

1 **Main Manuscript for**
2 **Title:** Ancestral and Contemporary Intertidal Mariculture Structures Marine Biodiversity.

3
4 **Authors:** Removed to support double-anonymized peer review
5

6 **This PDF includes:**

7 Main Text
8 Figures 1 to 5
9 Supplementary Text, Figure, and Tables

10
11 **Abstract**
12 The cultivation of seafood now outpaces extraction from wild populations. This novel
13 state in the history of human-marine ecosystem interactions highlights the importance of
14 identifying cultivation practices that balance production and conservation. Here, we test the
15 hypothesis that two shellfish cultivation practices, one that spans decades and the other
16 millennia, bolsters habitat complexity, which increases epifaunal (surface) invertebrate diversity.
17 To do so, we conducted multiple surveys of 24 First Nations clam gardens, shellfish aquaculture
18 farms, and non-walled or unmodified beaches along the west coast of Canada. We show that
19 habitat alterations specific to each cultivation practice restructure epifaunal communities at
20 several ecological and spatial scales. Distinct communities within clam gardens and shellfish
21 farms are a function of habitat complexity at 25-50 and 50-100 cm resolutions and changes in the
22 amount of gravel, bivalve shells, and seaweeds. Our findings highlight how resource cultivation
23 can contribute to achieving sustainable human-ecosystem interactions.

24 **Main text**

25 **Introduction**

26 Humans have managed aquatic and terrestrial ecosystems for millennia^{1,2}. Today,
27 anthropogenic activities influence the majority of marine and terrestrial ecosystems^{1,3}. Elevated
28 biological resource availability (*e.g.*, protein) within coastal regions relative to inland ecosystems
29 has contributed to a concentration of human influences along coastlines⁴. While coastal
30 communities have relied on mariculture for millennia, cultivating marine ecosystems has gained
31 global importance over recent decades and has, for the first time, outpaced the amount of seafood
32 extracted from wild populations^{5,6}. This shift signals the emergence of a novel state in the
33 history of human-marine ecosystem interactions. This expansion in cultivation has resulted in
34 remarkable accomplishments for humanity, including advancements in infrastructure, emergent
35 economies, and technology, but has also degraded many natural ecosystems^{7,8}. Balancing food
36 production with coastal resource management, ecosystem health, and population growth
37 represents an emerging challenge facing 21st-century global conservation efforts.

38 Despite numerous human-ecosystem interactions leading to species loss, disrupted
39 community dynamics, and environmental degradation, emerging research indicates that certain
40 anthropogenic activities can create ecological states that foster robust biological communities
41 ^{1,9,10}. These ecological states are predominately associated with human communities that have
42 developed management practices over dozens, if not hundreds of generations, and established an
43 intergenerational understanding of the ecosystem, often viewing themselves as an interconnected
44 part of the whole, as opposed to a separate or superior entity^{11,12}. The technologies and
45 management strategies that Indigenous Peoples of the northeastern Pacific established to increase
46 food production and ensure long-term sustenance, for example, have influenced ecosystems for

47 millennia^{11,13,14}. Along the coast of British Columbia, Indigenous Peoples have employed
48 practices such as intentional successive landscape burnings and plant translocations to enhance
49 forest productivity and plant species diversity^{11,13,15}. Similarly, shellfish cultivation methods
50 implemented over millennia increase the productivity of bivalve populations; a condition that
51 persists despite colonial policies that have disrupted traditional bivalve management by
52 Indigenous Peoples^{16,17}. This spatial-temporal model of how humans alter their environment
53 suggests that the legacy of these activities on ecological communities can persist for thousands of
54 years, even if management frequency or intensity varies^{9,17–19}.

55 Coastal Indigenous populations have stewarded marine resources along the coastlines of
56 the Pacific Northeast for generations^{11,16,20,21}. The enhancement, management, and harvesting of
57 bivalve populations are governed by complex socio-cultural systems within and among
58 communities^{16,17,22}. Beginning at least 3,800 years ago, Indigenous Peoples created and
59 enhanced clam habitat by building “clam gardens”— low intertidal rock walls and associated
60 soft-sediment terraces^{16,23,24}. Clam gardens, also commonly called sea gardens owing to the
61 diverse seafood found within, have been observed from Alaska to Washington State^{24–27}. Garden
62 walls increase intertidal sedimentation rates by up to fourfold, creating a flattened terrace on the
63 landward side of the wall that expands the amount of available clam habitat^{28,29}. The soft-
64 sediment terrace between the clam garden wall and the shoreline is maintained using a suite of
65 tending practices, including adding gravel and broken shells to produce conditions that increase
66 bivalve growth^{16,18,21,23}. This ancestral mariculture practice increases clam abundance and
67 productivity, providing predictable and stable shellfish populations adjacent to coastal
68 communities^{17,18,30}. Despite the extensive history of clam garden use, their existence and
69 distribution have only recently come to the attention of Western science^{16,22,25}.

70 In contrast, contemporary commercial shellfish farming in the northeast Pacific has
71 received considerable scientific attention^{5,6,8}. Westernized shellfish farming began in the mid-
72 1800s with the harvesting of Olympia oysters (*Ostrea lurida*). Overexploitation, foreshore
73 modifications, and disrupted settlement cues collapsed this fishery by 1960³¹. The Pacific oyster
74 (*Magallana gigas*), native to Japan, was introduced and cultivated by 1925³². The Manila clam
75 (*Ruditapes philippinarum*), initially introduced accidentally with *M. gigas*, was integrated into
76 the growing shellfish market in the 1980s³². Cultivating *M. gigas* and *R. philippinarum* involves
77 establishing and maintaining populations within intertidal beaches (*i.e.*, leased tenures) and
78 subtidal shellfish rafts that allow farmers to seed, grow, and harvest shellfish while ensuring
79 product quality and population viability^{6,33,34}. Plastic fences, anti-predator netting, and other
80 foreshore modifications (*e.g.*, rock walls, cages) are also often used in the intertidal to section off
81 outplants and increase habitat suitability^{7,33,34}. The co-occurrence of western commercial
82 shellfish and Indigenous clam gardens demonstrates the importance of bivalve cultivation within
83 the northeast Pacific and provides an opportunity to assess how differing bivalve management
84 systems influence local ecological conditions.

85 Here, we test the hypothesis that cultivating intertidal bivalves bolsters habitat
86 complexity and alters substrate composition, fostering increased diversity in non-target
87 communities (*i.e.*, taxa that are not the primary cultivation target). For this investigation, we
88 considered epifaunal (surface) invertebrates to be non-target communities but acknowledge that
89 non-target communities will differ between cultivation methods due to broader resource use
90 within clam gardens (*i.e.*, sea gardens that cultivate and harvest a range of taxa) and the use of
91 mono or co-culture approaches within shellfish farms. The co-occurrence of clam gardens,
92 shellfish farms, and beaches lacking physical modifications along British Columbia's coast

93 provides a natural experiment capable of testing this hypothesis. We quantified the diversity and
94 density of the epifaunal communities within 24 intertidal sites (6 clam gardens, 6 shellfish farms,
95 and 12 unmodified or non-walled beaches) within three regions along British Columbia's central
96 and south coast (Figure 1). We then evaluated the association of each site's epifaunal
97 communities with the complexity of the physical habitat and substrate composition. To do so, we
98 determined (1) the physical complexity of each intertidal site using structure-from-motion
99 photogrammetry to generate and analyze three-dimensional habitat models, (2) if and how
100 taxonomic diversity and community composition differ among cultivated and unmodified or
101 non-walled sites, and (3) the extent to which alterations in habitat complexity and substrate
102 composition influence biological communities within clam gardens and shellfish farms.
103 Collectively, this novel study examines how intertidal resource cultivation practices engineered
104 and implemented over decades, centuries, and millennia can shape contemporary ecosystems.
105

106 **Materials and Methods**

107 **Positionality of Authors**

108 The positionality statement has been removed to support double-anonymized peer review
109 and will be included if the manuscript is accepted for publication. We are comfortable to forgo
110 anonymized peer review if the reviewers wish to view this statement.

111

112 **Survey Locations**

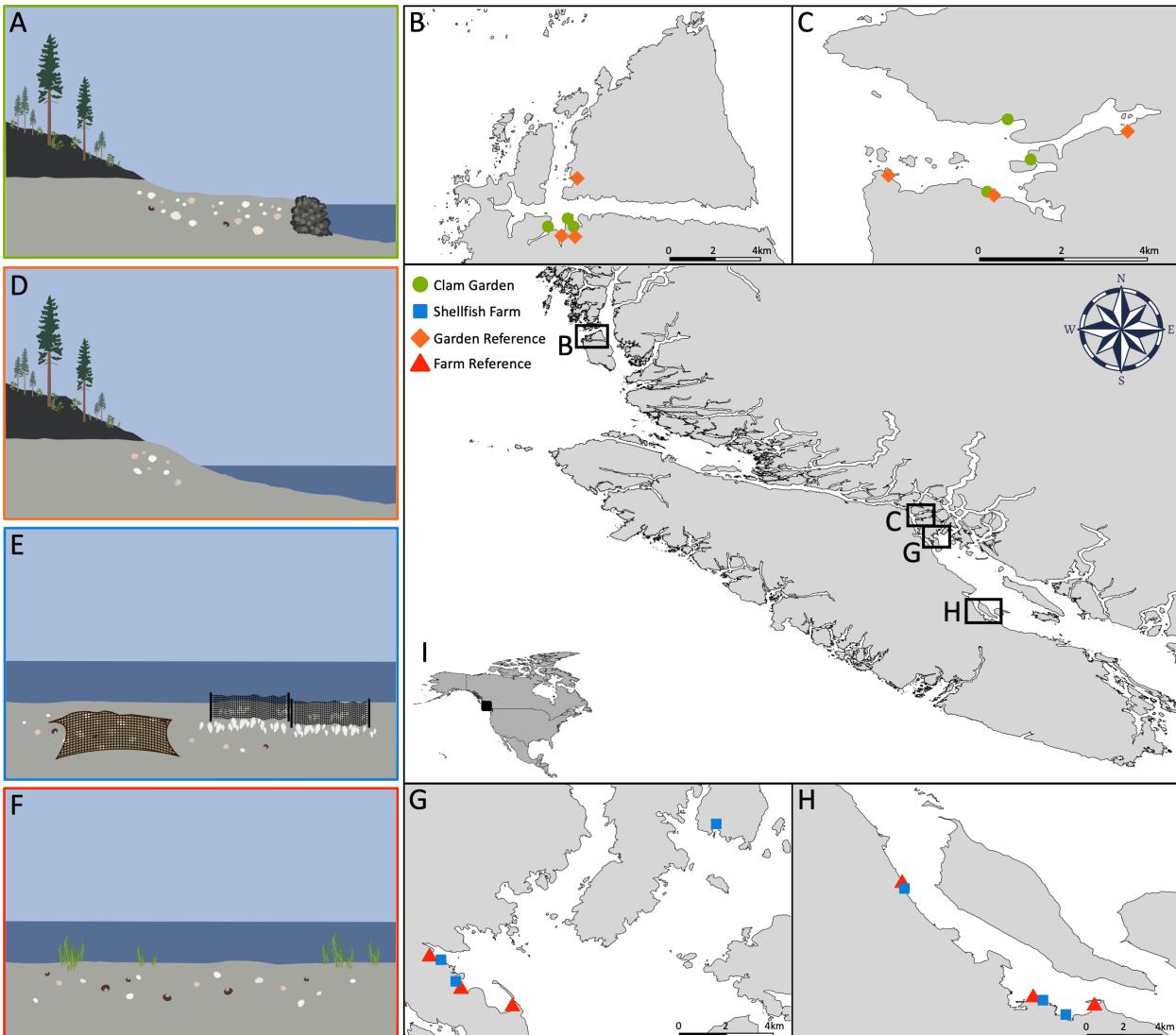
113 This study was conducted within three regions along British Columbia's central and
114 south coast: the Hakai Lúxvbálís Conservancy 'Calvert Island' (51.65606° N, -128.13427° W),
115 Quadra Island (50.21033° N, -125.26871° W) and Baynes Sound (49.52371° N, -124.82457° W)

116 (Figure 1). The 14,000-year continuous occupation of Calvert Island and the surrounding area by
117 Indigenous Peoples established expansive settlements, clam gardens, and other marine resource
118 harvesting sites^{9,30}. Further south on northern Quadra Island, extensive clam garden construction
119 has enhanced bivalve populations and increased settlement density in recent millennia^{18,24,26}.
120 Clam garden construction in the region began at least 3,800 years ago, with gardens built
121 continuously and used to the present day^{23,24}. Garden walls are found along 35% of the
122 shoreline, creating 113,000 m² of terrace beaches^{26,29}. Shellfish farms on Quadra Island mainly
123 cultivate *M. gigas* and *R. philippinarum*, and are predominantly located on the south end of the
124 island³⁴. On eastern Vancouver Island, Baynes Sound supports abundant shellfish farms,
125 producing over half of all shellfish cultured in British Columbia^{32,34}.

126 Twenty-four intertidal sites were surveyed in 2015, 2016, and 2017. The four site types
127 examined were clam gardens, non-walled clam garden reference beaches (hereafter, ‘garden
128 references’), shellfish farms, and unmodified shellfish farm reference beaches (‘farm references’)
129 (Figure 1). The primary comparisons of interest were between shellfish farms and farm reference
130 sites, and clam gardens and garden reference sites; however, differences between shellfish farms
131 and clam gardens were also considered. Surveys of the biological communities and substrate
132 composition occurred in 2015 and 2016. Habitat complexity surveys occurred in 2017. Long-
133 term monitoring of several sites indicated habitat complexity is conserved year to year. All
134 surveys occurred between May and July, and each regional comparison was surveyed over 5-8-
135 day tidal windows to minimize seasonal effects (e.g., Baynes Sound shellfish farms and
136 reference sites).

137

138



139
140 **Figure 1|** Study locations along British Columbia's central and south coasts and illustrations of
141 site types. Depictions of (A) clam garden, (D) unmodified clam garden reference beach, (E)
142 shellfish farm, and (F) unmodified shellfish farm reference beach. Study sites within (B) Calvert
143 Island and Hecate Island, (C) Northern Quadra Island, (G) Southern Quadra Island, and (H)
144 Baynes Sound. (I) Location of British Columbia coastline.

145

146 Field Surveys

147 Surveys were conducted in a similar manner to previous examinations of regions'
148 intertidal communities³⁵. In 2015, site assessments involved running 40-m parallel baselines
149 along the 3.0, 2.2, 1.5, and 0.8 m tidelines (above MLLW), and a perpendicular baseline from the
150 3.0 to the 0.8 m tidelines through the start of each parallel baseline (Figure S1). These baselines

151 established the high (3.0–2.2 m), mid (2.2–1.5 m), and low (1.5–0.8 m) tidal zones. If the
152 specific tidelines could not be accessed, baselines were laid as close to these tidal heights as
153 possible. Within each tidal zone, lines were extended at predetermined distances along the
154 perpendicular and parallel baselines. Distances along the perpendicular baselines were chosen *a*
155 *priori* using a random number generator, while parallel distances increased in increments of ten
156 meters to ensure the entire horizontal distance was covered. Assessments occurred at the
157 intersection of these extended lines, with each quantifying the biological community and
158 substrate composition (Figure S1). Five assessments within each zone were attempted, but only
159 three assessments occurred in some cases due to limited access to each intertidal zone. In 2016,
160 the same methodology was followed; however, based on the results of the previous year's
161 surveys, only the mid-zone was surveyed.

162

163 **Biodiversity Surveys**

164 Biodiversity surveys evaluated the epifaunal (surface) communities present at each of the
165 assessment locations. Assessments were done using a 0.5×0.5 m quadrat strung vertically and
166 horizontally every 5 cm to create 100 equal squares. Ten randomly selected 5×5 cm squares
167 were chosen from the 100 squares formed by the strung quadrat (Figure S2). All organisms
168 within each square were counted and identified. If multiple layers (*i.e.*, predator-exclusion nets,
169 oysters) were present, the top and bottom layers were assessed separately and combined,
170 representing the total epifaunal diversity present in the quadrat. The occurrence of multiple
171 layers was low (11 of 435 surveys). Sixty taxa (*e.g.*, species, genera) were observed across the
172 study sites (Table S1). Abundances were multiplied by ten to estimate the total abundance within
173 the quadrat. Despite extrapolation, this subsampling method accurately detects species diversity,

174 reduces assessment effort, and results in reliable species abundance estimates³⁵. Pacific oysters
175 (*M. gigas*) were the only species not subsampled as their densities are easily assessed and
176 respond poorly to extrapolation; thus, all oysters in each quadrat were counted. The resulting
177 biodiversity data were denoted as species diversity and abundances within the 0.25 m² area.

178

179 **Substrate Composition**

180 Percent cover of the substrate types observed within the 0.5 × 0.5 m quadrats was
181 determined to evaluate ecological covariates of the associated intertidal substrate. Each quadrat
182 was photographed before the biodiversity survey using a Nikon AW120 camera held 1 m above
183 the quadrat (resolution: 2,832 × 2,832 pixels). Substrate photos were analyzed using ImageJ to
184 derive surface cover metrics³⁶. Quadrat photos were processed in an unordered fashion to avoid
185 observer bias. Percent cover was determined by dividing each substrate's area by the total
186 quadrat area. Algal taxa were primarily denoted by genera, with *Gracilaria* spp., *Fucus*
187 spp., *Mastocarpus* spp., Phaeophyceae (Brown Algae), *Sargassum muticum*, *Ulva* spp.,
188 and *Zostera* spp. (eelgrasses) being observed. Habitat-forming calcareous shells and skeletons
189 (tests) were denoted as clam shells, Pacific oyster shells, and *Dendraster* (sand dollar) shells.
190 Sediments were classified using the Wentworth scale to identify the boulder, cobble, gravel,
191 sand, and mud/silt composition of each quadrat.

192

193 **Habitat Complexity Models**

194 The structural characteristics of the 24 clam gardens, shellfish farms, and reference
195 beaches were quantified using structure-from-motion (SfM) photogrammetry in 2017. This
196 method generates high-resolution georeferenced 3D reconstructions of the physical environments

197 using 2D images^{37,38}. A 10 × 10 m assessment area was established in the mid-intertidal region
198 at each site, with the top corners at the 2.2 m tideline (Fig S3). A detailed description of this
199 process is included within the supplemental material (Supplemental Text). Briefly, image
200 acquisition used a Canon SL1 digital SLR camera to photograph the 100 m² survey areas. Three-
201 dimensional reconstructions of the 24 sites were generated using Agisoft Metashape Standard
202 Edition (v1.7.4). The four key stages were: aligning photos, dense point cloud construction, mesh
203 construction, and building texture (Figure S4). The rendered 3D models of each of the 24 sites
204 were exported as wavefront files for further analysis.

205 The habitat models were analyzed using Rhinoceros 3D³⁹. The structural metrics
206 measured were rugosity and fractal dimension (D). Rugosity (R) uses an extendible chain
207 method to measure the topographic distance covered by a theoretical straight-line distance.
208 Consequently, linear R measurements are between 1 and 0, with lower values denoting more
209 complex surfaces. To avoid confusion, R was considered on an inverted scale (*i.e.*, 0-1), to allow
210 increases in R to reflect increases in complexity. Triplicate 9-m linear R measurements were
211 taken in both directions (6 total) using a virtual chain with a 2 cm link length (Figure S4B). The
212 mean linear R for each site was determined by averaging the six measurements. Fractal
213 dimension (D) measures how surface area changes with resolution by quantifying the slope of a
214 model's resolution relative to the surface area on a logarithmic scale (*i.e.*, how complexity varies
215 with scale). Measurements of D are between 2 and 3, with higher values signifying increased
216 heterogeneity. Fractal dimension was measured at four spatial resolutions, 2.5-5, 5-25, 25-50,
217 and 50-100 cm; effectively, this measures habitat complexity within these size ranges. Five D
218 measurements at the four spatial resolutions were taken for each model, one in each corner and

219 one in the middle (Figure S4C). These measurements were averaged to determine mean D at the
220 four spatial resolutions.

221

222 **Statistical Analyses**

223 All data analyses were conducted in RStudio version 3.6.1⁴⁰. Data visualizations and
224 analyses utilized the ‘ggplot2’, ‘vegan’, ‘mvp’ and ‘randomForestSRC’ packages^{40–44}.

225

226 *Community composition*

227 Epifaunal communities were characterized using Hill numbers (*i.e.*, richness, Shannon
228 diversity, and inverse Simpson) to examine the variability between the taxonomic diversity and
229 abundances at clam gardens, shellfish farms, and reference sites. The three indices were
230 represented by a q-value, which denotes the sensitivity of the measurement to the taxa’s relative
231 abundances where q = 0 is richness, q = 1 is Shannon diversity, and q = 2 is inverse Simpson
232^{35,45}. A function of order q (*i.e.*, q-value) until a maximum of five was generated for each site
233 type and regional comparison (*e.g.*, Quadra Island clam gardens and reference sites). The values
234 were plotted as diversity profile curves, illustrating diversity as a function of order q. The
235 resulting curve’s slope reflects community evenness, with steeper curves denoting uneven
236 abundances. Taxa unique to each site type, co-occurring between comparisons, and those present
237 among all habitats were examined using a Venn diagram, illustrating the allocation of landscape
238 species richness (gamma diversity) into the various ecological compartments. These analyses
239 considered only the 2015 and 2016 biodiversity surveys conducted within the mid-intertidal zone
240 to ensure a balanced sampling effort and minimize the confounding effect of tidal height (N =
241 235 quadrats).

Community composition was characterized using non-parametric multivariate analyses to examine the biological communities present at each site type. Analyses were conducted using the 'vegan' package⁴³, and again, only biodiversity surveys conducted within the mid-intertidal zone were considered to ensure a balanced sampling effort. Quadrat values for each year were averaged according to the site's mid-intertidal zone, and then the site-year values were averaged according to the site types (*e.g.*, clam garden, garden reference). A resemblance matrix of epifaunal densities was calculated using Bray-Curtis coefficients with a dummy variable of 1 added to correct for cells where no biota was observed. The community composition of each site type and regional comparison were visualized using non-metric multidimensional scaling (nMDS) plots. Permutational Multivariate Analysis of Variance (PERMANOVA) conducted on the resemblance matrix determined if community composition differed statistically among the site types and regions. Separate PERMANOVAs examined the site type's community dissimilarities observed within and among each of the three regions. Therefore, five PERMANOVAs were run: Clam Garden, Shellfish Farms, and Reference Sites; Calvert Island Gardens and Reference Sites; Quadra Island Gardens and Reference Sites; Quadra Island Shellfish Farms; and Baynes Sound Shellfish Farms. Site type, year, and the interaction between site type and year were included as fixed factors in each PERMANOVA, and an α of 0.05 was used to detect significance.

Percent dissimilarity between the site types and regions was calculated using a Similarity Percentages (SIMPER) analysis. SIMPER elucidates the differences in taxa between site types. The average dissimilarity (Diss) between each taxon over the standard deviation (SD) was measured as Diss/SD, determining a taxa's contribution to community dissimilarity. Values greater than one represent groups that consistently contributed to the observed differences

265 between site types⁴⁶. *Balanus glandula* and Barnacle Spp. (*i.e.*, unidentifiable barnacle species)
266 were merged during this analysis due to taxonomic resemblances; the majority of Barnacle Spp.
267 were likely juvenile *B. glandula* that could not be differentiated from juvenile *Chthamalus dalli*.

268

269 *Substrate-Epifaunal Community Associations*

270 Multivariate regression trees (MRTs) were used to analyze the association between the
271 abundances of epifaunal taxa and substrate composition. The MRTs were fitted in R-Studio
272 using the package ‘mvpart’⁴¹. The 60 taxa observed during the biodiversity surveys were
273 amalgamated into 24 higher-level taxonomic classifications to improve pattern visualization
274 (*e.g.*, family, order; Table S3). Densities were log-plus-one-transformed, following the addition
275 of a dummy variable of 1. Multivariate regression trees analyzed taxonomic densities within and
276 among site types. Garden and shellfish reference sites were pooled for this analysis to improve
277 the description of the substrate types that structure the ecological communities within these
278 habitats. Therefore, four separate MRTs were constructed: all sites combined, clam gardens,
279 shellfish farms, and reference sites. This approach identified the environmental characteristics
280 that predict taxonomic diversity within site types and among intertidal ecosystems. It also
281 allowed the high, mid, and low intertidal zone surveys (N = 435 quadrats) to be considered
282 without influencing the validity of comparisons (*e.g.*, creating an unbalanced sample
283 comparison).

284 Each MRT evaluated epifaunal taxonomic density as the response variable, and intertidal
285 zone, percent boulder, cobble, gravel, sand, mud/silt, clam shells, oyster shell, *Dendraster* (sand
286 dollar) shells, *Gracilaria* spp., *Fucus* spp., *Mastocarpus* spp., Phaeophyceae (Brown Algae),
287 *Sargassum muticum*, *Ulva* spp., and *Zostera* spp. as explanatory variables. The optimal tree size

288 for each MRT was determined following one-hundred-fold cross-validation. The three MRTs
289 considering each site type separately were pruned to the lowest cross-validation error rate. The
290 MRT with sites combined was pruned according to the one standard error rule, which states that
291 the most parsimonious model is one with an error rate within one standard error of the best
292 model⁴⁷. This multi-method approach to pruning provided a more informative description of the
293 substrate features important within each site type and a more conservative estimate of the
294 substrate features relevant across intertidal sites. The tree's splits were chosen using a sum of
295 squares criteria that minimizes each node's sums of squared distances. The four MTR trees were
296 pruned to 4-7 'leaves' to avoid overfitting. The taxa that contributed the most to each split in the
297 MTR with sites combined were determined using a discrimination analysis. This identified the
298 taxa that explain the most variance at each node, the directionality (*i.e.*, left versus right split) of
299 their contribution, and the probability that the contributed variance was non-random.
300

301 *Substrate variable importance*

302 A multivariate random forest (MRF) was constructed using survey data from all habitats,
303 intertidal zones, and the 'randomForestSRC' package to determine which of the substrate types
304 identified by the previous MRTs were the most important to epifaunal taxa⁴⁴. The MRF
305 considered the importance of percent cobble, gravel, clam shells, *Mastocarpus* spp., *Ulva* spp.,
306 oyster shell, mud/silt, *Dendraster* shells, and *Gracilaria* spp., for the surveyed 24 taxa (Table
307 S3). Site type, region, site, and intertidal zone were included in this investigation to identify the
308 extent to which features not captured in the substrate survey may be contributing to diversity
309 patterns. The MRF consisted of 6,000 trees grown to a maximum node depth of six to avoid
310 overfitting (Figure S5). The number of candidate variables randomly selected for splitting a node

311 was 4, following the default $p/3$ recommendation for regression, where p equals the number of
312 variables. The minimum terminal node size was 5, again, following the regression default. The
313 implications of different node sizes, number of trees, node depth, and candidate variables were
314 explored and had minimal influence on the outcomes. Variable importance was calculated by
315 randomly permuting values of the variables, running them through the model, and evaluating the
316 change in mean squared error (MSE). Variable importance was determined for each of the 24
317 taxa and averaged among taxa.

318 A subsequent analysis examined the ability of MRFs to predict species occurrences. The
319 predictive accuracy of the MRF was determined using 80% of the data to train a model and the
320 remaining 20% of the data to evaluate the model's predictions. Model construction used identical
321 parameters to the variable importance analysis. This analysis determined the MRF's capacity to
322 explain the variance of each taxa and the training data's error rate.

323

324 *Habitat complexity-epifaunal communities association*

325 The complexity metrics were averaged according to each site type to illustrate the
326 structural differences between the habitats. Each site's five D measurements (resolutions 2.5-5, 5-
327 25, 25-50, 50-100 cm) and linear R were averaged before determining mean D and mean linear R
328 for each site type. The D measurements illuminated complexity at fine and broad scales via
329 increasing resolutions. For example, an elevated D value within the 2.5-5 cm resolution would
330 indicate a high level of fine-scale complexity, whereas linear R denotes complexity as the
331 topographic distance divided by a 9 m chain, meaning the lower the value, the more complex the
332 surface.

333 An MRF analysis determined which of the habitat complexity measurements were the
334 most important to epifaunal communities. The analysis used the 2015 and 2016 mid-intertidal
335 zone epifaunal survey data to increase the spatial overlap between the measurements of the
336 rendered models and the surveys while ensuring a balanced sampling effort. Epifaunal survey
337 values were averaged according to the site's' mid-intertidal zone for each year, then the 2015 and
338 2016 values were averaged for each site. Epifaunal data were log10 transformed following the
339 addition of a plus one dummy variable. The MRF considered site type, region, average R, and
340 D2.5, D5, D25, and D50 for the surveyed 24 taxa. The 'site' term was not included in the MRF
341 as the biodiversity and complexity data were determined at the site level. The MRF consisted of
342 6,000 trees grown to a maximum node depth of six to avoid overfitting. The minimum terminal
343 node size was 3, which deviated from the default setting for regression based on the 'tune node'
344 functions recommendation. In keeping with previous MRFs, the importance of each variable was
345 calculated by randomly permuting the values of the variables, running them through the model,
346 and evaluating the change in mean squared error. Variable importance was determined for each
347 of the 24 taxa and averaged among the taxa. A subsequent analysis examined the extent to which
348 the MRF could predict species occurrences based on observed habitat complexity. The predictive
349 accuracy of the MRF was determined using 80% of the data to train a model and the remaining
350 20% of the data to evaluate the model's predictions. Model construction used identical
351 parameters as the previous variable importance analysis.

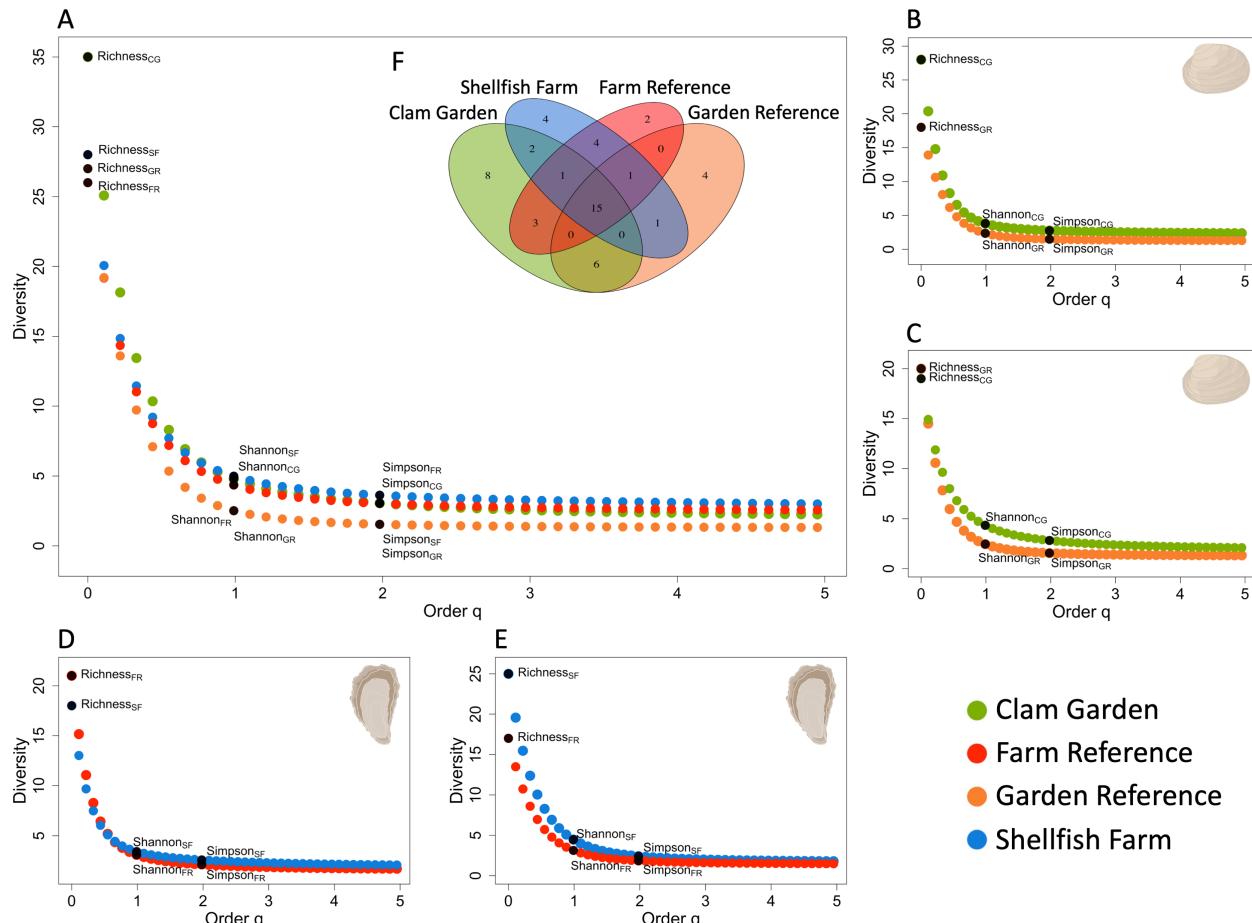
352

353 **Results**

354 **Community Composition**

355 Distinct epifaunal communities were found within the mid-intertidal zones of clam
356 gardens and shellfish farms relative to their respective reference beaches (Figure 2). However,
357 the extent to which observed communities differed varied among regions and according to
358 cultivation method. Across all regions, clam gardens had elevated taxonomic richness. Of 60
359 total observed taxa, clam gardens contained 35 taxa, whereas shellfish farms contained 28 taxa,
360 compared to the 27 and 26 taxa observed within garden and farm reference beaches, respectively
361 (Figure 2A, Table S1). Reduced diversity within garden reference beaches persisted when
362 comparing Shannon diversity and inverse Simpson; both indices were considerably lower within
363 reference sites (Figure 2A). Comparatively, shellfish farms, clam gardens, and shellfish farm
364 reference beaches exhibited relatively similar Shannon diversity and inverse Simpson values.
365 Cultivated sites exhibited more even communities, as evident by the slope of the order q line
366 stabilizing the Shannon diversity and inverse Simpson values (Figure 2). Elevated taxonomic
367 richness was more pronounced at clam gardens on Calvert Island and within shellfish farms in
368 Baynes Sound (Figure 2B, Figure 2D). Across the site types, unique taxa were present within
369 most of the ecological compartments considered (Figure 2F, Table S2). Eight taxa were unique
370 to clam gardens, four taxa were unique to shellfish farms, and fifteen taxa were common across
371 all site types (Table S2).

372
373



374
 375 **Figure 2|** Diversity profile curves illustrating mid-intertidal diversity as a function of order q
 376 values. Black dots denote Hill numbers: species richness ($q = 0$), Shannon diversity ($q = 1$), and
 377 Simpson inverse diversity ($q = 2$). The slope of the curve reflects community evenness. A)
 378 Diversity pooled across regions. B-E) Diversity within B) Calvert Island, C) Northern Quadra
 379 Island, D) Southern Quadra Island, and E) Baynes Sound. F) Venn diagram of taxa unique to
 380 each possible comparison. B-E) Illustrations depict a species cultivated within each site type B-
 381 C) Butter clams (*Saxidomus gigantea*), D-E) Pacific oysters (*Magallana gigas*).

382

383 There were significant differences in community composition between site types, years,
 384 and sites (Figure 3, Table S4). These differences were present among and within regions. The
 385 non-Metric Multi-Dimensional Scaling (nMDS) plots stress ranged from 0.08 to 0.14, indicating
 386 an appropriate model fit between comparisons (Figure 3). Among regions, the mid-intertidal
 387 communities observed within clam gardens, garden reference sites, shellfish farms, and farm
 388 reference sites differed (PERMANOVA, $F = 4.98$, $p = 0.018$, Figure 3A), as did the communities

389 observed annually and within each site (Table S4). Regionally, comparisons between the clam
390 gardens on Calvert Island, Baynes Sound shellfish farms, and their respective reference beaches
391 exhibited a high degree of divergence between communities (Clam Garden PERMANOVA, $F =$
392 3.42, $p = 0.029$; Shellfish Farm PERMANOVA, $F = 4.88$, $p = 0.005$; Figure 3, Table S4). Year
393 and site were different within all regional comparisons, except for the clam gardens and clam
394 garden reference beaches on Calvert Island (Figure 3; Table S4). Non-metric multidimensional
395 scaling plots of mid-intertidal substrate composition display similar differences in community
396 composition (Figure S6).

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

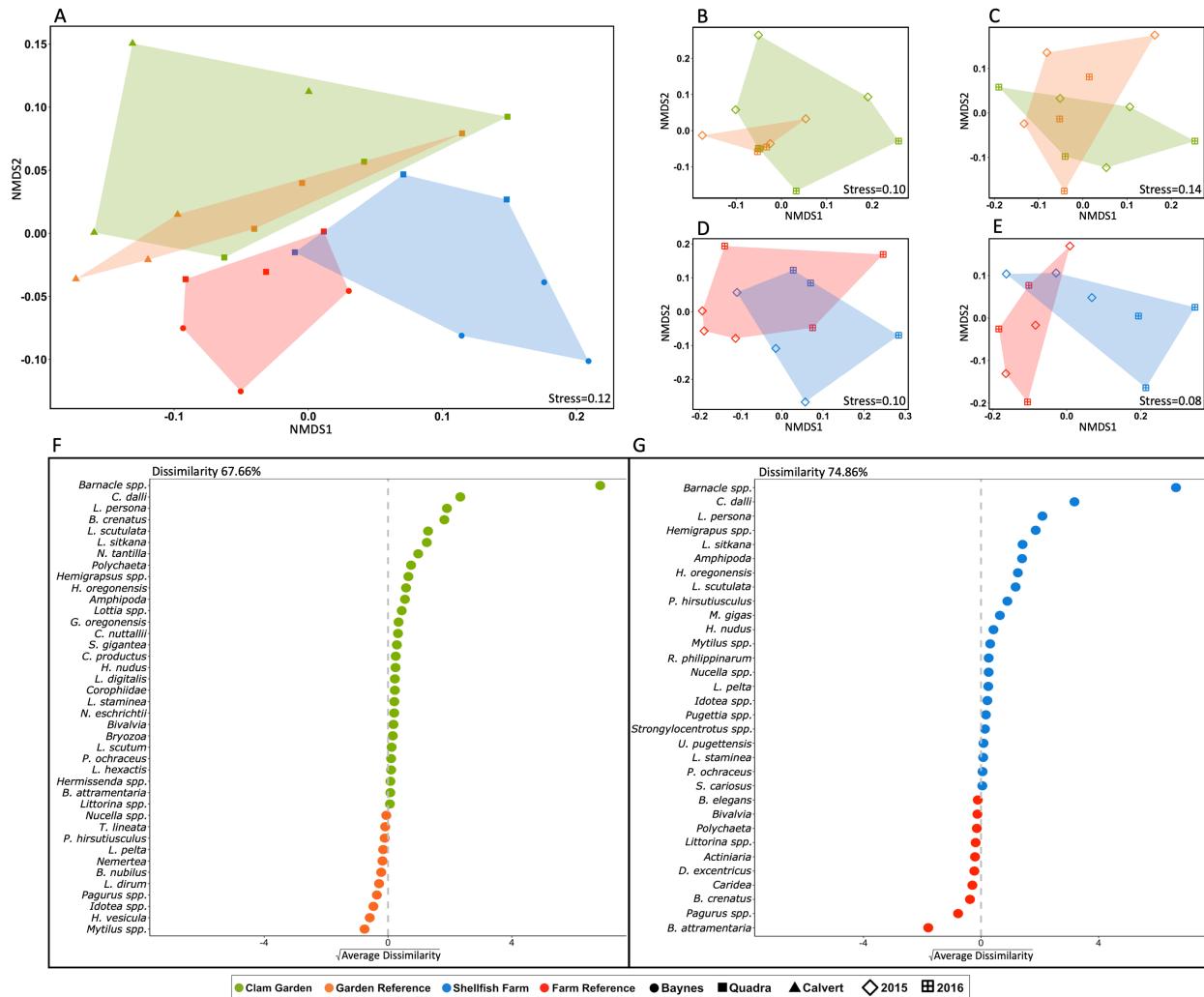
412

413

414

415

416



417
418
419
420
421
422
423
424
425
426
427

428 Taxon-specific dissimilarity varied substantially between site types, with most taxa
429 increasing in abundance within cultivated habitats (Figure S7). The SIMPER analysis determined
430 that clam garden and reference beach mid-intertidal communities were 67.66% dissimilar (Figure

431 3F). This dissimilarity was driven primarily by increased densities of *Balanus glandula*,
432 *Chthamalus dalli*, *Lottia persona*, *Balanus crenatus*, *Littorina scutulata*, and *Littorina sitkana*
433 (Figure 3F). Collectively, these taxa contributed over 90% of the cumulative dissimilarity, with
434 numerous taxa (e.g., *Chthamalus dalli*, *Balanus crenatus*, *Littorina scutulata*) exhibiting up to
435 a 4-fold increase in abundance (Table S5). Although contributing considerably less to cumulative
436 dissimilarity, clam gardens also displayed reduced abundances in several taxa, including *Mytilus*
437 spp., *Haminoea vesicula*, and *Idotea* spp. (Figure 3F, Table S5).

438 The SIMPER analysis of shellfish farms and reference sites determined that mid-
439 intertidal communities were 74.86% dissimilar (Figure 3G). Comparable to the analysis of clam
440 gardens, this dissimilarity was driven primarily by increased abundances of *Balanus glandula*,
441 *Chthamalus dalli*, *Lottia persona*, and *Littorina sitkana* (Figure 3G). Additionally, *Hemigrapsus*
442 spp. and Amphipoda abundances within shellfish farms increased by 1.5 and 2.4-fold,
443 respectively, accounting for 4.63% and 2.61% of the observed dissimilarity (Table S5). A
444 notable 2-fold increase in the introduced Japanese mud snail (*Batillaria attramentaria*)
445 abundances was observed within reference sites (Figure 3G). This increase accounted for 4.29%
446 of the observed dissimilarity and was the only instance in which an increase in the density of a
447 taxon within reference sites contributed more than 1% (Table S5). The comparison of Quadra
448 Island shellfish farms and reference beaches resulted in 77.30% dissimilarity, whereas the
449 Baynes Sound comparison resulted in 72.14% dissimilarity.

450

451 **Substrate-Epifaunal Community Associations**

452 The MRT analysis considering all sites and intertidal zones illustrated that the diversity
453 and density of the 24 higher-level taxonomic classifications were primarily associated with

454 gravel, oyster shell, cobble, and *Mastocarpus* spp. (Figure 4A, Table S3). The root node of this
455 tree identified gravel as the substrate type most closely associated with the epifaunal
456 communities. Littorinidae, Lottiidae, and Sessilia were the discrimination taxa informing this
457 split, all of which had higher right split mean values due to their association with gravel
458 percentages above 7.31% (Table S6). In habitats that met this gravel condition, the subsequent
459 decision node was dictated by the amount of cobble present. The co-occurrence of relatively high
460 gravel and cobble forms a terminal or ‘leaf’ node with a community comprised of the
461 discrimination taxa Decapoda, Mytilidae, and Batillariidae (Figure 4A). In habitats with
462 relatively low amounts of cobble, the abundance of Pacific oyster shells and gravel dictated
463 community composition. Specifically, an abundance of oyster shells promotes a terminal node
464 community comprised of discrimination taxa Decapoda, Sessilia, Ostreidae, Lottiidae, and
465 Asteriidae. The other terminal nodes were structured by combinations of gravel, oyster shells,
466 and *Mastocarpus* spp. (Figure 4A).

467 The MRF variable importance analysis determined the extent to which each substrate
468 type and spatial factor (*e.g.*, region, site) contributed to the resulting epifaunal communities.
469 Average variable importance, a measure of change in the mean squared error, ranged from 0.08
470 to 17.15% (Figure 4B), with region, gravel, *Mastocarpus* spp., site type, *Ulva* spp., and oyster
471 shell being the most important factors averaged across taxa. However, variable importance
472 differed considerably when considering taxa independently (Figure S8), with several robust taxon-
473 variable associations evident. For example, the importance of the associations between
474 *Mastocarpus* spp., region, and gravel for Amphilepidida, were 77.15%, 68.52%, and 42.46%,
475 respectively (Figure S8, Table S7). The variance explained by the MRF model differed
476 considerably among taxa, and as such, so did the model’s ability to predict taxonomic variability

477 (Table S7). Explained model variance was the highest in taxa that were consistently observed
478 across the study sites or exhibited a high degree of site type fidelity. For example, the random
479 forest model explained 48.64%, 46.43%, and 43.35% of the variability observed in Batillariidae,
480 Decapoda, and Sessilia abundances, respectively. The predictive capabilities of the trained model
481 mirrored this trend, with variance explained by the testing dataset proportional to the
482 performance of the full model (Table S7).

483

484

485

486

487

488

489

490

491

492

493

494

495

496

497

498

499

500

501

502

503

504

505

506

507

508

509

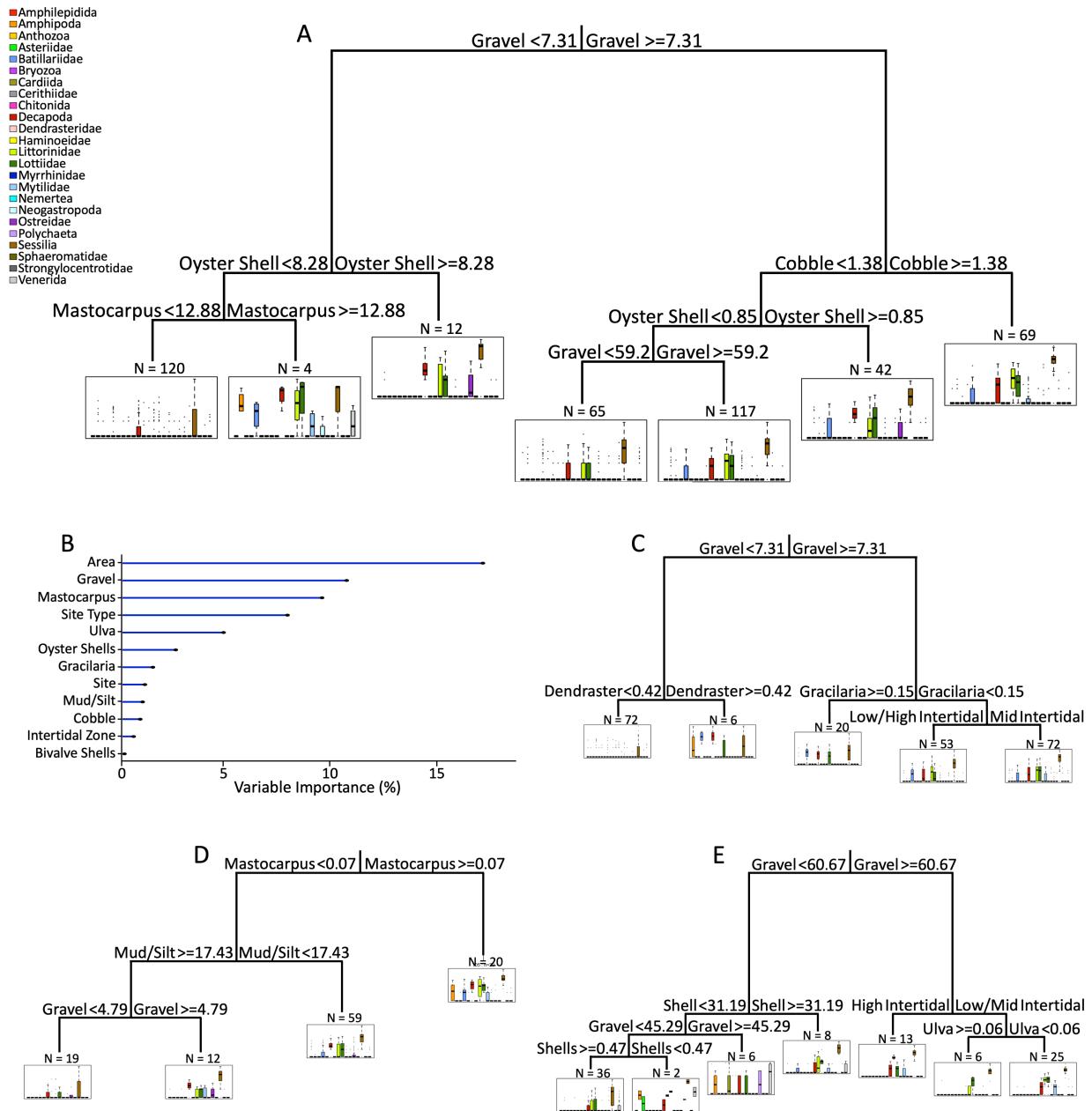


Figure 4 Multivariate regression trees (MRT) and multivariate random forest (MRF) variable importance analyses of the interaction between epifaunal communities and substrate composition. Each MRT's decision node denotes the split value for each respective substrate type. The MRT terminal node box plots illustrate log taxonomic densities. (A) MRT constructed using all regions and site-type data. (B) MRF relative importance of the predictor variables scaled by decreases in the mean squared error of the model when the variable is permuted. (C) MRT constructed for reference sites. (D) MRT constructed for shellfish farms. (E) MRT constructed for clam gardens.

520 The MRT analyses conducted on each site type separately identified unique associations
521 between epifaunal communities and the substrate variables. The MRT analysis of reference
522 beaches illustrated that gravel, *Dendraster* shells, *Gracilaria*, and intertidal zone (*i.e.*, tide
523 height) structure these biological communities (Figure 4C). The root node identified gravel as the
524 most influential substrate type. Low gravel percentages interacted with a *Dendraster* based
525 decision node, with increases in *Dendraster* generating the more diverse terminal node.
526 Substrates within high percentages of gravel were further structured by *Gracilaria*, which, if
527 abundant, interacted with intertidal zone to produce two terminal nodes. Within shellfish farms,
528 *Mastocarpus* spp. structured the root node with gravel, mud and silt forming subsequent
529 branches (Figure 4D). Higher *Mastocarpus* spp. abundances produced a diverse terminal node
530 with increases in Amphipoda, Batillariidae, Decapoda, Littorinidae, Lottiidae, Mytilidae, and
531 Sessilia. Low amounts of *Mastocarpus* spp. produced a decision node based on mud and silt,
532 which, at lower mud and silt percentages, interacted with gravel to form two terminal nodes—the
533 more taxonomically diverse and dense of these nodes corresponded to increases in the amounts
534 of gravel present. Within clam gardens, the root node of the MRT identified gravel at a relatively
535 high percentage of 60.67 % as the substrate type most influential for community composition
536 (Figure 4E). Habitats with amounts of gravel above this were structured by intertidal zone
537 and *Ulva* spp. Under the root node condition of lower gravel, bivalve shells structure
538 communities. If bivalve shells were abundant, gravel and bivalve shells function in combination
539 to structure communities with gravel constrained by the initial root condition. This interaction
540 generates four-terminal nodes exhibiting considerable taxonomic diversity and densities. Of
541 these nodes, the co-occurrence of gravel between 45.29 to 60.67%, and less than 31.19% bivalve

542 shell, produced the most diverse and abundant community, comprised of Amphipoda,
543 Cerithiidae, Decapoda, Lottiidae, Polychaeta, and Venerida.

544

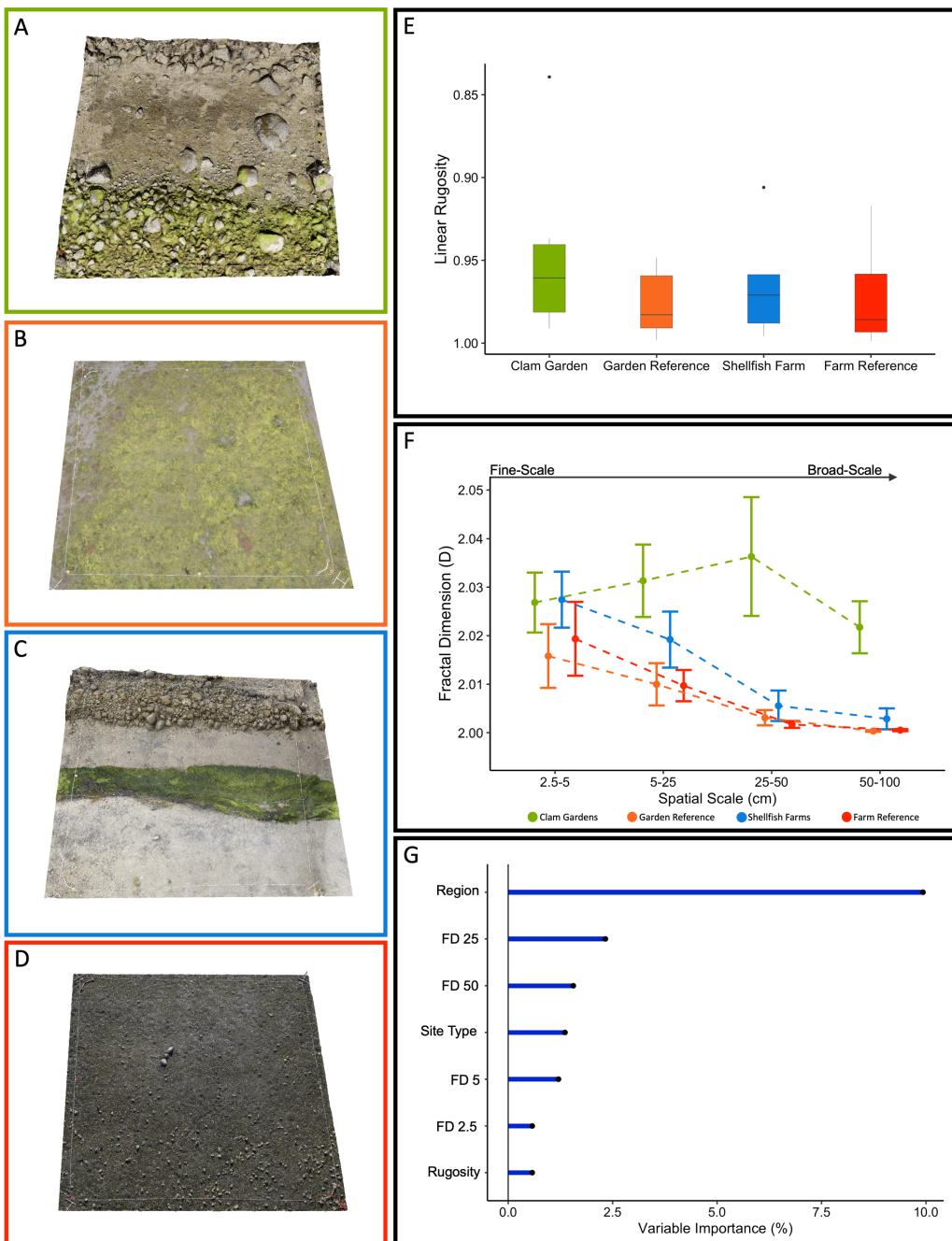
545 **Habitat Complexity-Epifaunal Community Associations**

546 Analyzing three-dimensional reconstructions of the 24 sites quantified multiple aspects of
547 each site's structural complexity and determined the importance of habitat structure for the
548 resident epifaunal communities (Figure 5). The reconstructions were more similar within than
549 among site types, although considerable variability was evident within each site type (Figure S9).
550 Linear rugosity was elevated within clam gardens and shellfish farms relative to the
551 corresponding reference sites, with clam gardens exhibiting the most rugged substrate (Figure
552 5E, Figure S10). Fractal dimension (D) among the site types exhibited a similar trend as linear
553 rugosity; complexity was elevated within clam gardens and shellfish farms (Figure 5F, Figure
554 S10). These increases in complexity were more prominent within clam gardens than shellfish
555 farms. Unmodified garden and farm reference sites had similar levels of complexity (Figure 5F).
556 Within each site type, most of the site's D complexity was highest at fine-scale resolutions and
557 declined with increasing resolution (Figure 5F). Clam gardens deviated from this trend the most
558 as 5-25 and 25-50 cm resolutions exhibited the highest complexity of the four spatial scales
559 considered.

560 The MRF variable importance analysis determined that of the complexity metrics
561 considered, D 25-50, D 50-100, and D 5-25 cm had the most notable impact on epifaunal
562 community structure (Figure 5G). However, variable order differed considerably for each taxon
563 (Figure S11), illuminating the unique combination of structural metrics that support each group.
564 Similarly, the variability explained by the MRF model and the model's predictive accuracy also

565 varied among taxa (Table S8). Model quality was strongly linked with population abundance,
566 whereby the MRF model explained more variability for taxa consistently observed across most
567 sites or exhibited a high degree of site type fidelity. Generally, high-quality models generated the
568 most accurate predictions. The MRF model was able to explain up to 39% of the variability in
569 taxonomic abundance and was relatively robust in predicting Decapoda, Batillariidae, Venerida,
570 and Cerithiidae (Table S8).

571



572
573
574
575
576
577
578
579
580
581

Figure 5| Habitat complexity analysis and the association between epifaunal communities and three-dimensional complexity. (A-D) Example three-dimensional reconstructions of the site types: (A) clam garden, (B) garden reference, (C) shellfish farm, (D) farm reference. (E) Site type's mean linear rugosity. (F) Fractal dimension of each site type at four spatial resolutions. Bar plots are of mean and standard error values. (G) Multivariate random forest (MRF) variable importance analyses. The relative importance of the predictor variables for epifaunal communities is scaled by decreases in the mean squared error of the model when the variable is permuted; higher bars equate to greater importance. Fractal dimension value and spatial resolutions are denoted as FD and respective cell size (e.g., FD 25 is the spatial scale 25-50 cm).

582

583 **Discussion**

584 We add to the growing body of evidence that the coastal ecosystems of the northeast
585 Pacific are shaped by intertidal resource cultivation practices engineered and implemented over
586 decades, centuries, and millennia. Evidence that contemporary ecological communities are a
587 function of human-ecosystem interactions is becoming increasingly vital to global conservation
588 efforts^{12,48,49}. Our examination demonstrates that clam gardens and shellfish farms restructure
589 epifaunal communities at several ecological (e.g., populations, communities) and spatial scales,
590 with community responses proportional to how each cultivation practice alters the habitat. This
591 work supports the supposition that traditional and contemporary intertidal resource cultivation
592 practices create distinct nearshore communities^{9,17,18,50}.

593 Shellfish cultivation alters the diversity and composition of intertidal epifaunal
594 communities, with clam gardens and shellfish farms producing distinct communities relative to
595 reference beaches. Several taxa, namely *Balanus glandula*, *Chthamalus dalli*, *Lottia persona*,
596 and *Littorina sitkana*, exhibited similar increases in abundance in response to both cultivation
597 methods. Conversely, numerous taxonomic responses were divergent. Convergent and divergent
598 responses were linked to the unique conditions created by each cultivation practice. Notably,
599 altered tidal heights within clam gardens are known to increase bivalve productivity^{18,30}, and
600 conceivably promote the proliferation of certain species. Altered tidal heights likely also exclude
601 taxa that occupy intertidal zones that are above or below optimal clam habitat (e.g., *Mytilus* spp.)
602 or occur within a habitat that would otherwise occupy the area (e.g., rocky intertidal). Clam
603 gardens further promote unique intertidal communities through the emergence of two substrate
604 compositions: elevated amounts of gravel and either abundant bivalve shells or growth of

605 macroalgae (e.g., *Ulva* spp.)^{18,21,23,28}. Although our analysis determined that bivalve shells and
606 macroalgae growth support diverse communities, bivalve shells are known to be more
607 ecologically beneficial than macroalgae. Specifically, the oral history of coastal Indigenous
608 Peoples, communicated by Kwakwaka'wakw Clan Chief Kwaxistalla Wathl'thla Adam Dick in
609 Deur *et al.*¹⁶, states that garden tending practices involve seaweed removal from the beach
610 surface and aerating the sediments through clam digging and increasing the density of shell
611 fragments^{21,22}. The MRT and MRF analyses reinforce this knowledge by illustrating that the
612 combination of 45-60% gravel and less than 31% bivalve shells promotes the most biologically
613 diverse communities observed within clam gardens.

614 Within shellfish farms, *Mastocarpus* spp., a common seaweed that grows on predator-
615 exclusion nets, fostered diverse communities that varied depending on the amount of gravel,
616 mud, and silt present. The role of sediment in this relationship is well-established. Broadly,
617 species diversity and density correlate positively with mud and silt percentages until increases in
618 fine-grain sediments facilitate oxygen depletion, resulting in toxic by-product accumulation and
619 organic loading that cause diversity to decline⁵¹. Therefore, under optimal conditions, increased
620 niche space provided by *Mastocarpus* spp. elevates biological diversity beyond the capacity of
621 reference beaches. Optimal conditions conceivably persist until density-dependent effects or
622 reduced water flow increase organic loading^{7,33,52}.

623 Elevated taxonomic richness within clam gardens relative to shellfish farms may be due
624 to the increased structural complexity observed at several spatial scales. Clam garden
625 construction can involve considerable foreshore modifications, including the input of large
626 cobbles and boulders to establish rock walls that alter the beach slope, increase sedimentation
627 rates, and stabilize shorelines^{23,28}. These cobble and boulders inputs are within the 25-50 and 50-

628 100 cm spatial scales that coincide with the observed increased complexity. The intertidal rock
629 wall and associated soft-sediment terrace are then managed for generations and adapted to meet
630 changing environmental conditions and community requirements ^{11,16,22}. Enhanced habitat
631 complexity and ongoing management interact to transform substrate composition by increasing
632 bivalve shells and gravel while removing excess algal growth. This process can transform a
633 range of intertidal habitats into clam gardens, including bedrock, otherwise lacking an
634 established clam population ²³. Alternatively, shellfish farming, a practice that began more
635 recently, usually occurs on beaches with existing bivalve populations and involves the addition
636 of predator exclusion nets, cages, and other low-lying structures into which shellfish broodstock
637 and juvenile non-native shellfish seeds are introduced ^{32,34}. Therefore, shellfish farming involves
638 comparatively fewer structural inputs within the 25-50 and 50-100 cm spatial scales, cultivation
639 occurs across a less dynamic range of intertidal habitats, and habitat alternations are limited to
640 recent decades.

641 Distinct physical features and biological communities within clam gardens and shellfish
642 farms benefit these ecosystems. Increases in habitat complexity provide available niche space,
643 offering refuge from adverse conditions and a range of exploitable resources ⁵³. The interaction
644 between increased complexity and altered substrate composition likely produces more
645 heterogeneous habitats. Specifically, structural inputs associated with clam garden or shellfish
646 farm construction and maintenance directly influence substrate composition (*e.g.*, abundance of
647 boulders, cobble, and soft sediments) but also occur independently of management practices that
648 alter the substrate (*e.g.*, seaweed removal, added shell). Therefore, the taxa residing within these
649 ecosystems respond to structural inputs, modified substrates, or the resulting habitat
650 heterogeneity. The extent to which clam gardens and shellfish farms benefit from this process

651 varies by cultivation method. Broadly, enhanced habitat complexity and altered substrate
652 composition prompted proportional responses within biological communities. These increases in
653 diversity and abundance suggest that the communities within clam gardens and shellfish farms
654 exhibit more functional redundancy and ecological resilience than their respective reference
655 beaches⁵⁴. Consequently, these communities may have an increased capacity to resist and
656 recover from disturbances, which increases the probability that these ecosystems maintain their
657 function (*i.e.*, bivalve production) despite increases in the severity and frequency of perturbations
658^{54,55}.

659 Ecological communities generally responded proportionally to cultivation intensity.
660 However, the prevalence of regional stressors may alter the magnitude of diversity responses.
661 For example, taxonomic richness was elevated at clam gardens on Calvert Island and shellfish
662 farms within Baynes Sound relative to the reference and cultivated beaches surrounding Quadra
663 Island. Calvert Island's nearshore ecosystems are less influenced by anthropogenic activities,
664 with minimal shoreline modifications, overwater structures, and industrial logging relative to
665 more southern regions^{56,57}. This difference suggests that the comparatively weaker ecological
666 responses within the Quadra Island sites may be due to anthropogenic stressors, specifically
667 industrial logging¹⁷. Conversely, the scale and magnitude of shellfish farming within Baynes
668 Sound surpasses northern counterparts, creating a novel ecosystem that maximizes ecological
669 responses to cultivation^{7,34,52}.

670 A considerable portion of the examinations of aquaculture focus on environmental
671 degradation, mismanaged introduced species, and declining ecosystem health^{7,52,58}. Shellfish
672 cultivation, however, is unique relative to finfish aquaculture in that shellfish require fewer
673 nutrient inputs, occupy a lower trophic position, and introduce fewer infectious agents⁵². These

674 characteristics may explain, in part, why ecological responses to shellfish cultivation persist
675 despite variability in frequency and intensity of management. Ecological responses may lessen
676 over time, but limited feed inputs or broodstock maintenance allows niche alterations attributed
677 to construction to persist. This is a particularly evident situation within clam gardens as the
678 primary cultivation species, *Saxidomus gigantea* and *Leukoma staminea*, occupy surrounding
679 habitats, allowing broadcast spawn to continue to seed beaches^{18,30,50}. Ecological responses to
680 shellfish cultivation may cause less degradation than other aquaculture systems, but
681 environmental impacts still occur. *Batillaria attramentaria*, introduced into the northeast Pacific
682 as early as 1928 alongside *M. gigas*⁵⁹, exhibits a 2-fold increase within reference sites.
683 Proliferation adjacent to the introduction site implies an invasion model in which the vector
684 distributes the invader into a suboptimal habitat. The introduced taxa then flourish once they
685 reach a more suitable habitat, in this instance, nearby mudflats. Functionally, this implies
686 invasive species management requires surveying beyond the site of introduction and that
687 numerous introduced taxa may be moving towards habitats that will support proliferation. Still,
688 biological communities' responses to shellfish farming and clam gardening indicate that of the
689 existing approaches to harvesting marine resources, shellfish cultivation represents a sustainable
690 balance between human-ecosystem interactions capable of providing access to protein for
691 millennia.

692 A series of local and global stressors threaten the cultivation of intertidal resources, many
693 of which have become increasingly predominant in recent decades. Warming ocean
694 temperatures, rising sea levels, increasing acidity, and lack of societal engagement in food
695 security threaten shellfish aquaculture^{34,58}. Humanity's ability to mitigate these ecological
696 challenges will improve significantly if Indigenous knowledge is at the forefront of management

697 plans^{11,12,34,48}. As exemplified by clam gardens and other Indigenous management systems,
698 traditional mariculture practices can be sustainable for millennia and withstand adapting to
699 changing climatic conditions^{17,21,60}. Therefore, the knowledge necessary to endure pending
700 disasters has been well-established by coastal Peoples. The cultural, economic, and
701 environmental knowledge developed during 3,800 years of clam garden construction and
702 management and the lessons gained over the last 200 years of shellfish farming pose an
703 opportunity to enhance local food security and mitigate environmental challenges^{17,18,24}. This
704 process is ongoing throughout the northeast Pacific, led by Indigenous shellfish farm ownership,
705 Nation-directed clam garden restoration projects, and the expansion of commercial shellfish
706 farming^{2,21,32,34}. For example, the Clam Garden Restoration project led by the Hul'q'umi'num
707 and WSÁNEĆ Nations, in partnership with Parks Canada, has restored gardens within the Gulf
708 Islands National Park Reserve using traditional practices guided by Elders and knowledge
709 holders^{20,21,61}. Our findings support the notion that these restoration and cultivation efforts
710 restore bivalve populations while creating biologically diverse seascapes that are evident at
711 several ecological and spatial scales.

712

713 **Conclusions**

714 Scientific evidence that the robust and dynamic history of human-ecosystem interactions
715 structures ecological communities is mounting^{9,17,19,62}. A fact well-known by many coastal First
716 Peoples, these interactions are not limited to the ecological communities and cultivation methods
717 described here, as fish weirs, root gardens, forest gardens, landscape terracing, and shellfish
718 cultivation are spatially and temporally abundant throughout the northeast Pacific^{9,11,14,29}. Here,
719 we show that intertidal resource management practices engineered and implemented over

720 decades, centuries, and millennia structure contemporary intertidal ecosystems. We propose that
721 the addition of habitat structural complexity and alterations to substrate composition that occur
722 as part of clam garden or shellfish farm construction and maintenance provide the increases in
723 available niche space required to foster distinct and diverse biological communities. Ecological
724 responses can be maintained with continual harvesting and management, elevated through
725 further intervention (*e.g.*, introducing broodstock, excluding predators), and may persist even if
726 reductions in management intensity occur. Understanding the robust history of enduring
727 intertidal resource cultivation practices is vital to facilitating resource management and
728 conservation strategies that can contribute to achieving balanced human-ecosystem interactions.
729 Shellfish cultivation exemplifies practices that can address diminishing marine resources and
730 declining marine biodiversity while achieving local and global food security.

731

732 **Acknowledgments**

733 The acknowledgments have been removed to support double-anonymized peer review
734 and will be included if the manuscript is accepted for publication.

735

736 **Author Contributions**

737 Author contributions have been removed to support double-anonymized peer review and
738 will be included if the manuscript is accepted for publication.

739

740 **Conflict of Interest**

741 The authors declare no competing interests.

742

743 **References**

- 744 1. Boivin, N. L. *et al.* Ecological consequences of human niche construction: Examining long-
745 term anthropogenic shaping of global species distributions. *Proc. Natl. Acad. Sci.* **113**, 6388–
746 6396 (2016).
- 747 2. Reeder-Myers, L. *et al.* Indigenous oyster fisheries persisted for millennia and should inform
748 future management. *Nat. Commun.* **13**, 2383 (2022).
- 749 3. Smale, D. A. *et al.* Marine heatwaves threaten global biodiversity and the provision of
750 ecosystem services. *Nat. Clim. Change* **9**, 306–312 (2019).
- 751 4. Bugnot, A. B. *et al.* Current and projected global extent of marine built structures. *Nat.*
752 *Sustain.* **4**, 33–41 (2021).
- 753 5. FAO. *The State of World Fisheries and Aquaculture 2020*.
754 <http://www.fao.org/documents/card/en/c/ca9229en> (2020) doi:10.4060/ca9229en.
- 755 6. Naylor, R. L. *et al.* A 20-year retrospective review of global aquaculture. *Nature* **591**, 551–
756 563 (2021).
- 757 7. Barrett, L. T., Swearer, S. E. & Dempster, T. Impacts of marine and freshwater aquaculture
758 on wildlife: a global meta-analysis. *Rev. Aquac.* **11**, 1022–1044 (2019).
- 759 8. van der Schatte Olivier, A. *et al.* A global review of the ecosystem services provided by
760 bivalve aquaculture. *Rev. Aquac.* 1–23 (2018) doi:10.1111/raq.12301.
- 761 9. Trant, A. J. *et al.* Intertidal resource use over millennia enhances forest productivity. *Nat.*
762 *Commun.* **7**, 12491 (2016).
- 763 10. Sullivan, A. P., Bird, D. W. & Perry, G. H. Human behaviour as a long-term ecological
764 driver of non-human evolution. *Nat. Ecol. Evol.* **1**, 0065 (2017).

- 765 11. Turner, N. J. From “taking” to “tending”: learning about Indigenous land and resource
766 management on the Pacific Northwest Coast of North America. *ICES J. Mar. Sci.* **77**, 2472–
767 2482 (2020).
- 768 12. Reid, A. J. *et al.* “Two-Eyed Seeing”: An Indigenous framework to transform fisheries
769 research and management. *Fish Fish.* **22**, 243–261 (2021).
- 770 13. Lepofsky, D. & Lertzman, K. Documenting ancient plant management in the northwest of
771 North America. *Botany* **86**, 129–145 (2008).
- 772 14. Armstrong, C. G., Earnshaw, J. & McAlvay, A. C. Coupled archaeological and ecological
773 analyses reveal ancient cultivation and land use in Nuchatlaht (Nuu-chah-nulth) territories,
774 Pacific Northwest. *J. Archaeol. Sci.* **143**, 105611 (2022).
- 775 15. Hoffman, K. M., Lertzman, K. P. & Starzomski, B. M. Ecological legacies of anthropogenic
776 burning in a British Columbia coastal temperate rain forest. *J. Biogeogr.* **44**, 2903–2915
777 (2017).
- 778 16. Deur, D., Dick, A., Recalma-Clutesi, K. & Turner, N. J. Kwakwaka’wakw “Clam Gardens”:
779 Motive and Agency in Traditional Northwest Coast Mariculture. *Hum. Ecol.* **43**, 201–212
780 (2015).
- 781 17. Toniello, G., Lepofsky, D., Lertzman-Lepofsky, G., Salomon, A. K. & Rowell, K. 11,500 y
782 of human–clam relationships provide long-term context for intertidal management in the
783 Salish Sea, British Columbia. *Proc. Natl. Acad. Sci.* **116**, 22106–22114 (2019).
- 784 18. Groesbeck, A. S., Rowell, K., Lepofsky, D. & Salomon, A. K. Ancient Clam Gardens
785 Increased Shellfish Production: Adaptive Strategies from the Past Can Inform Food Security
786 Today. *PLoS ONE* **9**, e91235 (2014).

- 787 19. Schang, K., Cox, K. & Trant, A. J. Habitation Sites Influence Tree Community Assemblages
788 in the Great Bear Rainforest, British Columbia, Canada. *Front. Ecol. Evol.* **9**, 791047 (2022).
- 789 20. Augustine, S. & Dearden, P. Changing paradigms in marine and coastal conservation: A case
790 study of clam gardens in the Southern Gulf Islands, Canada: A values-based approach to
791 coastal conservation. *Can. Geogr. Géographe Can.* **58**, 305–314 (2014).
- 792 21. H-GINPR. *Stutul’na’mut Report: Caring for our Beaches*. 1–15 (2016).
- 793 22. Lepofsky, D. *et al.* Ancient Shellfish Mariculture on the Northwest Coast of North America.
794 *Am. Antiq.* **80**, 236–259 (2015).
- 795 23. Smith, N. F. *et al.* 3500 years of shellfish mariculture on the Northwest Coast of North
796 America. *PLOS ONE* **14**, e0211194 (2019).
- 797 24. Holmes, K., Lepofsky, D., Smith, N. F., Crowell, T. D. & Salomon, A. K. Ancestral sea
798 gardens supported human settlements for at least 3,800 years on the Northwest Coast of
799 North America. *Front. Earth Sci.* **10**, 988111 (2022).
- 800 25. Harper, J. R., Haggarty, J. & Morris, M. *Broughton Archipelago Clam Terrace Survey*. 1–39
801 (1995).
- 802 26. Holmes, K. *et al.* Ancient Ecology: The Quadra Island Clam Gardens. *Fisheries* **45**, 151–156
803 (2020).
- 804 27. Stern, B. *The Lummi Indians of Northwest Washington*. (Columbia University Press, 1934).
- 805 28. Neudorf, C. M., Smith, N., Lepofsky, D., Toniello, G. & Lian, O. B. Between a rock and a
806 soft place: Using optical ages to date ancient clam gardens on the Pacific Northwest. *PLOS
807 ONE* **12**, e0171775 (2017).
- 808 29. Lepofsky, D. *et al.* Ancient Anthropogenic Clam Gardens of the Northwest Coast Expand
809 Clam Habitat. *Ecosystems* **24**, 248–260 (2021).

- 810 30. Jackley, J., Gardner, L., Djunaedi, A. F. & Salomon, A. K. Ancient clam gardens, traditional
811 management portfolios, and the resilience of coupled human-ocean systems. *Ecol. Soc.* **21**,
812 (2016).
- 813 31. White, J., Ruesink, J. L. & Trimble, A. C. The Nearly Forgotten Oyster: *Ostrea lurida*
814 Carpenter 1864 (Olympia Oyster) History and Management in Washington State. *J. Shellfish
815 Res.* **28**, 43–49 (2009).
- 816 32. Silver, J. J. Shellfish and coastal change: Pacific oysters and Manila clams in BC waters. *BC
817 Stud. Br. Columbian Q.* 83–103 (2014).
- 818 33. Munroe, D. & McKinley, R. S. Commercial Manila clam (*Tapes philippinarum*) culture in
819 British Columbia, Canada: The effects of predator netting on intertidal sediment
820 characteristics. *Estuar. Coast. Shelf Sci.* **72**, 319–328 (2007).
- 821 34. Holden, J. J. *et al.* Synergies on the coast: Challenges facing shellfish aquaculture
822 development on the central and north coast of British Columbia. *Mar. Policy* **101**, 108–117
823 (2019).
- 824 35. Cox, K. D. *et al.* Community assessment techniques and the implications for rarefaction and
825 extrapolation with Hill numbers. *Ecol. Evol.* **7**, 11213–11226 (2017).
- 826 36. Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. NIH Image to ImageJ: 25 years of image
827 analysis. *Nat. Methods* **9**, 671–675 (2012).
- 828 37. Bayley, D. T. I. & Mogg, A. O. M. A protocol for the large-scale analysis of reefs using
829 Structure from Motion photogrammetry. *Methods Ecol. Evol.* **11**, 1410–1420 (2020).
- 830 38. Burns, J., Delparte, D., Gates, R. & Takabayashi, M. Integrating structure-from-motion
831 photogrammetry with geospatial software as a novel technique for quantifying 3D ecological
832 characteristics of coral reefs. *PeerJ* **3**, e1077 (2015).

- 833 39. Young, G. C., Dey, S., Rogers, A. D. & Exton, D. Cost and time-effective method for multi-
834 scale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D
835 models. *PLOS ONE* **12**, e0175341 (2017).
- 836 40. R Core Team. R: A language and environment for statistical computing. (2019).
- 837 41. De'ath, G. Package 'mvpard'. (2014).
- 838 42. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag New York,
839 2016).
- 840 43. Oksanen, J. *et al.* *vegan: Community Ecology Package*. vol. R package version 2.5-6 (2019).
- 841 44. Ishwaran, H., Kogalur, U. & Kogalur, M. Package 'randomForestSRC'. (2021).
- 842 45. Chao, A., Chiu, C.-H. & Jost, L. Unifying Species Diversity, Phylogenetic Diversity,
843 Functional Diversity, and Related Similarity and Differentiation Measures Through Hill
844 Numbers. *Annu. Rev. Ecol. Evol. Syst.* **45**, 297–324 (2014).
- 845 46. Anderson, M. J., Gorley, R. N. & Clarke, K. R. *PERMANOVA+ for PRIMER: Guide to*
846 *Software and Statistical Methods*. 218 (2008).
- 847 47. Segal, M. & Xiao, Y. Multivariate random forests. *WIREs Data Min. Knowl. Discov.* **1**, 80–
848 87 (2011).
- 849 48. Artelle, K. A. *et al.* Supporting resurgent Indigenous-led governance: A nascent mechanism
850 for just and effective conservation. *Biol. Conserv.* **240**, 108284 (2019).
- 851 49. Diggon, S. *et al.* The Marine Plan Partnership: Indigenous community-based marine spatial
852 planning. *Mar. Policy* **132**, 103510 (2021).
- 853 50. Cox, K. D. *et al.* Infaunal community responses to ancient clam gardens. *ICES J. Mar. Sci.*
854 **76**, 2362–2373 (2019).

- 855 51. Hyland, J. *et al.* Organic carbon content of sediments as an indicator of stress in the marine
856 benthos. *Mar. Ecol. Prog. Ser.* **295**, 91–103 (2005).
- 857 52. Callier, M. D. *et al.* Attraction and repulsion of mobile wild organisms to finfish and
858 shellfish aquaculture: a review. *Rev. Aquac.* **10**, 924–949 (2018).
- 859 53. Stein, A., Gerstner, K. & Kreft, H. Environmental heterogeneity as a universal driver of
860 species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **17**, 866–880 (2014).
- 861 54. Biggs, C. R. *et al.* Does functional redundancy affect ecological stability and resilience? A
862 review and meta-analysis. *Ecosphere* **11**, (2020).
- 863 55. Bernhardt, J. R. & Leslie, H. M. Resilience to Climate Change in Coastal Marine
864 Ecosystems. *Annu. Rev. Mar. Sci.* **5**, 371–392 (2013).
- 865 56. Iacarella, J. C. *et al.* Anthropogenic disturbance homogenizes seagrass fish communities.
866 *Glob. Change Biol.* **24**, 1904–1918 (2018).
- 867 57. Shackelford, N., Standish, R. J., Ripple, W. & Starzomski, B. M. Threats to biodiversity
868 from cumulative human impacts in one of North America’s last wildlife frontiers. *Conserv.*
869 *Biol.* **32**, 672–684 (2018).
- 870 58. Murray, G. & D’Anna, L. Seeing shellfish from the seashore: The importance of values and
871 place in perceptions of aquaculture and marine social–ecological system interactions. *Mar.*
872 *Policy* **62**, 125–133 (2015).
- 873 59. Gillespie, G. Distribution of non-indigenous intertidal species on the Pacific Coast of
874 Canada. *Nippon Suidan Gakkaishi* **73**, 1133–1137 (2007).
- 875 60. Pacific Sea Garden Collective. Sea Gardens Across the Pacific: Reawakening Ancestral
876 Mariculture Innovations. Version 1. Washington Sea Grant at the University of Washington.
877 doi.org/10.6069/ZJB9-CG30 (2022).

- 878 61. Wickham, S. *et al.* Incorporating place-based values into ecological restoration. *Ecol. Soc.*
879 **27**, art32 (2022).
- 880 62. Cox, K. D. *et al.* Shellfish subsidies along the Pacific coast of North America. *Ecography* **43**,
881 668–681 (2020).
- 882
883
884
885
886
887
888
889
890
891
892
893
894
895
896
897
898
899
900
901
902
903
904
905
906
907

908 **Supporting Information For**

909 **Title:** Ancestral and Contemporary Intertidal Mariculture Structures Marine Biodiversity.

910

911 **This PDF file includes:**

912 Supplemental Text

913 Figures S1-S11

914 Tables S1-S8

915

916

917 **Supplemental Text**

918 **Intertidal Habitat Complexity**

919 *Survey region*

920 The structural characteristics of the 24 clam gardens, shellfish farms, and reference
921 beaches were quantified using structure-from-motion (SfM) photogrammetry in 2017. This
922 method generates high-resolution georeferenced 3D reconstructions of the physical environments
923 using 2D images¹. A 10 × 10 m assessment area was established at each site, with the top
924 corners at the 2.2 m tideline (Figure S3). This assessment location was within the mid intertidal
925 region, where most of the biodiversity surveys occurred. An elevated guideline was estimated
926 along each assessment area's perimeter to ensure the camera was held at a constant height. The
927 spatial location of ground control points (GCPs) placed at the corners and midpoints of the area
928 were recorded using GPS coordinates (Fig S3).

929

930 *Image acquisition*

931 Image acquisition used a Canon SL1 digital SLR camera with a 10–18 mm lens. The
932 camera was set to a focal length of 18 mm, a shutter speed above 1/100, an aperture of f/8-11 and

933 ISO as low as environmental conditions would allow. The 100 m² survey areas were
934 photographed until the entire area had been adequately covered ¹. Photographs were taken
935 continuously in a boustrophedonic pattern while holding the camera ~2 m above the substrate
936 (Figure S3). After completing this pattern, subsequent photos were taken from around the survey
937 area, aiming the camera at various acute angles relative to the substrate features. Between 440
938 and 2,030 images were captured depending on the complexity of the assessment area.

939

940 *3D habitat model generation*

941 Three-dimensional reconstructions of the 24 sites were generated using Agisoft
942 Metashape Standard Edition (v1.7.4). Model generation and subsequent analyses were completed
943 using a Dell Alienware Aurora R8 Desktop with 64GB RAM, an NVIDIA GeForce GTX 1070
944 Ti graphics card, and an Intel Core i7 8700 processor. Model generation followed the steps
945 outlined in Agisoft Metashape, further clarified in ² and ³. The four key stages were: aligning
946 photos, dense point cloud construction, mesh construction, and building texture (Figure S4A).

947 Rendering three-dimensional reconstructions of the 24 sites followed the workflow
948 developed by Agisoft Metashape and modified for ecological applications by Burns *et al.* ⁴,
949 Young *et al.* ² and Bayley and Mogg ³. The four key stages were: aligning photos, dense point
950 cloud construction, mesh construction, and building texture (Supplemental Figure S4). Prior to
951 photo alignment, images were reviewed in Metashape following a two-stage process to ensure a
952 minimum standard was met prior to the reconstruction process. First, survey images were
953 manually screened to remove poor quality images (*e.g.*, blurry, obstructions, dark). Metashape's
954 "Image Quality" was then used to exclude images with a quality value of less than 0.65.
955 Although exclusion of quality values of less than 0.5 is generally recommended, it became

956 evident that a higher quality standard is beneficial when modelling habitats with minute details
957 of interest.

958 Photo alignment produces a sparse 3D point cloud using the projections from the
959 different image orientations. The model's photo alignment deviated from the default settings,
960 using the highest accuracy, a key point limit of 0, and a tie point limit of 10,000. These settings
961 allowed Metashape to identify as many key points as possible within each image and for every
962 image to have an upper limit of 10,000 matching points. The tie points generated between
963 images allow them to be aligned and camera position estimated. This is done by algorithmic
964 detection of invariant features in multiple images, creating a geometrical projective matrix to
965 determine the camera's position and orientation¹. Ground control points (GCPs) were used to
966 create a local coordinate system for effective scaling and alignment of the point cloud, allowing
967 photos that failed to align correctly to be reset and aligned manually⁴. Sparse clouds were
968 trimmed considerably using Metashape's 'gradual selection' feature. Generally, reconstruction
969 uncertainty and projection accuracy were set to 10, and reproduction error was reduced by ~40%
970 of the initial value, which varied considerably across models. This feature had a substantial
971 influence on the resulting model quality. Cumulatively, photo alignment took several hours,
972 primarily due to the time required to realign photos.

973 Dense point cloud construction, mesh construction and texturing occurred in consecutive
974 order with setting defined to improve resulting model quality. Dense point cloud construction is
975 based on the triangulation of the tie points to identify pixels found in overlapping photos. The
976 cloud construction settings were high quality and mild depth filtering. Constructing each model's
977 dense cloud took between 5-10 minutes to generate the depth map and 20-40 minutes to create
978 the density cloud. Mesh construction interpolates surface areas surrounding points in the dense

979 point cloud. Mesh construction used a maximum number of polygons in the final mesh (face
980 count) as 10,000,000, with interpolation enabled and an arbitrary surface to account for variable
981 habitat types. Mesh construction took between 10-20 minutes. Texturing overlays the texture and
982 color of the original photos onto the mesh, with a 16,384-texture size and blending mosaic mode,
983 a process that, generally, took 10 minutes to complete. The rendered 3D models of each of the 24
984 sites were exported as wavefront files for further analysis.

985

986 *Quantification of spatial properties*

987 The habitat models were analyzed using Rhinoceros 3D (v7), a commercial 3D computer
988 graphics program developed for surface modelling. The structural metrics explored were rugosity
989 and fractal dimension (D). The habitat models were scaled using Rhinoceros ‘scale’ function and
990 the four 0.42 m scale bars within each model.

991 Rugosity (R) is measured using an extendible chain method to measure the topographic
992 distance covered by a theoretical straight-line distance. Consequently, linear R measurements are
993 between 1 and 0, with lower values denoting more complex surfaces. To avoid confusion, R was
994 considered on an inverted scale (*i.e.*, 0-1), to allow increases in R to reflect increases in
995 complexity. Triplicate 9-m linear R measurements were taken in both directions (6 total) using a
996 virtual chain with a 2 cm link length (Figure S4B). Measurements were taken using a custom
997 Python script adapted from Young *et al.*², allowing consistent application of the chains across
998 models. The mean linear R for each site was determined by averaging the six measurements.

999 Fractal dimension (D) measures how surface area changes with resolution by quantifying
1000 the slope of a model’s resolution relative to the surface area on a logarithmic scale (*i.e.*, how
1001 complexity varies with scale). Customizable dimensions allow for the consideration of different

1002 sizes. Dimensions can be selected based on species sizes, unique habitat characteristics, or a
1003 measure of complexity given multiple size categories. Measurements of D are between 2 and 3,
1004 with higher values signifying increased surface heterogeneity. Fractal dimension was measured
1005 at four spatial resolutions, 2.5-5, 5-25, 25-50, and 50-100 cm; effectively, this measures the
1006 complexity within these size ranges. Five D measurements at the four spatial resolutions were
1007 taken for each model, one at each corner and in the middle (Figure S4C). These measurements
1008 were averaged to determine mean D at the four spatial resolutions.

1009

1010 **Supplemental References**

- 1011 1. Westoby, M. J., Brasington, J., Glasser, N. F., Hambrey, M. J. & Reynolds, J. M. ‘Structure-
1012 from-Motion’ photogrammetry: A low-cost, effective tool for geoscience applications.
1013 *Geomorphology* **179**, 300–314 (2012).
- 1014 2. Young, G. C., Dey, S., Rogers, A. D. & Exton, D. Cost and time-effective method for multi-
1015 scale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D
1016 models. *PLOS ONE* **12**, e0175341 (2017).
- 1017 3. Bayley, D. T. I. & Mogg, A. O. M. A protocol for the large-scale analysis of reefs using
1018 Structure from Motion photogrammetry. *Methods Ecol. Evol.* **11**, 1410–1420 (2020).
- 1019 4. Burns, J., Delparte, D., Gates, R. & Takabayashi, M. Integrating structure-from-motion
1020 photogrammetry with geospatial software as a novel technique for quantifying 3D ecological
1021 characteristics of coral reefs. *PeerJ* **3**, e1077 (2015).

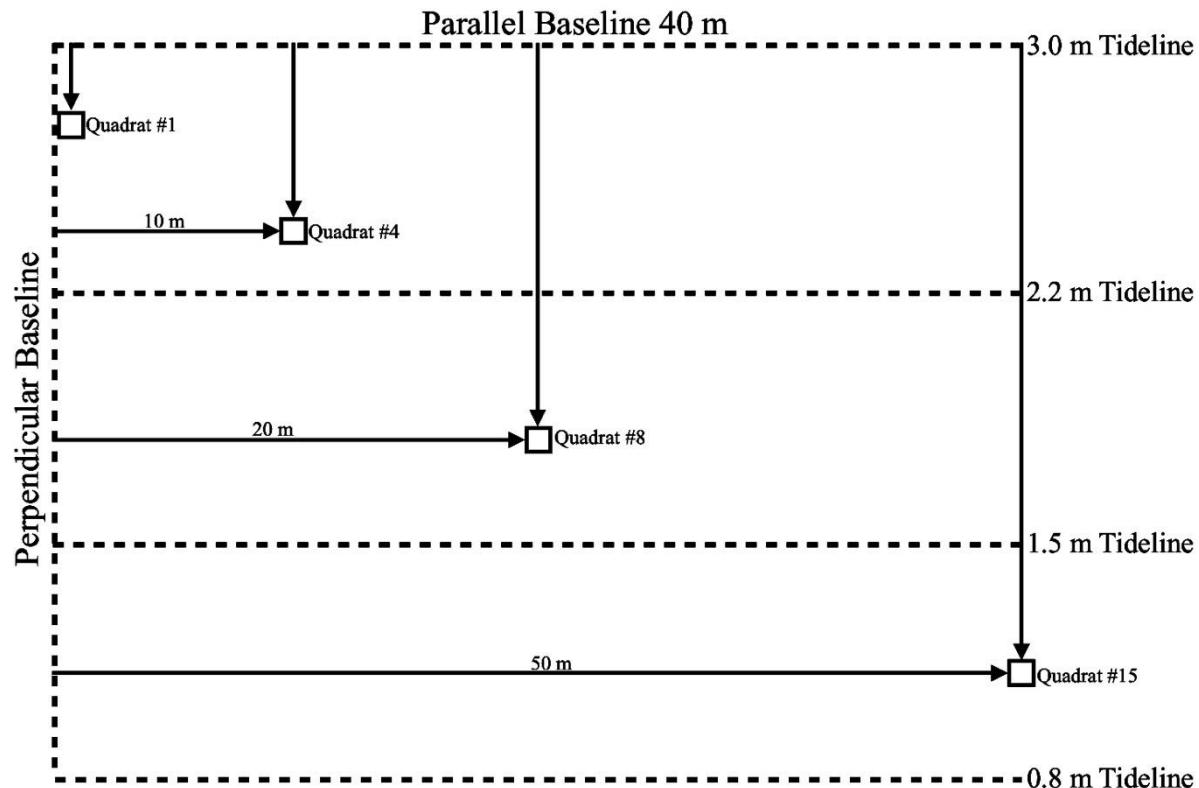
1022

1023

1024

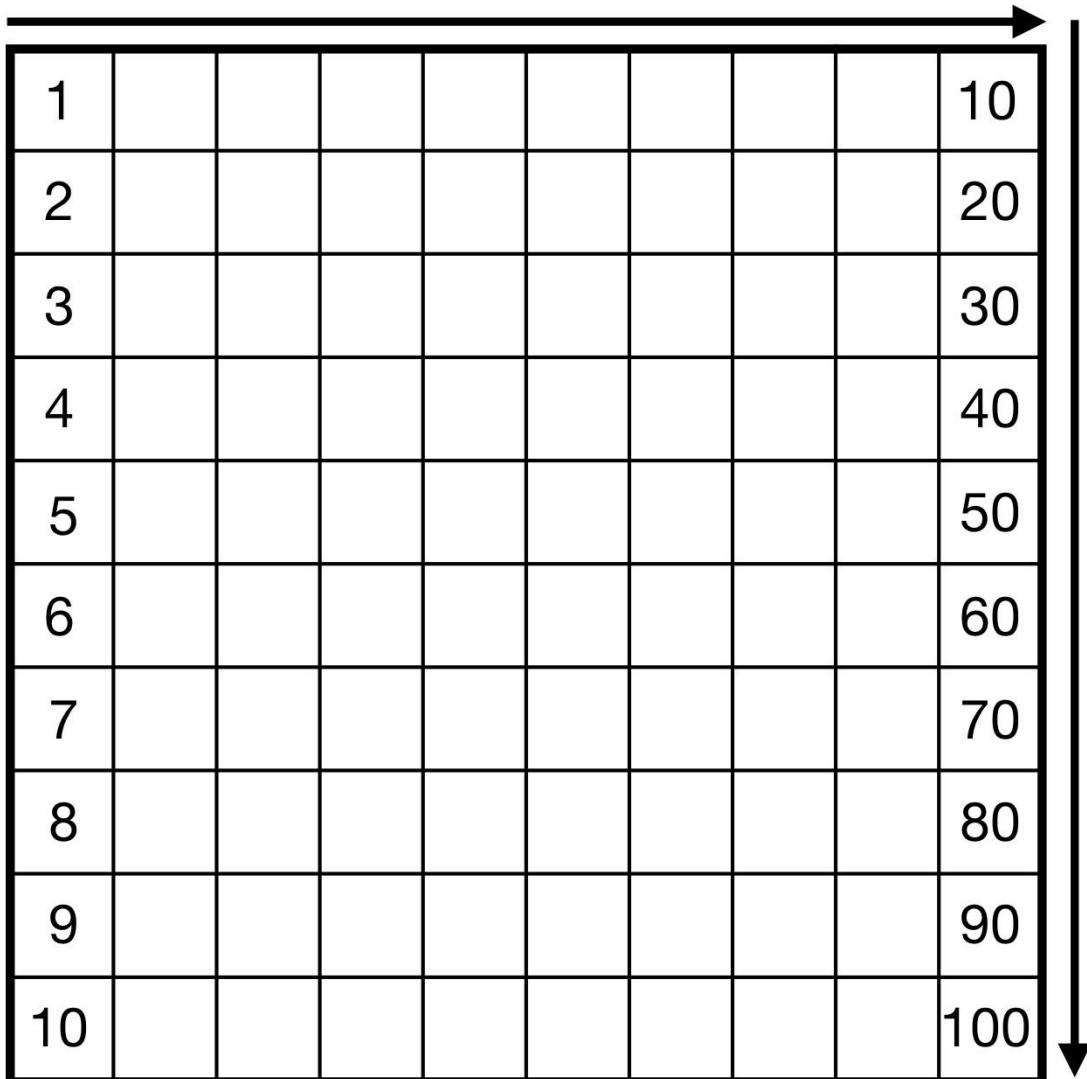
1025 **Supplemental Figures**

1026



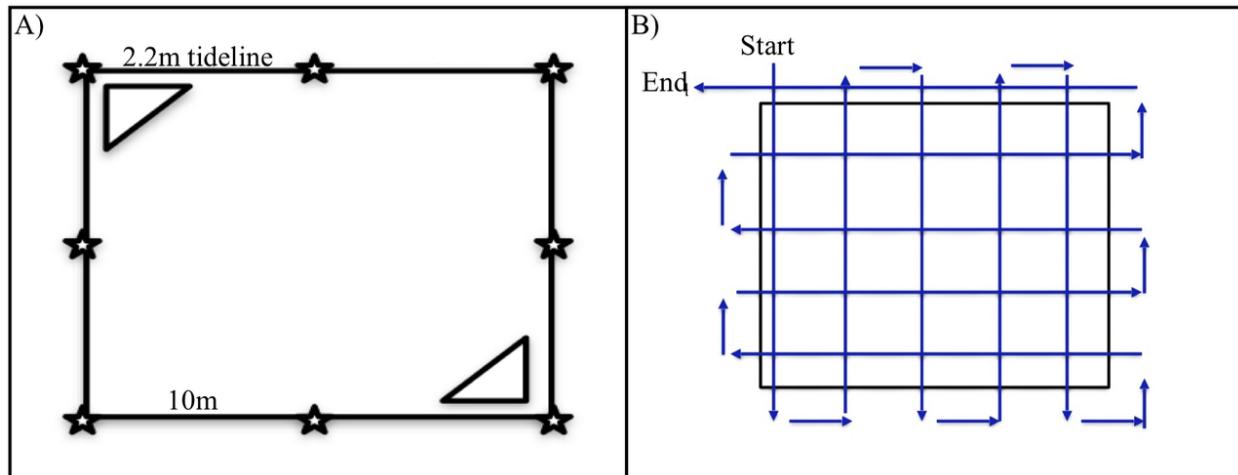
1027

1028 **Fig S1** | Site assessment area and quadrat placements used during the field surveys. Dashed lines
1029 denote horizontal and vertical baselines running parallel and perpendicular to the shoreline,
1030 respectively. Quadrat placement was at the intersection of perpendicular lines extended from the
1031 horizontal and vertical baselines. Examples of quadrat placement are illustrated by the placement
1032 of the 1st, 4th, 8th and 15th quadrats. Five quadrats were placed within each zone.
1033
1034
1035



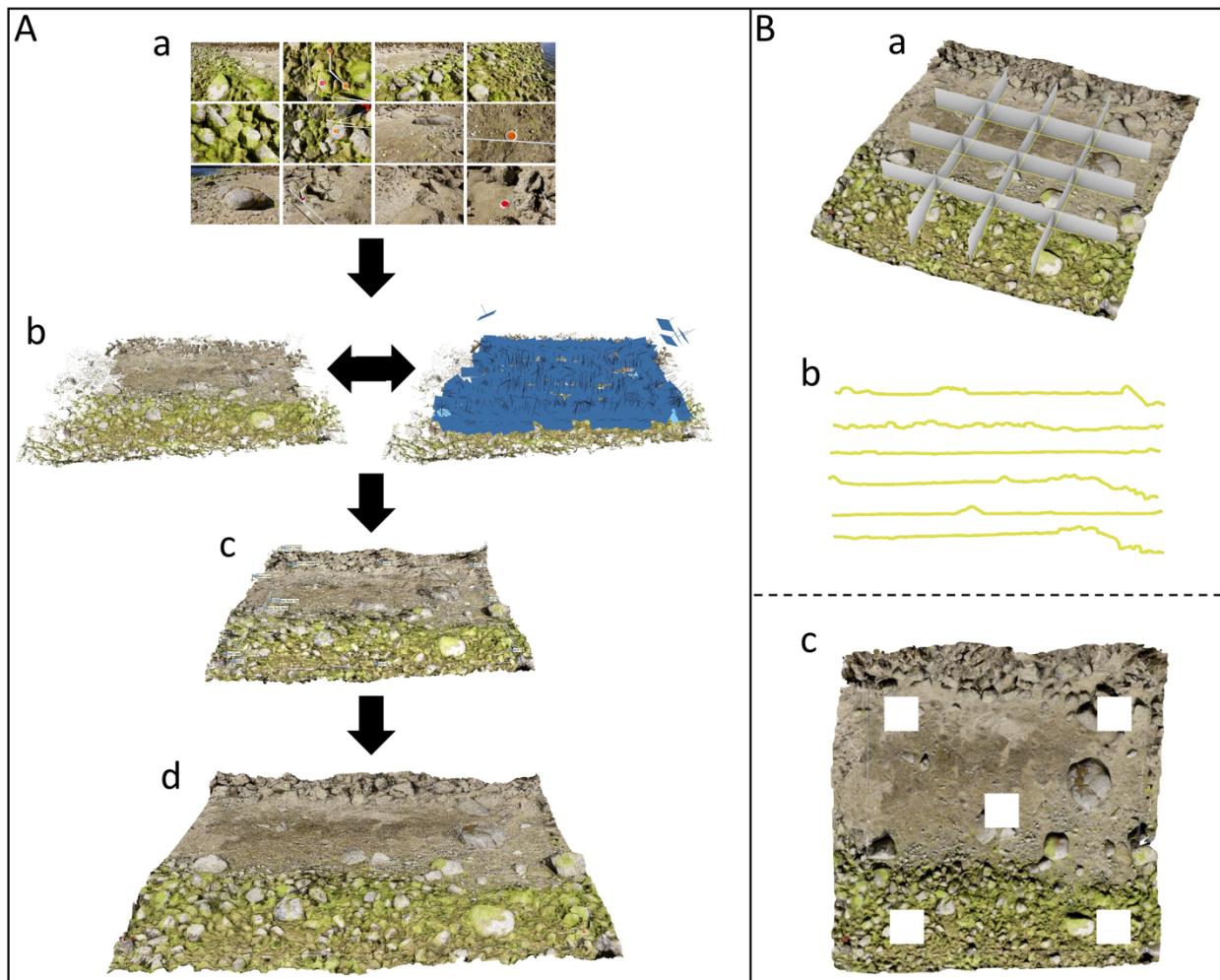
1036
1037
1038
1039
1040
1041

Fig S2 | Epifaunal taxonomic surveys 0.5×0.5 m strung quadrat diagram. Vertical and horizontal strings every 5 cm created 100 equal squares, of which ten squares were randomly selected and subsampled.



1042
1043
1044
1045
1046
1047
1048
1049
1050
1051
1052

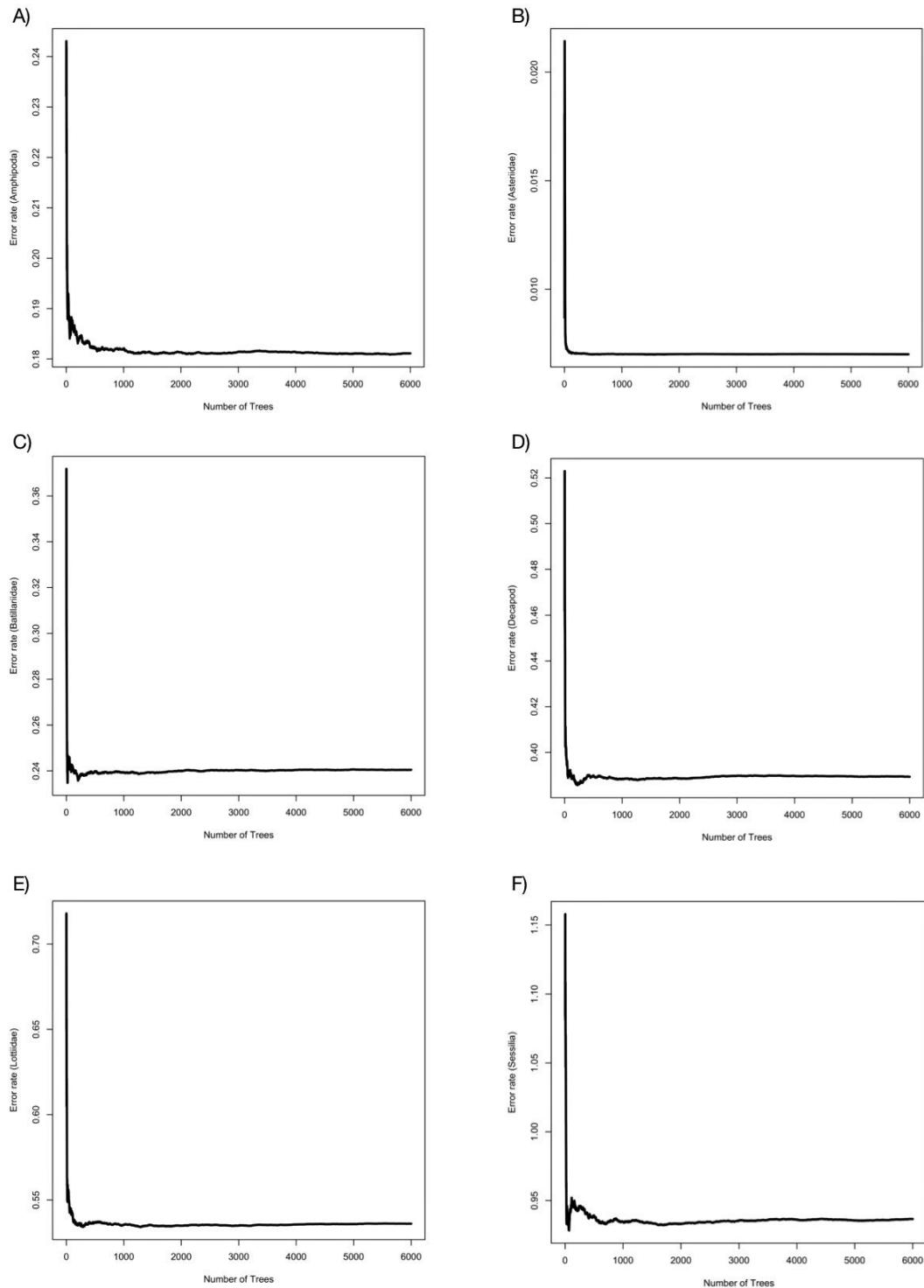
Fig S3 | Structure-from-motion (SfM) photogrammetry site assessment diagrams. A) 10×10 m SfM assessment area. Stars denote ground control point locations. Triangles indicate known length bars used for calibration. Bottom of area placed along the 1.0 m tideline. B) Ideal site assessment patterns used to ensure the entire assessment area was covered. Deviations from this pattern occurred if the assessment area responded poorly to trampling (e.g., intertidal mudflats).



1053
1054
1055
1056
1057
1058

Fig S4 | A) A flow diagram illustrating the a) image acquisition, b) image alignment and spare cloud generation, c) dense point cloud generation, and d) tiled mesh construction. **B)** Complexity analyses diagrams including a) six 9-meter rugosity chains laid out equidistantly across the model, b) curvatures resulting from interacting the model and chains, and c) five 1×1 m fractal dimension assessment locations.

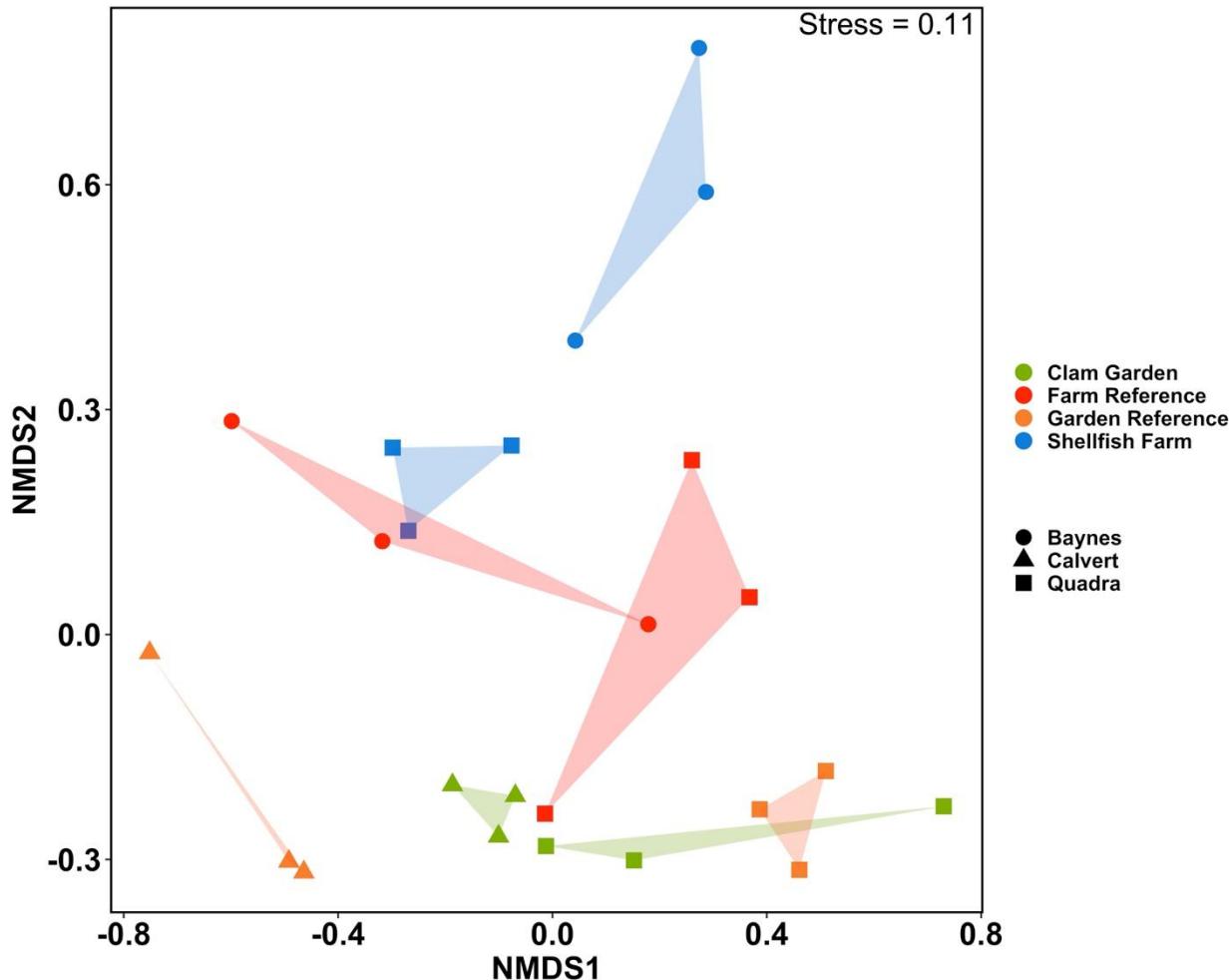
1059
1060
1061



1062
1063
1064
1065
1066

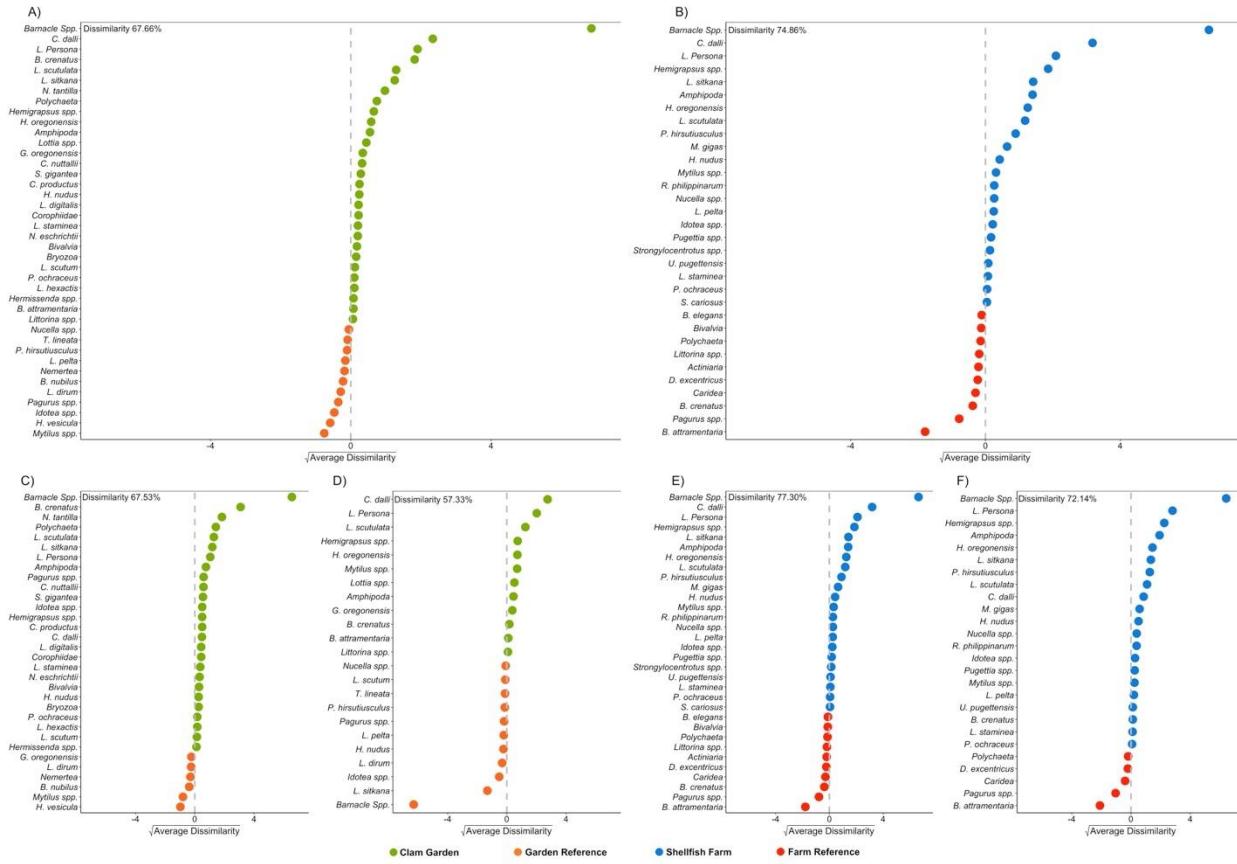
Fig S5 | Multivariate Random Forest number of trees selection process. The number of trees required was determined via a low and stable error rate. Six examples of the 24 taxa considered are depicted.

1067

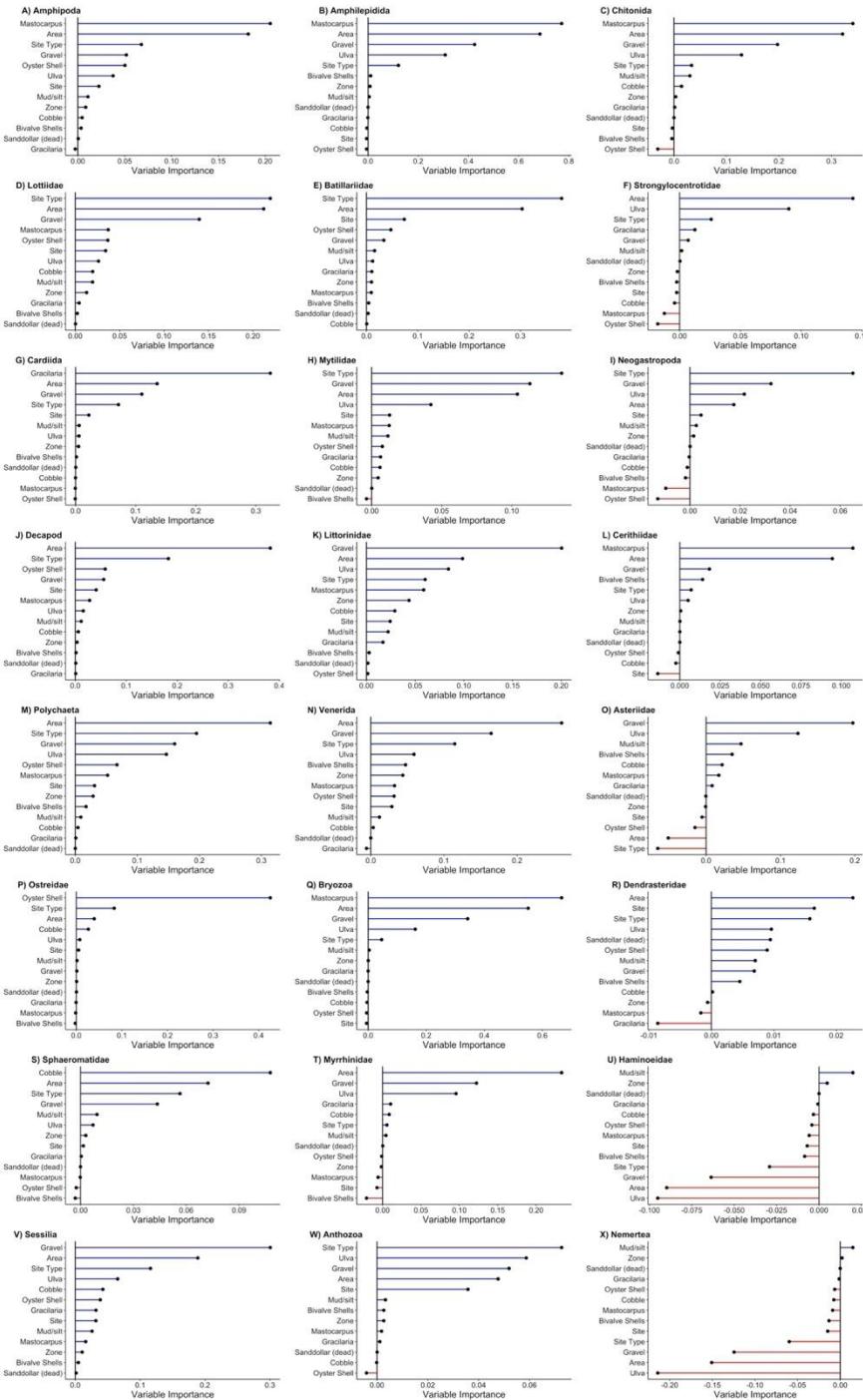


1068
1069
1070
1071
1072
1073
1074
1075

Fig S6 | Non-metric multidimensional scaling plots of mid-intertidal substrate composition averaged by site and illustrated accordingly to region and site type. Colors denote clam gardens (green), clam garden reference beaches (orange), shellfish farms (blue), and shellfish farm reference beaches (red). Shapes denote the study regions: Baynes Sound (circles), north and south Quadra Island (squares), and Hakai Lúxvbális Conservancy ‘Calvert Island’ (triangles).

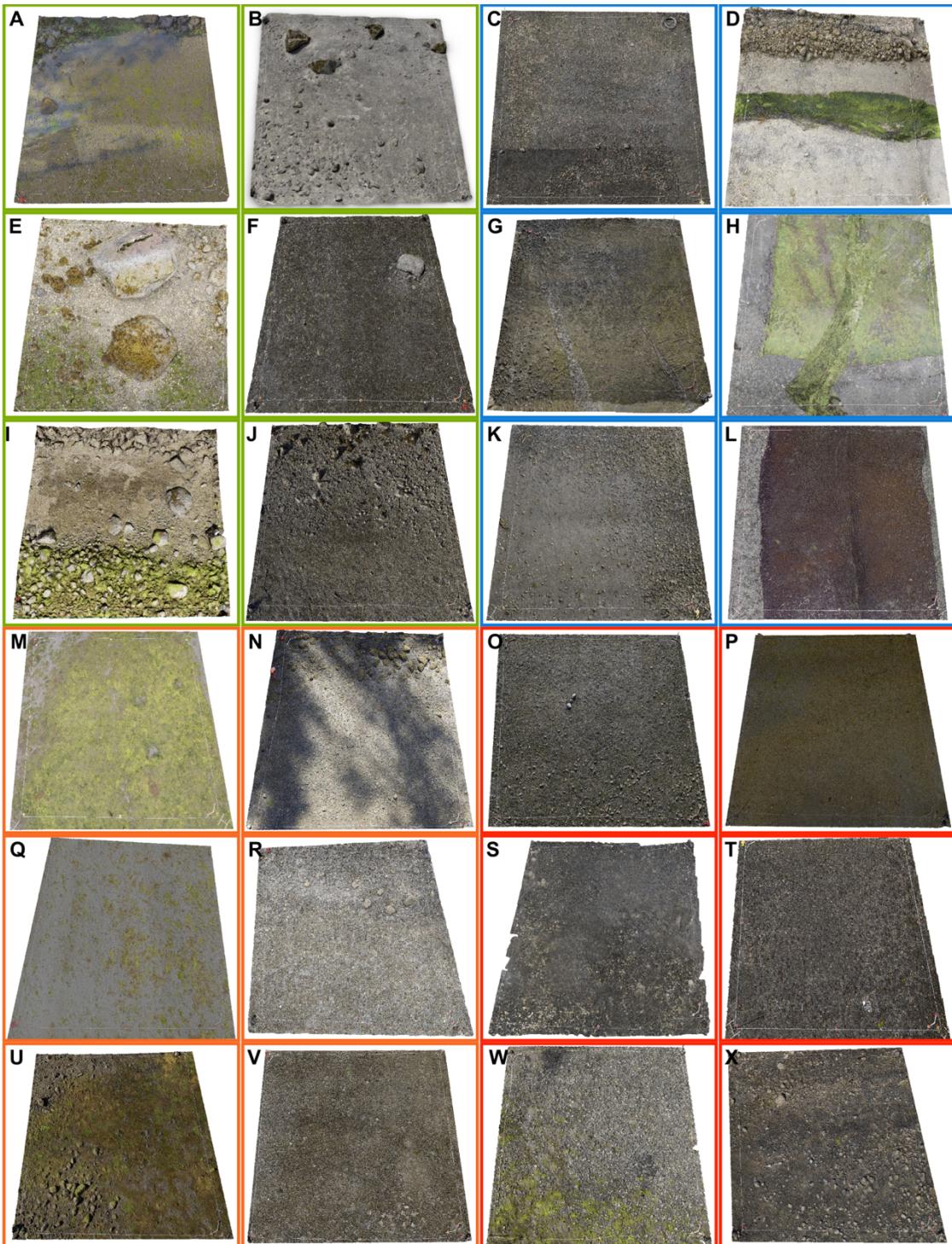


1076
1077 Fig S7 | Taxa-specific average dissimilarity between cultivated habitats and reference beaches
1078 derived from similarity percentage analyses. Square root of average dissimilarity plotted to
1079 improve visualization. Average densities increase in clam gardens (green) or reference beaches
1080 (orange). Average densities increase in shellfish farms (blue) or reference beaches (red). A)
1081 Clam gardens and clam garden reference beach comparison. B) Shellfish farms and shellfish
1082 farm reference beach comparison. Clam gardens and clam garden reference beach comparison
1083 within C) Hakai Lúxvbálís Conservancy ‘Calvert Island’ and D) northern Quadra Island.
1084 Shellfish farms and shellfish farm reference beach comparison within E) Southern Quadra Island
1085 and F) Baynes Sound.
1086
1087



1088
1089
1090
1091
1092
1093

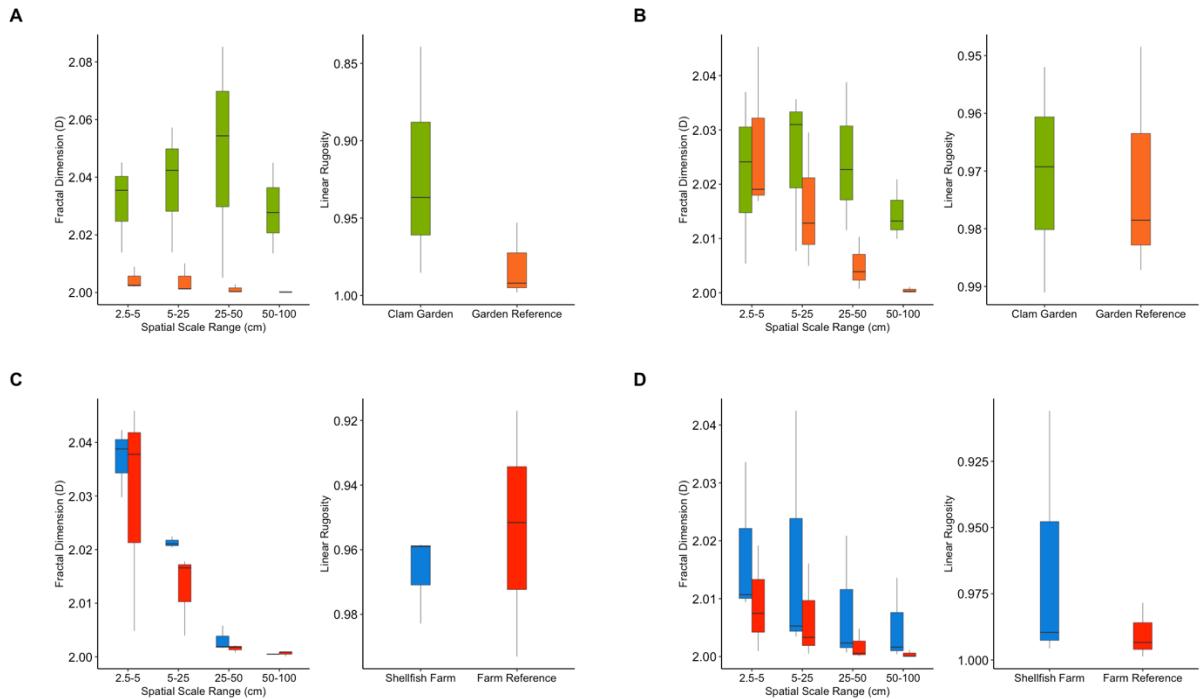
Fig S8 | Variable importance analyses of the interaction between epifaunal taxa and substrate composition. Derived from a multivariate random forest consisting of 6,000 trees. Variable importance depicted for the 24 taxa examined. Relative importance of the predictor variables scaled by decreases in the mean squared error of the model when the variable is permuted. Higher bars equate to greater variable importance.



1094
1095
1096
1097
1098
1099

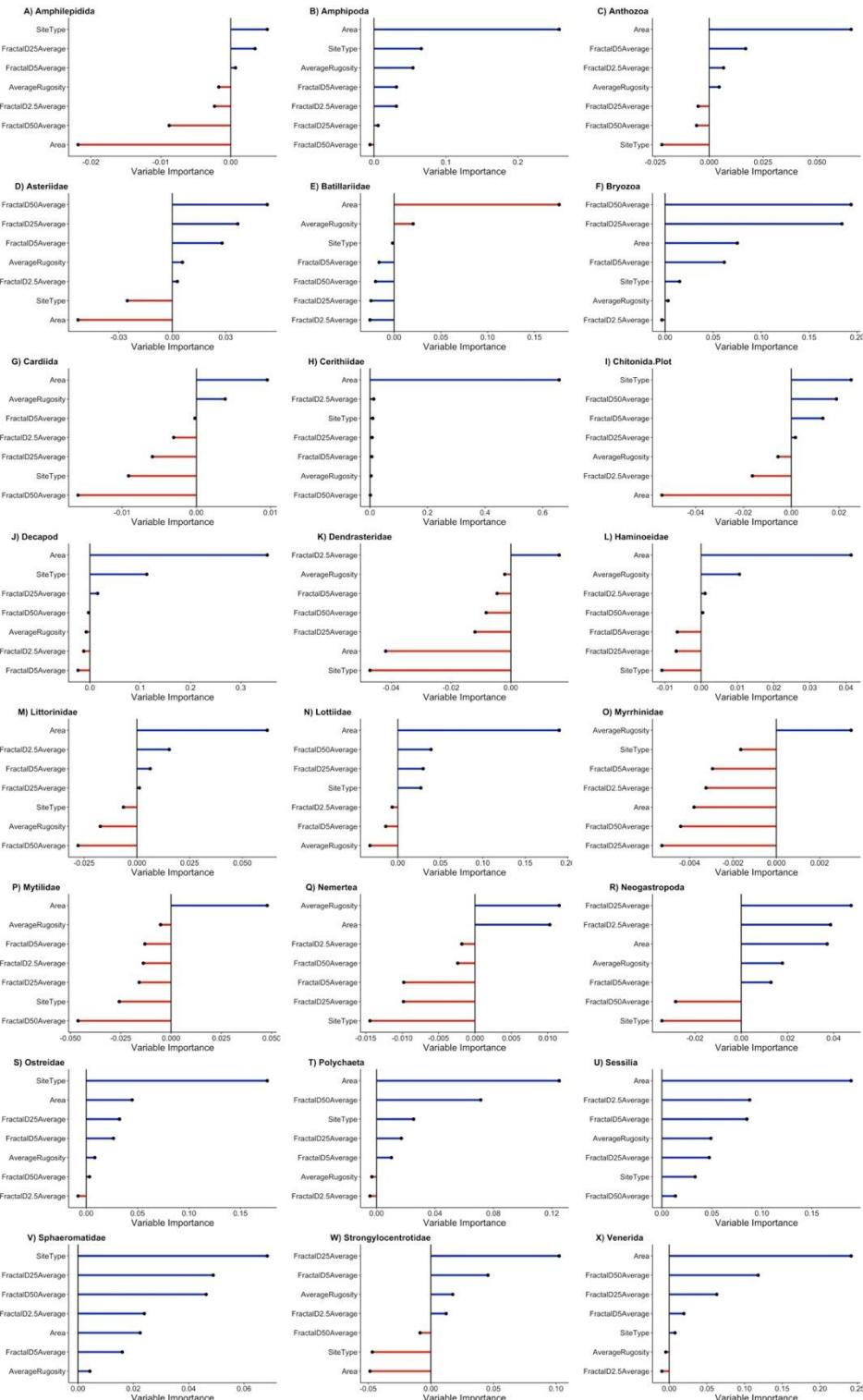
Fig S9 | Three-dimensional reconstructions of all 24 intertidal habitats. **A, E, I)** clam gardens on Calvert Island. **B, F, J)** clam gardens on Quadra Island. **C, G, K)** shellfish farms on Quadra Island. **D, H, L)** shellfish farms in Baynes Sound. **M, Q, U)** clam garden references on Calvert Island. **N, R, V)** clam garden references on Quadra Island. **O, S, W)** shellfish farm references on Quadra. **P, T, X)** shellfish farm references in Baynes Sound.

1100
1101



1102
1103
1104
1105
1106
1107
1108
1109

Fig S10 | Average fractal dimension and linear rugosity within each of the regions. Clam gardens (green), garden reference (orange), shellfish farms (blue), and farm references (red). A) Calvert Island, B-C) Quadra Island, and D) Baynes Sound.



1110
1111
1112
1113
1114
1115

Fig S11 | Variable importance analyses of the interaction between epifaunal taxa and habitat structural complexity. Derived from a multivariate random forest consisting of 6,000 trees. Variable importance depicted for the 24 taxa examined. Relative importance of the predictor variables scaled by decreases in the mean squared error of the model when the variable is permuted. Higher bars equate to great variable importance.

1116 **Supplemental Tables**

1117

1118 **Table S1** | Taxa observed within each habitat type.

Clam Garden	Shellfish Farm	Clam Garden Reference	Shellfish Farm Reference
Amphipoda	Amphipoda	Amphipoda	Amphipoda
<i>Balanus crenatus</i>	<i>Balanus crenatus</i>	<i>Balanus crenatus</i>	Anemone
<i>Balanus glandula</i>	<i>Balanus glandula</i>	<i>Balanus glandula</i>	<i>Balanophyllia elegans</i>
<i>Barnacle</i> spp.	<i>Barnacle</i> spp.	<i>Balanus nubilus</i>	<i>Balanus crenatus</i>
<i>Batillaria attramentaria</i>	<i>Batillaria attramentaria</i>	<i>Barnacle</i> spp.	<i>Balanus glandula</i>
Bivalvia	Caridean Shrimps	<i>Chthamalus dalli</i>	<i>Barnacle</i> spp.
Bryozoa	<i>Chthamalus dalli</i>	<i>Clinocardium nuttallii</i>	<i>Batillaria attramentaria</i>
<i>Cancer productus</i>	<i>Dendraster excentricus</i>	<i>Gnorimosphaeroma oregonensis</i>	Bivalvia
<i>Chthamalus dalli</i>	<i>Hemigrapsus nudus</i>	<i>Haminoea vesicula</i>	Caridean Shrimps
<i>Clinocardium nuttallii</i>	<i>Hemigrapsus oregonensis</i>	<i>Hemigrapsus nudus</i>	<i>Chthamalus dalli</i>
Corophiidae	<i>Hemigrapsus</i> spp.	<i>Hemigrapsus oregonensis</i>	<i>Dendraster excentricus</i>
<i>Gnorimosphaeroma oregonensis</i>	<i>Idotea</i> spp.	<i>Hemigrapsus</i> spp.	<i>Hemigrapsus nudus</i>
<i>Hemigrapsus nudus</i>	<i>Leukoma staminea</i>	<i>Idotea</i> spp.	<i>Hemigrapsus oregonensis</i>
<i>Hemigrapsus oregonensis</i>	<i>Littorina scutulata</i>	<i>Lirabuccinum dirum</i>	<i>Hemigrapsus</i> spp.
<i>Hemigrapsus</i> spp.	<i>Littorina sitkana</i>	<i>Littorina scutulata</i>	<i>Idotea</i> spp.
<i>Hermisenda</i> .spp.	<i>Lottia pelta</i>	<i>Littorina sitkana</i>	<i>Littorina scutulata</i>
<i>Idotea</i> spp.	<i>Lottia persona</i>	<i>Lottia pelta</i>	<i>Littorina sitkana</i>
<i>Leptasterias hexactis</i>	<i>Magallana gigas</i>	<i>Lottia persona</i>	<i>Littorina</i> .spp.
<i>Leukoma staminea</i>	<i>Mytilus</i> spp.	<i>Lottia scutum</i>	<i>Lottia pelta</i>
<i>Lirabuccinum dirum</i>	<i>Nucella</i> spp.	<i>Mytilus</i> spp.	<i>Lottia persona</i>
<i>Littorina scutulata</i>	<i>Pagurus hirsutiusculus</i>	Nemertea	<i>Magallana gigas</i>
<i>Littorina sitkana</i>	<i>Pagurus</i> spp.	<i>Neostyliidium eschrichtii</i>	<i>Mytilus</i> spp.
<i>Littorina</i> spp.	<i>Pisaster ochraceus</i>	<i>Nucella</i> spp.	<i>Pagurus hirsutiusculus</i>
<i>Lottia digitalis</i>	<i>Pugettia</i> spp.	<i>Nutricola tantilla</i>	<i>Pagurus</i> spp.
<i>Lottia pelta</i>	<i>Ruditapes philippinarum</i>	<i>Pagurus hirsutiusculus</i>	Polychaeta
<i>Lottia persona</i>	<i>Semibalanus cariosus</i>	<i>Pagurus</i> spp.	<i>Ruditapes philippinarum</i>

<i>Lottia scutum</i>	<i>Strongylocentrotus</i> spp.	<i>Tonicella lineata</i>
<i>Lottia</i> spp.	<i>Upogebia pugettensis</i>	
<i>Mytilus</i> spp.		
<i>Neostylidium eschrichtii</i>		
<i>Nutricola tantilla</i>		
<i>Pagurus</i> spp.		
<i>Pisaster ochraceus</i>		
Polychaeta		
<i>Saxidomus gigantea</i>		

1119
1120
1121
1122
1123
1124
1125
1126
1127
1128
1129
1130
1131
1132
1133
1134
1135
1136
1137
1138
1139
1140
1141
1142
1143
1144
1145
1146
1147
1148

1149 **Table S2** | Taxa observed across all habitat types, unique to each comparison, and unique to each
 1150 habitat type. Complements the Venn Diagram (Fig 2F). Shellfish Farms = SF, SFRB = Shellfish
 1151 Farm Reference Beaches, CG = Clam Garden, CGRB = Clam Garden Reference Beaches.
 1152

Common Taxa	Unique SF and SFRB Taxa	Unique CG and CGRB Taxa	Unique SF Taxa	Unique SFRB Taxa	Unique CG Taxa	Unique CGRB Taxa
Amphipoda	<i>Batillaria attramentaria</i>	<i>Clinocardium nuttallii</i>	<i>Pugettia</i> spp.	Anemone	Bryozoa	<i>Balanus nubilus</i>
<i>Balanus crenatus</i>	Caridean shrimps	<i>Gnorimosphaera romana</i> <i>oregonensis</i>	<i>Semibalanus cariosus</i>	<i>Balanophyllia elegans</i>	<i>Cancer productus</i>	<i>Haminoea vesicula</i>
<i>Balanus glandula</i>	<i>Dendraster excentricus</i>	<i>Lirabuccinum dirum</i>	<i>Strongylocentrotus</i> spp.		Corophiidae	Nemertea
<i>Barnacle</i> spp.	<i>Magallana gigas</i>	<i>Lottia scutum</i>	<i>Upogebia pugettensis</i>		<i>Hermissenda</i> spp.	<i>Tonicella lineata</i>
<i>Chthamalus dalli</i>	<i>Pagurus hirsutiusculus</i>	<i>Neostyliidium eschrichtii</i>			<i>Leptasterias hexactis</i>	
<i>Hemigrapsus nudus</i>	<i>Ruditapes philippinarum</i>	<i>Nutricola tantilla</i>			<i>Lottia digitalis</i>	
<i>Hemigrapsus oregonensis</i>					<i>Lottia</i> spp.	
<i>Hemigrapsus</i> spp.					<i>Saxidomus gigantea</i>	
<i>Idotea</i> spp.						
	<i>Littorina scutulata</i>					
	<i>Littorina sitkana</i>					
	<i>Lottia pelta</i>					
	<i>Lottia persona</i>					
	<i>Mytilus</i> spp.					
	<i>Pagurus</i> spp.					

1153
 1154
 1155
 1156
 1157
 1158
 1159

1160 **Table S3** | Higher-level taxonomic classifications to improve pattern visualization during
 1161 multivariate regression tree (MRT) and multivariate random forest (MRF) analyses. The 60
 1162 epifaunal taxa observed during the biodiversity surveys were amalgamated into 24 higher-level
 1163 taxonomic classifications as detailed below.
 1164

MRT and MFT Taxa	Classification	Included Taxa
Amphilepidida	Order	Amphilepidida
Amphipoda	Order	Gammaridae, Gammaridae, Amphipoda, Caprellidae
Anthozoa	Class	Anemone, <i>Balanophyllia elegans</i>
Asteriidae	Family	<i>Leptasterias hexactis, Pisaster ochraceus</i>
Batillariidae	Family	<i>Batillaria attramentaria</i>
Bryozoa	Phylum	Bryozoa
Cardiida	Order	<i>Macoma inquinata, Clinocardium nuttallii, Macoma spp.</i>
Cerithiidae	Family	<i>Neostylidium eschrichtii</i>
Chitonida	Order	<i>Mopalia muscosa, Mopalia ciliata, Tonicella lineata</i>
Decapoda	Order	<i>Cancer productus, Pugettia spp., Pagurus hirsutusculus, Pagurus spp., Pandalus platyceros, Pinnotheres pisum, Upogebia pugettensis, Hemigrapsus nudus, Hemigrapsus oregonensis, Hemigrapsus spp.</i>
Dendrasteridae	Family	<i>Dendraster excentricus</i>
Haminoeidae	Family	<i>Haminoea vesicula</i>
Littorinidae	Family	<i>Littorina sitkana, Littorina scutulata, Littorina spp.</i>
Lottiidae	Family	<i>Lottia scutum, Lottia spp., Lottia pelta, Lottia digitalis, Lottia persona, Idotea spp.</i>
Myrrhinidae	Family	<i>Hermissenda spp.</i>
Mytilidae	Family	<i>Mytilus spp.</i>
Nemertea	Phylum	Nemertea
Neogastropoda	Order	<i>Nucella spp., Lirabuccinum dirum</i>

Ostreidae	Family	<i>Magallana gigas</i>
Polychaeta	Class	Polychaeta
Sessilia	Order	<i>Balanus glandula, Chthamalus dalli, Balanus nubilus, Semibalanus cariosus, Balanus crenatus, barnacle spp.</i>
Sphaeromatidae	Family	<i>Gnorimosphaeroma oregonensis</i>
Strongylocentrotidae	Family	<i>Strongylocentrotus spp.</i>
Venerida	Order	<i>Saxidomus gigantea, Ruditapes philippinarum, Nutricola tantilla, Leukoma staminea, unidentified bivalve</i>
1165		
1166		
1167		
1168		
1169		
1170		
1171		
1172		
1173		
1174		
1175		
1176		
1177		
1178		
1179		
1180		
1181		
1182		
1183		
1184		
1185		
1186		
1187		
1188		
1189		
1190		
1191		
1192		
1193		
1194		
1195		
1196		

1197 **Table S4** | PERMANOVA (permutational multivariate analysis of variance) assessing if
 1198 epifaunal community composition varied between clam gardens, shellfish farms, and reference
 1199 beaches. A) Comparison of all habitat types. Comparison of clam gardens and clam garden
 1200 reference beaches within B) Hakai Lúxvbális Conservancy ‘Calvert Island’ and C) northern
 1201 Quadra Island. Comparison of shellfish farms and shellfish farm reference beaches within D)
 1202 Southern Quadra Island and F) Baynes Sound.

1203

A)	Comparison	Source	DF	SS	MS	Pseudo-F	p
Clam Garden, Shellfish Farms, and Reference Sites	Habitat Type	3	3.3	1.098	4.98	0.018	
	Year	1	1.5	1.495	6.78	0.001	
	Habitat Type: Site	20	18.1	0.904	4.1	0.001	
	Residuals	210	46.3	0.221			
B)	Comparison	Source	DF	SS	MS	Pseudo-F	p
Calvert Island Gardens and Reference Sites	Habitat Type	1	0.7	0.704	3.42	0.029	
	Year	1	0.49	0.491	2.39	0.056	
	Habitat Type: Site	4	1.31	0.328	1.59	0.085	
	Habitat Type: Site: Quad	32	8.7	0.272	1.32	0.086	
	Residuals	18	3.71	0.206			
C)	Comparison	Source	DF	SS	MS	Pseudo-F	p
Quadra Island Gardens and Reference Sites	Habitat Type	1	0.73	0.729	4.5	0.012	
	Year	1	0.52	0.518	3.2	0.029	
	Habitat Type: Site	4	1.67	0.417	2.58	0.011	
	Habitat Type: Site: Quad	44	7.75	0.176	1.09	0.382	
	Residuals	8	1.29	0.162			
D)	Comparison	Source	DF	SS	MS	Pseudo-F	p
Quadra Island Shellfish Farms and Reference Sites	Habitat Type	1	0.9	0.9	3.25	0.007	
	Year	1	3.69	3.69	13.36	0.001	
	Habitat Type: Site	4	0.88	0.22	0.8	0.73	
	Habitat Type: Site: Quad	42	11.62	0.28	1	0.488	
	Residuals	10	2.76	0.28			
E)	Comparison	Source	DF	SS	MS	Pseudo-F	p
Baynes Sound Shellfish Farms and Reference Sites	Habitat Type	1	1.08	1.081	4.88	0.005	
	Year	1	0.53	0.534	2.41	0.046	
	Habitat Type: Site	4	3.52	0.881	3.98	0.001	
	Habitat Type: Site: Quad	42	8.49	0.202	0.91	0.687	
	Residuals	11	2.44	0.221			

1204

1205

1206

1207

1208

1209

1210

1211 **Table S5** | SIMPER (Similarity Percentages) tables showing the contribution of each taxonomic
 1212 grouping to the observed differences between intertidal study site types (clam garden, shellfish
 1213 farms, and reference beaches) along the Central Coast of British Columbia, Canada. A) Clam
 1214 gardens and clam garden reference beach comparison. B) Shellfish farms and shellfish farm
 1215 reference beach comparison. Clam gardens and clam garden reference beach comparison within
 1216 C) Hakai Lúxvbálís Conservancy ‘Calvert Island’ and D) northern Quadra Island. Shellfish
 1217 farms and shellfish farm reference beach comparison within E) Southern Quadra Island and F)
 1218 Baynes Sound.
 1219

Taxa	Average Density	Average Density	Average Dissimilarity (%)	Contribution S.D	Average to S.D ratio	Contribution (%)	Cumulative (%)
(A) Barnacle Clam Gardens Reference Sites							
Average dissimilarity = 67.66%							
<i>spp.</i>	941.18	905.58	47.07	29.22	1.61	69.57	69.57
<i>C. dalli</i>	144.86	44.90	5.47	9.67	0.57	8.08	77.65
<i>L. persona</i>	75.91	50.32	3.62	4.66	0.78	5.36	83.01
<i>B. crenatus</i>	35.39	8.63	3.31	11.00	0.30	4.90	87.91
<i>L. scutulata</i>	45.39	15.92	1.67	2.35	0.71	2.47	90.38
<i>L. sitkana</i>	25.56	21.17	1.57	2.74	0.57	2.32	92.70
<i>N. tantilla</i>	5.39	1.85	0.95	3.81	0.25	1.40	94.10
<i>Mytilus</i> spp.	7.49	7.61	-0.57	1.28	0.45	0.85	94.94
<i>Polychaeta</i>	3.63	1.00	0.55	4.84	0.11	0.82	95.76
<i>Hemigrapsus</i> spp.	8.37	4.73	0.43	1.00	0.43	0.64	96.40
<i>H. vesicula</i>	1.00	2.69	-0.35	2.91	0.12	0.51	96.91
<i>H. oregonensis</i>	7.32	5.75	0.34	0.70	0.48	0.50	97.41
<i>Amphipoda</i>	2.75	2.02	0.30	1.47	0.20	0.44	97.85
<i>Idotea</i> spp.	3.28	3.88	-0.22	0.79	0.28	0.33	98.18
<i>Lottia</i> spp.	4.51	1.00	0.20	1.59	0.12	0.29	98.47
<i>Pagurus</i> spp.	1.53	1.68	-0.13	0.74	0.17	0.19	98.66
<i>G. oregonensis</i>	3.46	1.85	0.12	0.66	0.18	0.17	98.83
<i>C. nuttallii</i>	1.18	1.17	0.10	0.80	0.13	0.15	98.98
<i>L. dirum</i>	1.35	2.86	-0.08	0.33	0.25	0.12	99.10
<i>S. gigantea</i>	1.53	1.00	0.08	0.66	0.12	0.12	99.22
<i>C. productus</i>	1.18	1.00	0.06	0.64	0.10	0.09	99.31
<i>H. nudus</i>	2.05	1.51	0.06	0.18	0.32	0.09	99.40
Corophiidae	1.18	1.00	0.05	0.49	0.10	0.07	99.47
<i>L. digitalis</i>	1.18	1.00	0.05	0.49	0.10	0.07	99.54
<i>B. nubilus</i>	1.00	1.17	-0.05	0.52	0.09	0.07	99.61

<i>L. staminea</i>	1.35	1.00	0.04	0.30	0.13	0.06	99.68
<i>N. eschrichtii</i>	1.18	1.17	0.04	0.32	0.12	0.06	99.73
<i>Nemertea</i>	1.00	1.17	-0.03	0.32	0.10	0.05	99.78
<i>Bivalvia</i>	1.53	1.00	0.03	0.25	0.12	0.04	99.82
<i>L. pelta</i>	1.18	1.85	-0.02	0.14	0.17	0.04	99.86
<i>Bryozoa</i>	1.35	1.00	0.02	0.19	0.12	0.03	99.90
<i>L. scutum</i>	1.18	1.17	0.01	0.08	0.18	0.02	99.91
<i>P. hirsutiusculus</i>	1.00	1.17	-0.01	0.09	0.12	0.02	99.93
<i>L. hexactis</i>	1.18	1.00	0.01	0.08	0.12	0.01	99.95
<i>P. ochraceus</i>	1.18	1.00	0.01	0.08	0.12	0.01	99.96
<i>T. lineata</i>	1.00	1.17	-0.01	0.07	0.12	0.01	99.97
<i>Hermisenda</i> spp.	1.35	1.00	0.01	0.05	0.13	0.01	99.98
<i>B. attramentaria</i>	1.35	1.00	0.01	0.03	0.19	0.01	99.99
<i>Littorina</i> spp.	1.18	1.00	0.00	0.03	0.13	0.01	100.00
<i>Nucella</i> spp.	1.00	1.17	0.00	0.02	0.13	0.00	100.00

(B)	Shellfish Farms			Reference Sites				Average dissimilarity = 74.86%
	Farms	Reference	Sites					
Barnacle spp.	1765.56	939.44	43.98	28.81	1.53	58.75	58.75	
<i>C. dalli</i>	437.20	95.58	10.10	19.77	0.51	13.49	72.24	
<i>L. persona</i>	108.29	18.12	4.37	7.54	0.58	5.84	78.08	
<i>Hemigrapsus</i> spp.	50.66	34.83	3.46	6.42	0.54	4.63	82.71	
<i>B. attramentaria</i>	14.90	36.10	-3.21	8.21	0.39	4.29	87.00	
<i>L. sitkana</i>	33.03	16.08	2.00	4.98	0.40	2.68	89.67	
Amphipoda	24.22	10.17	1.96	5.42	0.36	2.61	92.29	
<i>H. oregonensis</i>	29.83	6.64	1.58	2.57	0.61	2.10	94.39	
<i>L. scutulata</i>	42.22	8.39	1.39	2.74	0.51	1.85	96.24	
<i>P. hirsutiusculus</i>	17.95	6.76	0.80	3.16	0.25	1.07	97.32	
<i>Pagurus</i> spp.	6.42	6.93	-0.61	2.02	0.30	0.81	98.13	
<i>M. gigas</i>	10.80	1.29	0.41	1.28	0.32	0.55	98.68	

<i>H. nudus</i>	4.22	1.41	0.18	0.55	0.32	0.24	98.92
<i>B. crenatus</i>	1.17	6.93	-0.14	1.05	0.14	0.19	99.11
<i>Mytilus</i> spp.	4.39	1.29	0.10	0.24	0.40	0.13	99.24
Caridea	1.17	1.68	-0.09	0.87	0.10	0.12	99.36
<i>R. philippinaru</i>							
<i>m</i>	2.36	1.17	0.07	0.30	0.22	0.09	99.45
<i>Nucella</i> spp.	2.02	1.00	0.07	0.34	0.20	0.09	99.54
<i>L. pelta</i>	2.03	1.12	0.06	0.27	0.22	0.08	99.62
<i>D. excentricus</i>	1.08	1.17	-0.05	0.41	0.13	0.07	99.69
<i>Idotea</i> spp.	1.68	1.51	0.05	0.22	0.21	0.06	99.75
Actiniaria	1.00	1.73	-0.04	0.26	0.16	0.06	99.81
<i>Littorina</i> spp.	1.00	2.53	-0.03	0.28	0.12	0.05	99.85
<i>Pugettia</i> spp.	1.17	1.00	0.03	0.25	0.11	0.04	99.89
Polychaeta	1.00	1.17	-0.02	0.22	0.09	0.03	99.92
<i>Strongyloco</i>							
<i>ntrotus</i> spp.	1.17	1.00	0.02	0.16	0.11	0.02	99.94
Bivalvia	1.00	1.17	-0.02	0.15	0.10	0.02	99.96
<i>B. elegans</i>	1.00	1.37	-0.01	0.10	0.12	0.02	99.98
<i>U. pugettensis</i>	1.17	1.00	0.01	0.06	0.12	0.01	99.99
<i>L. staminea</i>	1.17	1.00	0.01	0.04	0.13	0.01	99.99
<i>P. ochraceus</i>	1.17	1.00	0.00	0.02	0.13	0.00	100.00
<i>S. cariosus</i>	1.51	1.00	0.00	0.02	0.13	0.00	100.00

(C)	Clam Gardens			Average dissimilarity = 67.53%			
	Barnacle	Reference Sites					
Spp.	978.41	285.33	43.03	35.52	1.21	63.72	63.72
<i>B. crenatus</i>	71.74	16.00	9.57	19.01	0.50	14.17	77.89
<i>N. tantilla</i>	10.26	2.67	3.36	7.77	0.43	4.98	82.87
Polychaeta	6.56	1.00	2.02	10.10	0.20	3.00	85.87
<i>L. scutulata</i>	42.85	3.00	1.65	2.80	0.59	2.45	88.32
<i>L. sitkana</i>	18.41	3.33	1.40	4.02	0.35	2.08	90.39
<i>L. persona</i>	15.07	7.67	1.09	2.11	0.52	1.62	92.01
<i>H. vesicula</i>	1.00	4.33	-0.95	5.10	0.19	1.40	93.41
<i>Mytilus</i> spp.	3.59	6.67	-0.64	1.76	0.36	0.94	94.35
Amphipoda	2.11	1.67	0.57	2.88	0.20	0.84	95.19
<i>Pagurus</i> spp.	2.11	1.33	0.36	1.44	0.25	0.53	95.73

<i>C. nuttallii</i>	1.37	1.33	0.34	1.58	0.22	0.51	96.24
<i>S. gigantea</i>	2.11	1.00	0.30	1.46	0.21	0.45	96.69
<i>Idotea</i> spp.	1.37	1.33	0.25	1.32	0.19	0.37	97.06
<i>C. productus</i>	1.37	1.00	0.25	1.44	0.17	0.37	97.43
<i>Hemigrapsus</i> spp.	1.37	1.00	0.25	1.44	0.17	0.37	97.79
<i>C. dalli</i>	6.56	1.00	0.23	0.98	0.24	0.35	98.14
<i>Corophiidae</i>	1.37	1.00	0.19	1.06	0.18	0.27	98.41
<i>L. digitalis</i>	1.37	1.00	0.19	1.06	0.18	0.27	98.69
<i>B. nubilus</i>	1.00	1.33	-0.14	0.95	0.15	0.21	98.89
<i>L. staminea</i>	1.74	1.00	0.14	0.61	0.22	0.20	99.10
<i>N. eschrichtii</i>	1.37	1.33	0.10	0.56	0.19	0.15	99.25
<i>Nemertea</i>	1.00	1.33	-0.09	0.55	0.15	0.13	99.38
<i>Bivalvia</i>	2.11	1.00	0.08	0.44	0.19	0.12	99.50
<i>H. nudus</i>	2.11	1.00	0.07	0.24	0.28	0.10	99.60
<i>Bryozoa</i>	1.74	1.00	0.07	0.36	0.19	0.10	99.70
<i>L. dirum</i>	1.00	2.00	-0.06	0.35	0.17	0.09	99.79
<i>G. oregonensis</i>	1.00	2.33	-0.05	0.29	0.18	0.08	99.87
<i>L. hexactis</i>	1.37	1.00	0.03	0.15	0.19	0.04	99.91
<i>P. ochraceus</i>	1.37	1.00	0.03	0.15	0.19	0.04	99.95
<i>L. scutum</i>	1.37	1.00	0.02	0.11	0.19	0.03	99.98
<i>Hermisenda</i> spp.	1.74	1.00	0.01	0.07	0.20	0.02	100.00

(D)	Clam Gardens	Reference Sites			Average dissimilarity = 57.33%			
Barnacle spp.	907.67	1547.21	-39.66	26.32	1.51	69.17	69.17	
<i>C. dalli</i>	269.33	90.31	7.58	8.59	0.88	13.23	82.40	
<i>L. persona</i>	130.67	94.45	4.08	3.83	1.07	7.11	89.51	
<i>L. sitkana</i>	32.00	39.62	-1.73	2.36	0.73	3.02	92.53	
<i>L. scutulata</i>	47.67	29.28	1.57	1.98	0.79	2.74	95.27	
<i>Hemigrapsus</i> spp.	14.67	8.59	0.53	0.81	0.66	0.93	96.20	
<i>H. oregonensis</i>	13.00	10.66	0.51	0.73	0.70	0.88	97.08	
<i>Mytilus</i> spp.	11.00	8.59	0.48	0.78	0.62	0.84	97.92	
<i>Idotea</i> spp.	5.00	6.52	-0.26	0.64	0.41	0.46	98.38	
<i>Lottia</i> spp.	7.67	1.00	0.26	1.52	0.17	0.45	98.84	
Amphipoda	3.33	2.38	0.20	0.73	0.28	0.35	99.19	

<i>G.</i>							
<i>oregonensis</i>	5.67	1.34	0.14	0.65	0.21	0.24	99.43
<i>L. dirum</i>	1.67	3.76	-0.10	0.32	0.32	0.18	99.60
<i>H. nudus</i>	2.00	2.03	-0.05	0.13	0.40	0.09	99.70
<i>L. pelta</i>	1.33	2.72	-0.04	0.19	0.23	0.08	99.77
<i>Pagurus</i>							
spp.	1.00	2.03	-0.03	0.19	0.18	0.06	99.83
<i>B. crenatus</i>	2.67	1.00	0.03	0.16	0.18	0.05	99.88
<i>P.</i>							
<i>hirsutiuscul</i>							
<i>us</i>	1.00	1.34	-0.02	0.12	0.17	0.03	99.92
<i>T. lineata</i>	1.00	1.34	-0.02	0.09	0.17	0.03	99.94
<i>L. scutum</i>	1.00	1.34	-0.01	0.06	0.18	0.02	99.96
<i>B.</i>							
<i>attramentaria</i>							
<i>ia</i>	1.67	1.00	0.01	0.04	0.26	0.02	99.98
<i>Nucella</i> spp.	1.00	1.34	-0.01	0.03	0.19	0.01	99.99
<i>Littorina</i>							
spp.	1.33	1.00	0.01	0.03	0.18	0.01	100.00

(E)	Shellfish Farms	Reference Sites			Average dissimilarity = 77.30%		
Barnacle							
spp.	2562.30	1343.69	48.13	31.12	1.55	62.27	62.27
<i>C. dalli</i>	836.87	193.41	18.21	24.44	0.75	23.56	85.83
<i>L. sitkana</i>	25.00	21.34	2.53	7.08	0.36	3.27	89.10
<i>B.</i>							
<i>attramentaria</i>							
<i>ia</i>	17.67	15.52	1.95	5.45	0.36	2.52	91.62
<i>L. scutulata</i>	52.07	11.55	1.76	2.90	0.61	2.27	93.89
<i>Hemigrapsus</i>							
spp.	34.00	11.55	1.20	3.26	0.37	1.55	95.44
<i>H.</i>							
<i>oregonensis</i>	25.70	5.59	1.12	1.96	0.57	1.45	96.89
<i>L. persona</i>	31.33	12.03	0.89	1.67	0.53	1.15	98.04
<i>M. gigas</i>	7.53	1.59	0.46	1.56	0.29	0.60	98.64
<i>B. crenatus</i>	1.00	13.07	-0.26	1.48	0.18	0.34	98.98
<i>Mytilus</i> spp.	6.00	1.59	0.14	0.30	0.46	0.18	99.16
<i>Pagurus</i>							
spp.	2.00	2.72	-0.12	0.57	0.20	0.15	99.31
<i>H. nudus</i>	2.67	1.14	0.11	0.55	0.20	0.14	99.45
Actiniaria	1.00	2.48	-0.09	0.40	0.23	0.12	99.57
<i>L. pelta</i>	2.03	1.24	0.08	0.34	0.24	0.11	99.67
<i>Littorina</i>							
spp.	1.00	4.10	-0.07	0.39	0.17	0.09	99.76

<i>D.</i>							
<i>excentricus</i>	1.17	1.00	0.05	0.48	0.11	0.07	99.83
Bivalvia	1.00	1.34	-0.04	0.26	0.14	0.05	99.87
<i>Strongyloce</i>							
<i>ntrotus</i> spp.	1.33	1.00	0.03	0.21	0.16	0.04	99.92
<i>B. elegans</i>	1.00	1.76	-0.02	0.15	0.16	0.03	99.95
<i>Idotea</i> spp.	1.33	1.34	-0.02	0.08	0.23	0.02	99.97
Amphipoda	1.00	1.38	-0.02	0.11	0.16	0.02	100.00
<i>S. cariosus</i>	2.00	1.00	0.00	0.02	0.19	0.00	100.00

(F)	Shellfish Farms	Reference Sites			Average dissimilarity = 72.14%		
Barnacle							
Spp.	941.34	548.67	41.51	25.52	1.63	57.54	57.54
<i>L. persona</i>	187.90	24.00	8.02	9.48	0.85	11.11	68.65
<i>Hemigrapsus</i> spp.	67.90	57.33	4.87	6.49	0.75	6.76	75.41
<i>B.</i>							
<i>attramentaria</i>	12.03	56.00	-4.06	8.23	0.49	5.63	81.04
Amphipoda	48.24	18.67	3.66	6.51	0.56	5.08	86.12
<i>H.</i>							
<i>oregonensis</i>	34.10	7.67	2.13	3.25	0.65	2.95	89.07
<i>L. sitkana</i>	41.34	11.00	1.82	3.88	0.47	2.53	91.60
<i>P.</i>							
<i>hirsutiusculus</i>	35.48	12.33	1.61	4.17	0.39	2.23	93.83
<i>L. scutulata</i>	32.03	5.33	1.21	3.04	0.40	1.68	95.51
<i>Pagurus</i> spp.	11.00	11.00		2.51	0.42	1.48	96.98
<i>C. dalli</i>	23.76	1.00	0.75	3.12	0.24	1.04	98.03
<i>M. gigas</i>	14.17	1.00	0.35	0.96	0.36	0.48	98.51
<i>H. nudus</i>	5.83	1.67	0.27	0.60	0.45	0.37	98.88
<i>Nucella</i> spp.	3.07	1.00	0.15	0.53	0.29	0.21	99.09
Caridea	1.34	2.33	-0.15	0.93	0.16	0.21	99.30
<i>R.</i>							
<i>philippinarna</i>	3.76	1.33	0.15	0.44	0.33	0.20	99.50
<i>Idotea</i> spp.	2.03	1.67	0.07	0.28	0.27	0.10	99.61
<i>Pugettia</i> spp.	1.34	1.00	0.06	0.40	0.16	0.09	99.70
<i>Mytilus</i> spp.	2.72	1.00	0.06	0.16	0.35	0.08	99.77
<i>D.</i>							
<i>excentricus</i>	1.00	1.33	-0.04	0.29	0.14	0.06	99.83
<i>L. pelta</i>	2.03	1.00	0.04	0.15	0.26	0.05	99.89
Polychaeta	1.00	1.33	-0.03	0.23	0.15	0.05	99.93

	<i>U.</i>						
	<i>puggettensis</i>	1.34	1.00	0.02	0.09	0.18	0.02 99.95
	<i>B. crenatus</i>	1.34	1.00	0.02	0.08	0.18	0.02 99.98
	<i>L. staminea</i>	1.34	1.00	0.01	0.06	0.18	0.02 99.99
	<i>P.</i>						
	<i>ochraceus</i>	1.34	1.00	0.01	0.03	0.19	0.01 100.00
1220							
1221							
1222							
1223							
1224							
1225	Table S6 Analysis of the decision nodes formed during construction of the multivariate						
1226	regression tree (MRT). The respective MRT analyzed the interaction between epifaunal						
1227	communities and substrate composition. A) Discriminant taxa, left and right split means, and the						
1228	deviance explained at each node. B) Indicator species, directional clusters and the probability the						
1229	taxonomic cluster occurred randomly.						
1230							

(A)	Node	Discriminant Species	Explained Deviance (%)	Left Split Mean	Right Split Mean
	Root Node	Littorinidae	18.18	0.32	1.08
	Gravel = 7.305	Lottiidae	11.28	0.40	1.00
	Complexity = 12.45	Sessilia	61.17	1.05	2.45
	Left Node 1	Decapoda	24.73	0.42	1.61
	Oyster Shell = 8.275	Sessilia	54.35	0.89	2.66
	Complexity = 2.64				
		Amphipoda	19.95	0.11	1.76
	Left Node 2:	Decapoda	24.27	0.36	2.19
	Mastocarpus = 12.88	Littorinidae	14.39	0.22	1.63
	Complexity = 2.23	Lottiidae	21.86	0.28	2.01
	Right Node 1	Littorinidae	40.76	0.90	1.64
	Cobble = 1.384	Lottiidae	11.34	0.90	1.30
	Complexity = 3.01	Sessilia	43.92	2.26	3.04
		Decapoda	41.14	0.77	1.52
	Right Node 2	Lottiidae	13.21	0.82	1.25
	Oyster Shell = 0.8453	Ostreidae	17.55	0.00	0.50
	Complexity = 1.96	Sessilia	23.01	2.16	2.72
	Right Node 3	Littorinidae	36.65	0.49	1.18
	Gravel = 59.2	Lottiidae	14.54	0.54	0.98
	Complexity = 2.33				

	Sessilia	36.64	1.71
--	----------	-------	------

2.41

(B)	Node	Indicator Species	Cluster	Indicator Value	Probability
Root Node Gravel = 7.305 Complexity = 12.45	Cerithiidae	Left	0.04	0.004	
	Dendrasteridae	Left	0.02	0.028	
	Sessilia	Right	0.63	0.001	
	Littorinidae	Right	0.47	0.001	
	Lottiidae	Right	0.44	0.001	
	Decapoda	Right	0.40	0.001	
	Batillariidae	Right	0.24	0.002	
Left Node 1 Oyster Shell = 8.275 Complexity = 2.64	Mytilidae	Right	0.16	0.005	
	Decapoda	Right	0.73	0.001	
	Sessilia	Right	0.69	0.001	
	Lottiidae	Right	0.50	0.002	
	Ostreidae	Right	0.48	0.001	
	Littorinidae	Right	0.31	0.014	
Left Node 2 Mastocarpus = 12.88 Complexity = 2.23	Amphipoda	Right	0.94	0.001	
	Decapoda	Right	0.86	0.001	
	Littorinidae	Right	0.66	0.003	
	Lottiidae	Right	0.66	0.004	
	Batillariidae	Right	0.64	0.005	
	Mytilidae	Right	0.45	0.014	
Right Node 1 Cobble = 1.384 Complexity = 3.01	Venerida	Right	0.42	0.018	
	Littorinidae	Right	0.57	0.001	
	Sessilia	Right	0.56	0.001	
	Lottiidae	Right	0.45	0.003	
	Sphaeromatidae	Right	0.05	0.041	
Right Node 2 Oyster Shell = 0.8453 Complexity = 1.96	Decapoda	Right	0.58	0.001	
	Sessilia	Right	0.56	0.002	
	Ostreidae	Right	0.45	0.001	
	Lottiidae	Right	0.43	0.012	
	Asteriidae	Right	0.05	0.032	
Right Node 3 Gravel = 59.2 Complexity = 2.33	Venerida	Left	0.16	0.001	
	Polychaeta	Left	0.11	0.002	
	Cardiida	Left	0.05	0.042	
	Sessilia	Right	0.52	0.002	
	Littorinidae	Right	0.47	0.001	
	Lottiidae	Right	0.39	0.008	

1232 **Table S7** | Substrate composition-epifaunal community associations determined by taxa-specific
 1233 variability explained by the multivariate random forest (MRF) model, and the predictive
 1234 accuracy of the MRF determined. Eighty percent of the data were used to train a model and the
 1235 remaining 20% of the data to evaluate the model's predictions. Model construction used identical
 1236 parameters to the variable importance analysis.
 1237

Species	Random Forest Model			Prediction	
	Explained Variance (Percent)	Error Rate	Standardize Error Rate	Variance Explained	Test Set Error Rate
Batillariidae	48.64	0.24	0.51	48.17	0.3
Decapoda	46.43	0.39	0.54	45.51	0.41
Sessilia	43.35	0.94	0.57	36.14	1.13
Ostreidae	33.92	0.08	0.66	35.22	0.02
Littorinidae	33.77	0.61	0.66	30.68	0.66
Lottiidae	33.31	0.54	0.67	30.61	0.54
Cardiida	32.72	0.01	0.68	Inf	0
Amphipoda	27.67	0.18	0.72	23.26	0.21
Venerida	21	0.11	0.78	32.52	0.15
Mytilidae	12.27	0.19	0.88	14.41	0.13
Polychaeta	8.69	0.05	0.91	12.48	0.1
Anthozoa	4.7	0.01	0.95	6.26	0.02
Dendrasteridae	0.88	0.02	0.99	-2.47	0.01
Cerithiidae	0.71	0.02	0.99	-12.85	0.01
Haminoeidae	0.71	0.01	0.99	Inf	0
Sphaeromatidae	0.46	0.03	1	Inf	0
Neogastropoda	-1.4	0.05	1.02	-20.03	0.03
Strongylocentrotid ae	-3	0.01	1.03	-1.22	0.01
Asteriidae	-3.42	0.01	1.03	-0.22	0.02
Myrrhinidae	-3.93	0.01	1.04	-2.57	0
Chitonida	-5.83	0.01	1.06	-0.29	0.01
Amphilepidida	-7.89	0.01	1.08	0.52	0.03
Bryozoa	-8.79	0.01	1.08	1.04	0.04
Nemertea	-10.55	0	1.11	Inf	0

1238
 1239
 1240
 1241
 1242
 1243
 1244
 1245
 1246

1247 **Table S8** | Habitat complexity-epifaunal community associations determined by taxa-specific
 1248 variability explained by the multivariate random forest (MRF) model, and the predictive
 1249 accuracy of the MRF. Eighty percent of the data were used to train a model and the remaining
 1250 20% of the data to evaluate the model's predictions. Model construction used identical
 1251 parameters to the variable importance analysis.
 1252

Species	Random Forest Model			Prediction	
	Explained Variance (Percent)	Error Rate	Standardize Error Rate	Variance Explained	Test Set Error Rate
Amphilepidida	-23.81	0.2	1.24	Inf	0.01
Amphipoda	24.68	236.15	0.75	-409.1	86.55
Anthozoa	-6.16	1.79	1.06	Inf	0.12
Asteriidae	-19.45	0.14	1.19	-0.34	0.4
Batillariidae	6.67	530.33	0.93	46	138.83
Bryozoa	31.37	0.19	0.69	Inf	0.06
Cardiida	-23.78	1.01	1.24	Inf	0.32
Cerithiidae	38.68	0.08	0.61	23.77	0.21
Chitonida	-19.11	0.06	1.19	Inf	0.01
Decapoda	20.89	2778.45	0.79	69.85	846.8
Dendrasteridae	-12.94	4.14	1.13	0.51	0.2
Haminoeidae	-18.98	1	1.19	-2499.49	0.58
Littorinidae	-14.08	3972.49	1.14	-45.49	1087.28
Lottiidae	3.28	5450.76	0.97	-717.79	2363.69
Myrrhinidae	-23.53	0.21	1.24	-299.14	0.01
Mytilidae	-26.71	17.29	1.27	1.5	15.41
Nemertea	-22.66	0.01	1.23	Inf	0.01
Neogastropoda	-14.83	3.38	1.15	Inf	1.03
Ostreidae	5.05	105.48	0.95	-6859.78	15.35
Polychaeta	-7.85	20.95	1.08	12.25	55.96
Sessilia	27.97	851360.	0.72	64.67	284879.4
Sphaeromatidae	-2.94	1.34	1.03	7.98	0.74
Strongylocentrotidae	-11.08	0.03	1.11	63.77	0
Venerida	14.08	17.87	0.86	25.25	37.8

1253

1254

1255