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

98 considered to be attributed by deterministic factors such as habitat complexity (Syms and

99 Jones 2000).

100 Although the mangrove roots have been studied for their role as a nursery habitat,

101 little is known about the mangrove faunal communities relying upon fallen wood as a habitat;

102 in particular wood that has been attacked by teredinid bivalves. Teredinids create many

103 tunnels in LWD (Filho et al. 2008). When the teredinids die, the tunnels may support

104 biodiversity when vacant, for animals to exploit (Cragg and Hendy 2010, Hendy et al. 2013).

105 This means that LWD may provide an important ecosystem service as a bio-diverse micro-

106 habitat within intertidal areas (Storry et al. 2006). It is known that when trees fall in to

107 freshwater ecosystems they attract a high level of biodiversity (Roth et al. 2007). The riparian

108 zone is important as this habitat sustains many aquatic animals. Thus, LWD serves as an

109 important link between terrestrial and aquatic ecosystems (Roth et al. 2007), such as

110 important predation refugia (Hendy et al. 2013).

111 This study aims to investigate the ecological role of teredinid bivalves in creating

112 niches for fauna within LWD from Indonesian mangrove ecosystems. The complexity of the

113 mangrove forest determines the habitat for many fauna (Gratwicke and Speight 2005;

114 Nagelkerken et al. 2010). Thus, the engineered internal structural complexities within dead

115 wood created by teredinid tunnels was quantified and measured, and then correlated with

116 counts of animal abundance and number of species - to determine if increases of habitat

117 complexity created by teredinids can enhance ecosystem-level animal abundance and

118 numbers of species.

119 To increase biodiversity at ecosystem level the *engineering species,* in this case,

120 teredinids must create conditions not present elsewhere in the landscape, and other animals

121 must be able to live only in the engineer-created patches (Wright et al. 2002). Thus, this

122 study tested the hypotheses that;

123   1. the tunnels created by teredinids, when vacant are exploited by other fauna

124   2. with a greater number of teredinid tunnels there will be a greater level of animal

125   diversity within fallen wood

126   3. fallen wood provides a biodiversity mechanism for mangrove fauna, from

127   environmental buffering due to cooler internal temperatures

Materials and methods

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Assessing the effect of teredinid tunnelling on LWD in mangrove forests

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134   The abundance of animals and counts of species within teredinid tunnels was

135 estimated from five mangrove forests Langira, Kaluku, Loho, One Onitu and the Gili forest

136 in East Sulawesi, Indonesia (05° 12' - 06° 10' S, 123° 20' - 124° 39' E). Within each forest,

137 LWD samples were collected from five transects extending from the strandline out to the

138 seaward edge. Each transect was 4m wide, and between 50 and 100m apart. For details of

139 transect lengths and numbers of LWD samples collected, see Table 1. All wood was

140 measured and a sample from every piece of wood within the transects that fitted the criteria

141 for LWD (> 20 mm diameter) was removed from the forest for examination, and measured.

142 The proportion of sampled wood from the total volume of fallen wood in each of the transects

143 from each mangrove forest ranged from 1.4 to 5.5% of the total volume (Table 2B). Counts

144 of animals removed from within the tunnels in each sample of wood was estimated to 1 litre.

145   The LWD samples were carefully broken apart and all animals were collected and

146 identified. The percent of teredinid tunnels was used within the samples of LWD to

147 categorise the level of teredinid attack, by measuring the percentage of the surface occupied

148 by teredinid tunnels across the longitudinal section of each LWD sample using the digital

149   analysis package, Image Tool Version 3.00 (The University of Texas Health Science Centre

150   at San Antonio).

151   Within each mangrove forest, the substratum type that each LWD sample was

152   collected from was noted. Ground water salinities were measured using a Bellingham and

153   Stanley E-Line Aquatic hand-held refractometer, and the distance from the land (strandline)

154   of each LWD sample was recorded.

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

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158   A calibrated thermocouple thermometer (Oakton WD-35427-00 Temp 10 Type J) was

159   used to measure internal temperatures of 27 _in situ_ teredinid-attacked logs and outside air

160   temperatures in the Langira mangrove forest. The thermometer had 2 temperature probes: one

161   probe was placed upon the wood surface and the other placed in the centre of the wood. The

162   wood was very quickly split open and the probe placed in to the centre before closing the

163   split section. After 5 minutes of placing both probes in position, the temperature was

164   recorded. A sample of wood from each piece of wood that temperatures were recorded from

165   was taken back to the lab, and all animals within the vacant teredinid tunnels within the wood

166   sample were removed and counted. Temperatures were then matched with counts of animals

167   removed from the LWD samples.

168

Statistical data analysis

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171   The univariate and non-parametric multivariate techniques of the distance-based

172   linear modelling package (DistLM) contained in PRIMER 6.1 (PrimerE Ltd: Plymouth

173   Routines in Multivariate Ecological Research) were used to explore the animal abundance

174   and number of species removed from vacant teredinid tunnels in wood from five mangrove

175 forests, and tested against environmental variables: salinity, substrate type (mud, sand, and

176 calcareous mud), distance from land (D.F.L), % surface area of teredinid attack, mangrove

177 area and size of wood sample. Similarities of animal abundance and species between

178 mangrove forest sites were examined using PERMANOVA, based on square-root

179 transformed data in Bray-Curtis similarity matrices. DistLM was employed to verify

180 relationships between the abundance of fauna and number of species removed from teredinid

181 tunnels from each site with the environmental variables. DistLM produces a marginal test,

182 which assesses the variation each predictor (environmental variable) has on its own, and a

183 sequential test, assessing the variation of all the environmental variables (McArdle and

184 Anderson 2001). The most parsimonious model was identified using the selection criterion

185 R^2. Distance-based redundancy analyses (dbRDA) were used for visualizing the results as an

186 ordination, constrained to linear combinations of the environmental variables. The DistLM

187 was based on abundance and environmental data, with 4999 permutations.

188   To test for differences of abundances of animals and numbers of species between the

189 sites, a General Linear Model was used. A 1-way ANOVA was used to test for site-specific

190 variations of the percent surface area of teredinid tunnels, counts of animals removed from

191 wood and the numbers of species removed from wood. Regression analyses were used to test

192 for relationships of animal abundance and numbers of species within vacant teredinid tunnels

193 with environmental factors: distance from the land, volume of LWD, surface area of teredinid

194 tunnels and ambient air- and within wood- temperatures. A Pearson Correlation was used to

195 test for relationships with internal wood cooling and the abundance of fauna within wood. A

196 Paired t-test was used to determine temperature differences within wood and ambient air

197 temperatures. Tukey's *post-hoc* pairwise comparison tests separated values into statistically

198 distinct subsets for ANOVA. All data were checked for normality, residuals were inspected

199 to ensure that assumptions for ANOVA were not compromised. Count data were square root

200   transformed and all percentage data were arcsin transformed. Statistical analyses were

201   performed using MINITAB (MINITAB Inc, version 13.20).

Results

203   In total, 44 species, amounting to 1636 individuals were found in vacant teredinid

204   tunnels inside wood, which consisted of 9 phyla across the 5 mangrove forest localities

205   (Table 2A and B).

206   The kinds of animals found inhabiting teredinid tunnels in LWD samples were

207   diverse, and ranged from terrestrial species, such as coleopteran larvae and crickets (Insecta),

208   intertidal species including reef spiders, *Desis martensi* (Arachnida) and mussels (Bivalvia)

209   and aquatic species including moray eels, *Gymnothorax richardsonii* (Actinopterygii) and

210   octopods (Cephalopoda). In addition, different stages of animal development were found – as

211   many juvenile species were also found in the teredinid tunnels (Fig. 1).

212   A broad similarity between mangrove sites with the abundance of animals and

213   numbers of species removed from LWD samples was made responsible by one variable,

214   principally % surface area of teredinid attack explaining, 28% of the similarity between sites

215   (Fig. 2A, B and C, DistLM marginal test, $F = 74.2$, $p = <0.001$). The remaining variables

216   substrate type, LWD sample volume (L vol), site area, distance from land (D.F.L) and

217   salinity were each non-significant (Fig. 2B, sequential test, $p = >0.05$). The most

218   parsimonious model for the five sites explained 31% of the variation, with % surface area of

219   teredinid attack, again explaining 28% of the similarity between sites (DistLM sequential test,

220   $F = 74.2$, $p = <0.001$). Site area, substrate type and D.F.L each explained a negligible

221   similarity (DistLM marginal test, $F = 3–8$, $p = <0.05$).

222   No difference was found with the abundance of animals in wood when tested with

223   salinity, increasing distance from the land and with the total area of the mangrove forest

224   (Multi-regression, $p = >0.05$). However, a significant difference was found with greater

225   volumes of LWD when correlated with greater numbers of species and abundances ($F_{1, 193}$ =

226   8.12, p = <0.01), nonetheless a low relationship was found, R^2 (adj) = 4%. The strongest

227   relationship with best fit and significance for the numbers of species and abundance of

228   animals in LWD was the percentage surface area of teredinid tunnels (Fig. 3A, $F_{1, 193}$ =

229   159.34, p = <0.001, R^2 (adj) = 45% and Fig. 3B, $F_{1, 193}$ = 93.3, p = <0.001, R^2 (adj) = 32%

230   respectively). Also corroborated by a General Linear Model (p = < 0.001), with site and

231   percent surface area of teredinid attack as factors.

232   Distributions of the abundance and number of species removed from teredinid-

233   attacked LWD samples varied between each site (PERMANOVA, $F_{4, 190}$ = 3.5, p = <0.01).

234   These differences were found with the degree of teredinid-tunnelling in LWD samples

235   between the sites. Four of the mangrove forests were statistically indistinguishable, while the

236   % surface area of teredinid attack in the Gili forest was significantly lower than Langira,

237   Loho and Kaluku, 12.9% ± 3.6%, 28.1% ± 2.7%, 28.4% ± 3.2% and 32.3% ± 5.6%

238   respectively. The greatest degree of teredinid-tunnelling was found in LWD samples from the

239   Kaluku mangrove forest (Fig. 4A, 1-way ANOVA, $F_{4, 190}$ = 5.29, p = <0.001, mean ± SE).

240   The Gili forest had the least abundance (9.2 ± 2) and number of species (4 ± 0.8)

241   removed from the LWD samples, but Kaluku had significantly the greatest abundance (44.7 ±

242   16.4) and number of species (11.8 ± 3.6) within teredinid-attacked LWD (Fig. 4B and C, 1-

243   way ANOVA, $F_{4, 190}$ = 6, p = < 0.001 and $F_{4, 190}$ = 3.3, p = < 0.05, mean ± SE respectively).

244   Temperature measurements within wood was significantly cooler compared with the

245   ambient air temperature outside of the wood (Paired t-test, p = <0.001). As ambient air

246   temperature increased, internal wood temperatures were significantly cooler, with the greatest

247   difference being -9.5˚C (Fig. 5, Regression analysis R^2 = 82%, $F_{1, 25}$ = 116, p = < 0.001) and

248   the abundance of animals within wood increased with cooler temperatures (Regression

249   analysis R^2 = 19%, $F_{1, 25}$ = 5.9, p = < 0.05). The cooler the internal temperature within wood

250 relative to ambient air temperature, the greater the abundance of animals were found within

251 teredinid-attacked wood (Pearson Correlation, -0.5, p = <0.01).

252

Discussion

254   We support our hypotheses that vacant teredinid tunnels benefit many species in

255 Indonesian mangrove forests, and a greater surface area of tunnels will maintain a greater

256 number of species and abundance of fauna. Animal diversity is positively correlated with

257 increasing habitat complexity (Petren and Case 1998; Gratwicke and Speight 2005; Saha et

258 al. 2009). If it was not for the tunnels created by teredinids, LWD would have significantly

259 fewer animals due to the lack of niches, and a reduced nursery function, important for species

260 such as octopods, and dartfish (Hendy et al. 2013). Thus, the fauna collected from the

261 teredinid-attacked LWD in the mangrove forests from this study are maintained by a habitat-

262 specific structure – teredinid tunnels inside LWD.

263   Large woody debris within aquatic ecosystems are important constituents in the

264 structure and complexity of water ways and will probably become colonised by a wide

265 variety of animals (Hilderbrand et al. 1997; Storry et al. 2006; Hendy et al. 2013). Fallen

266 wood represents a vital resource providing a spatial subsidy for many animals within the

267 aquatic ecosystem (McClain and Barry 2014). Wood enhances habitat complexity (Shirvell

268 1990; Brooks et al. 2004), the deposition of sediments, and the retention of organic matter

269 (Bilby and Likens 1980; Smock et al. 1989). With the removal of wood however, sediment

270 discharge will increase and a reduction of ecosystem-level habitat structural complexity will

271 occur (Larson et al. 2001; Brooks et al. 2004). Large woody debris is therefore an important

272 component within aquatic ecosystems (Shields et al. 2006). Thus, a major threat to mangrove

273 ecosystems is wood harvesting (Valiela et al. 2001; Duke et al. 2007; Sanchirico and Mumby

274 2009), which could reduce ecosystem-level mangrove faunal diversity due to the reduced

275 wood volume (Benke et al. 1985; Wright and Flecker 2004; Hendy et al. 2013) and lack of

276 niches otherwise created by teredinids.

277 Indeed, the results from this study corroborate previous research that LWD does

278 increase animal diversity (Everett and Ruiz 1993; Wright and Flecker 2004). However, this

279 study is the first to link the association of the Teredinidae with enhancing ecosystem-level

280 biodiversity. Teredinids create niches as they consume LWD, by creating tunnels for a wide

281 range of animals – but only when those tunnels become vacant. As the number of teredinid

282 tunnels increase within LWD, the abundance and diversity of animals will become greater.

283 The great amounts of animal abundance and number of species found within increasing

284 numbers of teredinid tunnels may likely be due to a higher proportion of refuges from

285 predation (Willis et al. 2005; Hendy et al. 2013). For example, the refuge provided by woody

286 detritus is exploited by grass shrimp, as LWD significantly reduces their risk of predation

287 from predatory fish (Everett and Ruiz 1993). Vulnerable species have more options for

288 avoiding and escaping potential predation in habitats containing a greater number of niches.

289 Structurally complex habitats may also reduce visual contact, encounter rates and aggressive

290 behaviour between competitors (Jones et al. 2001; Willis et al. 2005).

291 Cryptic niches are typically exploited by animals to avoid predation (Ruxton et al.

292 2004), and animals may also exploit LWD to avoid extreme air temperatures. Many areas of

293 the mangrove environment may be affected by rapid fluctuations in temperature (Taylor et al.

294 2005; Bennett 2010). Yet, as air temperatures increased, the temperatures measured within

295 LWD became cooler creating a more desirable environment, and the numbers of animals in

296 cooler samples of LWD increased, which may also reduce their risks from desiccation.

297 Juvenile dartfish, *Parioglossus interruptus,* although able to tolerate high

298 temperatures, reside in the cooler teredinid tunnels during low tide (Hendy et al. 2013).

299 Under laboratory conditions, emerged LWD has an evaporative cooling process (Hendy et al.

300 2013). The fauna from this study may also benefit from a lower metabolic rate due to the

301 significantly lower temperatures within teredinid-attacked wood. Evidence of breeding within

302 the tunnels was found, and the cooler internal temperatures in LWD may provide a key

303 refuge for juveniles to escape high temperatures, as well as seeking relative safety from

304 predation.

305   Temperature is the primary factor affecting development of invertebrates (Smith et al.

306 2013). Previous studies have shown that survival rates of developing veliger gastropods

307 decrease with increasing temperatures due to higher energetic demands of development at

308 higher temperatures (Smith et al. 2013). In this study, we found many octopods with egg sacs

309 lining the vacant teredinid tunnels. Octopods in Indonesian mangrove forests may benefit by

310 residing inside cooler teredinid tunnels, as metabolic processes may be slower in cooler

311 temperatures, which may prolong octopod embryonic development – producing stronger

312 hatchlings (Robison et al. 2014).

313   The contribution of teredinid-attacked LWD, and the evaporative cooling within

314 wood (Hendy et al. 2013) to mangrove biodiversity maintenance is significant and

315 remarkable. Mangrove forest biodiversity is significantly enhanced by a large volume of

316 teredinid attacked LWD and the cooler temperatures in LWD may also enhance the

317 development of eggs and juveniles found in the teredinid tunnels. Non-tunnelled LWD has a

318 limited number of species and abundance of individuals due to the reduced niche availability.

319 A lack of teredinid tunnels within LWD maintains a reduced habitat complexity that may

320 likely increase predator-prey encounters. Differences of spatial structure will influence the

321 frequency of interactions such as predation or niche exploitation for animals (Warfe and

322 Barmuta 2004; Nurminen et al. 2007). This may also be the case for the spatial structure

323 teredinid tunnels provide in LWD, which explains the sharp change in animal assemblages

324 and diversity of animals in LWD without tunnels when compared to LWD with tunnels.

325 Biodiversity is dependent on the substratum sample size (Magurran 2004), as larger

326 samples are likely to contain additional resources and therefore greater numbers of species.

327 To effectively rule out the factor of sample size from this study all LWD samples were

328 standardised to the same volume. Even so, a greater amount of teredinid tunnels significantly

329 enhance the animal abundance and numbers of species within LWD samples of the same

330 volume.

331 Teredinid tunnelling will also influence faunal diversity at the whole ecosystem level

332 in Indonesian mangrove forests. The lowest overall level of teredinid attacked LWD was

333 recorded in the Gili forest, which also had the lowest counts of animal abundance and number

334 of species when compared with the other four mangrove localities. This is more apparent

335 when compared with Kaluku, which had the highest degree of teredinid tunnelling in LWD

336 combined with the greatest abundance of animals and number of species. Although LWD is

337 essential for the biodiversity of both the specialist and more generalist animals (Hilderbrand

338 et al. 1997; Kappes et al. 2009; Hendy et al. 2013); teredinid tunnels will increase the internal

339 structural complexity within LWD and the tunnels significantly enhance ecosystem-level

340 biodiversity.

341 Teredinid tunnels are home to many vulnerable animals (juveniles and adults), which

342 cannot bore into the very hard, un-decayed wood. Thus, the large numbers of animals that

343 rely on teredinid tunnels for predation refugia, or environmental buffering, or both, would not

344 be as abundant, or may not even be present in the mangrove ecosystem if it were not for the

345 tunnelled wood. With the data presented here, it is this reason we classify teredinids as

346 *ecosystem engineers*. Vacant teredinid tunnels within LWD in mangrove forests provide

347 many niches and the high complexity of tunnels lead to a broad range of co-existing animals

348 within LWD. Notwithstanding, the considerable turnover of large volumes of fallen wood by

349 teredinids in mangrove habitats – as the processed wood coupled with teredinid tissue and

350　faecal matter may significantly contribute to mangrove out-welling of nitrogen and carbon,

351　improving the productivity of near-shore adjacent ecosystems.

352　　　Spatial heterogeneity is a fundamental property of the natural world (Kostylev et al.

353　2005) and heterogeneity within an ecosystem is a vital component for the interaction of co-

354　existing animals (Petren and Case 1998; Gratwicke and Speight 2005). By comparison

355　structurally simple habitats are not able to support the same levels of biodiversity when

356　compared with habitats consisting of high levels of complexity and rugosity (Levin 1992). If

357　mangrove harvesting and wood removal persists, then Indonesian mangrove faunal

358　abundance and diversity will be significantly reduced at whole ecosystem levels.

359

Acknowledgements

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531 Table 1, The range of lengths (metres) of five transects extending from the strandline, and out
532 to the fringing edge from each mangrove forest locality, combined with the total number of
533 wood samples collected from the five transects in each mangrove forest.
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Site	Transect length (m)	Number of LWD samples
Langira	340 to 440	70
Kaluku	25 to 60	20
Loho	60 to 160	44
One Onitu	80 to 110	32
Gili	70 to 100	30

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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^3), 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 (m³)	% 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

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

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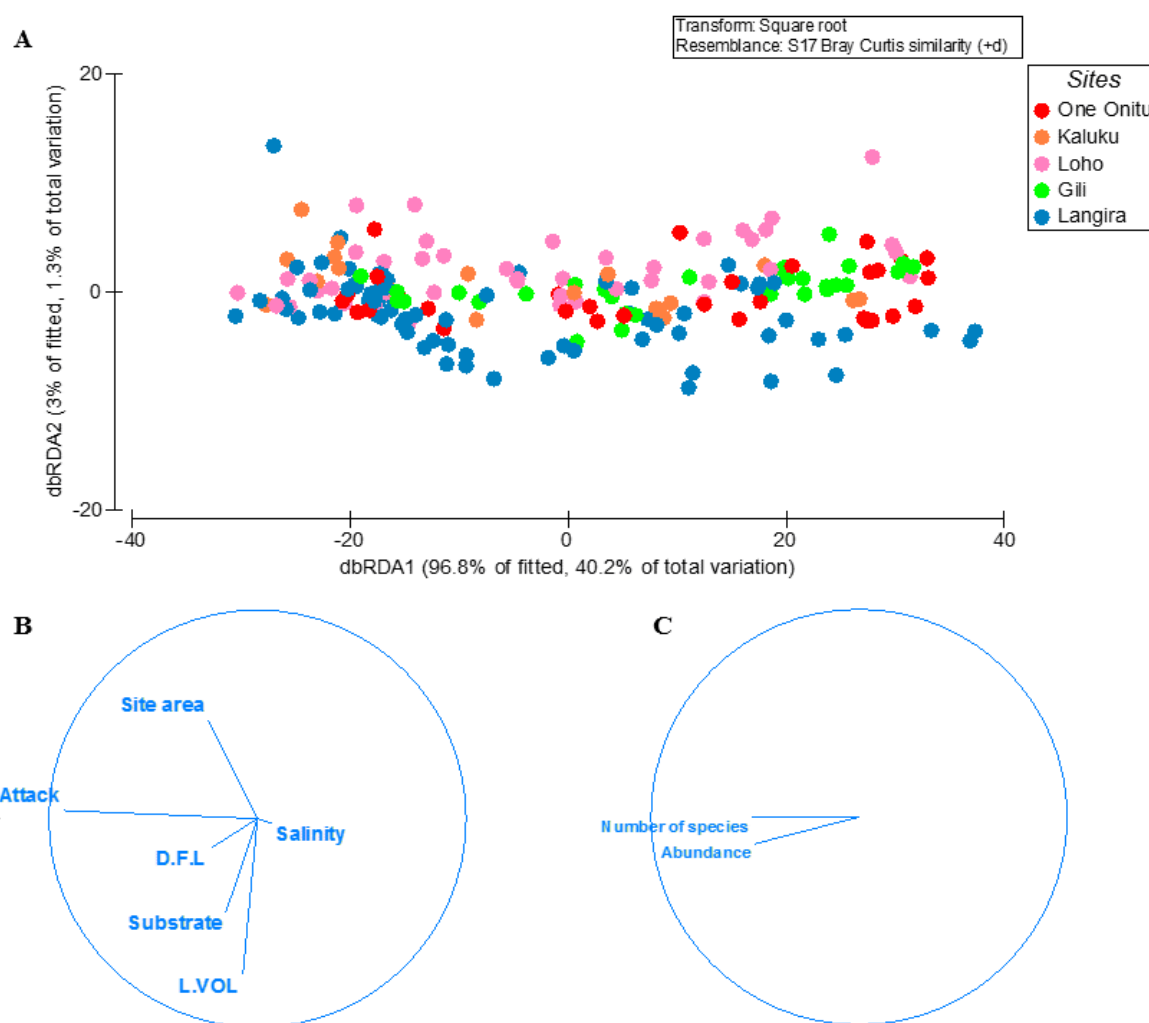
Figure 2, Distance-based redundancy analysis (dbRDA) expressed as ordinations. A, the variation of teredinid-attacked wood samples analysed from five mangrove sites in, relation to; B, measured environmental variables: teredinid-attack (attack), site area, distance from land (D.F.L), substrate type, 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.
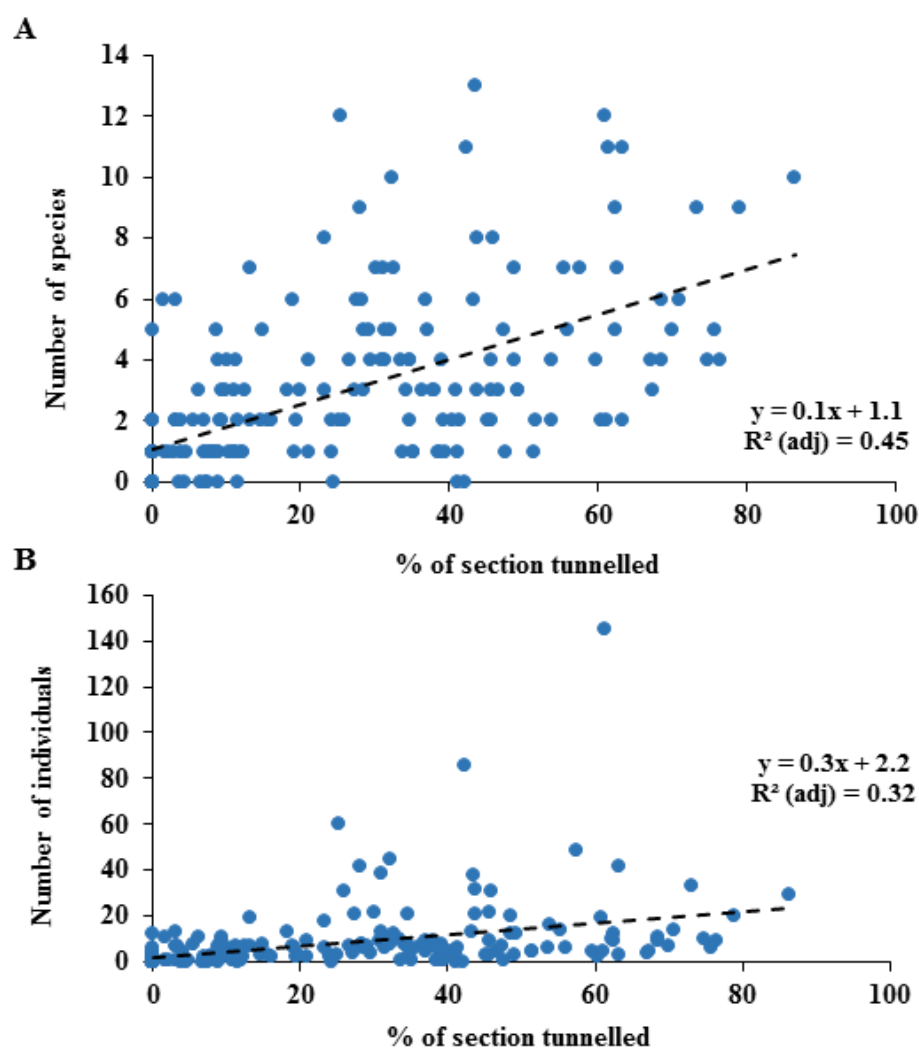
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657 Figure 3, Regression analyses of counts of animals removed from wood that has been
658 exposed to different levels of teredinid attack (numbers of teredinid tunnels expressed by the
659 % cross-sectional surface area of tunnels in each wood sample). A, the number of different
660 species ($p = <0.001$), and B. the total abundance of animals ($p = <0.001$), within wood
661 samples of different levels of teredinid-attack.
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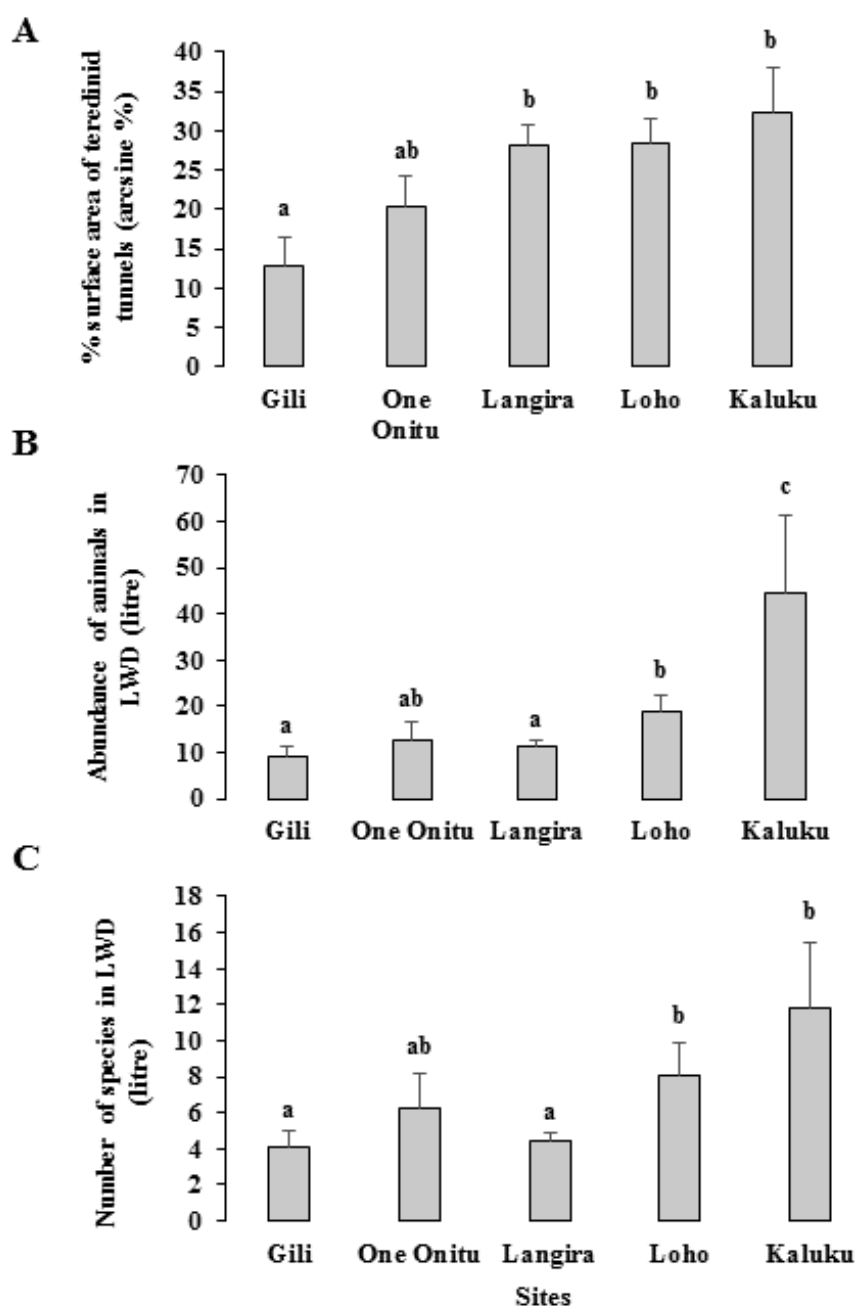664
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Figure 4, The effect from vacant teredinid tunnels on whole mangrove forest ecosystems. A, the percent of cross-sectional surface area of teredinid tunnels measured in wood from five mangrove forest localities (p = <0.001). B, the abundance of 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 ± SE).
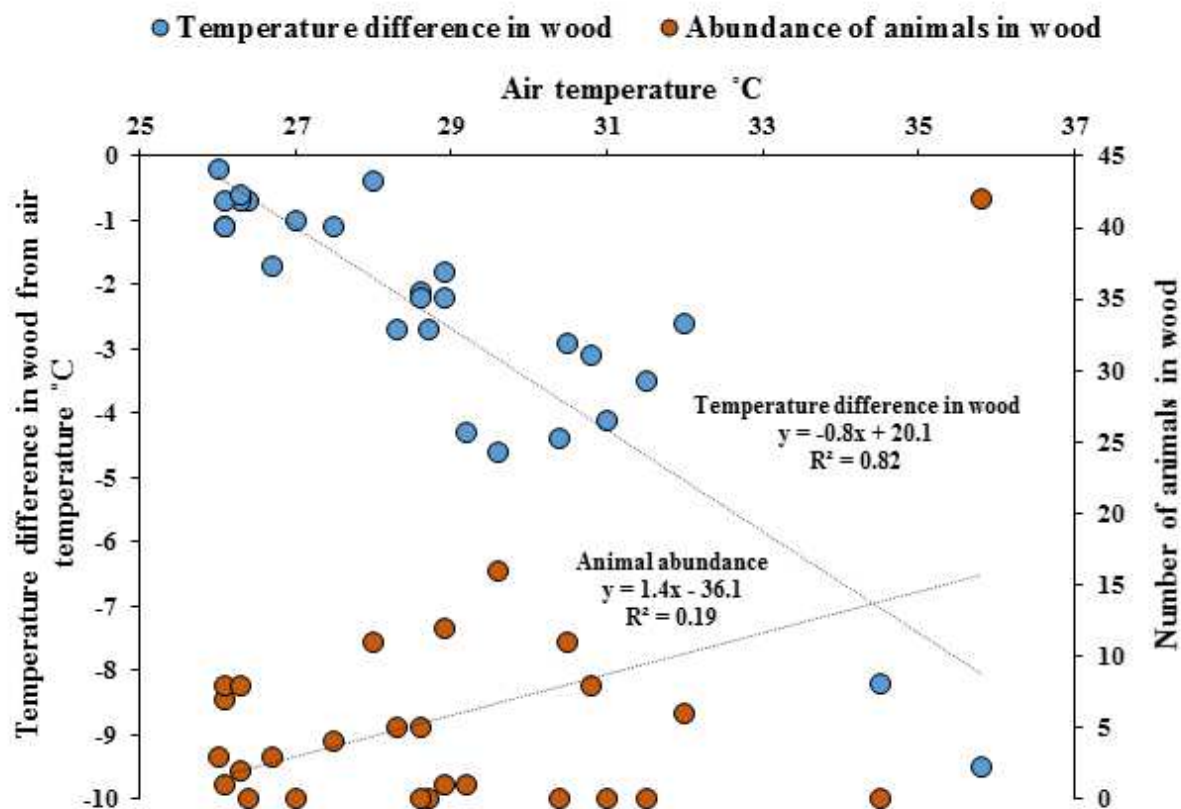
Figure 5, Corresponding in-wood and outside wood-surface air temperatures (˚C) of fallen logs (*n* = 27) attacked by teredinids in the Langira mangrove forest, with total counts of animals removed from samples of the same logs. As wood-surface temperature increases, internal wood-temperature is significantly cooler (*p* = <0.001) and the abundance of animals also significantly increase (*p* = <0.05).