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1 **Habitat creation and biodiversity maintenance in mangrove**
2 **forests: Teredinid bivalves as ecosystem engineers**

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4 Ian W. Hendy*, Laura Michie, & Ben W. Taylor

5 *Institute of Marine Sciences, University of Portsmouth, Ferry Road, PO4 9LY, UK*

6 *corresponding author

7
8
9 **email:** ian.hendy@port.ac.uk

10
11 **phone:** +44(0)23 92845799

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13 **Keywords:** mangrove wood, teredinid tunnels, cryptic fauna, biodiversity, niche creation,
14 refuge, nursery.

44 **Abstract**

45
46 Substantial amounts of dead wood in the intertidal zone of mature mangrove forests are
47 tunnelled by teredinid bivalves. When the tunnels are exposed, animals are able to use tunnels
48 as refuges. In this study, the effect of teredinid tunnelling upon mangrove forest faunal
49 diversity was investigated. Mangrove wood not containing teredinid-tunnels had very few
50 species and abundance of animals. However, with a greater cross-sectional surface area of
51 teredinid tunnels, the numbers of species and abundance of animals was significantly higher.
52 Temperatures within teredinid-attacked wood were significantly cooler compared with air
53 temperatures, and the animals in tunnels inside the wood may avoid desiccation by escaping
54 the higher temperatures. Animals co-existing in teredinid tunnelled wood ranged from
55 animals found in terrestrial ecosystems including centipedes, crickets and spiders, and
56 animals found in sub-tidal marine ecosystems such as fish, octopods and polychaetes. There
57 was also evidence of breeding within teredinid-attacked wood, as many juvenile individuals
58 were found, and they may also benefit from the cooler wood temperatures. Teredinid-
59 tunnelled wood is a key low-tide refuge for cryptic animals, which would otherwise be
60 exposed to piscivorous fishes and birds, and higher external temperatures. This study
61 provides evidence that teredinids are ecosystem engineers and also provides an example of a
62 mechanism whereby mangrove forests support intertidal biodiversity and nurseries through
63 the wood-boring activity of teredinids.

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72 Introduction

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

87 Studies in to the assessments of tropical habitat structure have shown that the
88 structural complexity maintains the greatest level of biodiversity (Gratwicke and Speight
89 2005; Fuchs 2013). Mangrove forests provide a wide number of niches that maintain a high
90 level of biodiversity, maintained by substrata such as mangrove roots (Gratwicke and Speight
91 2005). The complexity of root structures provides cover and protection for small and juvenile
92 fish communities (Ronnback et al. 1999; Correa and Uieda 2008; Wang et al. 2009) that
93 decrease their risk of becoming predated upon (Verweij et al. 2006; Tse et al. 2008;
94 MacDonald et al. 2009). Thus, the structural heterogeneity provided by the roots may either
95 impede the movement of hunting predatory fish or the prey-fish are able to reduce their
96 visibility by using the roots to hide behind (Laegdsgaard and Johnson 2001; Kruitwagen et al.
97 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

128 **Materials and methods**

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131 Assessing the effect of teredinid tunnelling on LWD in mangrove forests

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.

155

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

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

168

169 ***Statistical data analysis***

170

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).

202 **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, $12.9\% \pm 3.6\%$, $28.1\% \pm 2.7\%$, $28.4\% \pm 3.2\%$ and $32.3\% \pm 5.6\%$
 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 \pm 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 ($44.7 \pm$
 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 \pm 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

253 **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

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366

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529 fish diversity in a Venezuelan piedmont stream. *Biological Conservation*
530 120:439–44.

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
Kahuku	25 to 60	20
Loho	60 to 160	44
One Onitu	80 to 110	32
Gili	70 to 100	30

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571 Table 2 A, the Phyla and Class of animals removed from teredinid tunnels in wood from the
 572 five mangrove forest sites. * = present in that mangrove forest. B, details of the five
 573 mangrove forest sites, with the total area of each forest (hectares), the total area surveyed of
 574 the combined five transects (hectares), the total volume of fallen wood found in the five
 575 transects (metre³), the % of wood used to quantify animals and teredinid attack from the total
 576 volume of wood within the five transects, and the total number of species and abundance of
 577 animals removed from the wood samples, combined with the abundance of animals per
 578 sample within each mangrove forest locality.
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A

Phylum	Class	Langira	kaluku	Site Loho	One Onitu	Gili
Porifera	Homoscleromorpha			*		
Platyhelminthes	Rhabditophora	*	*	*		
Nemertea	Enopla	*	*	*		
Mollusca	Bivalvia	*	*	*		
	Gastropoda	*	*	*	*	*
	Polylacophora			*		
	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 ³)	% 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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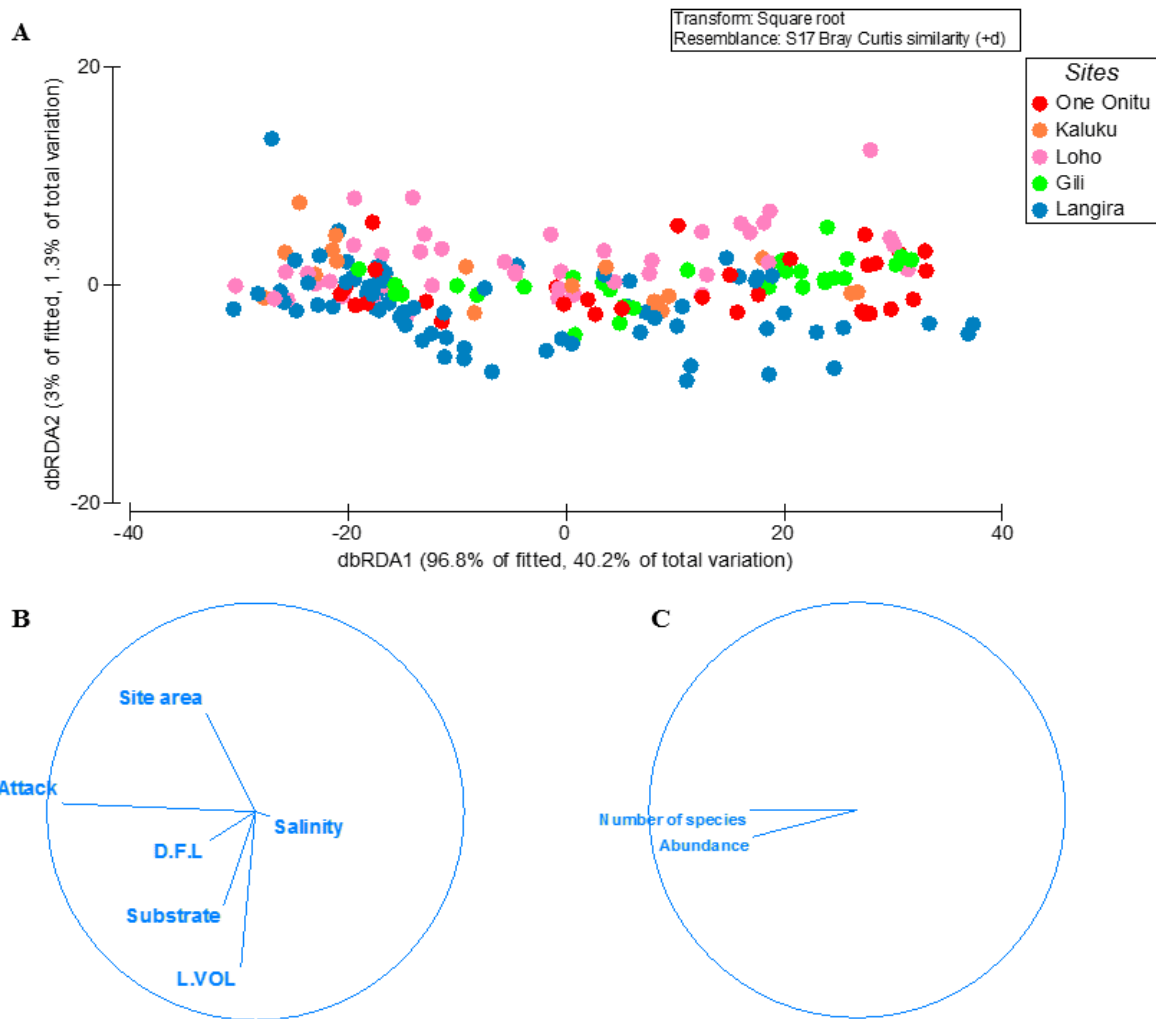
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629 Figure 2, Distance-based redundancy analysis (dbRDA) expressed as ordinations. A, the
 630 variation of teredinid-attacked wood samples analysed from five mangrove sites in, relation
 631 to; B, measured environmental variables: teredinid-attack (attack), site area, distance from
 632 land (D.F.L), substrate type, volume of wood sample (L vol) and salinity. The strongest
 633 relationship explaining the scatter of wood samples is correlated with teredinid attack, and C,
 634 a strong relationship is found with the number of species and abundance of animals found in
 635 the wood samples with teredinid attack.

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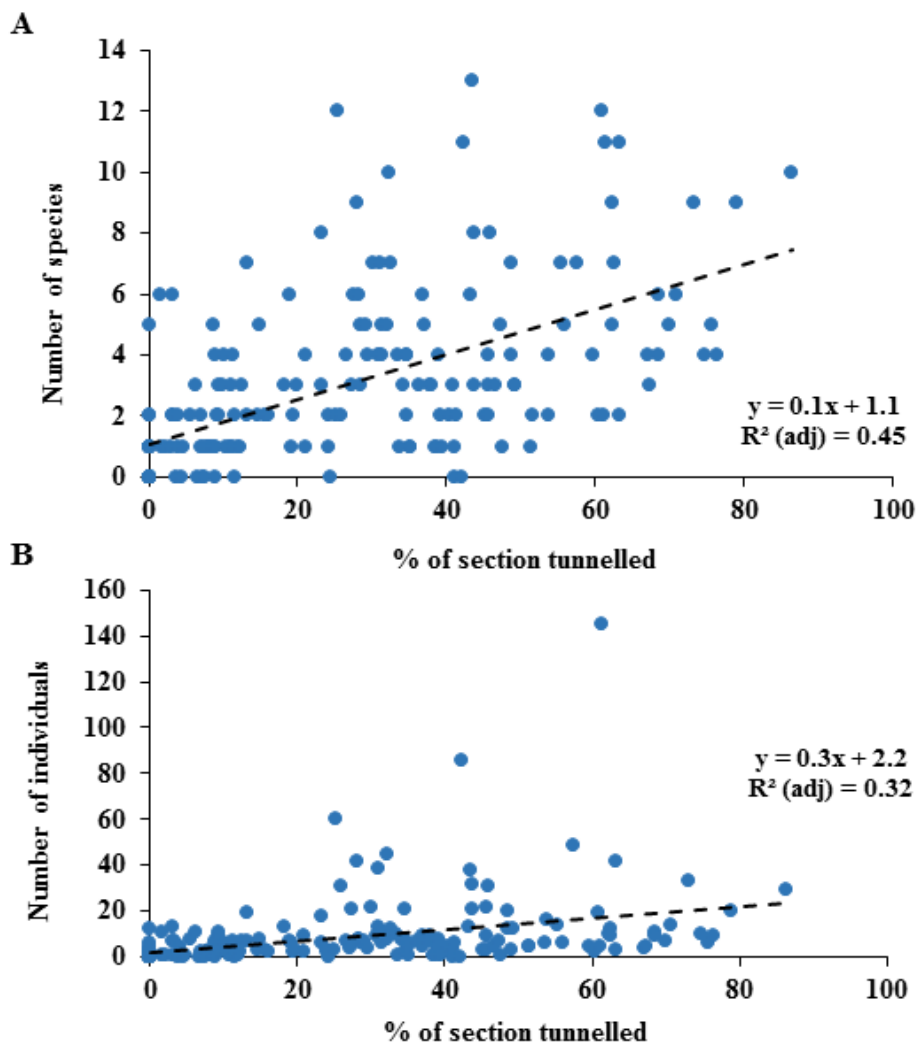
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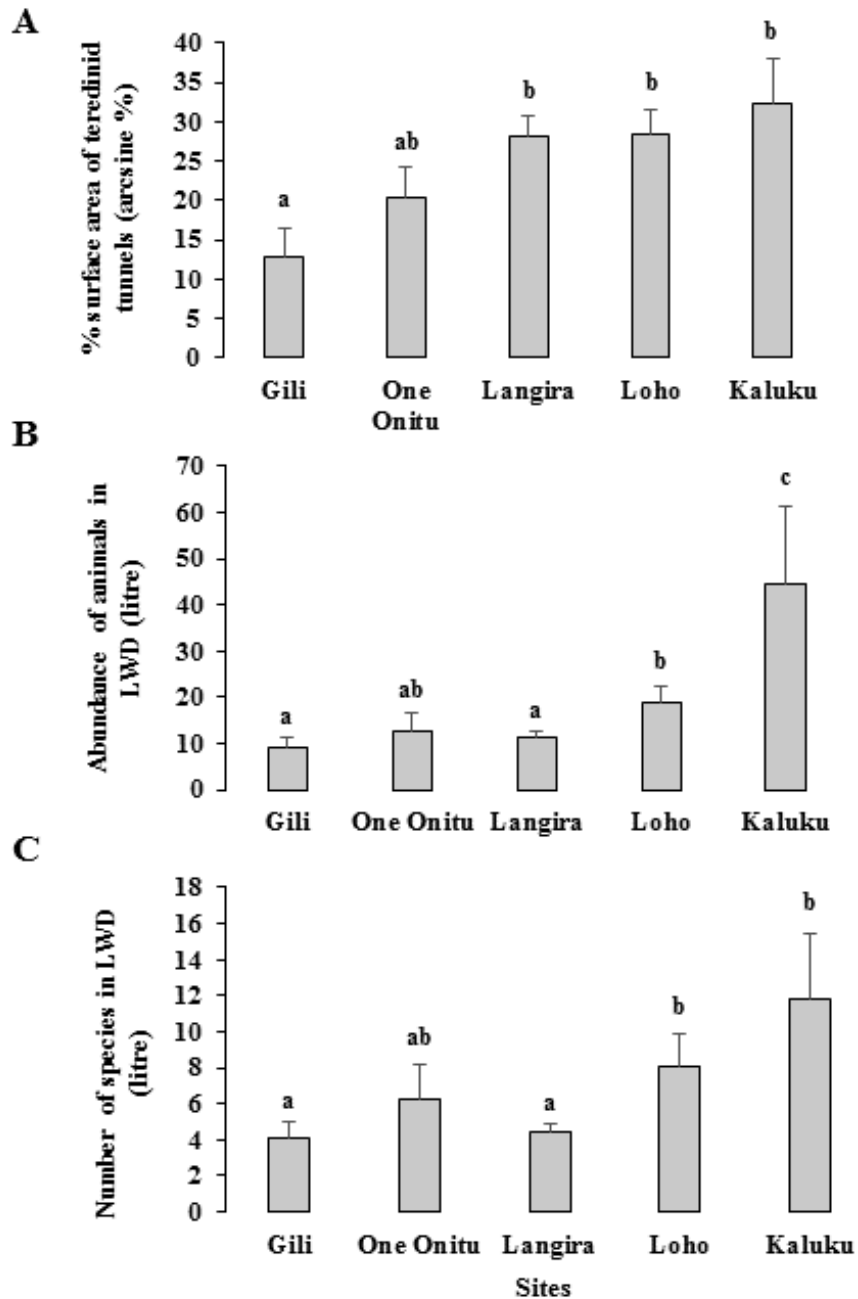
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Figure 3, Regression analyses of counts of animals removed from wood that has been exposed to different levels of teredinid attack (numbers of teredinid tunnels expressed by the % cross-sectional surface area of tunnels in each wood sample). A, the 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.



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674 Figure 4, The effect from vacant teredinid tunnels on whole mangrove forest ecosystems. A,

675 the percent of cross-sectional surface area of teredinid tunnels measured in wood from five

676 mangrove forest localities ($p = <0.001$). B, the abundance of animals removed and counted677 from samples of tunnelled wood (standardised to 1 litre) ($p = <0.001$) and, C, the number of678 species also removed and counted from samples of tunnelled wood (standardised to 1 litre) (p 679 $= <0.05$): from five mangrove forests (letters above the bars = Tukey's pairwise *post-hoc*680 comparisons, mean \pm SE).

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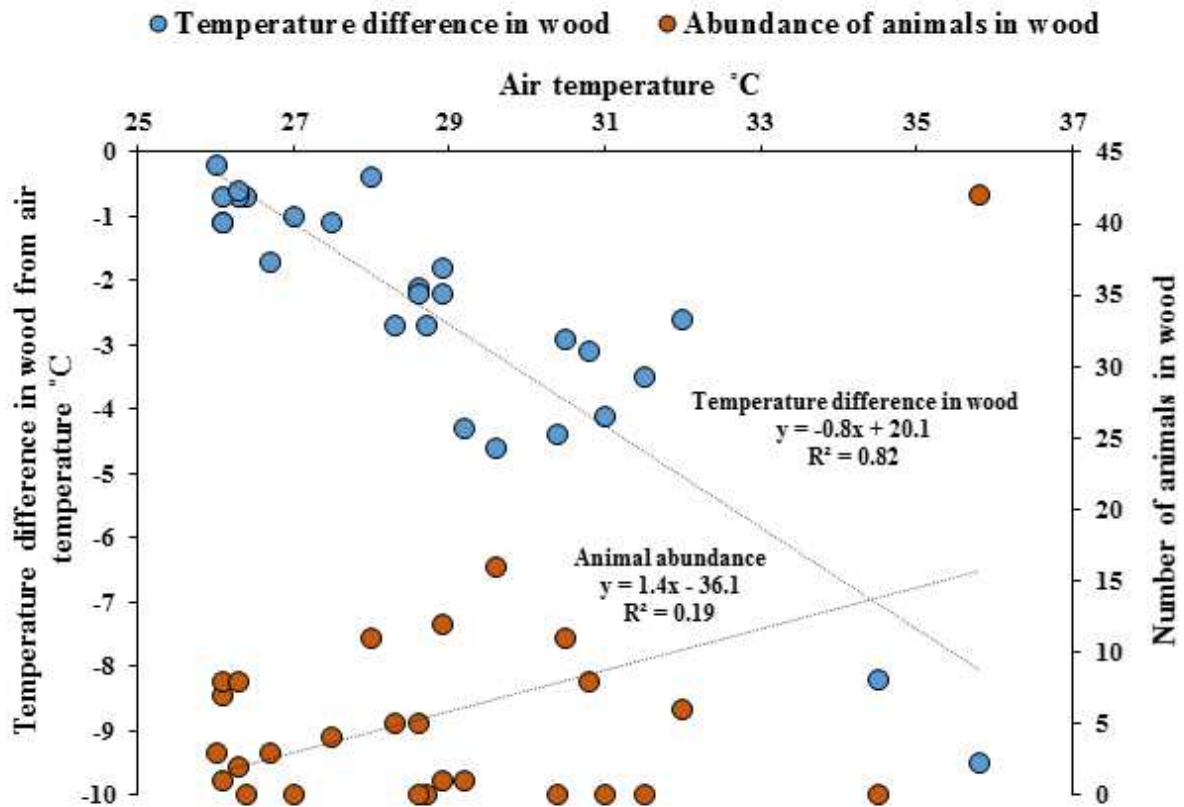
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Figure 5, Corresponding in-wood and outside wood-surface air temperatures ($^{\circ}\text{C}$) of fallen logs ($n = 27$) attacked by teredinids in the Langira mangrove forest, with total counts of animals removed from samples of the same logs. As wood-surface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