

Conus bonus! Facilitation of *Conus* gastropods by invasive mangroves in Mo'orea, French Polynesia

Eric C Witte ^{Corresp. 1}

¹ Department of Earth and Planetary Sciences, University of California, Berkeley, Berkeley, California, United States

Corresponding Author: Eric C Witte
Email address: e.witte@berkeley.edu

Background. Ecosystem engineers are organisms that modify habitats and in many cases community assemblages. Mangroves (*Rhizophora stylosa*) on Mo'orea displace native marsh grass habitats and affect the distribution of native and non-native gastropod species. This study aimed to determine the effect of mangrove facilitation on the expansion of geographic distribution of certain cone snail species (*Conus eburneus*, *C. frigidus*, *C. leopardus*, *C. miliaris*, and *C. pulicaris*).

Methods. Comparisons of temperature as well as cone snail abundance and diversity were conducted between marsh grasses, mangroves and sand flat habitats. The effects of short-term exposure to high temperatures on oxygen consumption were compared based on habitat parameters.

Results. While cone snails were absent from salt marshes, cone snails varied in abundance and diversity in mangrove and sand flat habitats. Cone snails were slightly more abundant in mangroves than paired sand flat habitats. *Conus* species assemblages were comparable in paired mangrove and sand flat habitats. One effect of mangrove ecosystem engineering is reduced thermal maxima and variance, which did not have a clear effect on oxygen consumption.

Discussion. Cone snails are excluded from salt marshes dominated by *Paspalum vaginatum*, however they are present in mangrove salt marshes. Habitat usage by cone snails is comparable between adjacent sites, suggesting that sand-specialized cone snails may receive the greatest benefit from mangrove facilitation due to proximity between possible habitats. Despite well documented effects of temperature variance on intertidal gastropods, this study did not find a direct effect of temperature variance on cone snails. This study contributes to efforts to understand effects of invasive ecosystem engineers on native community assemblages. Redistribution of species on a global scale has varied and complex implications; understanding these effects is crucial to predicting effects on biodiversity.

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3 Eric Witte
4 e.witte@berkeley.edu
5 *Department of Earth and Planetary Sciences, University of California, Berkeley, Berkeley,*
6 *California, 94720, USA*
7

8 **Abstract**

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31 Redistribution of species on a global scale has varied and complex implications; understanding
32 these effects is crucial to predicting effects on biodiversity.
33

34 **Introduction**

35 Our world is currently experiencing a period of unprecedented species redistribution (Viard,
36 David & Darling, 2016). Globalization has rapidly allowed species to overcome biogeographic
37 barriers and to extend their distributions beyond their native range (Mooney & Cleland, 2001).
38 The literature on invasion biology is extensive, with much of it focusing on interactions between
39 invasive and native species such as competition and predation (Ruiz *et al.*, 1999; Parker,
40 Simberloff & Lonsdale, 1999). The addition of non-native species can create more varied and
41 complex interactions within ecosystems. For example, Crooks (2002) highlights the role of
42 biological invaders as ecosystem engineers. Ecosystem engineers are defined as species that
43 modify biotic and abiotic factors in their habitat (Jones, Lawton & Shachak, 1994). Invasive
44 ecosystem engineers have varying effects, including facilitation of both native and non-native
45 species through habitat modification (Crooks, 2002; Rodriguez, 2006). Islands provide a natural
46 laboratory to study the complex effects of invasive organisms, since the proportional abundance

47 of invasive species on island communities is generally higher than in mainland environments
48 (Mooney & Cleland, 2001).

49 The invasion of some islands by mangroves is one example of an ecosystem engineer
50 introduction (Demopoulos & Smith, 2010). The establishment of the red mangrove (*Rhizophora*
51 *mangle*) in Hawai'i typifies impacts of invasive ecosystem engineers. *Rhizophora mangle*
52 modulates nutrient cycling and energy flow, which facilitates higher densities of introduced
53 macroinvertebrates (Simberloff, 1990; Demopoulos & Smith, 2010). The introduction of the
54 stilted mangrove (*Rhizophora stylosa*) to Vainaha Bay, Mo'orea in the 1930's aimed to employ
55 aerial prop roots for oyster culture (Acutt, 1995; Gershman, 1997). Despite the failure of
56 mangrove-facilitated oyster culturing, mangroves have become established in many sites around
57 Mo'orea (Acutt, 1995; Gershman, 1997).

58 Establishment of mangrove stands on Mo'orea is associated with changes in abiotic and
59 biotic modifications. Healthy mangrove ecosystems can offer structure as well as reduce
60 temperature fluctuations by providing canopy cover (Primavera, 1997; Gilma *et al.*, 2013).
61 Additionally, mangroves impact floral and faunal community assemblages. Kramer (1992)
62 documented loss of habitat of *Paspalum vaginatum*, a native marsh grass, due to mangrove
63 colonization. Mangrove stands demonstrated a disparate gastropod species assemblage from that
64 of marsh grasses or adjacent rocky intertidal zones (Gershman, 1997). Due to high relative
65 abundance of non-native species in mangrove stands, Gershman (1997) proposed that the
66 invasion of *R. stylosa* facilitates the expansion of geographic distribution of non-native species.

67 In addition to increasing the frequency of non-native species, invasive ecosystem
68 engineers can also create new habitat for native species. The genus *Conus*, also called cone
69 snails, contains 500 species of predatory gastropods, 38 of which are native to Mo'orea (Kohn,
70 1994; Moorea Biocode Project Database, 2016). Cone snails have diverse feeding patterns and
71 niche specializations (Duda & Alan, 2007) and can specialize in a variety of habitats, including
72 subtidal reef platforms, back reefs, barrier reefs, and sand flats (Kohn, 1959; Kelly-Garrick,
73 2010). Three of the species native to Mo'orea have been documented in sandy habitats, and are
74 therefore potential candidates to profit from a stilted mangrove invasion: *C. eburneus*, *C.*
75 *leopardus*, and *C. pulicarius* (Kohn, 1959; Marsh, 1970; Taylor, 1986; Kelly-Garrick, 2010).
76 Furthermore, prey specialization of native cone snails may allow for inferences into the trophic
77 ecology of the mangrove habitat since predators are constrained by prey distribution.

78 Cone snail biodiversity holds direct societal value, such as the development of cone snail-
79 derived medicines including pain and seizure treatment (Alonso *et al.*, 2003). Terlau and Olivera
80 (2004) estimate that there are more than 50,000 components of toxins employed by cone snails
81 with little overlap between species, suggesting that each species is a potential source for novel
82 pharmaceuticals. Venoms can even vary between geographic populations of the same species
83 (Duda *et al.*, 2009). In order to accurately determine pharmaceutical possibilities, more
84 information about the biodiversity and ecology of cone snails is necessary.

85 The current study adds to the understanding of invasive ecosystem engineers by
86 determining the effects of invasive ecosystem engineers on the distribution of native cone snails.
87 More specifically, this study focuses on the effects of invasive *Rhizophora stylosa* on cone snail
88 assemblages in Mo'orea's coastal ecosystems. The study will compare distribution of cone snails
89 in native marsh grass habitat, invasive mangrove habitat, and adjacent sand flat habitat. This
90 study will test whether ecosystem modulations will expand the geographic range of some, but
91 not all, *Conus* species in Mo'orea. Sand specialist species will gain the greatest advantage due to
92 sand flat proximity to mangroves as well as comparable substrate. Furthermore, significant

93 abiotic differences between marsh grass habitats and mangrove systems will limit distribution of
94 cone snails.

95

96 **Methods**

97 *Study sites*

98 The study was conducted on Mo'orea, a high volcanic island, surrounded by a barrier reef of
99 conglomerate coral in the Society Islands of French Polynesia. The invasion of the stilted
100 mangrove, *R. stylosa*, in Mo'orea provides opportunities to study the effects of invasive
101 ecosystem engineers. *Rhizophora stylosa* is established in a number of discrete sites; five sites
102 sampled in this study are shown in Fig. 1. Site 1 (17°29'31" S, 149°53'25" W) was located in
103 Papeto'ai in northwestern Mo'orea; Site 2 (17°33'17" S, 149°52'44" W) and Site 3 (17°33'22" S,
104 149°52'30" W) were located close to Ha'apiti on the southwestern part of the island; Site 4
105 (17°34'18" S, 149°51'59" W) was located South of Ha'apiti; Site 5 (17°34'59" S, 149°51'9" W)
106 was located near Vai'anae. Sites were selected by consulting maps of *R. stylosa* colonization and
107 initial surveys (Kramer, 1992). Sites were chosen for this study because they had coastal
108 mangroves stands as well as adjacent sand flat habitats. Sand flat habitats were a control for
109 bordering mangrove habitat. In addition, Sites 2 and 3 contained *P. vaginatum* marshes, which
110 were key for determining presence of cone snails in marsh grass-dominated
111 ecosystems. Mangrove and marsh grass habitats were selected to include monospecific stands as
112 well as 3 m of bordering sand. Sand flat habitats were selected to be parallel to shore, 10-15 m
113 from *R. stylosa* or *P. vaginatum* stands.

114

115 *Field surveys*

116 Timed transects were conducted for 30 minutes in each habitat at each site parallel to shoreline,
117 starting 10 minutes after sunset since cone snails are active at night (Kohn, 1959). Marsh grass
118 surveys were conducted until the entire habitat had been surveyed (8 minutes at Site 2, 17
119 minutes at Site 3). Surveys were conducted with two surveyors, walking or snorkeling if depth
120 permitted. Cone snails were identified and tallied by species. If a cone snail could not be
121 identified, it was collected with metal tongs and compared to a reference of known species in
122 Mo'orea, compiled from information in the Moorea Biocode Project (Moorea Biocode Project
123 Database, 2016).

124

125 *Temperature comparison*

126 Three HOBO 64K Temperature Loggers (Onset Computer Corporation, Bourne, MA, USA)
127 were placed in habitats of Site 2 to compare daily temperature fluctuations. Trackers were placed
128 next to marsh grass stands, in mangrove root structures and in the sand flat habitats. Each tracker
129 was secured with a zip tie and rope to a cinder block and buried under 3 inches of substrate.
130 Temperature was recorded every 30 min for four days (November 4-7, 2016).

131

132 *Temperature experiments*

133 Temperature experiments compared the effects of diurnal maxima on cone snail metabolic rate.
134 Twenty-seven *Conus eburneus* were collected from Site 2 and separated randomly using a
135 random sequence generator into three treatment groups of nine each: marsh grass, mangrove and
136 sand flat. Specimens were held in captivity for five days to acclimate to reduce systematic
137 change from capture (Mangum and Sassaman, 1968). Snails were placed in sealed 50 ml falcon
138 tubes for 30 min trials in water baths, as well as a blank tube. Data collected for temperature

139 comparisons (Fig. 2) was used to select daily maximum temperatures of each habitat for
140 respiration trials. Each water bath was kept at the average daily maximum temperature of the
141 habitat: 31 °C for sand flat habitat; 32 °C for mangrove habitat; and 41 °C for marsh grass
142 habitat. Respiration was determined by measuring dissolved oxygen content in the vial at the end
143 of the trial and comparing to blank tube. Water from falcon tubes was transferred to plates of a
144 Loligo Microplane Reader System, minimizing air contact. Dissolved Oxygen levels were
145 compared to initial samples of water to determine total respiration. Results were then normalized
146 using wet mass of the snail.

147

148 *Data analysis*

149 All statistical tests were conducted using R 3.3.1 (R Core Team, 2013). An ANOVA and a
150 Tukey's Posthoc Test were run between marsh grass presence and control site presence to
151 describe presence of cone snails in marsh grass ecosystems. A nested ANOVA was run to
152 compare abundance of cone snails in mangrove ecosystems to that of sand flats, followed by a
153 Tukey's Posthoc Test, which tested variance by site as well as by habitat. A correlation was used
154 to compare abundance between paired habitats of each site; a Regression Analysis, followed by a
155 Spearman's Rank Test were used to determine the significance of the relationship as well as the
156 strength of the correlation. An ANOVA and a Tukey's Posthoc Test were used to compare
157 species diversity between each site. An ANOVA was used to compare the daily maxima by
158 habitat, followed by a Tukey's Posthoc Test. Coefficients of variance were calculated by
159 dividing variance by mean values of each site. An ANOVA and a Tukey's Posthoc Test were
160 used to compare oxygen consumption of each treatment group.

161

162 **Results**

163 *Field survey*

164 Cone snails were present at all sand and mangrove habitats; however, none were found in any
165 marsh grass sites. Mean snail abundance in mangrove habitats was 32.0 ± 27.5 (N=5); sandy
166 habitat abundance was 25.4 ± 23.7 (N=5). Both were higher than abundance in marsh grass
167 habitats (ANOVA: $F=10^{31}$ (2, 9 df); $p<0.001$). Figure 3 shows significant variance of cone snail
168 abundance by site as well as by habitat (Tukey's Post Hoc Test). Significant differences occurred
169 between sites (Nested ANOVA: $F=83$ (4, 4 df); $p<0.001$), however certain sites shared some
170 overlap. Figure 3 shows abundances by site and habitat and represents the significant groupings
171 of sites. Figure 4 compares the same data, using correlation and a regression analysis.

172 Abundance in mangroves was correlated to adjacent sand flat habitat (Regression: $F=115$ (1, 3
173 df); $r^2=0.9661$; $p<0.01$).

174 As shown in Table 1, seven species of cone snails were represented in sand flat habitats;
175 five species were represented in mangroves; no individuals were found in marsh grass
176 ecosystems. Although more total species were found in control habitats, there is not a significant
177 relationship between paired habitat surveys (Welch's Two Sample t-Test: 7.4 df; $p=0.73$).

178 However, significant variation occurred between sites (Tukey's Post Hoc Test). Figure 5 shows
179 number of species by site as well as significant groupings. *Conus eburneus* was most common,
180 accounting for 58.1% of all individuals sampled.

181

182 *Temperature analysis*

183 Temperatures, as shown by Fig. 2, fluctuated in a diurnal pattern in all habitats sampled ranging
184 from 25 °C to 43 °C. Mean temperatures varied slightly between habitats: 28.6 °C in mangroves;

185 29.5 °C in sand flat habitat; 31.6 °C in marsh grasses. Coefficients of variation were more
186 distinct: 3.6% in sand flat habitat; 15.2% in mangroves; 77.5% in marsh grasses. Average
187 maxima of habitats were 31.0 °C in sand flat habitat, 32.0 °C in mangroves and 40.1 °C in marsh
188 grass. Marsh habitat had significantly higher daily maxima than both marsh and mangrove
189 ecosystems (ANOVA: $F=46.41$ (2, 9 df); $p<0.001$; $p<0.001$). No significant difference was
190 detected between sand and mangrove habitats ($p=0.65$).

191

192 *Temperature experiments*

193 Respiration rates varied greatly: 2-19 ppm Oxygen/gram body mass (Fig. 6). Mean values for
194 treatment groups were comparable: 8.5 ppm O₂/g for sand treatment, 11.1 ppm O₂/g for
195 mangrove treatment and 10.5 ppm O₂/g for marsh treatment. No significant difference was
196 detected between treatment groups (ANOVA: $F=1.64$ (2, 24 df); $p=0.22$). No snails died during
197 temperature trials.

198

199 **Discussion**

200 *Gastropod Distribution*

201 Previous comparative studies of gastropod assemblages in mangrove and marsh grass
202 communities of Mo'orea did not include the genus *Conus*, possibly due to diurnal sampling
203 (Gershman, 1997). Nocturnal hunting makes them difficult to identify during the day, therefore
204 diurnal surveys might not fully account for cone snail presence. The field survey expands on
205 previous studies by demonstrating the presence of five cone snail species in mangrove habitats
206 (Kelly-Garrick, 2010). Cone snail presence in mangroves demonstrates their ability to inhabit
207 mangrove-engineered ecosystems. Mangrove invasion of salt marshes facilitates cone snail's
208 expansion since mangroves convert habitat that was previously occupied by marsh grass
209 (Kramer, 1992).

210 Abundance is slightly higher in mangrove habitats than adjacent sand flats. This trend
211 may be due to reduced predation in mangrove habitats. For example, shrimp experience lower
212 predatory pressure due to shelter offered by mangrove prop roots (Primavera, 1997). *Conus*
213 species assemblages (Table 1) in mangroves are comparable to those found in adjacent sand flat
214 habitats. All five species of cone snail represented in the mangrove surveys (*C. eburneus*, *C.*
215 *pulicarius*, *C. miliaris*, *C. leopardus* and *C. frigidus*) were also found in control habitats. Three
216 of the species present in mangroves (*C. eburneus*, *C. pulicarius*, and *C. leopardus*) have been
217 documented in sandy habitats before (Kohn, 1959; Marsh, 1970; Taylor, 1986; Kelly-Garrick,
218 2010). Therefore, it appears that most of the cone snail species facilitated by mangroves are
219 present in sandy habitats.

220 The most common species in both mangrove and sand flat habitats was *C. eburneus*,
221 followed by *C. pulicarius* and *C. miliaris*. These three species are vermivorous, and feed chiefly
222 on polychaete worms (Marsh, 1970). Therefore, polychaete worms must be present in or near
223 mangrove habitats. *Conus leopardus* was present in lower numbers than other identified sand
224 specialists. However, its density and presence in sand flat habitats is consistent with previous
225 studies (Kelly-Garrick, 2010). *Conus leopardus* feeds on *Ptychodera flava*, an enteropneust
226 found throughout the Indo-Pacific (Kohn, 1959). Therefore, *C. leopardus* hunting in mangrove
227 habitats suggest the presence of enteropneusts. *Conus frigidus* preys on polychaetes, but has
228 previously been recorded in limestone reefs (Kohn & Nybakken, 1975). Presence of *C. frigidus*
229 in sand flats and mangrove habitats may reflect generalist behaviors on Mo'orea.

230 Two species of cone snails were found in sand flat habitats, but were absent from paired
231 mangroves. *Conus textile* and *C. flavidus* were recorded in low numbers at Site 2 and *C. flavidus*
232 was recorded in sand flats at Site 4. Therefore, sampling may have not have measured the low
233 abundance in mangrove habitats. Alternatively, it is possible that these two species are excluded
234 from mangrove habitats either by prey presence or for other physiological reasons. More
235 extensive observations would be required to determine the presence of *C. textile* and *C. flavidus*
236 in mangrove habitats.

237

238 *Temperature fluctuations*

239 According to Jones, Lawton, and Shachak (1994), an ecosystem engineer modifies resource
240 availability by physically altering biotic and abiotic resources. Moderating temperature
241 fluctuations is one way that mangroves engineer habitat on Mo'orea's coastline. Temperature, as
242 shown in Fig. 2, had higher coefficients of variance as well as significantly higher daily maxima
243 in marsh grass habitats compared to both mangroves and sand flats. Intertidal temperatures can
244 vary rapidly and can have effects on the physiology of intertidal invertebrates, including "heat
245 comas" and death if thermal ranges are exceeded (Broekhuysen, 1940; Newell, 1969; Clarke,
246 Mill, & Grahame, 2000; Davenport & Davenport, 2007). Reduced variance and daily maxima
247 may make mangrove habitat more hospitable to invertebrates, including cone snails and prey
248 species, such as polychaetes and enteropneusts. Therefore, range of cone snails may be directly
249 limited by thermal fluctuations, or indirectly by exclusion of prey species.

250

251 *Temperature experiments*

252 High temperatures are known to limit intertidal gastropod distribution, reduce activity
253 drastically, and even kill snails (Broekhuysen, 1940; Davenport & Davenport, 2007). Figure 6
254 shows oxygen consumption, which did not demonstrate significantly reduced activity in high
255 temperature trials. There was no death during the temperature trials. These results may be due to
256 air exposure while conducting measurements. Alternatively, it is possible that intertidal cone
257 snails tolerate wide temperature ranges, especially due to minimal diurnal activity. Diurnal rest
258 may be comparable to 'heat comas' described by Clarke, Mill and Grahame (2000) in other
259 gastropod species. However, trials did not account for the duration of diurnal temperature
260 fluctuations. Trials lasted thirty minutes and may have ignored effects of long term exposure.
261 Conducting two hour trials in 40 °C conditions, Broekhuysen (1940) found 100% mortality rates
262 of five of the six South African intertidal gastropod species he studied. Although these values
263 cannot be directly compared, this demonstrates the effects of lasting heat exposure on a variety
264 of gastropods. Longer exposures at high temperature may demonstrate higher mortality rates in
265 cone snail species of Mo'orea.

266

267 *Conclusion*

268 Mangroves altered salt marsh community assemblages and facilitated the colonization of cone
269 snail species. The species of cone snail that colonize mangrove habitats are: *C. eburneus*, *C.*
270 *pulicarius*, *C. miliaris*, *C. leopardus*, and *C. frigidus*. These species are also present in adjacent
271 sand flat habitats. However, cone snails are not present in marsh grass ecosystems. Marsh grass
272 habitats have significantly higher temperatures and higher coefficients of variance. Thermal
273 parameters may make marsh grass ecosystems inhospitable to cone snail species or prey species.
274 Future studies should fully assess the thermal effects on distribution to determine factors limiting
275 distribution of cone snails in marsh grass habitats. Additional studies should study the effects of

276 long-term heat exposure on cone snail survivorship. Additionally, surveys should compare the
277 presence of prey species— polychaetes and enteropneusts— in marsh grass habitats to that of
278 mangrove habitats to determine the effects of ecosystem engineers by trophic level.

279 This study addresses the role of invasive *R. stylosa* in habitat and *Conus* gastropod
280 community assemblage modification in Mo'orea. These conclusions are valuable for
281 understanding trophic ecology in mangrove habitats. More globally, this is a complex
282 relationship of an invasive species facilitating geographic expansion of a native species. Invasive
283 ecosystem engineers can have indirect, yet drastic, effects on the distribution of another
284 species. Modification of abiotic factors can alter standard nutrient flow, temperature, and other
285 factors. This can expand or reduce habitat for native species. Additionally, it can alter biotic
286 factors by removing prey species, or increasing predation. Therefore, evaluation of invasive
287 species impacts must include many biotic and abiotic variables that may indirectly affect
288 biodiversity.

289

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Figure 1(on next page)

Map of Mo'orea and study sites.

Site 1: 17°29'31" S, 149°53'25" W; Site 2: 17°33'17" S, 149°52'44" W; Site 3: 17°33'22" S, 149°52'30" W; Site 4: 17°34'18" S, 149°51'59" W; Site 5: 17°34'59" S, 149°51'9" W

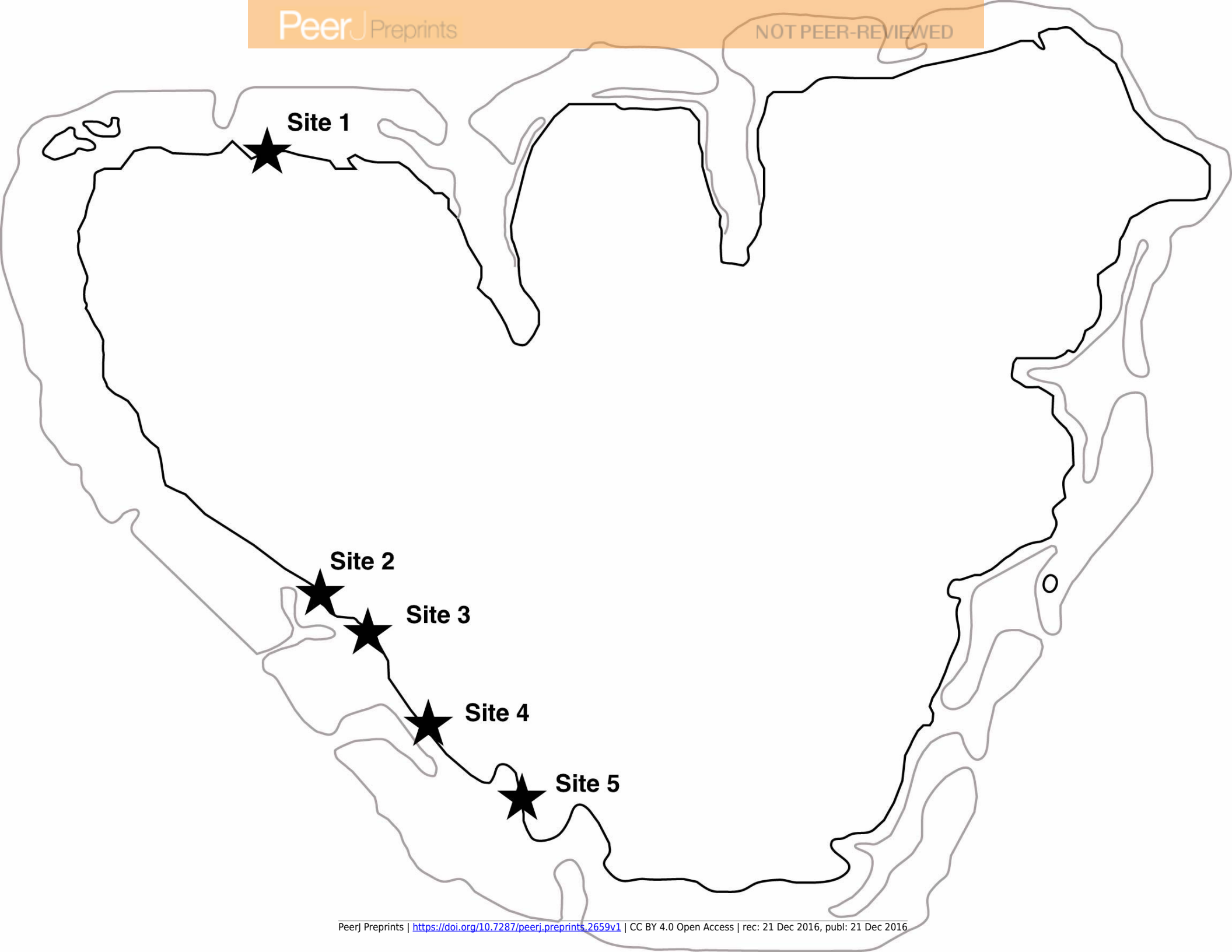


Figure 2 (on next page)

Temperature with respect to time in sand flat, mangrove, and marsh habitats.

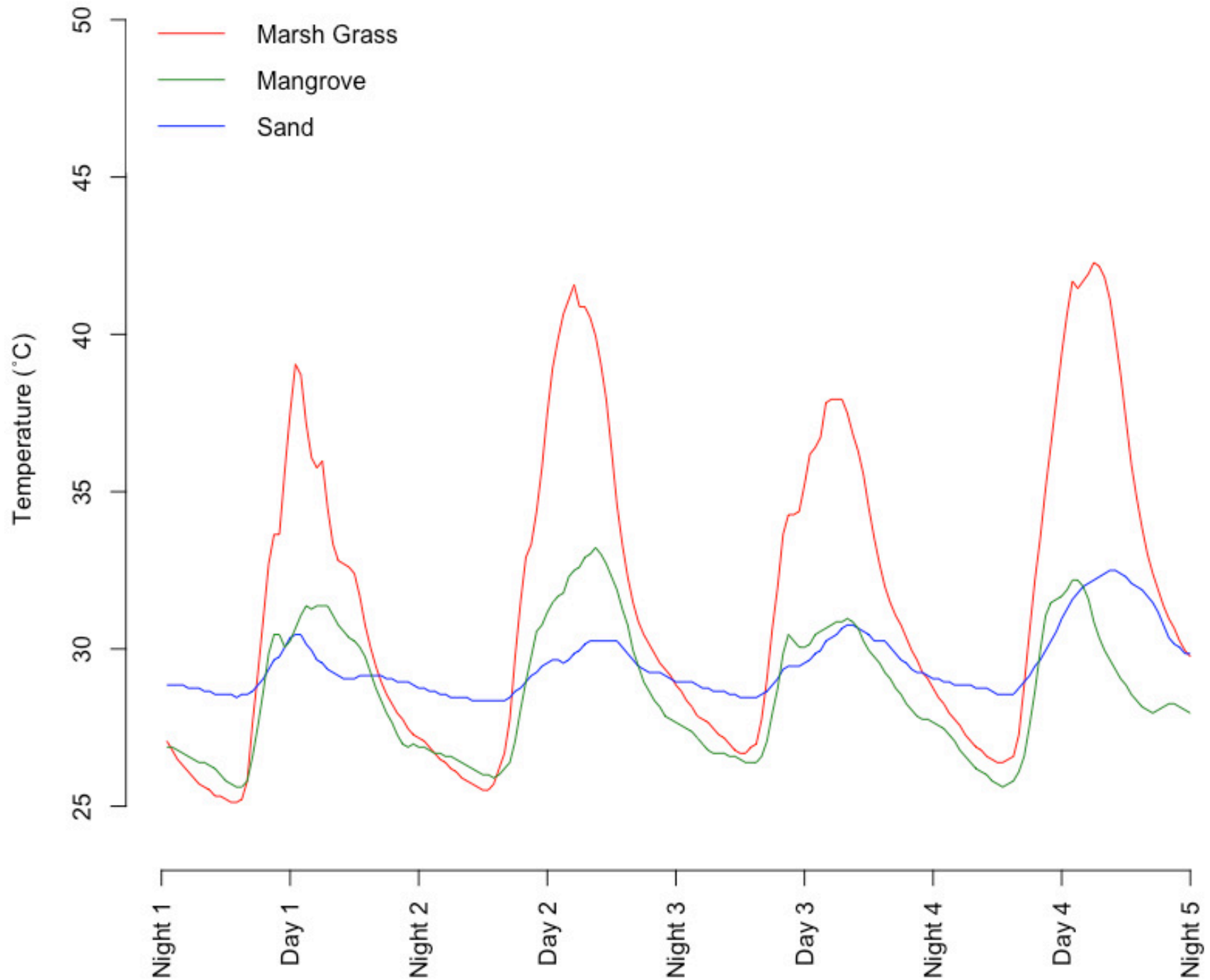


Figure 3 (on next page)

Abundance of cone snails by site and habitat.

Letters dictate significant groups.

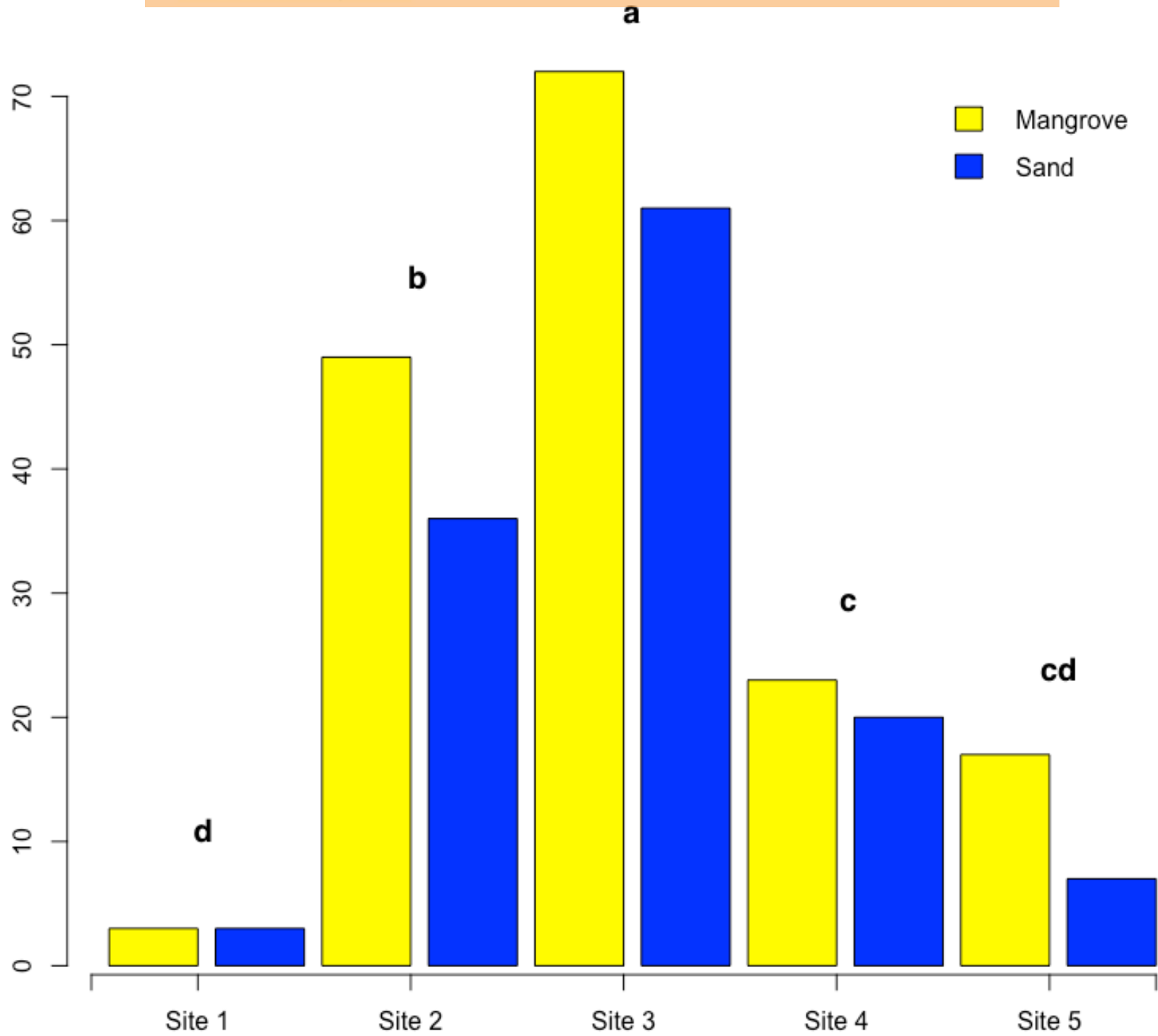


Figure 4(on next page)

Correlation of mangrove abundance to control abundance.

Mangroves correlate closely to paired sand flat sites, but have slightly higher abundance ($y=1.146x+3.682$; $r^2=0.9661$; $p<0.01$).

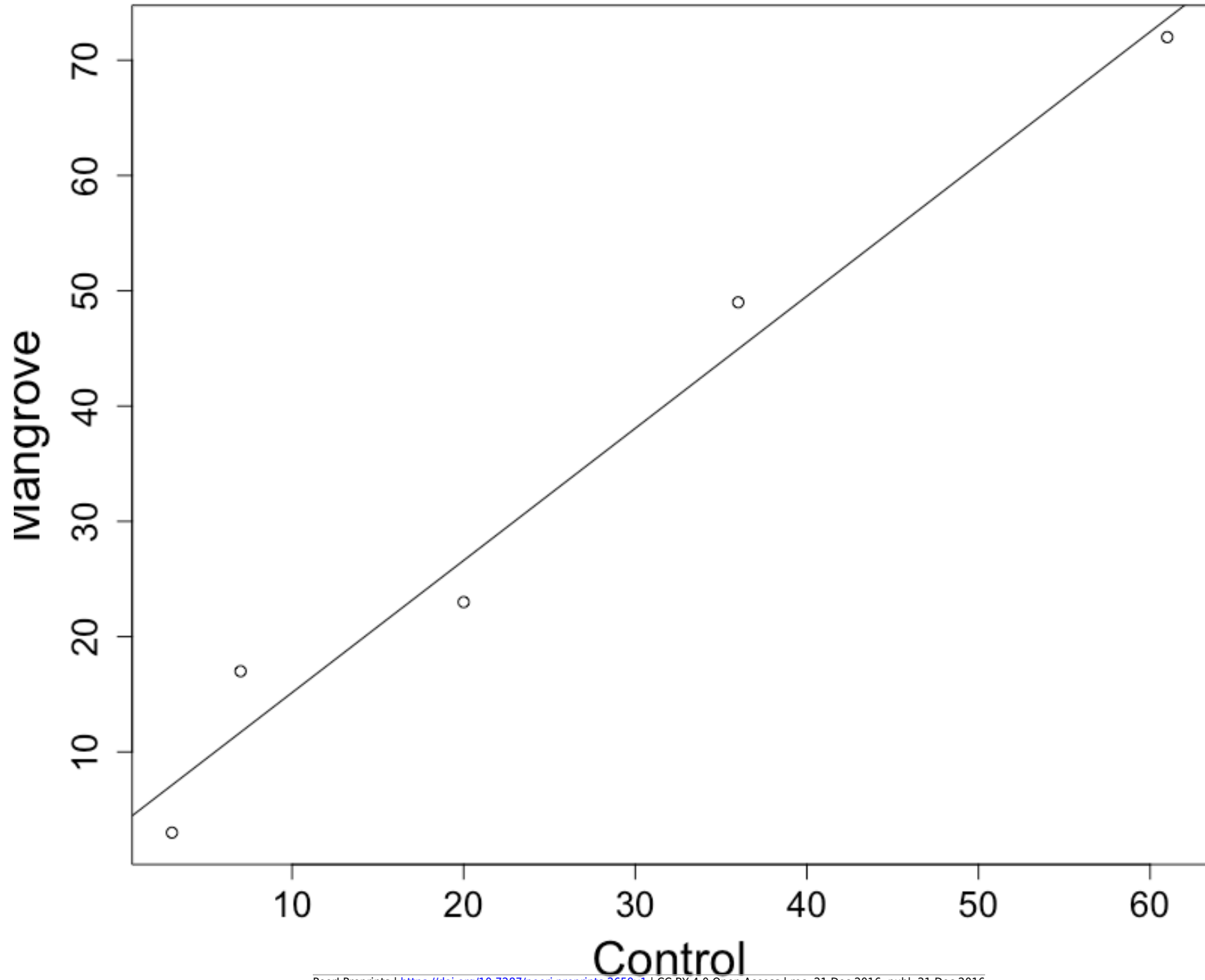


Table 1 (on next page)

Abundance of *Conus* species in each mangrove and sand habitats.

1

| Sites | Site 1 | | Site 2 | | Site 3 | | Site 4 | | Site 5 | |
|----------------------|----------|------|----------|------|----------|------|----------|------|----------|------|
| Habitat | Mangrove | Sand | Mangrove | Sand | Mangrove | Sand | Mangrove | Sand | Mangrove | Sand |
| <i>C. eburneus</i> | 3 | 1 | 32 | 9 | 53 | 49 | 9 | 10 | 2 | 1 |
| <i>C. pulicarius</i> | 0 | 2 | 10 | 11 | 15 | 8 | 9 | 7 | 10 | 6 |
| <i>C. miliaris</i> | 0 | 0 | 6 | 6 | 2 | 3 | 1 | 1 | 5 | 0 |
| <i>C. leopardus</i> | 0 | 0 | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 0 |
| <i>C. frigidus</i> | 0 | 0 | 0 | 5 | 1 | 0 | 2 | 0 | 0 | 0 |
| <i>C. flavidus</i> | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 |
| <i>C. textile</i> | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

Figure 5 (on next page)

Species diversity by site.

Letters show significant groups.

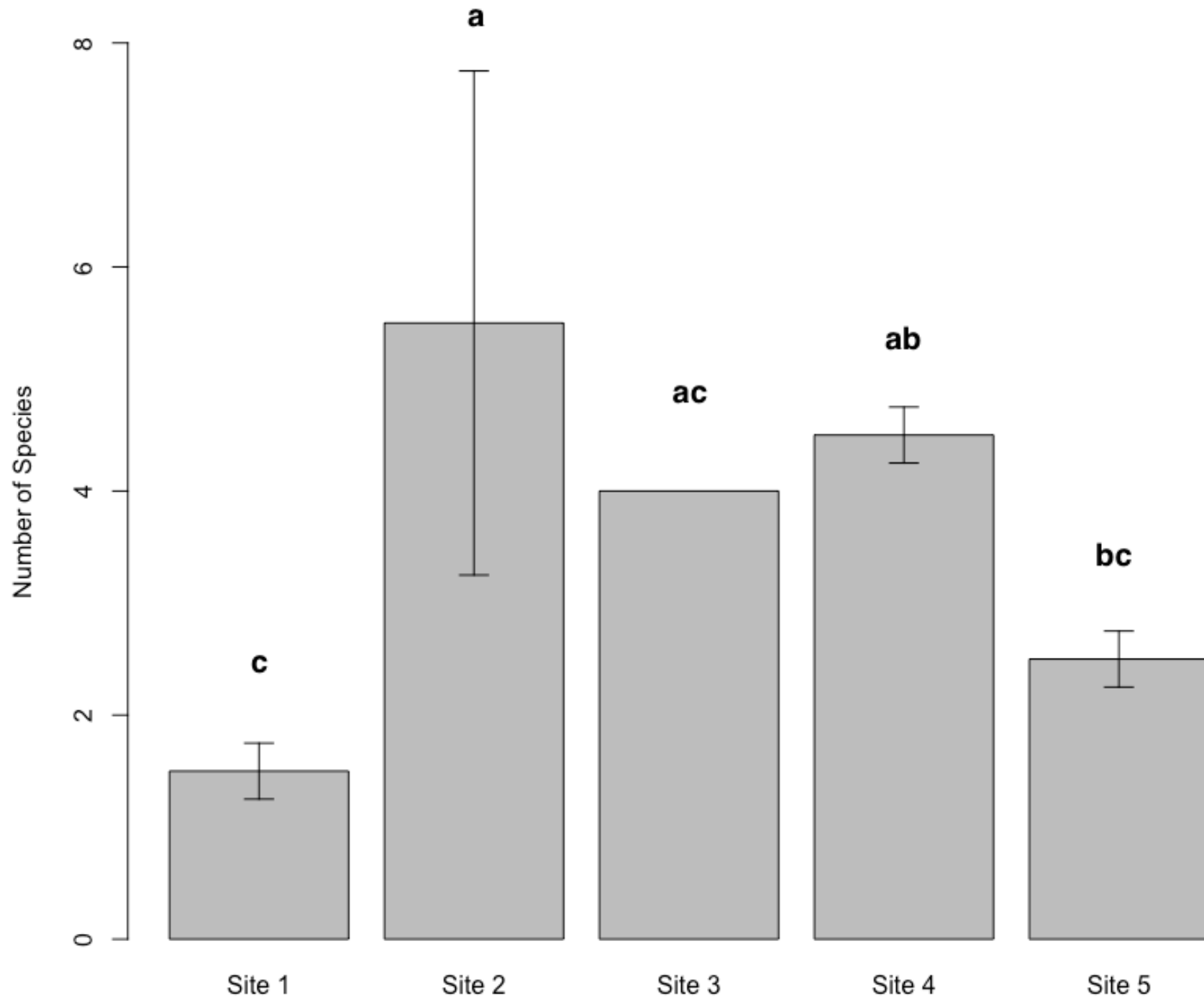


Figure 6 (on next page)

Respiration rates by treatment

