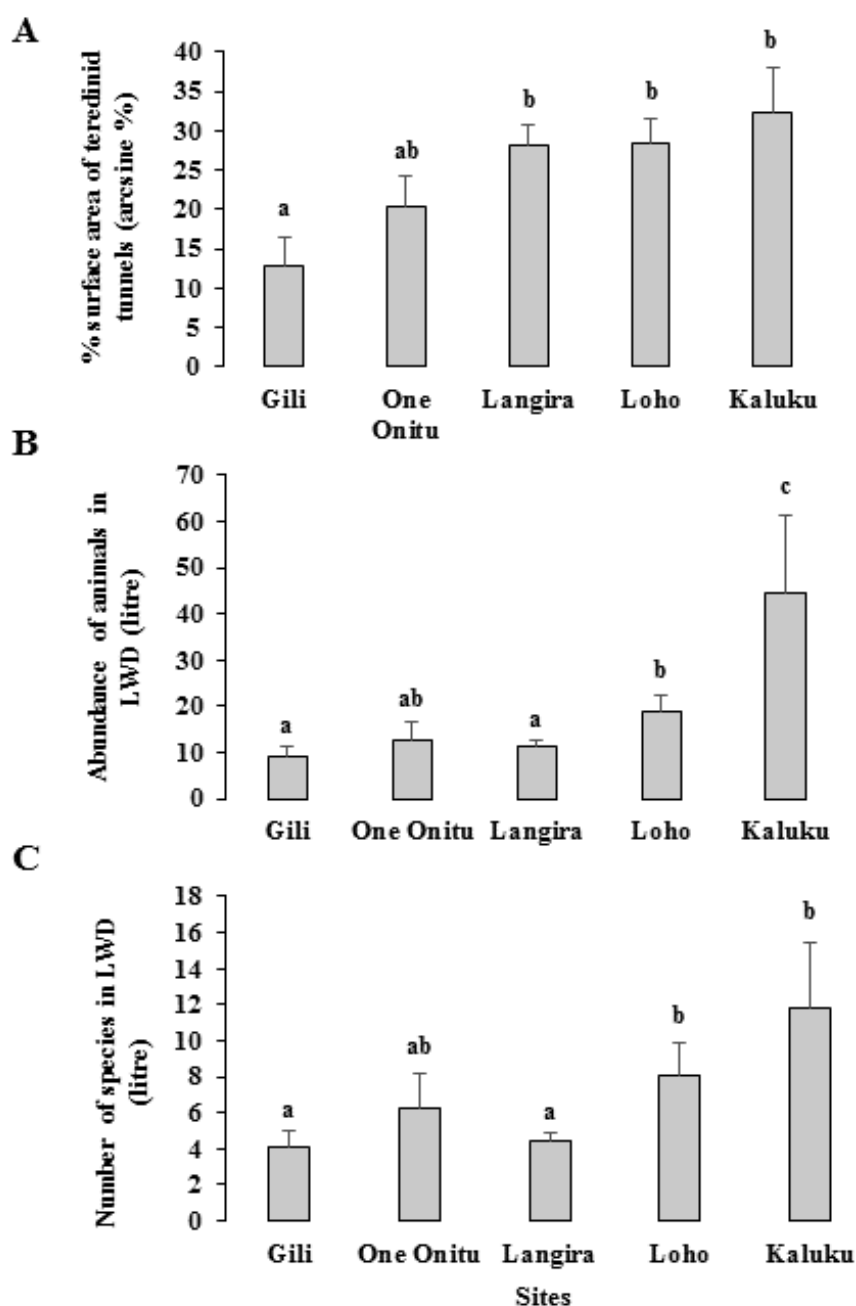
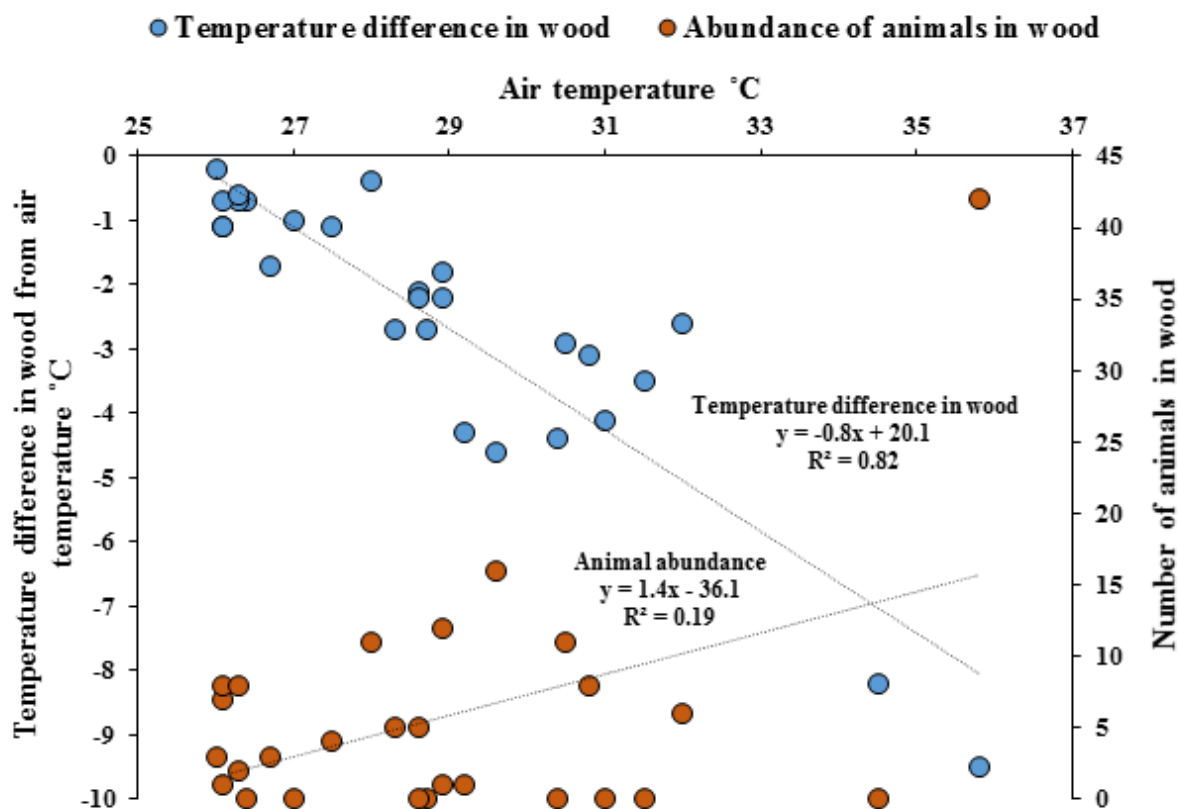


Figure 3, Regression analyses of counts of animals removed from wood that has been exposed to different levels of teredinid attack (numbers of teredinid tunnels expressed by the % cross-sectional surface area of tunnels in each wood sample). A, the number of different species ( $p = <0.001$ ), and B, the total abundance of animals ( $p = <0.001$ ), within wood samples of different levels of teredinid-attack.



**Figure 4.** The effect from vacant teredinid tunnels on whole mangrove forest ecosystems. A, the percent of cross-sectional surface area of teredinid tunnels measured in wood from five mangrove forest localities ( $p = <0.001$ ). B, the abundance of animals removed and counted from samples of tunnelled wood (standardised to 1 litre) ( $p = <0.001$ ) and, C, the number of species also removed and counted from samples of tunnelled wood (standardised to 1 litre) ( $p = <0.05$ ); from five mangrove forests (letters above the bars = Tukey's pairwise *post-hoc* comparisons, mean  $\pm$  SE).



**Figure 5.** Corresponding in-wood and outside wood-surface air temperatures (°C) of fallen logs ( $n = 27$ ) attacked by teredinids in the Langira mangrove forest, with total counts of animals removed from samples of the same logs. As wood-surface temperature increases, internal wood-temperature is significantly cooler ( $p = <0.001$ ) and the abundance of animals also significantly increase ( $p = <0.05$ ).