Title

Species identity drives ecosystem function in a subsidy-dependent coastal ecosystem

Authors

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Abstract

Declines in species diversity carry profound implications for ecosystem functioning. Communities of primary producers and consumers interact on evolutionary as well as ecological time scales, shaping complex relationships between biodiversity and ecosystem functioning. In subsidized ecosystems, resource inputs are independent of consumer actions, offering a simplified view of the relationship between species diversity and function for higher trophic levels. With food webs supported by substantial but variable inputs of detritus from adjacent marine ecosystems, sandy beaches are classic examples of subsidized ecosystems. We investigated effects of consumer species diversity and identity on a key ecological function, consumption of kelp wrack from nearshore giant kelp (*Macrocystis pyrifera*) forests. We assessed effects of species richness on kelp consumption by experimentally manipulating richness of six common species of invertebrate detritivores in laboratory mesocosms and conducting field assays of kelp consumption on beaches. Consumer richness had no effect on kelp consumption in the field and a slight negative effect in laboratory experiments. Kelp consumption was most strongly affected by the species composition of the detritivore community. Species identity and body size of intertidal detritivores drove variation in kelp consumption rates in both experiments and field assays. Our results provide further evidence that species traits, rather than richness per se, influence ecosystem function most, particularly in detrital-based food webs with high functional redundancy across species. On sandy beaches, where biodiversity is threatened by rising sea levels and expanding development, our findings suggest that loss of large-bodied consumer species could disproportionally impact ecosystem function.

Keywords

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49   Biodiversity, Generalist Consumers, Body Size, Detrital Subsidies, Sandy Beach

50

51   **Introduction**

52   Biodiversity is declining at local to global scales (Cardinale et al. 2012; Gonzalez et al.

53   2016) and understanding the ecological implications of these losses is an urgent challenge

54   (Worm et al. 2006; Hooper et al. 2012). Numerous empirical, experimental and modeling studies

55   have evaluated the extent to which biodiversity affects ecosystem functioning (BEF, reviewed by

56   Naeem 2002; Srivastava et al. 2009; Tilman et al. 2014; Duffy et al. 2017). Many of these

57   studies have focused on how species richness of plant communities affects primary production

58   (Naeem et al. 1996; Reich et al. 2001; Cardinale et al. 2004; Cardinale et al. 2007), and nutrient

59   dynamics (Tilman et al. 1996; Hooper and Vitousek 1998; Bracken and Stachowicz 2006;

60   Kahmen et al. 2006). Far fewer BEF studies have examined higher trophic levels, multitrophic

61   systems or naturally assembled communities (Duffy 2002; Duffy et al. 2007; Lefcheck et al.

62   2015; Soliveres et al. 2016; van der Plas 2019).

63   Consumers maintain critical functions in ecosystems, stimulating primary production and

64   facilitating the transfer of energy and nutrients across trophic levels (Duffy 2002; Duffy et al.

65   2007; Hensel and Silliman 2013; Allgeier et al. 2017). However, evaluations of relationships of

66   biodiversity with ecosystem function across multiple trophic levels are greatly complicated by

67   the reality that consumers are often embedded in a complex food web, vary widely in their

68   relative functional dominance, and interact with a diverse set of primary producers (e.g., Hooper

69   et al. 2005; Thebault and Loreau 2006; Duffy et al 2007; Creed et al. 2009; Edwards et al. 2010;

70   Filip et al. 2014; Lefcheck and Duffy 2015; Brose and Hillebrand 2016; Daam et al. 2019).

71   Consumer and resource dynamics are not independent in these systems, and the effect of

72 consumers on resources can impact future consumption, production and ecosystem functioning

73 (Dyer and Letourneau 2003). For example, herbivore and predator diversity may interact to

74 affect basal functions, such as net primary production (Finke and Denno 2005; Ives et al. 2005;

75 Stachowicz et al. 2007; Griffin et al. 2013). These interactions feed back to affect community

76 properties on both ecological and evolutionary timescales, adding complexity (Douglass et al.

77 2008; Matthews et al. 2011; Gravel et al. 2011; Walsh et al. 2012). As a consequence,

78 experimental studies on consumer diversity, and particularly multitrophic diversity, are

79 logistically difficult and often confined to modeling and experiments using microorganisms

80 (Naeem et al. 2000; Downing and Leibold 2002; Gamfeldt et al. 2005; Brose 2008).

81   Not all ecosystems and food webs, however, are characterized by two-way interactions

82 between consumers and producers. Food webs with consumers that depend on allochthonous

83 subsidies, often detritus, as their main resource supply typically have no influence on detrital

84 production or input (Polis et al. 1997; Cebrian and Lartigue 2004; Moore et al. 2004; Leroux and

85 Loreau 2008; Srivastava et al. 2009) although they are strongly affected by subsidy supply

86 (Hoekman et al. 2019). Nevertheless, such subsidized ecosystems can support food webs with a

87 high diversity and abundance of consumers, as reported in streams (Wallace et al. 1997),

88 submarine canyons (Vetter 1995), desert islands (Polis and Hurd 1995), and sandy beaches

89 (Dugan et al. 2003). In these subsidized ecosystems, primary consumers play a vital role,

90 incorporating detrital inputs into the food web and making energy available to higher-level

91 consumers (Heck et al. 2008; Spiller et al. 2010; Hagen et al. 2012). Across terrestrial and

92 aquatic ecosystems, detritus increases the standing stock of all trophic levels by supporting

93 detritivores and providing energy and habitat to predators (Hagen et al. 2012). The separation in

94 space between producers and consumers for subsidized ecosystems means that the effect of

95 consumers can be quantified without ecological or evolutionary feedback or response from the

96 resource donor (Wallace et al. 1997), simplifying the evaluation of BEF relationships.

97   Sandy beach ecosystems are a widespread coastal interface between marine and

98 terrestrial realms (Luijendijk et al. 2018). Characterized by low *in situ* primary production,

99 beaches are a classic example of subsidized ecosystems with food webs that rely primarily on

100 marine subsidies (Brown & McLachlan 2006). Where nearshore productivity is high, drift

101 macrophytes (macroalgae and seagrass), or wrack, cast ashore by waves and tides can sustain

102 rich productive communities of intertidal detritivores on beaches (Dugan et al 2003; Ince et al.

103 2007; Schlacher et al. 2017). In turn, these consumer populations support higher trophic levels

104 including predatory arthropods, reptiles, and shorebirds (Tarr and Tarr 1987; Polis and Hurd

105 1996; Dugan et al. 2003; Spiller et al. 2010). By acting as detritivores and shredders that process

106 macrophyte wrack inputs (Griffiths and Stenton-Dozey 1981; Lastra et al. 2008), facilitating

107 recycling of nutrients in beach sand and nearshore waters (Dugan et al. 2011; Gomez et al. 2018;

108 Lowman et al. 2019), and supporting coastal food webs (Dugan et al. 2003), these abundant

109 invertebrates perform key ecological functions.

110   To explore BEF relationships in this detritus-based ecosystem, we evaluated the influence

111 of intertidal consumer diversity on a key ecosystem service, wrack processing. We used the

112 consumption rate of the primary subsidy to beaches in our region, drift kelp from highly

113 productive nearshore forests of giant kelp (*Macrocystis pyrifera*) to estimate this ecological

114 function. We hypothesized that consumer species richness would positively influence kelp

115 consumption rates due to facilitation and/or species-specific feeding differences (e.g. scraping vs

116 shredding). To test this prediction we manipulated the richness of six species of common

117 intertidal beach detritivores in laboratory mesocosm experiments. We further evaluated this

118   prediction by comparing field consumption rates of kelp detritus on six beaches spanning a

119   gradient of species richness and abundance of these invertebrates. We assessed the relative role

120   of diversity and species composition on ecosystem function using analyses that separated species

121   richness from species identity.

122   **Methods**

123   *Study Site and Organisms*

124   Sandy beaches of Santa Barbara, California, USA, are characterized by large but variable

125   inputs of stranded giant kelp (*Macrocystis pyrifera*), or wrack (>500 kg m^{-1} yr^{-1}, Dugan et al.

126   2011) from highly productive nearshore kelp forests. This major subsidy to beaches is consumed

127   by a diverse assemblage of highly mobile intertidal detritivores (Lastra et al. 2008; Michaud et

128   al. 2019). We focused on six intertidal arthropod species that make up >90% of abundance of

129   invertebrate detritivores on these beaches: four congeneric species of talitrid amphipods (two

130   large-bodied species, *Megalorchestia corniculata* and *M. californiana,* and two smaller species

131   *M. minor* and *M. benedicti*), a tenebrionid beetle (*Phaleria rotundata*) and an oniscid isopod

132   (*Alloniscus perconvexus*). These taxa are representative of families of important intertidal

133   detritivores on sandy beaches worldwide (Brown and McLachlan 2006).

134   *Richness Experiment*

135   To experimentally evaluate effects of intertidal consumer species richness on the

136   consumption of giant kelp (*Macrocystis pyrifera)* wrack*,* we used a replacement design where

137   consumer abundance in treatments was held constant at 12 individuals, and five levels of species

138   richness (1, 2, 3, 4 & 6 species) were established in which the abundance of a given species

139   decreased correspondingly to maintain the same total abundance (12, 6, 4, 3 & 2 individuals,

140   respectively). Given the size range of the consumer species we tested it was not possible to hold

141   biomass constant in the treatments. We tested all possible species combinations, resulting in 57

142 unique treatments, each of which was run concurrently in triplicate. Experimental designs to test

143 the effects of diversity on ecosystem function can include maintaining biomass rather than

144 abundance, maintaining the abundance of one species when adding another, and using unique

145 species in each richness level (Allison 1999; Benedetti-Cecchi 2004). We addressed this tradeoff

146 by using a replacement design (Duffy et al. 2003) which allowed us to maintain species evenness

147 within each richness level and evaluate the effect of species identity on function. Our goal was to

148 understand the effect of changing biodiversity on an ecosystem function, not consumption per

149 unit consumer biomass.

150   Our treatment mesocosms were plastic tubs (19 cm x 17 cm x 9 cm) filled to ~6 cm depth

151 with sieved (1.5mm) dry sand from Campus Point beach (34.41 N, 119.84 W), mixed with

152 filtered seawater to achieve a moisture level of 10-15% by weight, approximately equivalent to

153 that of the 24-hour high tide line where the densest aggregations of these intertidal wrack

154 consumers are typically found. Fresh blades of giant kelp and live consumers were collected by

155 hand on each morning the experiments were set up. Kelp blades were cut into square pieces of

156 ~2g wet weight and weighed individually. This amount was chosen after preliminary

157 experiments, to ensure that the entire piece was not consumed during the experimental period.

158 We removed a subsample from each piece of kelp, weighed it to the nearest mg, dried it at 60˚C

159 for at least 48 hours, and then ashed it in a muffle furnace at 500˚C for four hours to obtain the

160 ash weight. The subsample provided a dry:wet ratio and an inorganic:organic ratio for each piece

161 of kelp that was used to calculate consumption rates (see below). Consumer species were added

162 in their prescribed numbers to the mesocosms and observed for 5-10 minutes until all had

163 burrowed into the sand, upon which time we added the square of kelp to each mesocosm. The six

164 consumer species we used are largely nocturnal; all experimental units were run for 3 nights and

165   began and ended in the morning. Trials were run over the course of three weeks during August

166   2016 and all replicates of a given treatment were run at the same time to ensure no treatment

167   differences were driven by the differences in animal collections. Changes in the condition of

168   animals collected over the three-week experimental period was unlikely as environmental

169   conditions are most stable during this time of year. We conducted the trials in an

170   environmentally controlled room kept at 20˚C and set to a 14:10 hour light:dark cycle,

171   approximating natural conditions at the time of the experiment. Each treatment was misted daily

172   with filtered seawater to maintain moisture levels in the sand and kelp.

173   At the end of each experiment, the remaining kelp in each mesocosm was removed,

174   gently rinsed, placed into pre-weighed foil packets and dried at 60˚C for at least 48 hours to

175   obtain dry mass. The dried kelp was then ashed in a muffle furnace at 500˚C for four hours to

176   obtain the ash weight of the unconsumed kelp plus any attached sand. Extensive rinsing of the

177   unconsumed kelp would have removed all attached sand but also a significant portion of the kelp

178   biomass. Therefore, we used the dry:wet and inorganic:organic mass ratios of the initial

179   subsamples to remove the sand mass from the blade mass consumed (B_C) in each replicate as

180   follows:

181    $$B_C = B_i - B_f$$

182   where B_i is initial blade dry mass, taken as the wet mass of kelp measured at the beginning of the

183   assay multiplied by the dry:wet mass ratio of the subsample, and B_f is final blade dry mass,

184   corrected as:

185    $$B_f = B_T - S$$

186 where B_T is total dry mass of the remaining blade material and S is sand mass, estimated as the

187 inorganic ash weight of B_T minus the inorganic kelp fraction, calculated as the organic mass of

188 B_T multiplied by the inorganic:organic fraction of the sand-free subsample.

189   During the experiments six control mesocosms were run for each trial using an identical

190 setup as described above but with no animals, to account for any kelp biomass loss due to

191 handling or microbial decomposition of the blades. Each trial was corrected using trial-specific

192 controls by subtracting mean control mass loss from each treatment (Silliman and Zieman 2001).

193 The average mass loss from all controls was small, averaging $4.0 \pm 1.5\%$ dry mass (6.0 ± 2.5

194 mg).

195   The consumers were collected from each treatment and frozen for 24 hours, after which

196 they were rinsed, dried at 60˚C for at least 48 hours to obtain dry mass, and then ashed at 500˚C

197 for four hours to obtain ash-free dry weight (AFDW).

198 *Field assays*

199   As a comparative approach to evaluating the effect of species richness on ecosystem

200 function, we conducted feeding assays on six sandy beaches located on a 22 km stretch of

201 shoreline in Santa Barbara County in October 2016 and April 2017 (map in Electronic

202 Supplementary Material S3). To assess field consumption rates, six freshly collected kelp blades

203 were prepared as for the experiments described above, except entire kelp blades were used.

204 Feeding assays were conducted on a falling tide series such that the next high tide would not

205 wash away the kelp blades. Replicate kelp blades were placed on the sand surface at the high tide

206 line on the six beaches before sunset and collected just after sunrise. The kelp remaining in each

207 kelp blade after the overnight assay was processed as above to determine the consumed dry mass

208 for each replicate.

209   Prior to each field consumption test, we quantitatively surveyed macrophyte wrack cover

210   and the species richness and abundance of macroinvertebrates in the upper beach zone of the six

211   beaches using methodology adapted from Dugan et al. (2003). Wrack cover was estimated using

212   the line-intercept method (Dugan et al. 2003). Invertebrates were surveyed by collecting 20

213   evenly spaced cores (10 cm diameter, 20 cm depth) from the upper beach boundary (cliff base or

214   dune toe) to the lowest extent of upper beach invertebrates on six haphazardly placed shore-

215   normal transects. Core samples were aggregated and sieved in 1.5 mm mesh in the field to

216   remove sand and then frozen before sorting in the lab, where animals were identified to species

217   and counted. Counts were converted to number of individuals per meter of shoreline based on the

218   number of cores and their spacing rather than per m^2 to better account for changing beach widths

219   across sites and time (Brown and McLachlan 1990, Schlacher et al. 2008, Dugan et al. 2013).

220   Mean site values were calculated across the six transects for each time point.

221   *Data Analysis*

222   To compare feeding rates of the six detritivore species, we analyzed consumption rates

223   from the six single species treatments (n = 18 total replicates) using one-way ANOVA followed

224   by a Tukey post-hoc test and generation of a compact letter display for the pairwise comparisons.

225   The relationship between kelp consumer rates and consumer biomass was explored with linear

226   regression analysis for the single species replicates (n = 18) and for all treatment replicates (n =

227   171). The effect of consumer diversity on kelp consumption rates was evaluated with ANOVA,

228   where kelp consumption was the response variable and richness the explanatory variable. To

229   further explore the relationship between species richness and identity we employed a hierarchical

230   nested ANOVA model adapted from Reiss et al. (2011) and Bailey and Reiss (2014) that

231   separated species richness from species identity and species composition. This set of models tests

232   species richness alone, species identity, the interaction of richness and identity, and species

233   combinations as drivers of observed kelp consumption. The richness model depends only on the

234   number of species. The species identity model assigns each species its own effect, which is

235   multiplied by the number of individuals of that species present, thereby considering species'

236   abundance, and in polyculture treatments considers these effects to be additive. The richness and

237   identity interaction allows species identity effects to differ at each richness level, and tests for

238   interactions between species due to the changing number of species present at each richness

239   level. Lastly, species combination considers the species identities and their treatment

240   combinations. These related models form a hierarchical structure with increasing complexity

241   (more degrees of freedom). We used ANOVA to compare the goodness of fit for each model

242   with the goodness of fit for the next most complex model in the hierarchy (Grafen and Hails

243   2002; Reiss et al. 2011). Additional detail on the model structure is in the Electronic

244   Supplementary Material S2.

245   We evaluated relationships between diversity and abundance of detritivores and kelp

246   consumption rates across the six survey sites using linear mixed effects modeling. We first

247   assessed the relationship between kelp blade consumption (n = 6) and our two random factors of

248   site (n = 6) and month (n = 2). Then, we independently tested the effects of three site-level

249   variables;1) total richness of upper beach detritivores, 2) richness of the six species used in the

250   laboratory mesocosm experiment and, 3) the proportional abundance of the two largest species

251   relative to total abundance of detritivores. Each of the three linear mixed effects models were

252   then compared to the model with random factors only using ANOVA and provided that the

253   models explained significantly different proportions of the variance, the model with the lowest

254   Akaike Information Criterion (AIC) value was selected. Data display for the field assay consists

255   of site-level values rather than replicates for ease of distinguishing the various sites and

256   timepoints. Analyses were conducted using base R v. 3.5 (R Core Team 2013), the Tidyverse

257   package (Wickham et al. 2019), multcomp (Hothorn et al. 2008), lme4 (Bates et al. 2015), and

258   lmerTest (Kuznetsova et al. 2017).

259   **Results**

260   *Mesocosm Experiment*

261   Adult body size of the wrack detritivores varied over more than an order of magnitude

262   among the six species we tested (mean individual AFDW ± SE, 2.7 ± 0.1 mg to 46.9 ± 2.5 mg,

263   Figure 1a). Consumption rates of kelp varied over an order of magnitude and differed

264   significantly among the six species in the single species treatments (Figure 1b, one-way

265   ANOVA, F value = 12.3, $p < 0.001$, df = 5 and 12). The Tukey post-hoc test indicated that

266   differences in consumption among the six consumer species were driven by the two largest

267   talitrid species (Electronic Supplementary Material S1). These two species, *Megalorchestia*

268   *corniculata* and *M. californiana*, consumed kelp at the highest mean rates, 3.1 ± 0.3 and 2.1 ±

269   0.5 mg dry mass individual^{-1} day^{-1}, respectively, in single species treatments while the two

270   smaller species, *M. benedicti* and *M. minor*, consumed much less kelp on average, 0.2 ± 0.1 and

271   0.6 ± 0.3 mg dry kelp individual^{-1} day^{-1}, respectively. The isopod *Alloniscus perconvexus* and the

272   beetle *Phaleria rotundata* consumed kelp at similar rates, averaging 0.9 ± 0.2 mg individual^{-1}

273   day^{-1} despite their large difference (>4x AFDW) in average body size (mean individual AFDW =

274   12.3 ± 0.3 mg and 2.7 ± 0.1 mg, respectively) (Figure 1a,b). The relationship between consumer

275   biomass and kelp consumption rates was significant for the single species treatments (n = 18, r^2 =

276   0.5, $p < 0.001$, df = 1 and 16) and all treatments (n = 171, $r^2 = 0.15$, $p < 0.0001$, df = 1 and 169).

277   We evaluated the effect of biodiversity on an ecological function, in this case kelp

278   consumption rate, using replicated combinations of the six consumer species across five levels of

279   species richness. A linear regression between consumption rate and species richness suggested a

280   weak, albeit significant, negative effect of diversity on kelp consumption ($r^2 = 0.02$, $p = 0.05$)

281   (Figure 2a). Using species-specific kelp consumption rate values from the single species

282   treatments, we estimated expected consumption values for every mixed species treatment and

283   compared them to the actual consumption values and found that, on average species mixtures

284   generally underperformed their expected kelp consumption rates by 24.6% (Figure 2b).

285   The suite of models adapted from Reiss et al. (2011) and Bailey and Reiss (2014)

286   confirmed that species richness alone did not explain observed rates of kelp consumption (Table

287   1). The model results indicated that species combinations (df = 32, $p < 0.00001$) and species

288   identity (df = 5, $p < 0.00001$) were significant drivers of kelp consumption, whereas richness was

289   not. The significance of species combinations is consistent with the finding that species mixtures

290   tended to underperform predicted consumption rates. Additionally, if the monocultures

291   (combined with richness levels) predict the polyculture outcomes, then the model "Richness +

292   Identity" should account for everything apart from random error. Therefore, we compared this

293   model with all treatment outcomes (i.e. "Species Combinations"), and found that, although

294   monoculture consumption rates explain much of the consumption rates in mixed species

295   assemblages, species combinations still noticeably underperformed the expected consumption

296   rates predicted by the monoculture consumption rates (Species combinations | Richness +

297   Identity, df = 47, F = 2.99, $p < 0.00001$).

298   *Field consumption assay*

299   Background levels of macrophyte wrack cover on the six study beaches varied greatly

300 ranging from 1.3 – 4.7 m^2 m^{-1} (mean 3.0 m^2 m^{-1}) in October and 0.1 – 2.3 m^2 m^{-1} (mean 0.8 m^2

301 m^{-1}) in April. However, cover of the primary food resource, giant kelp, was less variable over

302 time ranging from 0.2 – 1.1 m^2 m^{-1} (mean 0.56 m^2 m^{-1}) in October and 0.08 – 1.9 m^2 m^{-1} (mean

303 0.56 m^2 m^{-1}) in April. Species richness of intertidal detritivores varied from 5 to 15 species in

304 surveys of the six beaches in October 2016 and April 2017. Total abundance of detritivores

305 ranged from 3,300 to 29,000 individuals m^{-1} of shoreline among the study sites, and the six

306 species we evaluated in our BEF experiments made up 92-100% of the total abundance. The

307 fraction of total abundance of the kelp detritivore community composed of the two large-bodied

308 talitrid amphipods, *Megalorchestia corniculata* and *M. californiana*, ranged from 10% to 84%

309 among sites and dates.

310   Mean values of overnight consumption of kelp in field feeding assays varied greatly

311 across the six study beaches, ranging from 180-2,549 mg dry kelp day^{-1}. Site and month were not

312 significant drivers of the observed variability in kelp consumption rates (p = 0.11). There was no

313 relationship between total consumer richness and overnight kelp consumption (Figure 3a, p =

314 0.08) across the six beaches; this result also held when richness was limited to the six species of

315 detritivores used in the mesocosm experiment (Figure 3b, p = 0.68). Neither of these models

316 explained more of the observed variance than the site and month model (p = 0.14 and p = 0.78,

317 respectively). Species identity, however, was a strong predictor of the observed consumption of

318 kelp in our field assays: the relative abundance of the two species of large-bodied talitrid

319 amphipods explained a significant portion of the variation in kelp consumption among beaches

320 (Figure 3c, t = 5.7, p < 0.0001, trendline displayed represents simple linear regression (also

321   significnant) for display purposes). This model was also a significant improvement over the site

322   and month model (chi-square = 20.8, p < 0.0001).

323   **Discussion**

324   Our results from laboratory experiments and field assays suggest that species richness of

325   intertidal detritivores does not strongly influence the rate of processing of marine detrital

326   subsidies, a key ecological function on sandy beaches. Rates of kelp wrack consumption in both

327   mesocosm experiments and the field assays were better predicted by species identity than by

328   diversity. In mesocosm experiments, kelp consumption rates in mixed-species treatments were

329   nearly 25% below predicted values based on the single species treatments. In the field,

330   processing of kelp wrack by intertidal consumers was strongly influenced by the relative

331   abundance of the two largest species of talitrid amphipods, rather than the species richness of the

332   intertidal detritivore community. Our finding that species identity is relevant to how ecosystem

333   functioning may change if one species were substituted for another points to the role of

334   consumer body size, but also indicates that results of BEF studies are context dependent based on

335   the community metrics varied. While our focus was on the effect of changing community

336   richness with evenness maintained, data indicate that community biomass is also an important

337   variable in the magnitude of this ecosystem function.

338   Ecosystem function may be strongly influenced by the number of species present if

339   different processes require functionally distinct species (Perkins et al. 2015) or if the actions of

340   one or more species facilitate others (Tonin et al. 2018). Given that feeding habits, intertidal

341   habitat, and other functional traits of the invertebrate consumers in this experiment were similar

342   and individual biomass varied greatly, our finding that species richness was not a strong driver of

343   ecosystem function on beaches is perhaps not surprising. Our results are consistent with those

344   from detritivore communities in a variety of terrestrial and aquatic ecosystems including

345   grasslands, floodplains, streams and salt marshes (Cragg and Bardgett 2001; Reiss et al. 2010;

346   Treplin et al. 2013; O'Connor et al. 2016; Little and Altermatt 2018). Instead, species identity

347   was a better predictor of ecosystem functioning than richness in our sandy beach ecosystem. A

348   strong role of species identity in function has been reported in a variety of systems (Handa et al.

349   2014; Gagic et al. 2015), including leaf litter breakdown by freshwater detritivores (Jonsson and

350   Malmqvist 2000; Stoker et al. 2017; Santonja et al. 2018), grazing of marine algal biomass

351   (Duffy et al. 2001; O'Connor and Crowe 2005; Godbold et al. 2009), urban food litter

352   consumption by arthropods (Youngsteadt et al. 2014), and nutrient regeneration by marine

353   bioturbators (Ieno et al. 2006).

354   Patterns of resource dynamics in subsidized ecosystems and the species traits of

355   consumers that rely on these resources may underlie these findings. In ecosystems with stable

356   and diverse primary producer communities, the resulting resource heterogeneity and stability is

357   conducive to specialization by consumers (Reboud and Bell 1997; Kassen 2002). Niche

358   partitioning by these specialists results in complementarity as different species use different

359   resources (Finke and Snyder 2008) and increasing diversity leads to greater overall resource

360   exploitation and ecosystem functioning (Thebault and Loreau 2003; Ives et al. 2005; Finke and

361   Snyder 2008; Filip et al. 2014). In contrast, when the type or availability of resources is more

362   stochastic, as in many subsidized food webs, generalist consumers tend to have an advantage

363   (Reboud and Bell 1997; Ma and Levin 2006; Narwani and Mazumder 2010). The highly

364   dynamic supply of kelp wrack and other marine subsidies on sandy beaches may thus promote a

365   relatively high abundance of generalist consumer species (Hutchinson 1961; Mihuc and Minshall

366 1995; Verberk et al. 2010), weakening BEF relationships due to greater functional redundancies

367 across the community (Ives et al. 2005; Novotny et al. 2010; Filip et al. 2014).

368   The underperformance of observed relative to predicted rates of kelp consumption in our

369 laboratory mesocosm experiments (Figure 2b) suggests that negative interspecific competitive

370 interactions may have increased with species richness (Bond and Chase 2002; Bastian et al.

371 2008; Gessner et al. 2010). Competition for shared resources can be high in communities

372 comprised of generalist consumers (Thebault and Loreau 2003; Ives et al. 2005). Species may

373 respond to interspecific competition by shifting their diet (Finke and Snyder 2008) or their

374 behavior across time and space (Mihuc and Minshall 1995; Mihuc 1997). Although giant kelp is

375 the primary form of macroalgal detritus on southern California beaches (Dugan et al. 2003;

376 Dugan et al. 2011), other drift macroalgae and seagrasses, as well as carrion, are consumed by

377 sandy beach invertebrates (Lastra et al. 2010; Bessa et al. 2014; Michaud et al. 2019). The

378 intertidal consumer species we investigated all readily consumed blades of giant kelp; however,

379 in nature they may adjust their behavior or diet to avoid interspecific competition. Such niche

380 partitioning would represent a form of complementarity (Loreau and Hector 2001; Thebault and

381 Loreau 2003; Poisot et al. 2013; Tonin et al. 2018) that would not be observed in a study

382 considering a single resource type. Although not tested here, this type of complementarity could

383 result in greater total detritus consumption when multiple detritivore species and types of wrack

384 detritus are present.

385   The ecological function of kelp wrack consumption was largely driven by the relative

386 abundance of the largest detritivore species in our field study. Body size is a key species trait

387 (Brose et al. 2006; Norkko et al. 2013) and large-bodied species often make disproportionately

388 high contributions to ecosystem function (Seguin et al. 2014; Brose et al. 2016; Tonin et al.

389   2018). Indeed, species traits or functional attributes are better predictors of ecological functions

390   in multitrophic systems (Lefcheck and Duffy 2015). Species that contribute significantly more to

391   an ecosystem function tend to be the dominant species in a community while rare species that are

392   generally low in abundance contribute much less (Smith and Knapp 2003, Dangles and

393   Malmqvist 2004, Klemmer et al. 2012, Wohlgemuth et al. 2016). When function is driven by

394   species identity and a dominant species is present, ecosystem functioning is expected to be

395   negatively correlated with diversity (Creed et al. 2009). The highest functioning species must

396   also be the dominant species for process rates to be high at the ecosystem scale (Creed et al.

397   2009, Treplin et al. 2013). Our finding that an important ecological function was maximized

398   when the two highest functioning species were the dominant species adds to the growing

399   evidence supporting the role of species identity and dominance in the provisioning of key

400   ecosystem functions, especially in soft-sediment ecosystems (Henderson et al. 2019, Schenone

401   and Thrush 2020).

402   Threats to biodiversity from a changing climate are well recognized (Thomas et al. 2004),

403   but our understanding of impacts on key species traits, like body size, is lacking. Warming

404   temperatures associated with climate change can lead to decreases in animal body size due to

405   higher metabolic rates and faster development, particularly in ectotherms (Gardner et al. 2011;

406   Sheridan and Bickford 2011; Ohlberger 2013). For example, a significant negative relationship

407   between sea temperature and body size has been reported for populations of sandy beach

408   invertebrates, including a talitrid amphipod, across a wide latitudinal gradient (Jaramillo et al.

409   2017). Large-bodied species may also be particularly vulnerable to extinction as the climate

410   warms (Cardillo 2006; Brose et al. 2016). Consequently, as these key species disappear,

411   ecosystem functioning may decline more than predicted by diversity losses alone.

412   Globally, sandy beach ecosystems are threatened by sea level rise, urbanization, erosion

413   and coastal armoring (Schlacher et al. 2007; Defeo et al. 2009; Dugan et al. 2017; Schooler et al.

414   2017; Vitousek et al. 2017). In combination or alone, impacts from these threats commonly

415   result in the degradation or loss of the upper beach zone required by intertidal wrack consumers

416   (Dugan et al. 2008; Myers et al. 2019). On beaches worldwide, especially along highly

417   developed shores, coastal management regimes that remove wrack (grooming or raking) and

418   armor the shore to protect coastal development and infrastructure (Defeo et al. 2009) increase

419   disturbance and reduce beach biodiversity (Dugan et al. 2003; Jaramillo et al. 2012; Schooler et

420   al. 2019). On urbanized beaches in southern California, where intertidal diversity is lower than

421   beaches in less developed areas, the two large-bodied talitrid species that we found to be the

422   most effective kelp consumers are often sparse or absent (Schooler et al. 2019), suggesting that

423   impacts to these key species from coastal management and climate change are already

424   significantly degrading sandy beach ecosystem function on developed coasts.

425   Biodiversity is often used as a primary metric to set goals, establish baselines and

426   measure success of conservation efforts (Schwartz et al. 2000; Srivastava and Vellend 2005).

427   Our results, however, reinforce the need to also consider the roles of individual species and

428   species traits in ecosystem functioning (Cadotte et al. 2011; Henderson et al. 2019). In many

429   ecosystems, including the subsidized sandy beach communities studied here, ecosystem function

430   and services may depend mainly on dominant and high-functioning species (Winfree et al.

431   2015). Identifying these key species and traits is necessary to predict the impacts of species loss

432   on ecosystems and their vital functions, and to prioritize them for conservation and management.

433

446 **Conflicts of Interest**: The authors declare that they have no conflict of interest.

447 Ethics Approval: All applicable institutional and/or national guidelines for the care and use of

448 animals were followed.

449 **Availability of data and material**: The datasets generated during and/or analyzed during the

450 current study are available from the corresponding author on reasonable request.

451

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851

852 **Table 1**.

853 Results of ANOVA for nested model set derived from Reiss et al. (2011) and Bailey and Reiss

854 (2014) on laboratory mesocosm results for response variables of trial, richness, identity and

855 species combination. Trial refers to the week the treatment was conducted, richness is the

856 number of species, identity is the species-specific effect, and species combination refers to the

857 specific assemblage composition of each treatment. Each row in the table corresponds to a

858 difference between two models. The number in parentheses is the number of model parameters,

859 the "|" means "given", and degrees of freedom is the difference between the numbers of

860 parameters in the two models. See Appendix S1 for more model information.

861

Comparison	Degrees of Freedom	Sum of Squares	Mean Square	F	p
Trial (3) | Constant (1)	2	350.2	175.1	4.13	0.02
Richness (5) | Trial (3)	2	143.4	71.68	1.69	0.2
Identity (6) | Constant (1)	5	4246.7	849.34	20.04	<0.00001
Richness*identity (25) | Richness + Identity (10)	15	1652.9	110.19	2.6	0.002
Species combination (57) | Richness*Identity (25)	32	4309.8	134.68	3.18	<0.00001
Residuals	114	4830.9	42.38		

862

Figure Legends

864   **Fig. 1 (a)** Mean values (n=3) of species-specific individual ash-free dry weights (AFDW, mg).

865   **(b)** Mean values (n = 3) of species-specific kelp consumption rates from single species

866   mesocosm treatments. Error bars are standard error and letters identify groups of non-significant

867   pairings determined by the TukeyHSD post-hoc test. Species codes: P = *Phaleria rotundata*, B =

868   *Megalorchestia benedicti*, M = *Megalorchestia minor*, A = *Alloniscus perconvexus*, Co =

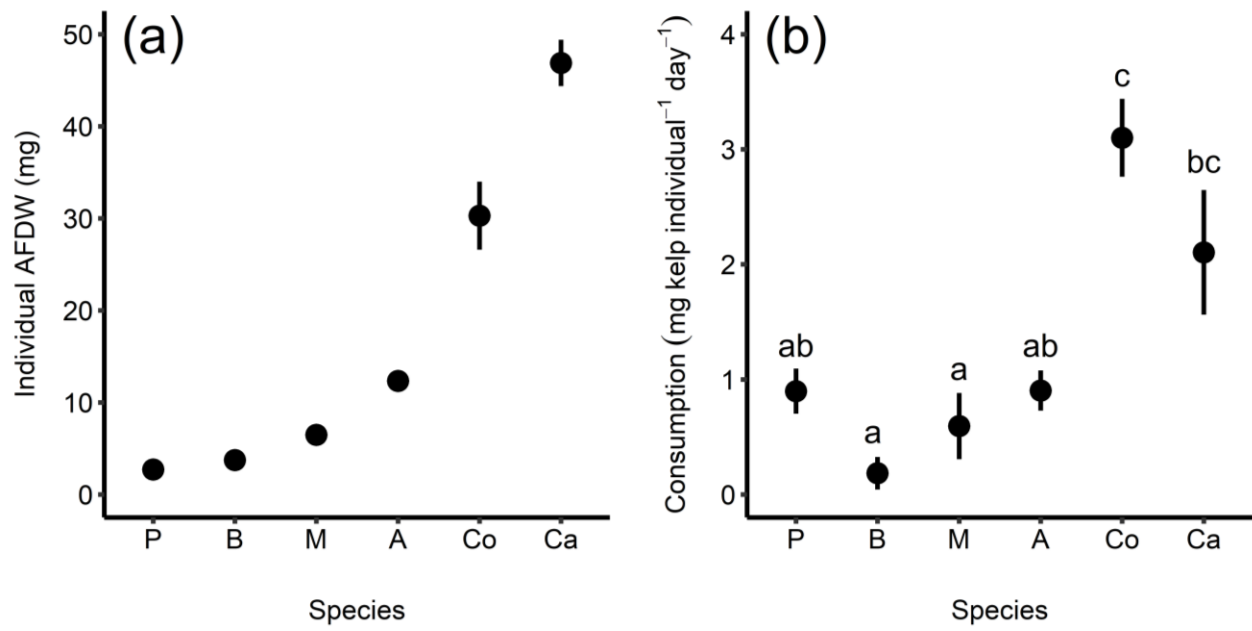869   *Megalorchestia corniculata*, Ca = *Megalorchestia californiana*

870

871   **Fig. 2 (a)** Kelp consumption rates (mg dry kelp individual^{-1} day^{-1}) as a function of species

872   richness in mesocosm experiments. The line represents a linear regression (r^2 = 0.02, p = 0.04).

873   **(b)** Observed kelp consumption rates in mesocosm experiments compared to expected kelp

874   consumption rates based on species' performance in single species treatments. Dashed line

875   represents 1:1 line

876   **Fig. 3 (a)** Overnight kelp consumption for field assays compared to total observed richness of

877   upper beach detritivores for six beaches in October 2016 (unfilled) and April 2017 (filled) (site

878   symbols: R Beach - circle, Isla Vista – square, East Depressions - diamond, East Goleta -

879   triangle, Arroyo Burro West – inverted triangle, Arroyo Burro East – cross (circled cross in

880   April, un-circled in October). A site map is available in the Electronic Supplemental Material

881   S3). **(b)** Overnight kelp consumption for field assays compared to observed richness of the six

882   common species used in the mesocosm experiment. **(c)** Overnight kelp consumption for field

883   assays compared to the fraction of the abundance of the six consumer species occupied by the

884   two large talitrid amphipod species (*Megalorchestia corniculata* and *Megalorchestia*

885   *californiana*) (Linear mixed effects model, t = 5.7, p < 0.0001). The simple linear regression

886   between site means (also significant) is shown for display purposes ($r^2 = 0.59$, $p < 0.01$). Error

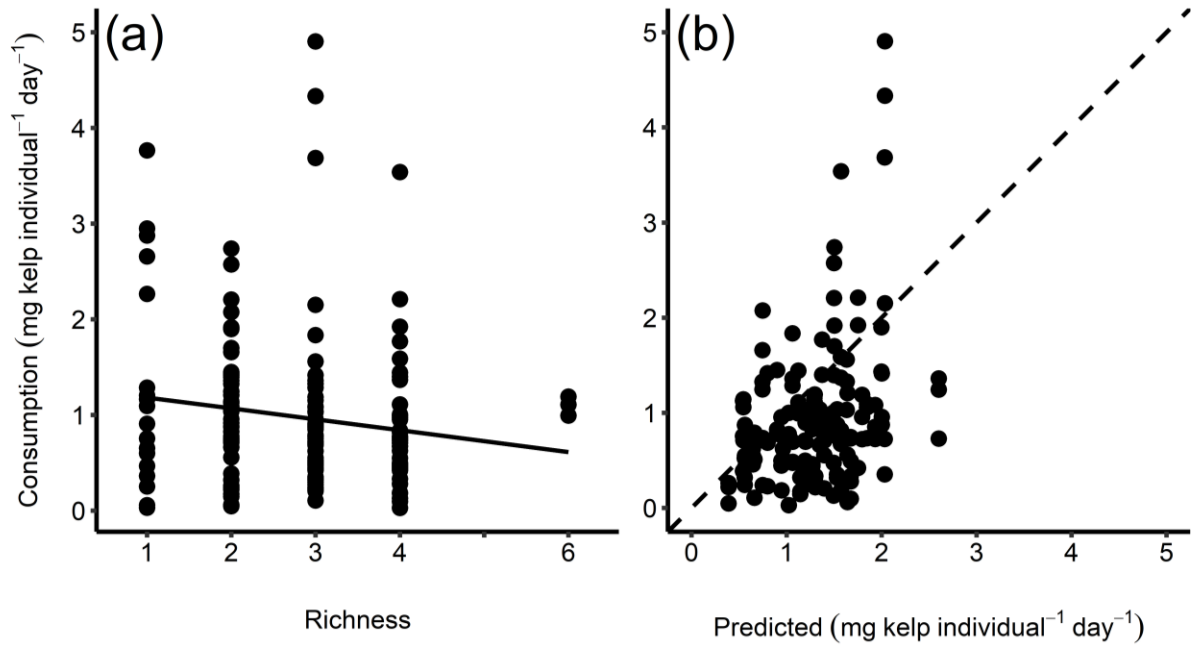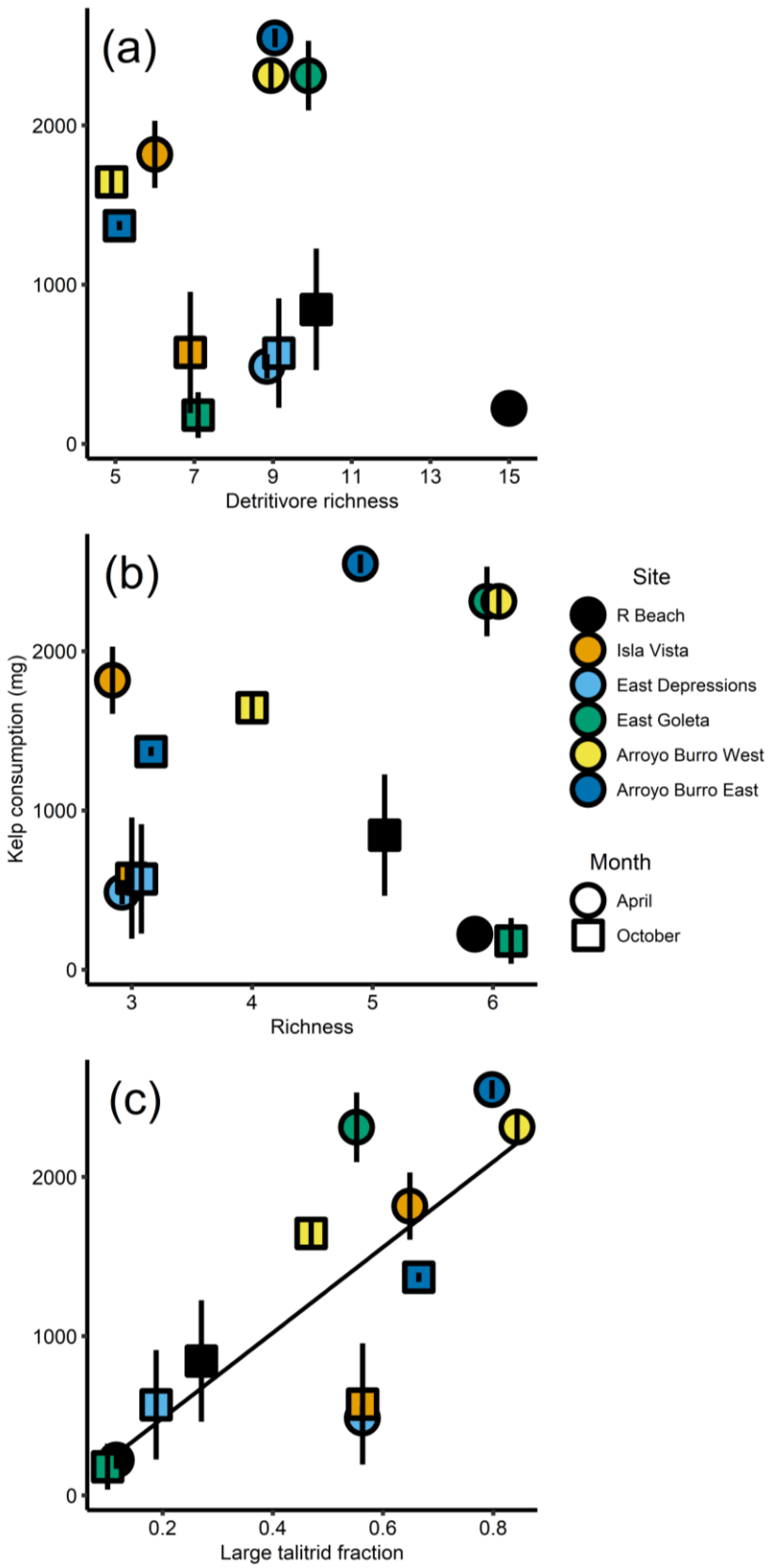887   bars are standard error of consumption rates ($n = 6$)

888   **Fig. 1**

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890

Fig. 2

Fig. 3