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Title: Disturbance size and frequency mediate the coexistence of benthic spatial competitors

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1 **Abstract.** Disturbance plays a key role in structuring community dynamics and is central to
2 conservation and natural resource management. However, ecologists continue to debate the
3 importance of disturbance for species coexistence and biodiversity. Such disagreements may arise in
4 part because few studies have examined variation across multiple dimensions of disturbance (e.g.,
5 size, frequency) and how the effects of disturbance may depend on species attributes (e.g.,
6 competitiveness, dispersal ability). In light of this gap in understanding and accelerating changes to
7 disturbance regimes worldwide, we used spatial population models to explore how disturbance size
8 and frequency interact with species attributes to affect coexistence between seagrass (*Zostera marina*)
9 and colonial burrowing shrimp (*Neotrypaea californiensis*) that compete for benthic space in estuaries
10 throughout the west coast of North America. By simulating population dynamics under a range of
11 ecologically-relevant disturbance regimes, we discovered that intermediate disturbance
12 (approximately 9–23% of landscape area per year) to short-dispersing, competitively-dominant
13 seagrass can foster long-term stable coexistence with broad-dispersing, competitively-inferior
14 burrowing shrimp via the spatial storage effect. When holding the total extent of disturbance constant,
15 the individual size and annual frequency of disturbance altered landscape spatial patterns and
16 mediated the dominance and evenness of competitors. Many small disturbances favored short-
17 dispersing seagrass by hastening recolonization, whereas fewer large disturbances benefitted rapidly-
18 colonizing burrowing shrimp by creating temporary refugia from competition. As a result, large,
19 infrequent disturbances generally improved the strength and stability of coexistence relative to small,
20 frequent disturbances. Regardless of disturbance size or frequency, the dispersal ability of the superior
21 competitor (seagrass), the competitive ability the inferior competitor (burrowing shrimp), and the
22 reproduction and survival of both species strongly influenced population abundances and coexistence.
23 Our results show that disturbance size and frequency can promote or constrain coexistence by altering
24 the duration of time over which inferior competitors can escape competitive exclusion, particularly
25 when colonization depends on the spatial pattern of disturbance due to dispersal traits. For coastal
26 managers and conservation practitioners, our findings indicate that reducing particularly large
27 disturbances may help conserve globally-imperiled seagrass meadows and control burrowing shrimp
28 colonies that can threaten the viability of oyster aquaculture.

29

30 **Keywords:** *biodiversity; burrowing shrimp; dispersal; estuary; intermediate disturbance hypothesis;*
31 *population dynamics; seagrass; sensitivity analysis; spatial ecology; storage effect*

32

33 **Introduction**

34 Understanding how spatial processes promote or constrain species coexistence is an enduring
35 challenge in ecology. According to theory, coexistence of competitors at landscape scales requires
36 that differences among species in competitive abilities are offset by niche or life-history differences,
37 such as their dispersal ability, resource use, or response to disturbance or natural enemies (Holt 1985,
38 Chesson 2000, Amarasekare 2003, Kneitel and Chase 2004, Roxburgh et al. 2004). For example,
39 when species exhibit competition–colonization trade-offs, inferior competitors rapidly colonize
40 available patches and disperse offspring prior to being displaced by slow-colonizing superior
41 competitors (Levins and Culver 1971, Tilman 1994). For long-term stable coexistence, dominant
42 competitors cannot occupy all space but instead must suffer loss from disturbances, senescence, or
43 natural enemies that cause spatiotemporal heterogeneity in the stages of succession (Amarasekare
44 2003, Roxburgh et al. 2004).

45 Disturbances (i.e., discrete events that change resources or the physical environment and
46 disrupt ecosystem structure; White and Pickett 1985) have been focal to the study of coexistence
47 because they often simultaneously mediate competitor abundance and resource availability. For
48 example, disturbance to dominant plants can alter competitive dominance and resources to reorganize
49 communities in forests (Ellison et al. 2005), grasslands (Collins 2000), and coastal marine ecosystems
50 (Williams 1990, Castorani et al. 2014, 2018). Despite strong evidence that disturbance often mediates
51 community structure, there has been mixed support for the longstanding hypothesis that intermediate
52 levels of disturbance foster coexistence and enhance biodiversity (Connell 1978, Huston 1979, 2014,
53 Mackey and Currie 2001, Hughes et al. 2007, Mayor et al. 2012, Fox 2013, Sheil and Burslem 2013).
54 However, investigations of the intermediate disturbance hypothesis typically focus on individual
55 elements of disturbance (e.g., size, frequency; Miller et al. 2011, 2012, Zhang and Shea 2012,
56 Castorani et al. 2018) or treat them as interchangeable (Connell 1978, Miller 1982, Amarasekare
57 2003). Hence, disagreements and uncertainty in disturbance–diversity relationships may be partly

58 resolved if different disturbance elements vary in their effects on coexistence or if effects depend
59 upon relevant species attributes (e.g., competitiveness, dispersal ability).

60 Resolving how variation in different elements of disturbance mediates coexistence is a
61 pressing challenge because humans alter disturbance regimes in many ecosystems (Turner et al. 2003,
62 Ellison et al. 2005). Moreover, the severity (size or magnitude of impact) and frequency (number of
63 events within a time period) of many disturbances have increased or are forecast to increase due to
64 climate change (Ummenhofer and Meehl 2017). Clarifying the ways that different disturbance
65 elements influence the persistence of competitors is also valuable to biodiversity conservation and
66 natural resource management. For example, depressing disturbance frequency (e.g., fire suppression)
67 can improve the recovery of target species (Coffin and Lauenroth 1988) or threaten the persistence of
68 conserved taxa with low competitive rank (Collins 2000). Similarly, increasing disturbance frequency
69 can diminish richness (Turner et al. 2003), enhance richness (Cavender-Bares and Reich 2012), or
70 both depending on species attributes (Castorani et al. 2018). Manipulating disturbance regimes can
71 also aid in the control of undesired species, such as agricultural pests and non-native species (Zhang
72 and Shea 2012).

73 In light of these basic and applied challenges, we explored how variation in disturbance size
74 (individual diameter), frequency (number per year), and their interaction alter long-term landscape-
75 scale coexistence. We focused on competition for space because it is a limiting resource in numerous
76 ecosystems (or a proxy for other spatially-constrained resources such as light, water, or food) and is
77 commonly mediated by disturbance to space-holding organisms. Specifically, we explored how
78 disturbance structures coexistence between seagrass and colonial burrowing shrimp that compete for
79 dominance of benthic habitats in estuaries and shallow seas worldwide (Suchanek 1983, Harrison
80 1987, Dumbauld and Wyllie-Echeverria 2003, Siebert and Branch 2006, Berkenbusch et al. 2007).
81 Seagrass and burrowing shrimp are ideal study species because they exhibit a classic competition-
82 colonization trade-off (Castorani et al. 2014) and benthic disturbance is commonly managed to
83 promote seagrass conservation (Waycott et al. 2009) or burrowing shrimp eradication (Dumbauld et
84 al. 2006). By using this well-described empirical system to investigate how ecologically-relevant
85 variation in disturbance size and frequency structures coexistence, our approach aims to bridge the
86 divide between findings from models and data (e.g., Mackey and Currie 2001, Hughes et al. 2007,

87 Mayor et al. 2012, Fox 2013, Huston 2014) and brings advantages of realism over prior theoretical
88 studies that used generic competition models (e.g., Banitz et al. 2008, Miller et al. 2012, Liao et al.
89 2016; but see Moloney and Levin 1996).

90 Within the context of our study system, we asked the following questions: (1) How does the
91 total extent of disturbance influence the coexistence of spatial competitors and does biodiversity peak
92 at intermediate levels of disturbance? (2) Do changes in disturbance size and frequency mediate the
93 effects of disturbance extent in structuring the coexistence and relative abundance of competitors? (3)
94 What mechanisms promote stable coexistence? (4) How important is intraspecific variation in
95 biological attributes (e.g., demographic parameters) and is this importance mediated by variation in
96 disturbance size or frequency?

97 To address these questions, we varied disturbance using spatially-explicit population models
98 because conducting sufficiently large, numerous, or frequent disturbances in the field can be
99 impractical and unethical, while natural experiments commonly conflate multiple disturbance
100 attributes (Castorani et al. 2018). We varied disturbance size and frequency to determine their
101 combined effects on long-term coexistence and used sensitivity analysis to assess how biological
102 attributes affect species abundances. Our results broaden theory on biodiversity in heterogeneous
103 landscapes by comprehensively investigating how the size and frequency of disturbance interact with
104 variation in competitiveness, dispersal ability, and demographic processes to structure species
105 coexistence.

106

107 **Methods**

108 **Study system.** Throughout the west coast of North America, the bottoms of shallow estuaries
109 and coastal lagoons are commonly dominated by undersea meadows of seagrass (eelgrass *Zostera*
110 *marina*), dense colonies of burrowing shrimp (ghost shrimp *Neotrypaea californiensis*), or a co-
111 dominant patch mosaic of both species (Fig. 1A; Appendix S1; Harrison 1987, Swinbanks and
112 Luternauer 1987, Castorani et al. 2014). These two benthic species exhibit a competition–colonization
113 trade-off. Ghost shrimp are locally excluded by the physical structure of eelgrass rhizomes and roots
114 (which inhibit surface burrows; Brenchley 1982, Castorani et al. 2014) but rapidly colonize areas
115 where eelgrass is lost to disturbances (Harrison 1987, Castorani et al. 2014) such as storms that cause

116 wave scour or sand burial, marine heatwaves, algal blooms, overgrazing, and coastal development,
117 which are common in shallow estuaries (Short and Wyllie-Echeverria 1996). Although competitively
118 dominant, eelgrass can be relatively slow to recover from such disturbances due to limited distances
119 of rhizome elongation ($\leq 2\text{--}3$ m/y; Marbà and Duarte 1998) and seed dispersal (typically $\leq 5\text{--}10$ m;
120 Orth et al. 1994, Ruckelshaus 1996, Furman et al. 2015; but see Källström et al. 2008), particularly
121 when compared to the much broader scales of ghost shrimp larval recruitment (Kozuka 2008) and
122 adult lateral movement (about 1–13 m/y; Posey 1986b, Weitkamp et al. 1992, Castorani et al. 2014).
123 Hence, field experiments support the hypothesis that the extent and pattern of eelgrass disturbance
124 mediate competitive exclusion of burrowing shrimp (Harrison 1987, Castorani et al. 2014).

125 Eelgrass and other seagrasses are focal to coastal conservation due to their global declines
126 from anthropogenic activities in spite of high value as habitat-forming foundation species (Waycott et
127 al. 2009). Although native, ghost shrimp are the target of eradication in some regions of commercial
128 oyster aquaculture because their bioturbation kills young bottom-cultured oysters (Feldman et al.
129 2000). Since adult ghost shrimp can migrate up to a meter below the sediment surface, they are highly
130 resistant to disturbances that cause eelgrass loss, as evidenced by decades of unsuccessful attempts to
131 control burrowing shrimp colonies by mechanical disturbance or compaction of sediments
132 (Washington State Department of Ecology 2015).

133 **Population dynamics.** To explore how the total extent, size, and frequency of disturbance
134 interact with biological attributes to structure the coexistence and abundance of competing seagrass
135 and burrowing shrimp, we developed spatially-explicit population models (Fig. 2) using data on both
136 species' demography, growth, reproduction, competition for space, and mortality (due to disturbance
137 and non-disturbance factors). Specifically, we used a set of discrete-time difference equations to
138 model the annual population dynamics of seagrass shoots ($S_{ij,t}$) and seeds ($E_{ij,t}$), and burrowing shrimp
139 adults ($B_{ij,t}$) and juveniles ($Y_{ij,t}$) in each year (t) and patch (patch i, j centered at location x_i, y_j in a two-
140 dimensional landscape). We used a stage-structured model for both species to account for differences
141 in dispersal ability, interactions, and susceptibility to disturbance of each stage. We parameterized our
142 model using data or estimates from the literature and simulated population dynamics across a range of
143 disturbance regimes that differed in the individual size and annual frequency of ecologically-relevant
144 disturbances to seagrass. In particular, we simulated disturbances that cause the complete mortality of

145 seagrass shoots (all aboveground and belowground tissues), such as severe storms. Lastly, to assess
146 how intraspecific variation in the biological attributes of both species affects competitor abundances,
147 we performed a global sensitivity analysis under multiple disturbance regimes (Harper et al. 2011).

148 Seagrass populations grow through both sexual and asexual reproduction. A proportion of
149 seagrass shoots develop into senescent flowering shoots and produce seeds, together leading to per
150 capita reproduction σ (Olesen 1999). We assumed seagrass per capita reproduction was constant over
151 space because, in general, flowering effort does not differ based on seagrass patch size or shape
152 (Livernois et al. 2017, Stubler et al. 2017), seed production does not vary based on patch size or with-
153 patch location (Harwell and Rhode 2007; Stubler et al. 2017), and germination is not density-
154 dependent (Orth et al. 2003). Seeds dispersed radially from all source patches (i', j') following a
155 Gaussian probability density function (PDF) with standard deviation ω . Because eelgrass seeds are
156 not viable after about 12 months (Moore et al. 1993, Jarvis et al. 2014), non-germinating seeds
157 suffered total mortality after one year. Hence, seed abundance each year depended entirely on
158 production from flowering seagrass shoots in the same year according to:

159
$$E_{ij,t} = \sum_{i'=1}^{n_i} \sum_{j'=1}^{n_j} \left[\sigma S_{i',j',t} \cdot \frac{1}{\pi\omega^2} e^{-\left(\sqrt{(x_i-x_{i'})^2 + (y_j-y_{j'})^2}/\omega\right)^2} \right]. \quad (\text{Eq.}$$

160 1)

161 A fraction (γ) of seeds germinated and survived to adulthood (i.e., became seagrass shoots). To
162 account for additional mortality of young seed recruits through sediment reworking by ghost shrimp
163 (Dumbauld and Wyllie-Echeverria 2003), we integrated the instantaneous rate of bioturbation-driven
164 mortality (ψ) per adult burrowing shrimp over one year. Seagrass shoots propagated new shoots
165 asexually in proportion (α_s) to the local (i.e., within-patch) abundance of adult shoots (Marbà and
166 Duarte 1998). Of these new clonal shoots, a proportion ($1 - l$) remained within their natal patch and
167 the remainder (l) spread laterally and uniformly contributed to populations in N neighboring patches,
168 defined as those separated by distances less than the annual rate of rhizome elongation (d). Existing
169 seagrass shoots experienced constant, density-independent mortality due to non-disturbance factors,
170 such as senescence or herbivory (Olesen and Sand-Jensen 1994a), with proportion μ_s surviving.
171 Combining surviving shoots with those produced from sexual and asexual reproduction yielded the
172 new seagrass shoot population:

173 $F_S(S_{ij,t}, E_{ij,t}, B_{ij,t}) = \alpha_S(1-l)S_{ij,t} + \frac{\sum_{i=1}^{n_i} \sum_{j=1}^{n_j}}{\sqrt{(\alpha_i - x_i)^2 + (\alpha_j - y_j)^2} < d} \left(\alpha_S \left[\frac{l}{N} \right] S_{ij',t} \right) + \gamma e^{-(\psi B_{ij,t})} E_{ij,t} + \mu_S S_{ij,t} . \quad (\text{Eq. 2})$

174 New and surviving seagrass shoots underwent Beverton-Holt density-dependent competition
 175 for space, saturating at $1/\beta_S$ (Table 1). Shoots suffered complete mortality within disturbed patches
 176 (i.e., $D_{ij,t} = 0$ for disturbance in patch ij and year t ; otherwise $D_{ij,t} = 1$). Thus, the abundance of
 177 seagrass shoots after density dependence and disturbance was:

178
$$S_{ij,t+1} = \frac{F_S(S_{ij,t}, E_{ij,t}, B_{ij,t})}{1 + \beta_S F_S(S_{ij,t}, E_{ij,t}, B_{ij,t})} \times D_{ij,t} . \quad (\text{Eq. 3})$$

179 3)

180 Young burrowing ghost shrimp mature through a series of pelagic larval stages. After being
 181 released by adult females during spring and summer, larvae develop in nearshore waters for 4–6
 182 weeks (Johnson and Gonor 1982, Dumbauld et al. 1996, Morgan et al. 2011). Larvae then return to
 183 estuaries and settle to the bottom as juveniles. Because ghost shrimp larval recruitment depends upon
 184 the adult population size but is highly variable over time (Dumbauld et al. 1996, Feldman et al. 1997,
 185 2000, Dumbauld and Bosley 2018), we assumed that the annual abundance of juveniles was
 186 determined by a time-varying stochastic process in proportion ($\alpha_{B,t}$) to the total abundance of adults
 187 (i.e., the population was demographically closed). We further assumed that recruitment was uniform
 188 across the landscape (Dumbauld and Bosley 2018). Juveniles matured (i.e., left the juvenile class) at
 189 rate ρ . Both juvenile and adult burrowing shrimp experienced constant, density-independent mortality
 190 (μ_B) from processes including predation and senescence (Posey 1986b, Weitkamp et al. 1992,
 191 Dumbauld et al. 2008, Castorani et al. 2014). Combining new recruits with surviving juveniles that do
 192 not mature yielded the juvenile population of burrowing shrimp:

193
$$Y_{ij,t+1} = \alpha_{B,t} \sum_{i=1}^{n_i} \sum_{j=1}^{n_j} \left(\frac{B_{ij',t}}{n} \right) + \mu_B e^{-\rho} Y_{ij,t} . \quad (\text{Eq. 4})$$

194 Adult ghost shrimp can rapidly colonize adjacent habitats by burrowing laterally (Harrison
 195 1987, Castorani et al. 2014, Dumbauld and Bosley 2018) and thus we approximated the radial
 196 movement of adult burrowing shrimp populations as a Gaussian PDF dependent on the annual lateral
 197 movement rate (ζ). Seagrass competition caused local declines in adult burrowing shrimp abundance
 198 at rate ϕ per seagrass shoot (Castorani et al. 2014). Combining newly maturing juveniles with
 199 surviving burrowing shrimp adults yielded:

200 $F_B(S_{ij,t}, B_{ij,t}, Y_{ij,t}) = \left([1 - e^{-\rho}] Y_{ij,t} + \sum_{i'=1}^{n_i} \sum_{j'=1}^{n_j} \left[\frac{1}{\pi \zeta^2} e^{-\left(\frac{d_{ij,i'j'}}{\zeta} \right)^2} \right] B_{ij,t} \right) \mu_B e^{-\phi S_{ij,t}} . \text{ (Eq. 5)}$

201 Newly recruited and surviving burrowing shrimp underwent Beverton-Holt density-dependent
 202 competition for space (Dumbauld et al. 1996), saturating at $1/\beta_B$ (Table 1), leading to the new adult
 203 burrowing shrimp abundance:

204
$$B_{ij,t+1} = \frac{F_B(S_{ij,t}, B_{ij,t}, Y_{ij,t})}{1 + \beta_B F_B(S_{ij,t}, B_{ij,t}, Y_{ij,t})} . \text{ (Eq. 6)}$$

206 **Disturbance.** We varied the individual size (all integers from 1 to 40 m diameter, inclusive)
 207 and annual frequency (all integers from 1 to 1604 per year, inclusive) of disturbance to seagrass using
 208 all possible combinations that resulted in approximately 0–50% of the total landscape area disturbed
 209 per year (2,577 unique combinations), representing disturbance regimes characteristic of our study
 210 system (Short and Wyllie-Echeverria 1996). For each year and simulation, we varied the location of
 211 disturbance centroids across the landscape by randomly sampling (without replacement) from a
 212 uniform distribution of all possible patches. Disturbances falling outside of landscape boundaries or
 213 overlapping with other disturbances were not redistributed elsewhere within the landscape. Therefore,
 214 to avoid any biases from areas of disturbance ‘lost’ outside of landscape boundaries or overlapping
 215 with other disturbances, in all analyses we investigated the effect of the actual proportion of the total
 216 landscape area disturbed per year and averaged these across all years within each simulation (i.e., the
 217 output values of realized disturbance, not the input values of the simulated disturbance regime).

218 **Simulations.** We simulated the model landscape in R 3.4.4 (R Core Team 2018) with a two-
 219 dimensional lattice of regular hexagonal patches ($n = 3,600$ patches, simulating $60 \text{ m} \times 60 \text{ m}$; Fig. 1B)
 220 characteristic of the scale of interspecific interactions (diameter = 1 m; area = 0.866 m^2 ; Castorani et
 221 al. 2014). We discretized space using a hexagonal tessellation because it has ideal patch-neighbor
 222 symmetry and approximates radial dispersal more accurately than Cartesian grids (Birch et al. 2007).
 223 We indexed patches using integer hexagonal coordinates (i, j) and measured inter-patch distances
 224 using the location of patch centroids in Cartesian space (x_i, y_j).

225 Dispersal beyond landscape boundaries resulted in mortality because eelgrass dies from light
 226 stress at depth (Dennison 1987), and temperature or desiccation stress in the intertidal (Marsh et al.
 227 1986, Boese et al. 2005). Likewise, predation can restrict ghost shrimp from colonizing deep zones

228 (Posey 1986b, Weitkamp et al. 1992), and bait fishing or pesticide application can limit intertidal
229 distributions (Peterson 1977, Dumbauld et al. 1996).

230 For each disturbance regime we performed 20 numerical simulations of annual population
231 dynamics for 250 years, which was sufficient for populations to reach quasi-equilibria given
232 environmental and demographic stochasticity. Additional replicate simulations (up to 200) and longer
233 durations (up to 10,000 years) did not change mean abundances or coexistence predictions (Appendix
234 S2: Figs. S1–S2). We initiated all simulations by randomly selecting each patch to start with either a
235 small number of seagrass shoots or a small number of adult burrowing shrimp (other starting
236 conditions changed the time needed to reach quasi-equilibria, but did not change coexistence or
237 abundances at quasi-equilibria). During each simulation we tracked the annual landscape-scale
238 densities of seagrass shoots ($S_t = \sum_{i=1}^{n_i} \sum_{j=1}^{n_j} \left[\frac{S_{ij,t}}{n} \right]$) and adult burrowing shrimp ($B_t = \sum_{i=1}^{n_i} \sum_{j=1}^{n_j} \left[\frac{B_{ij,t}}{n} \right]$).
239 For both species, we normalized abundances by dividing annual densities by the maximum observed
240 density across all simulations ($\bar{S}_t = \frac{S_t}{S_{max}}$; $\bar{B}_t = \frac{B_t}{B_{max}}$). As an index of the strength of coexistence and
241 relative parity in normalized abundances we also measured species evenness using Simpson's E
242 (Simpson 1949), which ranged from 0.5 to 1. Lastly, to characterize landscape-scale population
243 patterns we measured the spatial autocorrelation of normalized seagrass and burrowing shrimp
244 abundances using Moran's I (Moran 1950). For each disturbance regime, we calculated metric
245 averages across simulations at quasi-equilibria.

246 **Parameterization and sensitivity analysis.** To parameterize the biological components of our
247 model, we obtained values from the peer-reviewed literature and used the mean of these estimates for
248 our simulations (Table 1). We estimated the seagrass seed dispersal parameter (ω) by fitting a
249 Gaussian kernel to *in situ* eelgrass seed dispersal data (Appendix S3: Fig. S1). We approximated
250 stochastic variation in burrowing shrimp recruitment among years by randomly choosing the annual
251 recruitment density parameter ($\alpha_{B,t}$) from a truncated normal distribution of possible values (Table 1).
252 We estimated the effect of seagrass competition on burrowing shrimp (φ) by fitting a negative
253 exponential relationship to *in situ* density data (Appendix S4: Fig. S1). For seagrass populations, we
254 parameterized β_S (which sets the saturation point of Beverton-Holt density dependence) as $\beta_S =$
255 $\frac{\mu_S + \alpha_S - 1}{(\mu_S + \alpha_S)k_S}$ so that the equilibrium seagrass population density in the absence of shrimp was near the

256 observed carrying capacity (k_s). Likewise, for burrowing shrimp populations we parameterized β_B as
257 $\beta_B = \frac{\mu_B + \alpha_B - 1}{(\mu_B + \alpha_B)k_B}$. We estimated the shrimp maturation rate ρ as the inverse of the average time to
258 maturity (2–4 years; Pimentel 1986, Dumbauld et al. 1996).

259 To quantify the relative influence of variation in species attributes on competitor abundances,
260 we performed a global sensitivity analysis (GSA) by randomly drawing all biological parameter
261 values from uniform distributions across their estimated ranges (Table 1). For each of the resulting
262 2,000 randomly drawn combinations, we measured landscape-scale abundances of seagrass shoots
263 and adult burrowing shrimp, and species evenness at quasi-equilibria. We analyzed these results with
264 a GSA method that incorporates non-additive and interactive effects using random forest
265 nonparametric bootstrapping (Harper et al. 2011). Using several R packages (*randomForest* 4.6-12,
266 Liaw and Wiener 2002; *rpart* 4.1-12, Therneau and Atkinson 2018; *rpart.plot* 2.1.1, Milborrow
267 2017), we produced multiple pruned classification and regression trees and used these to rank
268 parameters according to their total effect on species abundances (Harper et al. 2011). We calculated
269 the relative importance of each parameter by comparing the prediction accuracy of trees with and
270 without the parameter and rescaled all importance values so that they summed to one. To assess how
271 disturbance size and frequency affected the importance of biological parameters, we used this GSA
272 approach under four disturbance regimes that supported strong coexistence and parity (Simpson's $E \geq$
273 0.9) with mean-estimated parameter values: many small disturbances (783 1-m disturbances per year);
274 several medium disturbances (102 3-m disturbances per year); a few large disturbances (13 7-m
275 disturbances per year); and a single very large disturbance (one 21-m disturbance per year).

276 **Stability of coexistence.** We evaluated whether coexistence was stable by calculating the
277 realized (stochastic) per-capita growth rates for each species when rare (i.e., Lyapunov exponents).
278 Coexistence occurs when each species can increase when rare and in the presence of its competitor
279 (Chesson 2000). To calculate realized growth rates, for each species we ran stochastic simulations in
280 which the abundance of the focal species was set to zero and the competing species was present at
281 normal abundance. From these simulations we determined the density-independent growth factor (i.e.,
282 the projected total population size, for all demographic stages in all patches and without intraspecific
283 competition, at the subsequent time point divided by the total population size at the previous time
284 point, if it was non-zero) through time as $\lambda_{X,t}$ for species X . Hence, we calculated the average realized

285 growth factor as $\overline{\lambda_X} \approx \frac{1}{T_f} \sum_1^{T_f} \ln(\lambda_{X,t})$, given T_f time points (150 years) following a burn-in period (100
286 years), for all 68 disturbance regimes ($n = 20$ simulations each) that appeared to support moderate to
287 strong coexistence in the multi-species simulations ($E > 0.6$). Stable coexistence occurs when $\overline{\lambda_X} > 0$
288 for both species (Roth and Schreiber 2014, Benaïm and Schreiber 2019).

289 ***Coexistence mechanisms.*** To understand how disturbance structures biodiversity, it is
290 important to clarify the general mechanisms promoting coexistence (Amarasekare 2003). We
291 hypothesized that the ‘spatial storage effect’ could be an important mechanism underlying
292 disturbance-mediated regional coexistence of seagrass and burrowing shrimp. Under this theory,
293 spatially-varying environmental conditions (e.g., disturbance) favor different species in different
294 patches, and high population growth in favorable patches buffer against low population growth in
295 unfavorable patches (Chesson 2000, Sears and Chesson 2007). Hence, we evaluated whether
296 disturbance promoted coexistence through the spatial storage effect by assessing three requirements:
297 (1) differential responses to the environment, (2) buffered population growth, and (3) covariance
298 between the environment and competition (Chesson 2000).

299 The first criterion was satisfied because species-specific differences in response to the
300 environment were a fundamental part of the model, as seagrass was killed by disturbance but
301 burrowing shrimp were unaffected. The second criterion was also satisfied because buffered
302 population growth is inherent to spatial population models (Chesson 2000). To evaluate the third
303 criterion, we tested for covariance between the response to the environment and the strength of
304 interspecific competition by simulating population dynamics for each species in the presence and
305 absence of its competitor (using the parameterization described previously) for all 68 disturbance
306 regimes that appeared to support moderate to strong coexistence in the multi-species simulations ($E >$
307 0.6). Then, for the individual and combined demographic stages of each species at $t = 250$, we
308 characterized the environmental response as the natural log of local (patch-scale) abundance in the
309 absence of interspecific competition (i.e., single-species simulations) and characterized the
310 competitive response as the log response ratio of local abundance in single-species (absence of
311 competition) and multi-species (presence of competition) simulations (Sears and Chesson 2007,
312 Berkley et al. 2010). We averaged environmental and competitive responses within each disturbance

313 regime and estimated the strength of covariance using linear regressions (Sears and Chesson 2007,
314 Berkley et al. 2010).

315

316 **Results**

317 ***Effects of the total extent, size, and frequency of disturbance.*** Increases in the total annual
318 extent of disturbance (i.e., the combined landscape area disturbed each year) caused gradual
319 reductions in seagrass abundance and, beyond a threshold, increases in burrowing shrimp abundance
320 (Figs. 3, 4). Disturbance exceeding about 23% of the total landscape extent per year caused effective
321 extinction of seagrass (i.e., < 1% of the of the observed maximum abundance; Figs. 3A, 4B).
322 Disturbance below about 9% of the total landscape extent per year resulted in the effective extinction
323 of ghost shrimp as a result of being locally outcompeted by seagrass (Figs. 3B, 4C). Ghost shrimp
324 persisted when the total normalized seagrass abundance across the landscape was less than about 0.1
325 (i.e., 10% of the observed maximum abundance of seagrass; Fig. 5). Hence, coexistence was strongest
326 when about 10–20% of the landscape extent was disturbed per year (cf. green areas in Figs. 4A with
327 warm-colored areas in Fig. 4D). Such disturbance regimes supported coexistence that was generally
328 stable (see *Stability of coexistence*, below) and remained consistent for at least 10,000 years
329 (Appendix S2: Fig. S2).

330 Disturbance size and frequency mediated how the total annual extent of disturbance affected
331 the abundance and coexistence of seagrass and burrowing shrimp. When holding the total annual
332 extent of disturbance constant, disturbance regimes characterized by fewer large disturbances resulted
333 in less seagrass (Figs. 3A, 4B, 5) and more burrowing shrimp (Figs. 3B, 4C, 5) than regimes with
334 many small disturbances. As a result, larger disturbances generally improved parity in competitor
335 abundance (i.e., increased evenness; Figs. 4D, 5), increased the stability of coexistence (see *Stability*
336 *of coexistence*, below), and broadened the range in the total extent of disturbance that led to
337 coexistence (cf. Figs. 3A and 3B). A single species (seagrass or burrowing shrimp) dominated the
338 landscape for all but a narrow combination of disturbance sizes and frequencies (i.e., areas in Fig. 4D
339 where species evenness exceeds about 0.5).

340 Disturbance size mediated seagrass abundance when the total extent of disturbance was below
341 about 23% per year (Fig. 3A), but this effect was most pronounced under moderate disturbance

342 regimes (about 5–14% of area per year; Fig. 3A). For example, despite the total extent of disturbance
343 being equivalent at about 10% per year, landscapes impacted by a single 22-m disturbance per year
344 resulted in 82% less seagrass than landscapes impacted by nearly 350 1-m disturbances per year
345 (normalized abundance of seagrass = 0.08 and 0.41, respectively; cf. Figs. 4A and 4B). Within the
346 zone of coexistence (about 9–23% of landscape extent disturbed per year; Fig. 3), increases in the
347 individual size of disturbance were matched by strong increases in burrowing shrimp abundance
348 despite no changes in overall seagrass abundance (Fig. 5).

349 The spatial autocorrelation of seagrass and burrowing shrimp increased with both the
350 individual size and annual frequency of disturbance (Fig. 6). When disturbances were small and
351 frequent, both species were nearly randomly dispersed across the landscape (Moran's $I \approx 0$). Larger
352 infrequent disturbances caused greater clustering (Moran's $I > 0$) for both species, although burrowing
353 shrimp were always more clustered than seagrass (cf. Figs. 6A and 6B). Clustering was also more
354 variable for seagrass, particularly for large, infrequent disturbances (Fig. 6A). For all disturbance
355 regimes, both species were never perfectly dispersed but instead either randomly dispersed or
356 clustered across the landscape (i.e., Moran's I was always positive).

357 ***Relative importance of biological parameters.*** For the four tested disturbance regimes that
358 supported strong coexistence, random forest GSA explained 75% of the variance in relative seagrass
359 abundance and 50% of the variance in relative burrowing shrimp abundance. Parameters describing
360 seagrass reproduction (asexual shoot production, seed production, and seed recruitment), equilibrium
361 shoot density, and shoot survival were most important to seagrass populations, whereas other seagrass
362 parameters and all burrowing shrimp parameters were of little importance to seagrass populations
363 (compare parameters in Fig. 7A). The rate of seagrass lateral spread was among the most important
364 parameters for burrowing shrimp populations, along with those describing burrowing shrimp survival,
365 reproduction, and equilibrium density (Fig. 7B). Interestingly, the ability of burrowing shrimp to
366 inhibit seagrass seed germination via bioturbation was fairly important for burrowing shrimp
367 populations (Fig 7B).

368 In contrast to large differences among parameters in their importance to seagrass and
369 burrowing shrimp populations, variation in the size and frequency of disturbance had modest effects
370 on parameter importance values, causing small changes in their relative importance but not changing

371 their order of importance (compare bars of different shades in Fig. 7). Large, infrequent disturbances
372 slightly enhanced the importance of parameters promoting overall seagrass abundance (equilibrium
373 density, shoot survival, asexual reproduction) relative to those promoting rapid seagrass recovery
374 (shoot spread, seed production, seed recruitment). These shifts may have arisen because larger
375 disturbances *per se* depressed overall seagrass abundance, thereby enhancing the importance of
376 factors controlling the size of the seagrass population remaining after disturbance. In contrast, the
377 relative effects of these parameters were more similar when disturbances were small and frequent. For
378 burrowing shrimp, larger disturbances slightly diminished the importance of shrimp equilibrium
379 density and slightly enhanced the importance of seagrass seed mortality by shrimp burial, possibly
380 because larger disturbances enhanced burrowing shrimp persistence within disturbed patches. For all
381 other parameters, variation in disturbance size and frequency had weak or inconsistent effects.

382 ***Stability of coexistence.*** Coexistence was stable for the large majority of disturbance regimes
383 that yielded moderate to high species evenness ($E > 0.6$). Average realized low-density per capita
384 growth rates were always positive for seagrass and positive for burrowing shrimp in 88% of
385 simulations (Appendix S5: Fig. S1). Large, infrequent disturbance regimes generally enhanced growth
386 factors for both species relative to small, frequent disturbances, where burrowing shrimp occasionally
387 had slightly negative growth factors (Appendix S5: Fig. S2). Still, on average, coexistence was stable
388 for all disturbance regimes with moderate to high species evenness.

389 ***Coexistence mechanisms.*** Consistent with theory, patterns of covariance between the
390 environment and competition indicated that coexistence was promoted through the spatial storage
391 effect. Individual and combined abundances of adult and juvenile burrowing shrimp exhibited
392 positive covariance between their responses to the environment and competition ($R^2 = 25.3\%$ for
393 adults, $R^2 = 63.5\%$ for juveniles, and $R^2 = 39.7\%$ for adults and juveniles combined; Appendix S6:
394 Fig. S1), indicating that interspecific competition limits the growth of burrowing shrimp populations
395 in suitable patches (Chesson 2000, Sears and Chesson 2007). Consistent with the inferior competitive
396 strength of burrowing shrimp, individual and combined abundances of seagrass shoots and seeds
397 exhibited weak environment-competition covariance ($R^2 \leq 8\%$; Appendix S6: Fig. S1).

398

399 **Discussion**

400 Disturbances vary in their size and frequency across a broad range of ecosystems (Turner et al.
401 2003, Ellison et al. 2005). Despite accelerating changes to disturbance regimes globally (Ummenhofer
402 and Meehl 2017), resolving how such disturbance elements interact with species attributes to structure
403 coexistence and biodiversity has remained a persistent challenge in community ecology (Miller 1982,
404 Chesson 2000, Amarasekare 2003, Miller et al. 2012, Huston 2014, Castorani et al. 2018). Our
405 findings help narrow this gap by supporting three general conclusions about how disturbance can
406 structure the coexistence of species with competition–colonization trade-offs. First, intermediate
407 extents of disturbance (about 9–23% of landscape extent per year) to short-dispersing, competitively
408 dominant seagrass can foster long-term spatial coexistence with broad-dispersing, competitively
409 inferior burrowing shrimp via the spatial storage effect. Second, when holding the total extent of
410 disturbance constant, the individual size and annual frequency of disturbance can alter the overall
411 spatial pattern of seagrass loss across the landscape and thereby mediate the dominance, evenness,
412 and clustering of these spatial competitors. Numerous small disturbances favor seagrass by reducing
413 the time required for recolonization, allowing it to quickly fill in gaps and exclude burrowing shrimp.
414 Conversely, fewer large disturbances can cause time lags in seagrass recovery due to its
415 comparatively limited dispersal, favoring rapid-colonizing burrowing shrimp by creating temporary
416 refugia from competition. Third, irrespective of disturbance size or frequency, the dispersal ability of
417 superior competitors (seagrass), the competitive ability of inferior competitors (burrowing shrimp),
418 and the reproduction and survival of both competitors can be important to mediating coexistence.

419 Together, these findings indicate that disturbance size, frequency, and their interaction can
420 mediate coexistence by altering the duration of time over which inferior competitors can escape
421 competitive exclusion. Beyond the many coastal ecosystems home to seagrass and burrowing shrimp,
422 our conclusions may apply broadly to heterogeneous landscapes containing competitive communities
423 with clear interspecific differences in the response to disturbance, the strength of competitive
424 exclusion, and the rate of colonization, especially when recovery depends on the spatial pattern of
425 disturbance due to species dispersal attributes. Our results also suggest that management of
426 disturbance size and frequency can maximize landscape-scale biodiversity or, alternatively, tip the
427 balance of competition to favor the conservation of imperiled species (e.g., seagrass) or eradication of
428 pests (e.g., burrowing shrimp) or non-native taxa.

429 Our findings demonstrate that intermediate extents of annual disturbance can maximize
430 coexistence and evenness in our two-species competition–colonization trade-off system through the
431 spatial storage effect (Chesson 2000, Roxburgh et al. 2004, Sears and Chesson 2007). This result
432 supports the intermediate disturbance hypothesis (Connell 1978) and is consistent with earlier
433 theoretical and empirical studies showing that patchy disturbance improves coexistence by reducing
434 competition for limiting resources (summarized in Amarasekare 2003, Roxburgh et al. 2004, Sheil
435 and Burslem 2013, Huston 2014). In our study, disturbance to seagrass did not simply delay eventual
436 competitive exclusion, but instead yielded long-term stable coexistence (Appendices S2 and S5). Our
437 results also align with non-spatial competition models showing that agents of density-independent
438 mortality, such as disturbance, can strongly mediate coexistence (Holt 1985).

439 We found that coexistence was possible only within a fairly limited combination of
440 disturbance sizes and frequencies in which burrowing shrimp were able to colonize disturbed patches
441 and reproduce prior to being displaced by encroaching seagrass. The delicate balance of disturbance
442 characteristics that we found necessary for coexistence is consistent with an earlier generic
443 competition–colonization trade-off model which showed that long-term coexistence was only possible
444 for a narrow range of intermediate disturbance frequencies (Roxburgh et al. 2004). Importantly,
445 however, competitive communities in nature may not be characterized by equilibrium conditions and
446 a much broader set of disturbance regimes may delay competitive exclusion long enough for other
447 local and regional coexistence mechanisms to sustain biodiversity (Huston 1979, 2014).

448 Examinations of the intermediate disturbance hypothesis typically focus on variation in only
449 one aspect of disturbance (Mackey and Currie 2001, Hughes et al. 2007), such as studies showing that
450 intermediate disturbance extent increases boreal plant diversity (Mayor et al. 2012), intermediate
451 disturbance frequency promotes the coexistence of sessile rocky intertidal flora and fauna (Sousa
452 1979), and intermediate disturbance intensity enhances the coexistence of desert plants (Guo 1996).
453 Our study builds upon these earlier works by demonstrating that multiple disturbance attributes (size
454 and frequency) can interact to structure biodiversity in competitive communities. Variation in the
455 individual size and annual frequency of disturbance changed the spatial pattern of seagrass loss,
456 thereby mediating the persistence of burrowing shrimp and the relative dominance of both species.
457 Under similar total extents of disturbance, large infrequent disturbances tended to improve the

458 strength and stability of coexistence over smaller frequent ones. These results agree with and extend
459 earlier theoretical work showing that increasing spatial correlation of disturbance can favor species
460 with broad dispersal and disadvantage those with limited colonization ability (Moloney and Levin
461 1996, Banitz et al. 2008, Miller et al. 2012, Liao et al. 2016).

462 Across all disturbance regimes, burrowing shrimp showed greater spatial clustering than
463 seagrass, probably because they were outcompeted at relatively low seagrass densities, forcing them
464 to the core of disturbed areas, as observed in field studies (Castorani et al. 2014). The positive effect
465 of spatially-autocorrelated disturbance for inferior competitors may be stronger for species in which
466 settlement and recruitment are positively associated with the local density of adults (Banitz et al.
467 2008), such as organisms that respond positively to conspecific settlement cues (Woodin 1976). These
468 findings for seagrass and burrowing shrimp may extend to other systems characterized by regular,
469 repeated disturbance and clear interspecific competition–colonization trade-offs, especially when rates
470 of recovery depend on the spatial pattern of disturbance, such as competition between vegetatively-
471 spreading and wind-dispersed plants (Liao et al. 2016).

472 Sensitivity analysis indicated that, within the range of coexistence, abundances of competing
473 species may be governed chiefly by the competitiveness of the fast-colonizing inferior competitor
474 (burrowing shrimp), the colonization rate of the slow-colonizing superior competitor (seagrass), and
475 the reproduction, survival, and carrying capacity of both species. Disturbance size and frequency had
476 only modest effects on the relative importance of these and other biological parameters. Our finding
477 that reproduction is important to the persistence of both species is consistent with generic
478 competition–colonization trade-off models (e.g., Klausmeier 1998) and empirical metapopulation
479 models (e.g., Castorani et al. 2017, Johnson et al. 2018) which show that variation in propagule
480 production can be as important or more important than variation in successful long-distance dispersal.

481 Our results are consistent with earlier studies demonstrating that the rate of competitor
482 recovery from disturbance can mediate coexistence (Huston 1979, 2014). Within the context of our
483 study system, this finding supports the notion that processes that reduce seagrass clonal spread (e.g.,
484 light limitation; Ochieng et al. 2010) will enhance the persistence of burrowing shrimp. By contrast,
485 variation in the strength of seagrass competitive exclusion had minimal importance to burrowing
486 shrimp populations because even low densities of eelgrass rapidly exclude ghost shrimp (Brenchley

487 1982, Harrison 1987, Castorani et al. 2014). Likewise, processes that enhance the survival and
488 reproduction of burrowing shrimp (e.g., reduced predation; Posey 1986b, Dumbauld et al. 2008) or
489 increase sediment turnover and burial of seagrass seeds by burrowing shrimp (e.g., warming;
490 Berkenbusch and Rowden 1999) should promote burrowing shrimp populations. Hence,
491 understanding seagrass–burrowing shrimp interactions would be improved by resolving how ghost
492 shrimp bioturbation affects seagrass seedling mortality (which has only been addressed in a single
493 study; Dumbauld and Wyllie-Echeverria 2003). Our finding that variation in the lateral movement
494 rate of burrowing shrimp was unimportant to their populations supports the idea that over broad
495 scales, larval recruitment has an overwhelming influence on the colonization of disturbances to
496 seagrass, whereas post-settlement movement is probably more important over smaller scales in space
497 and time (Castorani et al. 2014, Dumbauld and Bosley 2018). Our results suggest that seagrass
498 persistence is insensitive to variation in burrowing shrimp parameters and depends only upon changes
499 in survival and reproduction (chiefly clonal propagation, but also seed production and recruitment).
500 More generally, our finding that variation in species traits is vital to structuring coexistence and
501 biodiversity reinforces conclusions drawn from competitive communities of annual plants (Turnbull
502 et al. 2004), ants (Stanton et al. 2002), birds (Rodríguez et al. 2007), parasitic trematodes (Mordecai et
503 al. 2016), and sessile invertebrates (Edwards and Stachowicz 2010).

504 Results from this and earlier studies (Banitz et al. 2008, Liao et al. 2016) indicate that altering
505 the size and frequency of disturbance can be a useful tool for landscape-scale management of
506 biodiversity and natural resources. In general, reducing the size of disturbance may support the
507 persistence of slow-colonizing competitive dominants, such as many habitat-forming foundation
508 species. Conversely, prescribing the total extent, individual size, and frequency of disturbance may
509 aid in the eradication of undesired species, such as agricultural pests or non-native taxa, depending on
510 their relative competitive rank and colonization ability. However, we stress caution in managing
511 disturbances because competitive coexistence can be structured by interspecific differences in
512 multiple traits (Seifan et al. 2013).

513 Within the context of our coastal benthic study system, our results suggest that reducing large
514 disturbances to seagrass and promoting conditions that enhance reproduction (e.g., improved water
515 quality) will maximize the persistence of seagrasses, which are imperiled globally (Waycott et al.

516 2009). In Washington State (USA), pesticides have been used for decades to eradicate burrowing
517 shrimp from aquaculture sites because their bioturbation kills young oysters and reduces shellfish
518 production (Feldman et al. 2000, Dumbauld et al. 2006). This practice has raised environmental
519 concerns and recently caused conflict among oyster growers, managers, fishing communities, and the
520 public (Baker 2016). Together with prior field studies (Harrison 1987, Swinbanks and Luternauer
521 1987, Castorani et al. 2014), the results of our model sensitivity analysis indicate that management
522 actions that increase the rate of seagrass spread, such as seeding, transplantation, or restoration of
523 water quality, may reduce local burrowing shrimp abundances. Likewise, conservation of benthic
524 marine predators such as Dungeness crab, cutthroat trout, sculpin, flounder, leopard sharks, and grey
525 whales may help lower burrowing shrimp populations by reducing adult survival, reproductive output,
526 and density (Posey 1986b, Weitkamp et al. 1992, Feldman et al. 2000, Dumbauld et al. 2008,
527 Dumbauld and Bosley 2018). Similarly, our findings suggest that conservation of the many fish
528 species that prey upon ghost shrimp larvae, such as herring and salmon, may constrain ghost shrimp
529 populations (Feldman et al. 2000). Feedbacks between seagrass expansion, enhanced fish abundance,
530 lower burrowing shrimp abundance, improved sediment stability, and improved water quality may
531 lead to synergy among goals in seagrass conservation, oyster aquaculture, and fisheries management.
532

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538

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Table 1. Description of model parameters and values of mean and range used. Sources for parameter values are listed below table.

Description	Notation	Values			Units	Sources
		Estimate	Min.	Max.		
Seagrass parameters						
Equilibrium density of adult leaf shoots	k_S	1,000	700	3,845	shoots per m ²	1–7
Annual survival of adult leaf shoots	μ_S	0.507	0.450	0.730	unitless	8
Annual asexual production of new leaf shoots	α_S	0.956	0.551	1.455	unitless	8
Annual distance of lateral shoot spread	d	1.26	0	2.26	m per y	7, 9–11
Annual proportion of asexually-produced shoots spreading laterally	l	0.05	0.01	0.20	unitless	7
Equilibrium density of seeds	k_E	9,321	7,997	13,700	seeds per m ²	12–15
Annual seed production	σ	2.42	0	17	seeds per leaf shoot per y	3, 14, 16–18
Standard deviation of seed dispersal kernel	ω	3.19	3.10	3.27	m	19, 20
Seed recruitment	γ	0.0128	0	0.36	leaf shoots per seed per y	13, 14, 19, 21–23
Burrowing shrimp parameters						
Equilibrium density of adults	k_B	250	5	700	adults per m ²	7, 24–33
Annual survival of adults and juveniles	μ_B	0.62	0.24	0.79	unitless	32, 33
Annual production of juveniles*	$\alpha_{B,t}$	2.8 ± 2.0	0	4.9	unitless	32, 34, 35
Annual distance of adult lateral movement	ζ	6.0	1.63	13.0	m	7, 28, 36

Maturation rate	ρ	$\frac{1}{3}$	$\frac{1}{4}$	$\frac{1}{2}$	per year	32
Species interactions						
Reduction in burrowing shrimp abundance due to competition with seagrass	ϕ	0.0668	0.0123	0.121	per seagrass leaf shoot per m ² per y	7
Mortality of seagrass seedlings due to burrowing shrimp bioturbation	ψ	0.0046	0.0016	1	per adult burrowing shrimp per m ² per y	37

References: ¹Kentula and McIntire 1986; ²Olesen and Sand-Jensen 1994a; ³Poumian-Tapia and Ibarra-Obando 1999; ⁴Reusch and Williams 1999; ⁵Krause-Jensen et al. 2003; ⁶Huntington and Boyer 2008; ⁷Castorani et al. 2014; ⁸Olesen and Sand-Jensen 1994b; ⁹Olesen and Sand-Jensen 1994c; ¹⁰Marbà and Duarte 1998; ¹¹Boese et al. 2009; ¹²Keddy 1987; ¹³Harrison 1993; ¹⁴Olesen 1999; ¹⁵Greve et al. 2005; ¹⁶Churchill and Riner 1978; ¹⁷Phillips et al. 1983; ¹⁸Silberhorn et al. 1983; ¹⁹Orth et al. 1994; ²⁰Ruckelshaus 1996; ²¹Harrison 1991; ²²Moore et al. 1993; ²³van Lent and Verschuure 1994; ²⁴Peterson 1977; ²⁵Bird 1982; ²⁶Peterson 1984; ²⁷Posey 1986a; ²⁸Posey 1986b; ²⁹Harrison 1987; ³⁰Swinbanks and Luternauer 1987; ³¹Griffis and Suchanek 1991; ³²Dumbauld et al. 1996; ³³Feldman et al. 2000; ³⁴Feldman et al. 1997; ³⁵Dumbauld and Bosley 2018; ³⁶Weitkamp et al. 1992; ³⁷Dumbauld and Wyllie-Echeverria 2003.

*Annual proportional production of juvenile burrowing shrimp is shown as mean \pm standard deviation because recruitment varied stochastically among years. This parameter was drawn randomly from a truncated normal distribution (see *Methods*).

Figure legends

Figure 1. Seagrass populations experience disturbances that vary in their size and frequency, and this variation was approximated using spatial population models. (A) Aerial images of seagrass meadows in northern California, USA, show patterns consistent with fewer large disturbances (left) and many small disturbances (right). Inset photograph in panel A shows a dense burrowing shrimp colony. (B) Simulated landscapes mimicked such variation in disturbance to seagrass (relative densities of seagrass and burrowing shrimp are shown in shades of green and pink, respectively; white areas show recent disturbances to seagrass). Photo credit: M.C.N. Castorani.

Figure 2. Population models captured the essential processes governing the dynamics of seagrass and burrowing shrimp populations, as well as their interactions. See *Methods* and *Table 1* for descriptions of state variables and parameters. Note that not all parameters are shown.

Figure 3. Increasing the total annual extent of disturbance (i.e., the combined area of the landscape disturbed each year; x -axis) caused (A) gradual declines in seagrass populations and (B) increases in burrowing shrimp populations beyond a threshold, but this effect was mediated by the individual size of disturbances (warmer colors indicate larger disturbances; note log scale). Abundances represent normalized (i.e., rescaled to a maximum of one) landscape-scale adult population sizes at quasi-equilibria. The zone of long-term coexistence, in which abundances of both species are $>1\%$ of population maxima, is between the vertical dashed lines.

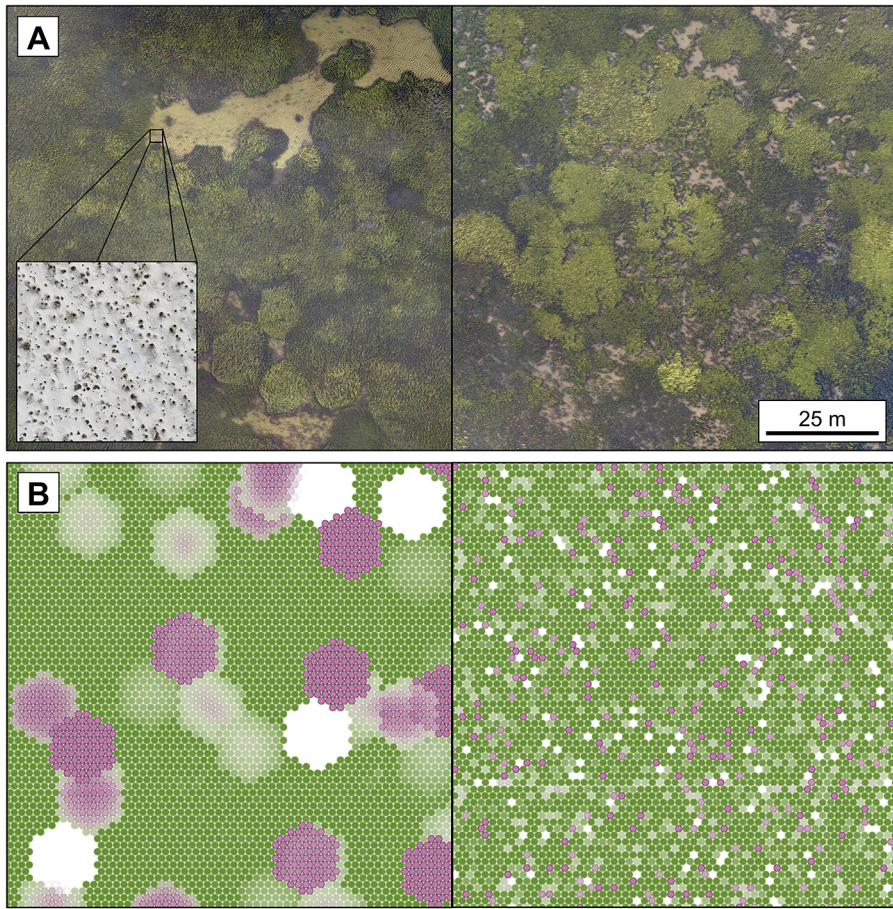
Figure 4. The size and frequency of disturbances interacted to alter (A) the total annual extent of disturbance across the landscape, (B) seagrass abundance, (C) burrowing shrimp abundance, and (D) species evenness (Simpson's E). Note that both axes are on a log scale. Abundances are normalized as in Fig. 3.

Figure 5. The individual size of disturbances mediated the negative effect of seagrass (x -axis; note log scale) on burrowing shrimp at the landscape scale. Hence for a given abundance of seagrass,

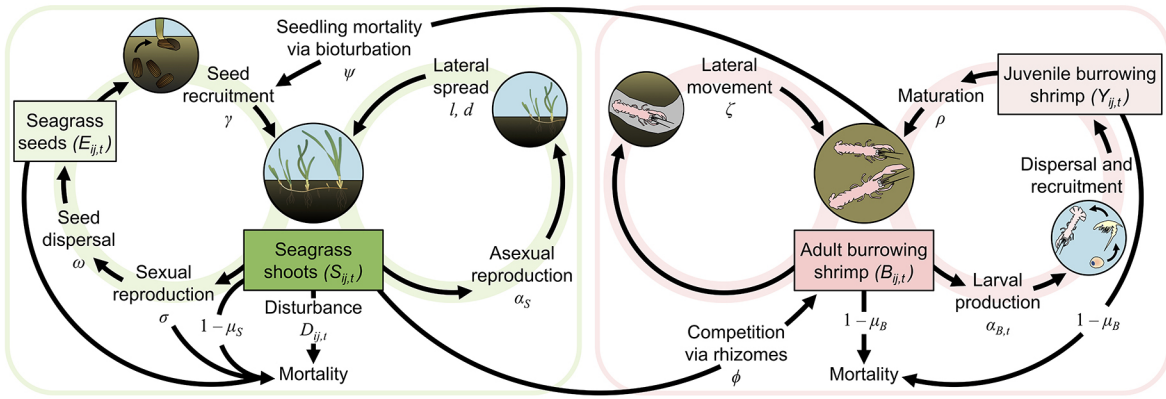
larger disturbances (warmer colors; note log scale) resulted in a greater abundance of burrowing shrimp. Abundances are normalized as in Fig. 3.

Figure 6. Larger, less frequent disturbances enhanced the spatial autocorrelation of (A) seagrass and (B) burrowing shrimp populations when compared to smaller, more frequent disturbances (larger values of Moran's I indicate greater spatial clustering). Burrowing shrimp were nearly always more clustered than seagrass because of strong competitive exclusion that forced burrowing shrimp to the interiors of areas experiencing seagrass loss (see Fig. 5 and Appendix S4: Fig. S1). Note that the color bar represents disturbance frequency on a log scale.

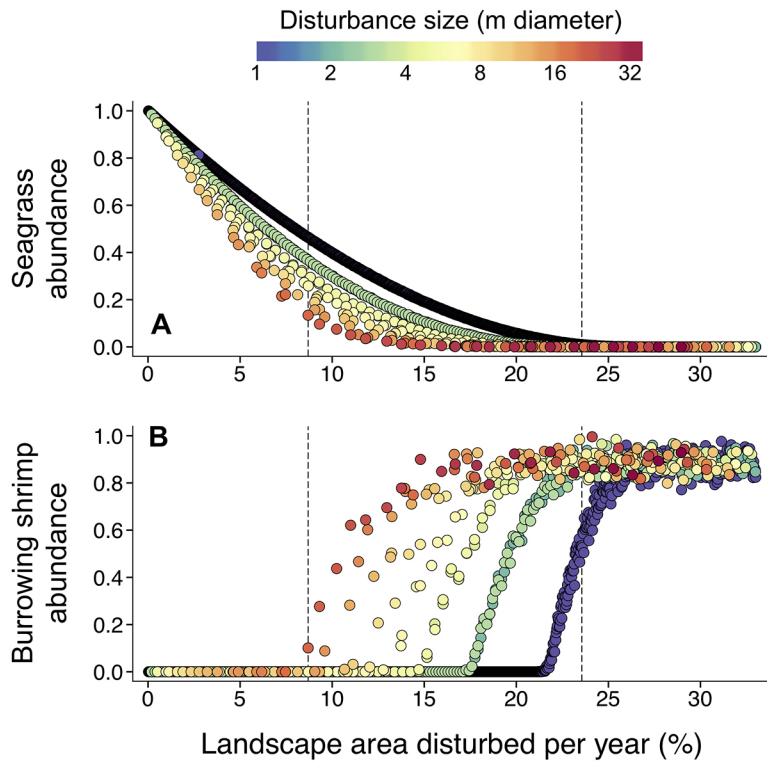
Figure 7. Results from the global sensitivity analysis showing the normalized relative importance of each biological parameter and its interactions with all other parameters in determining the abundance of seagrass (A; left panels) and burrowing shrimp (B; right panels) under four disturbance regimes that supported strong coexistence: a single very large disturbance (frequency = 1 per year, size = 21 m diameter); a few large disturbances (frequency = 13 per year, size = 7 m diameter); several medium disturbances (frequency = 102 per year, size = 3 m diameter); many small disturbances (frequency = 783 per year, size = 1 m diameter).



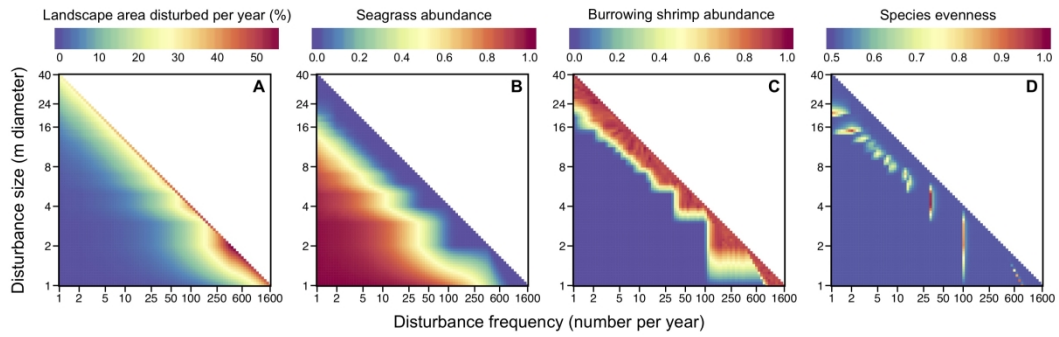
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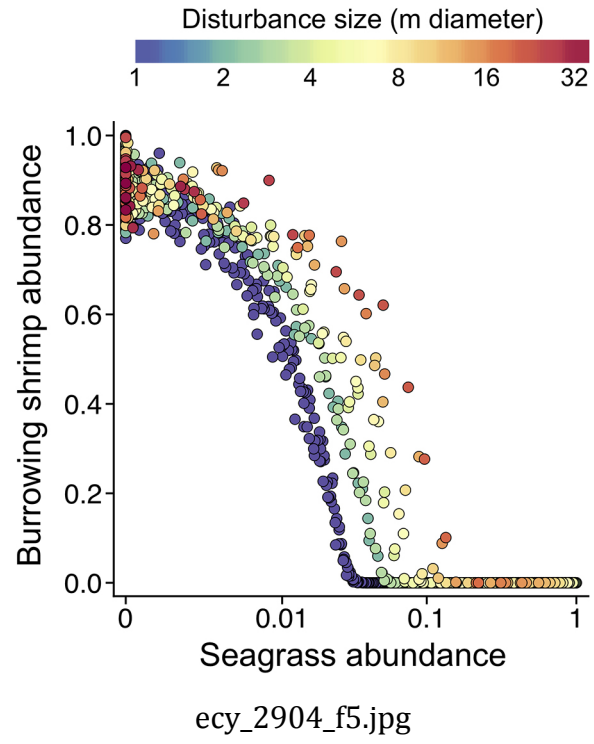
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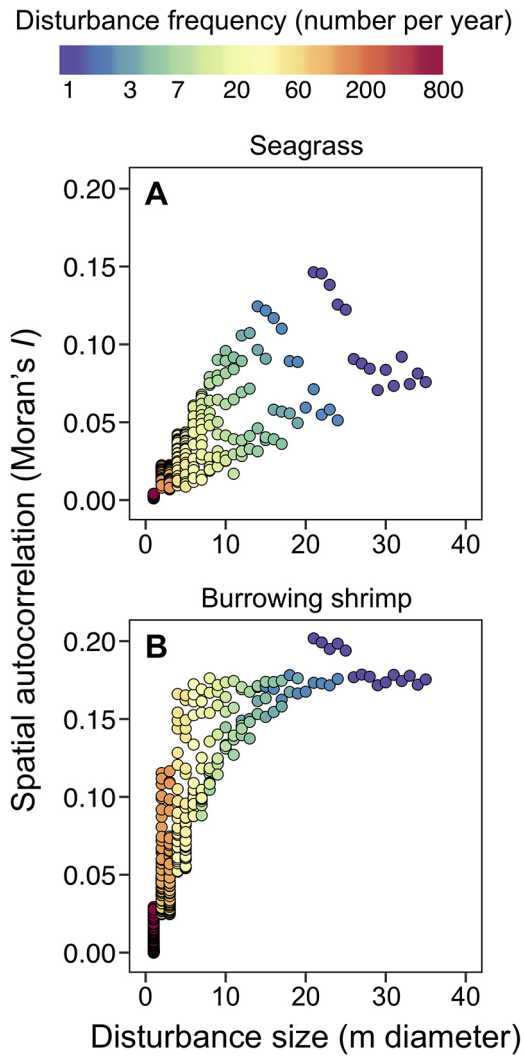


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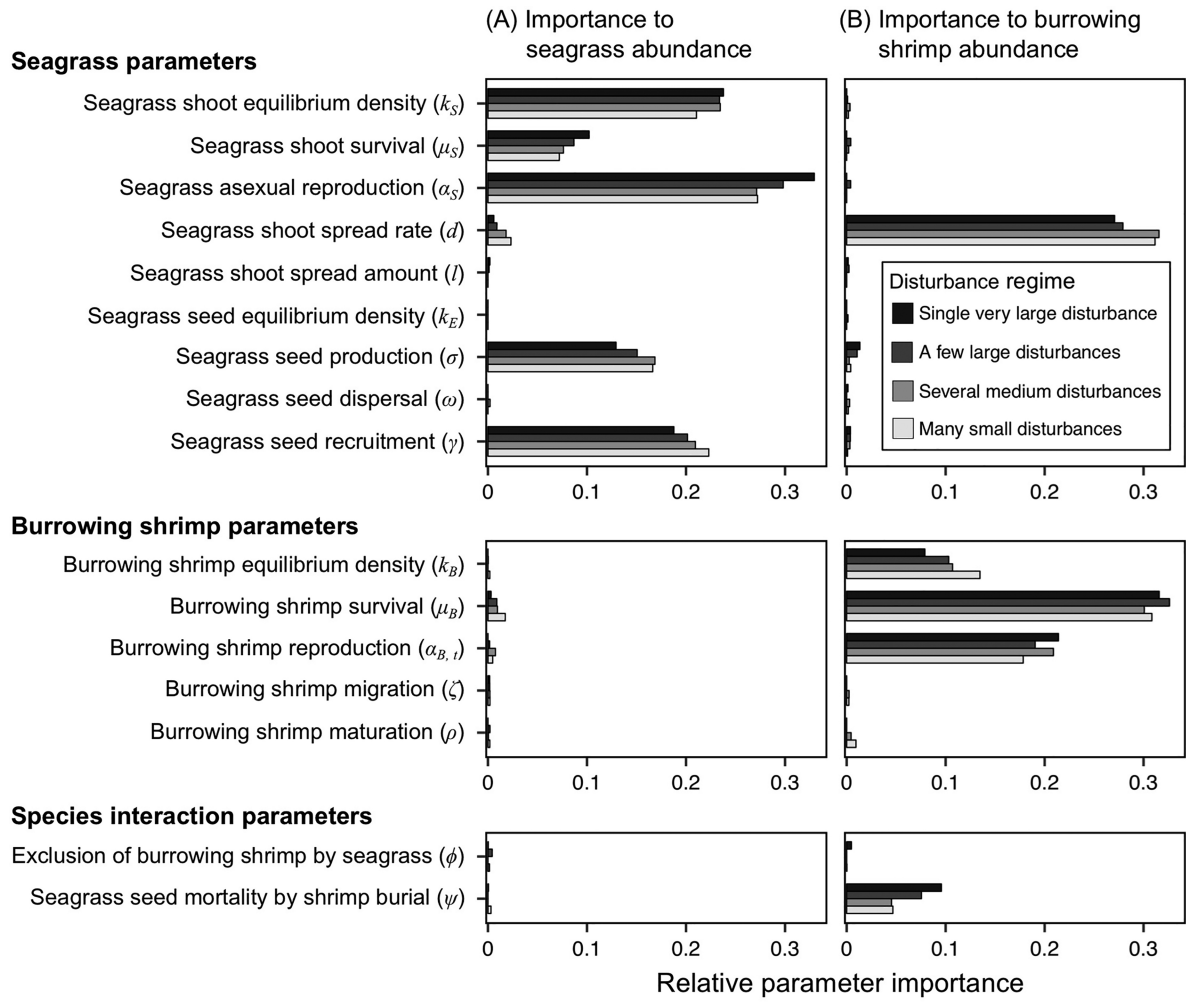


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