

1 **Running head:** Species co-occurrence networks

2 **Title:** Species co-occurrence networks: can they reveal trophic and non-trophic interactions in
3 ecological communities?

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39 **Abstract**

40 Co-occurrence methods are increasingly utilized in ecology to infer networks of species
41 interactions where detailed knowledge based on empirical studies is difficult to obtain. Their use
42 is particularly common, but not restricted to, microbial networks constructed from metagenomic
43 analyses. In this study, we test the efficacy of this procedure by comparing an inferred network
44 constructed using spatially intensive co-occurrence data from the rocky intertidal zone in central
45 Chile to a well-resolved, empirically-based, species interaction network from the same region.
46 We evaluated the overlap in the information provided by each network and whether there is a
47 bias for co-occurrence data to better detect known trophic or non-trophic, positive or negative
48 interactions. We found a poor correspondence between the co-occurrence network and the
49 known species interactions with overall sensitivity (probability of true link detection) equal to
50 0.469, and specificity (true non-interaction) equal to 0.527. The ability to detect interactions
51 varied with interaction type. Positive non-trophic interactions such as commensalism and
52 facilitation were detected at the highest rates. These results demonstrate that co-occurrence
53 networks do not represent well classical ecological networks in which interactions are defined by
54 direct observations or experimental manipulations. Co-occurrence networks provide information
55 about the joint spatial effects of environmental conditions, recruitment, and, to some extent,
56 biotic interactions, and among the latter, they tend to better detect niche-expanding interactions
57 such as positive non-trophic interactions including habitat engineering. Detection of links
58 (sensitivity or specificity) was not higher for well-known intertidal keystone species than for the
59 rest of consumers in the community. Thus, as observed in previous empirical and theoretical
60 studies, patterns of interactions in co-occurrence networks must be interpreted with caution,
61 especially when extending interaction-based ecological theory to interpret network variability

62 and stability. Co-occurrence networks may be particularly valuable for analysis of community
63 dynamics that blends interactions and environment, rather than pairwise interactions alone.

64 **Keywords:** species interactions, non-trophic interactions, food webs, ecological networks, co-
65 occurrence, intertidal, keystone species, anthropogenic impacts

66 **Introduction**

67 Most past ecological research on the network of species interactions within communities has
68 focused on small subsets of interacting species, and usually on those interactions that can be
69 easily inferred from observation of an organism's diet or physical contact between species, such
70 as predation, pollination, and fruit dispersal (Bascompte and Jordano 2104, Dunne et al 2002,
71 Montoya and Solè 2002). Since such approaches usually require extensive efforts in data
72 collection, and because many types of interactions or ecological systems cannot be readily
73 observed (e.g. microbial communities, endoparasites), it is increasingly common to infer or
74 reconstruct interaction networks from pattern in species co-occurrence in either time or space
75 (e.g. Stephens et al. 2009, Araujo et al., 2011, Faust and Raes 2012, Borthagaray et al. 2014).

76 Species co-occurrence is a simple and long sought after approach to infer species interactions
77 within ecological systems (Morales-Castilla et al., 2015, Cazelles et al., 2016, Sander et al.,
78 2017). Significant spatial co-occurrence is considered evidence of positive or mutualistic
79 interactions, and co-exclusion considered evidence of negative (e.g. competitive) interactions
80 (Faust et al., 2015, Fuhrman et al 2015). However, co-occurrence patterns within a single
81 ecosystem can also be interpreted in terms of species response to environmental factors (Peres-
82 Neto et al. 2001) or dispersal limitation (Ulrich 2004). The premise of the co-occurrence
83 approach is that if species in a community are interacting with each other in a way that affects
84 each others' abundance or presence over space, thereby influencing local community assembly

85 patterns, then they will have non-random co-occurrence that could be revealed through an
86 appropriate sampling design and statistical tests (e.g. Ulrich & Gotelli 2013, Borthagaray et al.
87 2014). For example, predators might be observed with their prey more frequently, and
88 competitors might be observed together less frequently than expected from random assembly.
89 This approach is closely related to the development of assembly rules (Diamond 1975) and null
90 models in ecology (Graves and Gotelli 1996). While our understanding of co-occurrence patterns
91 and the processes underlying community assembly is much more sophisticated and multifactorial
92 than originally envisioned (de Bello et al., 2012, Chase 2012, Cazelles et al., 2016), the basic
93 premise from the point of view of building ecological networks from such patterns is essentially
94 the same (Peres-Neto et al 2001).

95 The pattern of interactions among members of an ecological community has consequences
96 for population dynamics and persistence of species, for network stability and for the maintenance
97 of ecological function (e.g. Allesina and Pascual 2008, Faust and Raes 2012, Slessarev et al.,
98 2016). It is therefore important to understand to what extent patterns of co-occurrence of species
99 (or Operational Taxonomic Units in the case of microbes) reflect species interactions. In other
100 words, to what extent ecological networks built from co-occurrence patterns, for microscopic or
101 metazoan organisms, are commensurate with those built through direct observation, such as gut
102 content analyses, direct observations of consumption, stable isotope analyses, or experimental
103 manipulations (Dunne et al 2008, Kéfi et al 2015, 2016, Sander et al., 2017)?

104 There are important ecological and methodological reasons as to why ecological interactions
105 may not translate into easily discernible patterns of co-occurrence. The method of constructing
106 ecological networks from co-occurrence data has explicit spatial assumptions built into its
107 design, which should be scrutinized further so that we better understand the limitations of the

108 approach when it comes to interpreting network structure and dynamics. Predator and prey are
109 expected to positively correlate over some spatial scale that allows predators to maximize prey
110 encounters. Yet, over some smaller scale, effective predators should reduce or completely
111 eliminate prey, sometimes restricting them to refuges beyond predator reach, generating strong
112 negative associations. The actual spatial scale over which the direction of species correlation
113 changes across an environmental or biotic gradient will also change depending on biological
114 attributes of the species involved, such as body size and dispersal capacity (Borthagaray et al
115 2014). This makes it quite challenging to detect such correlations across multiple-species
116 assemblages using a fixed sampling size. In addition, species interaction networks, especially
117 food web networks, are directed, which means the matrix of species interactions can be
118 asymmetric (Cazelles et al 2016). Covariance structures estimated from spatial co-occurrence
119 can only infer symmetric interactions. Further, species can coexist and exhibit a correlation in
120 their abundances through either time or space because they are affected by a third species (as in
121 apparent competition, e.g., Holt and Bonsall 2017), or through a common environmental factor,
122 even if the species pair does not interact directly. Moreover, spatial variability in dispersal and
123 subsequent settlement and recruitment can by itself generate spatial correlation patterns between
124 species (e.g. de Bello et al., 2012, Shinen & Navarrete 2014). The multi-species interactive
125 nature of real communities, where each species simultaneously interacts with many others and in
126 different ways (Berlow et al 2004, Kéfi et al 2016), adds additional complications when trying to
127 construct patterns of paired interaction from co-occurrence (Azaele et al 2010). In this context, it
128 is of great importance to understand the robustness of the network reconstructions based upon
129 co-occurrence data.

130 Despite these limitations, one can still argue that if species interactions are important in

131 determining the presence of species, then non-random patterns of co-occurrence must reflect the
132 multiplicity of interactions, especially after controlling for environmental effects and indirect
133 effects of third species (Peres-Neto et al 2001, Azaele et al 2010). Co-occurrence analyses can be
134 particularly valuable because they have the potential to reveal which species respond in similar
135 ways to ecosystem conditions. Indeed, many ‘true’ observed links (e.g. a predator incidentally
136 consuming a prey species) may be feeble and have little relevance in modulating prey abundance
137 (but see Berlow 1999). In this sense, significant patterns of co-occurrence may reveal strong
138 ecological interactions and filter out many weak effects.

139 Here we provide an empirical test of inferring species interactions from correlational studies
140 using a well-resolved and comparatively specious empirically-based ecological network from the
141 wave exposed rocky shore of central Chile. We focus on examining the types of interactions for
142 which there is the greatest correspondence between correlation-based and empirical approaches
143 to species interactions. The only other study to conduct such an analysis focused on machine
144 learning approaches and comparison to different ecosystems (Sander et al 2017). We elucidate
145 the aspects of the intertidal ecosystem that relate most directly to species co-occurrence.

146 We examine whether patterns of species co-occurrence, obtained through intensive field
147 surveys conducted at multiple sites, may reflect the documented species interactions in the
148 network. Importantly, not only consumptive interactions among the members (hereafter food
149 web) of the local community have been considered, but also non-trophic interactions (hereafter
150 NTI), such as facilitation, interference, or habitat provisioning have been described (Kéfi et al.,
151 2015, 2016). Since many of the documented interactions in ecological communities are non-
152 trophic, such as mutualistic relations and competition, we examine whether spatial co-occurrence
153 patterns reflect best trophic, positive NTI or negative NTI type of interactions. Moreover, we

154 assess whether known strong interactions are better resolved by spatial co-occurrence patterns, as
155 well as assess the performance of the methods across strong environmental gradients.

156 **Method**

157 *Network*

158 The approach we follow here is to use a 'known', independently constructed ecological
159 network of species interactions for the wave-exposed rocky shore of central Chile (see Castilla
160 and Durán 1985 and Castilla 1999 for an overview of this system) and examine whether such a
161 network can be reconstructed from extensive species co-occurrence data. The interaction
162 structure for this community is composed of the trophic interactions, negative NTIs, and positive
163 NTIs recorded in Kéfi et al. (2015). Like all ecological networks, there is uncertainty as to the
164 significance of some of the links connecting species in the network (see discussion in Kéfi et al.
165 2015), but the network used here represents one of the most complete networks yet published in
166 which both food web (trophic) interactions and non-trophic interactions are determined from
167 long-term analysis of species' natural history, surveys and observations, and experimental
168 studies. Further methodological details and analyses of the network structure can be found in
169 Kéfi et al. 2015, 2016 and in <http://beta.mappr.io/play/chile-marine-intertidal-network>.

170 *Field surveys in rocky shore communities*

171 The spatial data is from surveys of species at multiple sites over multiple years along the
172 rocky shores of central Chile. A total of 49 sites and 3847 quadrats were considered in our
173 analyses (Figure 1). Out of these 49 sites, 46 sites were sampled during the time periods 1998-
174 2000, 2003-2005, and 2010, 7-15 quadrats of 50 by 50 cm placed haphazardly along a 20-30
175 meter long transect at each low and mid, and occasionally high, intertidal zones were sampled.
176 This sampling effort was sufficient to capture the full species richness at each site (Broitman et al

177 2011). Note that not every site was sampled every year and a different number of quadrats were
178 sampled during each survey. Details of the surveys, methods and distribution of sites sampled
179 can be found in Broitman et al. (2001, 2011), Navarrete et al., (2005), and Wieters et al. (2009).
180 In 2013, three additional sites around the region of Copiapó (27°S) were surveyed. This time, 25
181 quadrats of 50 by 50 cm at three different tidal levels (high, mid, and low tide) along 50 meter
182 transects were sampled. For all surveys, mobile species were counted as individual organisms
183 while sessile species were recorded as percent cover.

184 *Inferring links from spatial structure*

185 We used Pearson correlations on presence/absence data to test for spatial association between
186 species. The sign and magnitude of the association is that of the correlation coefficient. Note
187 that for presence/absence data, Pearson correlation is equivalent to Spearman and Kendall's tau
188 correlations. We assigned a $\alpha = 0.1$ significance threshold, privileging a greater number of
189 significant links over precision. The results are insensitive to alterations in this value, however it
190 should be noted that 10% of the inferred associations are likely due to statistical effects.

191 In the results section that follows, and for ease of presentation, we describe to what extent the
192 species interactions recovered from co-occurrence data revealed 'true' links as previously
193 described in the intertidal ecological network, using the Pearson correlation approach and note
194 the differences with the null model approach. Of course, as discussed above, identification of
195 such 'true' links are not free of assumptions (see Kéfi et al., 2015 for detailed discussion). We
196 adopt the terminology of 'interaction' for links in the 'true' network and 'association' for links in
197 the co-occurrence network.

198 We present heatmaps of the full results in the Appendix S1, figures S2-S6 and present and
199 discuss condensed versions of these results in the body of the manuscript.

200 Sensitivity, or the probability of detection of a true link, is computed as the ratio of the
201 number of links that are correctly identified as ecological interactions (true positives) to the total
202 number of links in the empirical network. Specificity, or the true negative rate, is the ratio of the
203 number of links that are correctly identified non-interactions (true negatives) to the total number
204 of non-interactions in the empirical network. Sensitivity and specificity are defined for any given
205 subnetwork, including for single species, by counting only the links that connect to species
206 within that subnetwork (links may originate or end outside of the subnetwork).

207 There is a plethora of approaches for reconstructing species interactions from
208 presence/absence data, but most have the covariance matrix, the object of analysis in this study,
209 as a common underpinning. An alternative conceptual approach, the “probabilistic approach”, is
210 to measure association based on significant deviations from the expected probability of co-
211 occurrence of two species based on the occurrence of single species (Araujo 2011, Veech 2014).
212 Significant deviation from the expectation can be determined using a null model approach
213 (Gotelli and Graves 2000), or an exact p-value if there are very few samples (Veech 2014). To
214 complement our analysis we used both the correlation and the probabilistic approach described
215 above.

216 *Strong Interactions*

217 The keystone species in this ecosystem that have been identified through experimental
218 manipulations (Paine et al. 1966, Castilla and Duran 1985, Navarrete and Castilla 2003, Oliva
219 and Castilla 1986, Aguilera and Navarrete 2012) are carnivores: the seastar *Heliaster helianthus*
220 and the muricid whelk *Concholepas concholepas*, and grazers: *Fissurella crassa* and *Fissurella*
221 *limbata*. It should be noted that these grazers are highly omnivorous (Camus et al., 2008, 2014).
222 There are also 14 species that are harvested by humans, including three of the keystone species

223 (*C. concholepas*, *F. crassa*, and *F. limbata*).

224 **Results**

225 *Inferring links of the ecological network from non-random co-occurrence*

226 The probabilistic approach performs substantially worse than the correlation-based approach
227 due to a high false-positive rate (specificity of 0.283). It has slightly higher sensitivity (0.692)
228 than the correlation-based approach, particularly for rare species, but much lower specificity.
229 Consequently, we focus on analyzing the performance of the better-performing correlation
230 method and present these results in appendix S1, figures S7 and S8.

231 The overall sensitivity using the correlation-based approach with a significance of $\alpha = 0.1$ is
232 0.469, meaning just under half of the interactions in the empirical network are detected as
233 significant associations. The specificity is 0.527, meaning that slightly over half of the detected
234 non-associations are not interactions. The lowest specificity (0.367) was in the sessile-sessile
235 interactions, which are mostly negative NTIs. In comparison to other interactions, there are
236 relatively few interactions where a sessile species affects a mobile species and both specificity
237 (0.558) and sensitivity (0.531) are highest for these interactions.

238 As a species becomes more common across the region, sensitivity increases rapidly at first
239 and then appears to level off around an occurrence of 1000 quadrats out of the total of 3847
240 quadrats (Figure 2a). Similarly, specificity rapidly declines, i.e. more false or spurious
241 interactions are detected with increasing occurrence of the species in the field surveys up to
242 about 1000 quadrats, where it levels off to between 0.2- 0.3 (20-30% of non-interactions
243 correctly classified as non-interactions) (Figure 2b). The specificity does not fall off as quickly
244 as sensitivity increases; a linear best fit between the two metrics for each individual species
245 compared to all interaction types has a slope of -0.861 (Figure 2c). The detection is best for

246 positive non-trophic interactions (Figure 2c, purple line). We find no relationship between the
247 total number of potential interactions and the average effect size (Appendix S1; Figure S1).

248 *Detection by interaction type*

249 The ability to correctly detect a true link (i.e. sensitivity) varies across different interaction
250 types with positive non-trophic interactions being most detectable by co-occurrence. Of the
251 known positive non-trophic interactions, 77.4% were detected (Figure 3). Negative non-trophic
252 interactions and trophic interactions are less detected with 46.7% and 44.4% of the known
253 interactions detected, respectively (Figure 3).

254 At the spatial scale of the quadrats (0.25m²), the sign of significant correlation coefficients
255 that correspond with trophic interactions is mainly positive, suggesting that the co-occurrence
256 approach is best able to detect instances where species co-occur with their prey more often than
257 they exclude their prey (Figure 4c). This may be a general principle for this system, but we
258 would need to collect additional evidence to support this hypothesis. The strongest positive
259 association observed was between the kelp *Lessonia spp* (*L. spicata* and *L. heteroana*) and the
260 grazing limpet *S. scurra*, which lives almost exclusively on the kelp. These species thus also
261 share a positive non-trophic interaction. Almost all of the asymmetrical interactions in the
262 interaction network are trophic interactions. Only 614 of the significant associations correspond
263 to asymmetrical interactions; consequently 614 of 2888 false positives are possibly accounted for
264 by asymmetry in interactions.

265 Of the 120 positive non-trophic interactions detected as a significant association, 14 were
266 detected as negative associations (Figure 4d). Of these, 4 were species pairs that have both
267 positive and negative non-trophic interactions (*Corallina officinalis* -> *Perumytilus purpuratus*,
268 *Phragmatopoma spp.* -> *Ulva rigida*, *Porphyra spp.* -> *Semimytilus algosus*, *Semimytilus*

269 *algosus* -> *Porphyra spp.*). Four of the positive NTIs that were detected as significant negative
270 correlations are positive interactions initiated by *P. purpuratus*, which is both a strong
271 competitor for space and a habitat engineering species.

272 Negative non-trophic interactions detected as significant associations in the co-occurrence
273 analysis were overwhelmingly and incorrectly identified as positive associations (Figure 4a). In
274 the low intertidal zone, negative non-trophic interactions were more likely to be identified as
275 negative associations in the surveys than at any other tidal height.

276 *The intertidal stress gradient*

277 The gradient from low to high intertidal zone represents a strong environmental stress
278 gradient for intertidal organisms of marine origin (Connell 1961). We therefore performed
279 separate analyses per tidal height, which is one way of controlling for or reducing the influence
280 of environmental conditions.

281 Overall, a smaller percentage of the links were detected when separate analyses were
282 conducted for the high, mid, and low shore heights, especially a lower percentage of positive
283 non-trophic interactions and of trophic interactions (Figure 3). The lower percentage of links
284 detected is due, at least in part, to reduction in statistical power due to the smaller sample sizes.
285 There are 1610 quadrats for each of the low and mid tidal heights and 627 quadrats at the high
286 tidal height. In order to control for the effects of reducing the sample size on the statistical
287 power, we performed the co-occurrence analysis on 500 random subsamples with the same
288 number of quadrats as were available for each shore height, 1610 quadrats for comparison to the
289 low and mid tidal zone and 627 quadrats for comparison to the high tidal zone. For all interaction
290 types, a lower percentage of interactions were detected with a random subsample than with all
291 samples, indicating that there is a reduction of statistical power with a reduced sample size.

292 From these analyses we found that species co-occurrence detected $34.6 \pm 0.0187\%$ of the negative
293 non-trophic interactions with 627 randomly selected samples and $38.2 \pm 0.0152\%$ of the negative
294 non-trophic interactions with 1610 samples, $60.2 \pm 0.0338\%$ of the positive non-trophic
295 interactions with 627 samples and $66.3 \pm 0.0616\%$ of the positive non-trophic interactions with
296 1610 samples. Finally, species co-occurrence detected $28.0 \pm 0.0141\%$ of the trophic interactions
297 with 627 samples and $33.8 \pm 0.010\%$ of the trophic interactions with 1610 samples. These
298 numbers should be compared with Figure 3 to understand the interaction of tidal height and
299 interaction type for detectability. Co-occurrence using just samples from the high tidal height
300 detects a higher proportion of the known negative non-trophic and trophic interactions than a
301 sample across the environmental gradient of the same size. Using the low and mid tidal elevation
302 samples, co-occurrence detects fewer links than in a sample of the same size across the
303 environmental gradient for all interaction types.

304 *Indirect interactions*

305 The empirical network is dense, with 4458 links representing both trophic and non-trophic
306 interactions, resulting in a connectance of 0.47. Consequently, indirect interactions are extremely
307 abundant in this system. At path length 4, the network is complete (every species is connected to
308 every other species by a path of length 4). An indirect interaction of path length 2 is an
309 interaction between two species that is mediated by a third species (e.g. species A and species B
310 have an interaction, species C and species B have an interaction, so the interaction between
311 species A and species C is a path length two indirect interaction). There are 8833 interactions of
312 path length two; of these, 1537 correspond to significant co-occurrences that did not correspond
313 to links in the empirical networks of known direct interactions (“false positives”), making them
314 likely candidates for pairwise co-occurrence driven by interactions with a third species. One

315 example of an indirect interaction is competition for prey. In this network, 1324 path-length-two
316 indirect interactions are between predators that share prey. Of these 1324 links, 496 links were
317 discovered as significant association between species.

318 *Strong interactions: keystone species, anthropogenic effects, and effect size*

319 We did not find that the keystone species are distinguishable in either the specificity or
320 sensitivity from other species in the community. Harvested species tend to have a slightly larger
321 effect size (stronger correlation) for a given node degree (Figure 5), whereas no noticeable
322 distinction between keystone and other species was observed in terms of the effect size (Figure
323 5). The median effect size of correlations increases with increasing detected node degree and
324 sessile species show a more gradual increasing trend than mobile species. The species with the
325 largest median effect sizes were small generalist herbivores, the barnacles *N. scabrosus* and *J.*
326 *cirratus*, and the algae *M. laminarioides* and *Porphyra spp.*.

327 **Discussion**

328 The construction of ecological networks from patterns of species co-occurrences is rapidly
329 expanding in the microbial ecological and biomedical sciences (Fuhrman et al 2015), and
330 spreading to metazoan communities (Araujo et al., 2011, Borthagary et al 2014). There is no
331 doubt that such co-occurrence networks reveal aspects of a local community that have important
332 bearing on network dynamics, stability and resilience (Faust and Raes 2012), and, in the case of
333 microbial environmental genomic studies, there are as of now few other sensible approaches to
334 get a glimpse into the complex matrix of interactions among the members of these highly diverse
335 communities. Our results do not dispute the importance of such networks. However, in many
336 ways, authors have interpreted co-occurrence as revealing ‘classical’ species interaction
337 networks (e.g. competition, predations, facilitation). Our results complement and expand recent

338 empirical findings (Sander et al., 2017), which suggest this to be highly unlikely by using a
339 spatially extensive dataset that reflects the type of presence-absence data that is commonly
340 available for co-occurrence studies.

341 *Inferring links*

342 Given the multiplicity of ecological and environmental processes that affect species
343 assemblages, the prevalence of weak links in the empirical network, and the potentially large
344 number of species in this community, the result that many species interactions are still
345 detectable, with 25-70% of species interactions detected, depending on the interaction type and
346 data subset used, is indicative of a strong role of species interactions in this community.

347 There are distinct reasons, statistical and artefactual, for why there may be false positives as
348 opposed to false negatives. The correlation test can only infer symmetric interactions but true
349 interactions can be asymmetrical, leading to false positives. In addition, some of the false
350 positives could represent correlations based on shared environmental preference, common
351 settlement patterns, or indirect interactions. Indirect interactions could also result in false
352 negatives, if multiple interactions cancel out (Cazelles et al 2016). There may be other reasons
353 for the lack of sensitivity, such as a priority effect operating on sessile or highly territorial
354 species, for instance. If a priority effect is important, then the order of arrival of larva to the
355 shore, a stochastic process that may also depend on species-specific life history traits, may matter
356 more for coexistence than does the outcome of competitive interactions among juveniles or
357 adults once on the shore (Berkeley et al. 2010, Aiken and Navarrete 2014, Orostica et al 2014).

358 Increasing occurrence of individual species decreases the specificity while increasing
359 sensitivity. This diminishing return has both statistical and biological explanations. As
360 occurrence increases, more information is available about new species combinations, but as

361 occurrence asymptotes to match the number of samples, there is less information available again.
362 The saturating relationships in Figure 2a,b is likely a unimodal relationship with zero sensitivity
363 as occurrence goes to one and as occurrence goes to the number of samples. We cannot verify
364 this hypothesis since no species were present in all samples. This suggests that there is a limit to
365 detectability of interactions when using occurrence alone, a limitation that in theory could be
366 resolved with quantitative abundance data. Previous studies have attributed similar results based
367 on occurrences to significant ecological processes, hypothesizing that less common species are
368 more affected by biotic interactions than by environmental preferences (Azaele et al 2010). This
369 may be the reason why including both biotic and abiotic predictor variables usually improves the
370 modeling of species interactions and spatial distribution (Gonzalez-Salazar et al. 2013, Stephens
371 et al. 2017). In our system, we have no information that could help us test this hypothesis.
372 Further work along this research direction should be encouraged.

373 We found that the Pearson's correlation test performed better than the probabilistic approach.
374 The robustness of Pearson's correlation has been noted in other studies. Notably, Sander et al
375 (2017) found that two machine-learning approaches were not superior to using Pearson's
376 correlation.

377 *Niche-based and interaction-based processes*

378 Positive non-trophic interactions are more detectable than either negative non-trophic
379 interactions or trophic interactions. The fact that over 70% of positive non-trophic interactions
380 were correctly detected indicates the usefulness of occurrence data to infer species interactions.
381 A similar result was also obtained by Sanders et al. (2017) using occurrence data and both
382 Pearson's correlation and Dynamic Bayesian Networks to infer non-trophic interactions (positive
383 and negative pooled), which suggest that the increased sensitivity of occurrence data for this type

384 of data may be a general phenomenon. Positive non-trophic interactions generally ameliorate
385 environmental stress or provide habitat for other species, in effect expanding the possible niche
386 for the species involved (Jones et al. 1994, Wright et al, 2002, Hastings et al., 2007, Stachowicz
387 2012). Trophic and non-trophic interactions can only operate within the niche defined by
388 environmental constraints. This may be a key attribute of positive non-trophic interactions that
389 makes them more detectable when sampling across space and environmental variability.

390 Power to detect species interactions decreases when controlling for tidal height except in the
391 high tidal zone. Many of the detected co-occurrences may be mainly driven by shared
392 environmental preferences rather than species interactions. Controlling for tidal height might
393 have been expected to increase the detectability of interactions because the interaction network is
394 modular with the modules related to the height at which species are found (Kéfi et al 2015,
395 2016). However, many strong interactions occur between tidal levels and lead to tidal
396 segregation of species as shown in Chile and in other rocky shore communities, i.e. predators
397 delimiting lower end of mussels (e.g. Paine 1966, Castilla & Duran 1985, Menge et al, 1994,
398 2004), competitive monopolization or domination of the mid-tidal zone restricting other species
399 to higher, or lower elevations (Connell 1961, Berlow & Navarrete 1997, Branch & Steffani 2004,
400 Navarrete & Castilla 1990). This tidal segregation between strong interactors would go
401 undetected when examining within tidal levels. In addition, the overlap between environmental
402 preference and potential species interactions may artificially inflate detection of species
403 interactions when samples from all tidal heights are included.

404 Habitat preferences and environmental processes may be especially important for shaping
405 species distributions if biotic interactions are weak (Shinen & Navarrete 2014). There are
406 considerably more negative non-trophic interactions and trophic interactions in the empirical

407 network than there are positive non-trophic interactions, so there may also be proportionally
408 more weak negative non-trophic and trophic interactions (Berlow et al. 2004, Lopez et al. 2017).
409 Weak interactions may have either less of an impact or a more variable impact on the spatial
410 structure of the community (Berlow, 1999). While weak interactions can be quite important for
411 population dynamics and community stability, they may be less detectable using co-occurrence
412 alone, especially if there are many and diverse weak interactions. One implication of this work is
413 that studies based on pairwise interactions may not be generalizable to understanding the whole
414 community composition.

415 *Indirect interactions*

416 The pattern of species co-occurrence is affected by indirect interactions (those mediated by a
417 third species) in addition to direct interactions (Cazelles et al. 2016). Exploitation competition
418 for prey might affect predator co-occurrence, while the effects of multiple consumers on a single
419 prey species might blur the relationship between a single consumer species and its prey. In terms
420 of non-trophic interactions, a species' competitors are also likely competing with each other due
421 to the density of the negative non-trophic interaction network.

422 Indirect interactions mediated by the habitat provisioning species can be very strong. For
423 example, of the species that have significant associations with both *Lessonia. spp* and *P.*
424 *purpuratus*, 55 of 64 species have negative association with one and a positive association with
425 the other. *Lessonia* and *P. purpuratus* compete for space on the low shore and have a negative
426 non-trophic interaction. The reversed sign of the association might be an indirect interaction
427 mediated by the competition between *Lessonia* and *P. purpuratus*.

428 Lack of significant co-occurrence could be generated by indirect interactions if multiple
429 interactions between species cancel the effects of pairwise interactions. If this were the case, one

430 would expect that species with many interactions (high node degree) would have fewer links
431 detected than species with fewer interactions (low node degree). In this analysis, we find no
432 relationship between total node degree and the percent of links detected. There is a weak inverse
433 relationship between outgoing node degree and the percent of links detected, suggesting that
434 specialist predators are more likely to co-occur with their prey, since trophic interactions are the
435 main asymmetrical interactions in this network. This is most likely related to mobility patterns of
436 these predators.

437 *Strong interactions: keystone species, anthropogenic influence, and effect size*

438 Harvested species have a larger effect size of realized co-occurrences than would be expected
439 based on the number of links detected. This might be related to perturbations in the system
440 aiding detection because species interactions are most evident as the species occurrences return
441 to equilibrium after a disturbance. It may also reflect the fact that humans usually remove the
442 larger bodied species within a given assemblage, which may have stronger effects than other
443 species in the assemblage.

444 The median of the absolute value of the effect size increases as the number of detected
445 interactions increases (Figure 5) and there is no relationship between the total number of
446 potential interactions and the average effect size (Appendix S1; Figure S1). These results largely
447 contradict the assertion by Cazelles et al. (2016) that “the strength of an interaction decreases
448 with the total number of interactions a species experiences”. The trend of increasing effect size
449 as the detected node degree increases could be statistical; when there are many links, strong links
450 are more likely to be detected. In sectors of the interaction matrix with few interactions (e.g.
451 sessile species affecting mobile species), there is high specificity and high sensitivity, indicating
452 that when there are fewer interactions at the community level, interactions may be more

453 detectable. More generally, these results indicate that co-occurrence may mostly identify
454 interactions above a certain threshold and miss truly weak links.

455 We find that small grazers have the largest median effect size of correlations. This is in line
456 with the conclusions of Borthagaray et al 2014 that smaller species form tightly linked subgroups
457 (here manifested as large effect size) and could be an effect of the relatively small quadrats,
458 which may capture the co-occurrence of smaller-sized species better than larger species. There is
459 also slightly higher edge density among the species in the steeply increasing section of Figure 5
460 (0.25) as compared to edge density between those species and the species on the slowly
461 increasing section of the trend (0.11). We additionally demonstrate that habitat engineering
462 sessile species can also form tightly linked subgroups, but that not all sessile species form tightly
463 linked groups. Most sessile species have relatively weak co-occurrence with other species.

464 We do not find a distinct signal of keystone species. We would have expected keystone
465 species to have large effect size (Menge et al., 1994, Power et al, 1996), however it is possible
466 that keystone species instead have large effect size only when abundance is taken into account,
467 or they may have strong effects only on a small subset of the species with which they interact.
468 Moreover, it is possible that the effect of keystone species may be more noticeable on indirect
469 than direct interactions. It is important to keep in mind, however, that the ability to detect a
470 predator-prey interaction using spatial co-occurrence depends not only on the strength of the
471 interaction, but also on how homogeneous or variable are across space the other factors that
472 simultaneously influence species distribution, such as recruitment and environmental tolerances.

473 **Conclusions**

474 Co-occurrence networks do not reproduce interaction networks, but they do provide
475 interesting and interpretable information about community assembly. In cases in which spatial or

476 environmental effects operate synergistically with species interactions to determine the presence
477 and absence of species (or other interacting biological component such as a protein or an OTU),
478 a co-occurrence network can be a valuable object of analysis, albeit at times difficult to interpret
479 due to the influence of indirect interactions and stochastic processes.

480 Both ecological and statistical effects can limit the interpretability of co-occurrence
481 networks. As the occurrence of a given species increases, the probability of detecting a greater
482 number of statistically significant associations increases as well. However, these associations
483 may not necessarily correspond to interactions; both the number of true positives and false
484 positives increases as the occurrence of a species increases. In terms of the important ecological
485 effects, both environmental effects, including here recruitment, and species interactions
486 determine the species range in the intertidal zone. Consequently, it can be difficult to disentangle
487 which associations are related to interactions and which are related only to shared environmental
488 preferences or correlated settlement. We suggest that environmental and settlement preferences
489 may possibly outweigh biotic interactions in determining whole community co-occurrences. This
490 is not to say that environment is more important in structuring communities than biotic
491 interactions, but that environmental variability may leave a more discernable signal in spatial co-
492 occurrence patterns. Having said this, habitat engineering species and non-trophic positive
493 interactions may leave a more detectable signal than other interaction types because they expand
494 or create niche spaces for the species with which they interact.

495 In summary, ecological patterns observed in co-occurrence networks must be interpreted
496 with caution, especially when extending interaction-based ecological theory to interpret network
497 variability and stability. Co-occurrence networks may be particularly valuable for analysis of
498 community dynamics as an epiphenomenon combining interactions and environment, rather than

499 simply as the result of pairwise interactions.

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509

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633 **Figure Legends**

634 Figure 1. Community surveys were done at 49 distinct coastal intertidal sites during the years
635 1998-2013. Not all sites were surveyed in all years and a different number of samples were taken
636 during each survey. The figure indicates the latitude of sampling sites, which should be projected
637 on the coast for the actual sampling location.

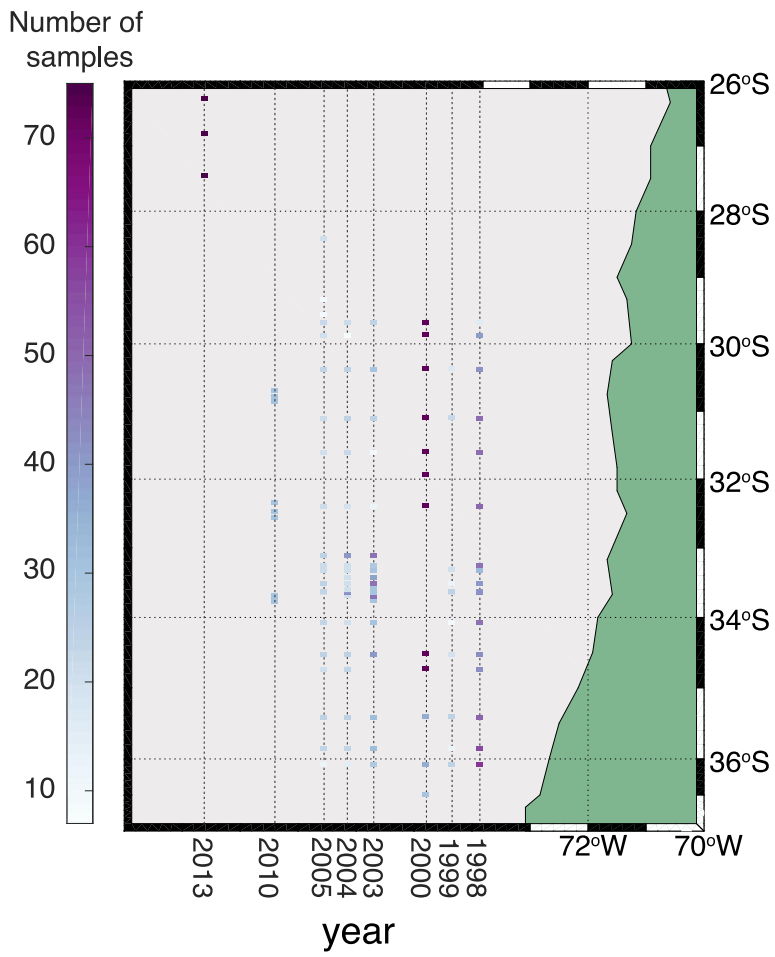
638 Figure 2 (a). Sensitivity, or percentage of links detected plotted against the total number of
639 occurrences for a given species. (b). Specificity, or percentage of non-interactions detected as
640 non-interactions plotted against the total number of occurrences for a given species. In these
641 plots, each point is a different species. Blue dots are mobile species, green dots are sessile
642 species. Darker dots are harvested species and species outlined in black are keystone species. (c).
643 Specificity plotted against sensitivity. Each point is a different species. The colors indicate which
644 network, trophic interactions (TI), positive non-trophic interactions (NTI+), negative non-trophic
645 interactions (NTI-), or all interaction types is used as the 'true' network. The dashed lines are
646 best fit lines for each interaction type. The black line is a 1:1 line. Points above the 1:1 have
647 better detection than random while point below the 1:1 line have worse detection than average.

648 Figure 3. The bars show the number of links of each type including species found at all
649 heights along the intertidal and species only present in the high, medium, and low heights in all
650 samples. The white bars show the number of links detected using co-occurrence of species.
651 Proportions above each bar are the proportion of links of each type detected using co-occurrence.

652 Figure 4. Links between species inferred using three different data subsets (only high tide
653 samples, only mid tide samples, and only low tide samples) for each of three interaction types (a)
654 negative non-trophic interactions, (b) positive non-trophic interactions, and (c) trophic
655 interactions. Species are arranged on the axes from inward to outward by high to low trophic

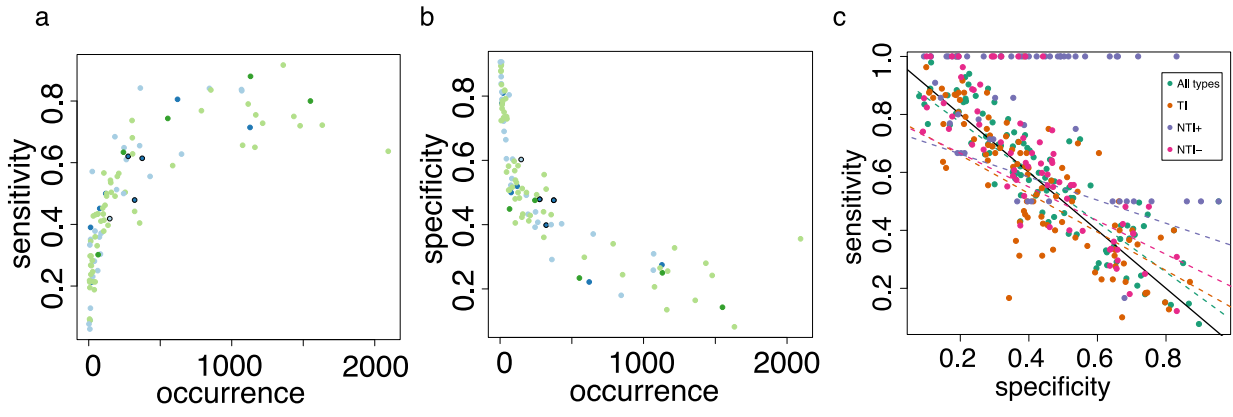
656 position. The preferred tidal height of each species is indicated by the node color. Blue edges
657 indicate an inferred positive association while red edges indicate an inferred negative
658 association. (d) Network showing all positive non-trophic interactions. Blue edges indicate a
659 positive association inferred by co-occurrence, red edges indicate a negative association inferred
660 by co-occurrence, and black edges indicate no association. The node size represents the number
661 of samples in which each species occurred while node color is the preferred tidal level for each
662 species.

663 Figure 5. True positives, plotted against the median effect size (correlation intensity) of all
664 detected links. A true positive is a known species interaction that is also detected as a significant
665 association. This analysis only includes the most common species (occurrence greater than 62
666 quadrats). 62 occurrences was chosen because it is the inflection point in Figures 2a,b, in order to
667 avoid the loss of power at low occurrence. Blue dots are mobile species, green dots are sessile
668 species. Darker dots are harvested species and species outlined in black are keystone species.



669

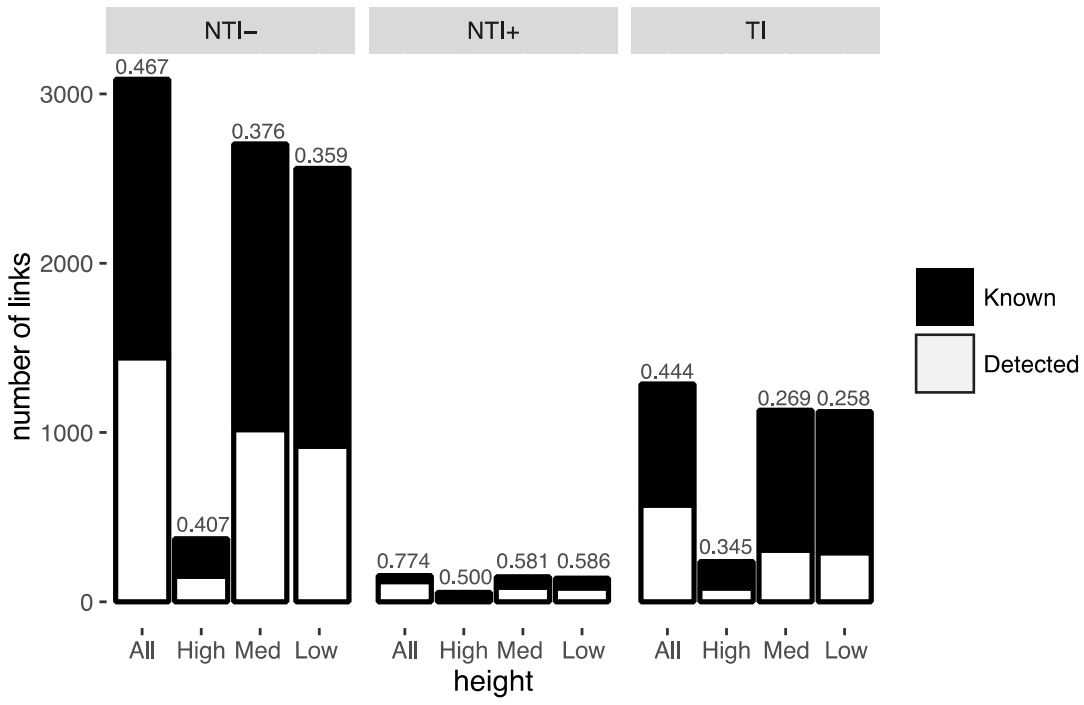
670 Figure 1.



671

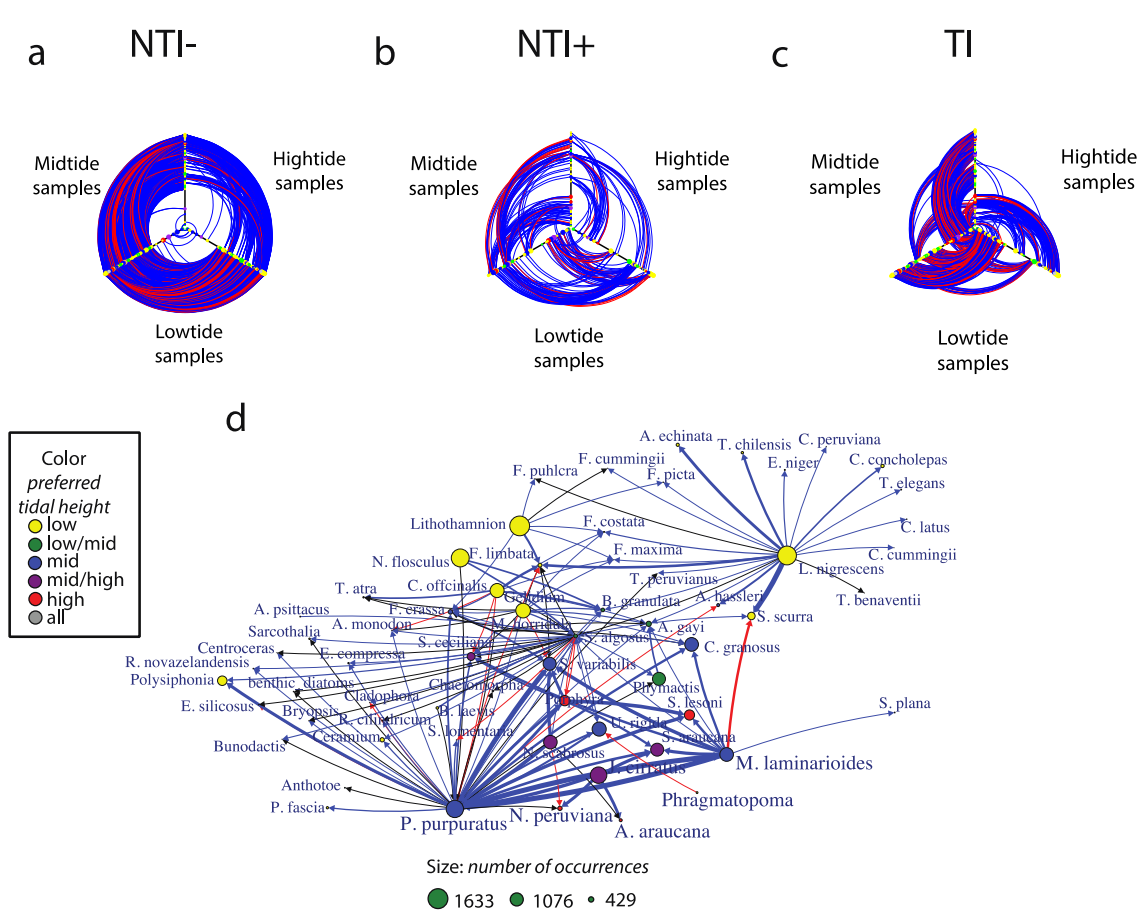
672 Figure 2

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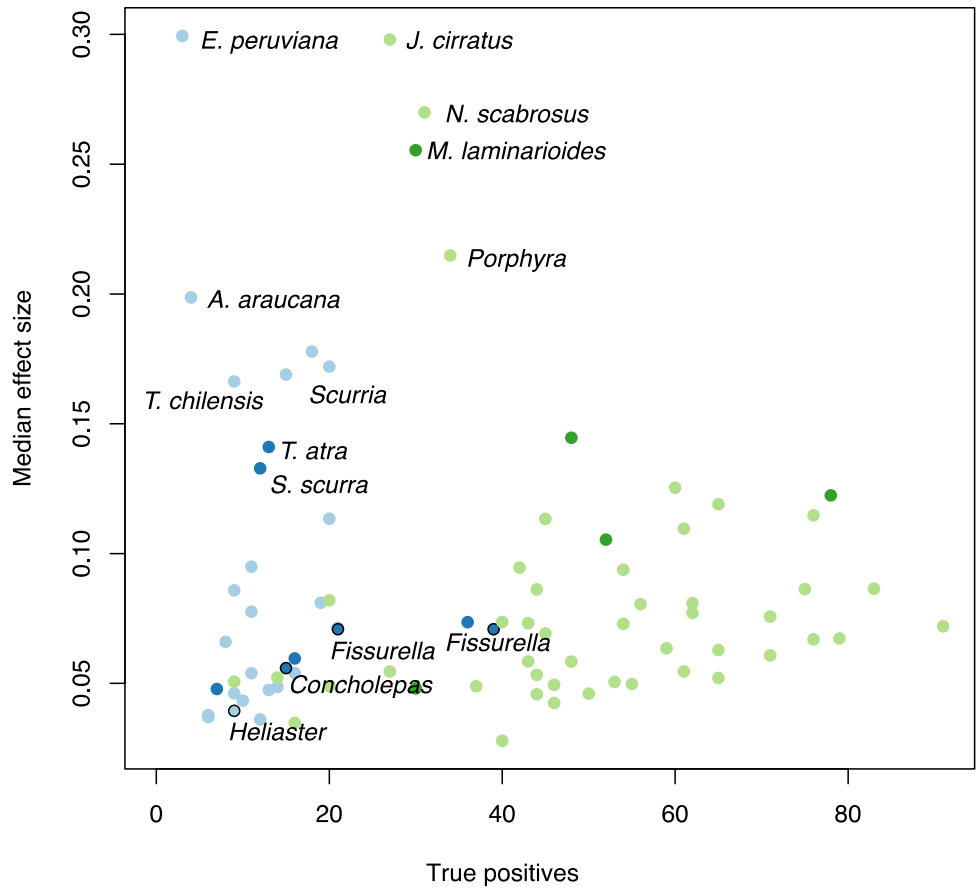
674

675 Figure 3



676

677 Figure 4.



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679 Figure 5