Ancestral and contemporary intertidal mariculture practices support marine biodiversity in the northeast Pacific

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Kieran D. Cox [1,2] ✉, Hailey L. Davies [1], Ben Millard-Martin[2], Morgan Black[1,2], Margot Hessing-Lewis[2], Nicole F. Smith[2], Francis Juanes [2] & Sarah E. Dudas[1,2,3]

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

Humans have managed aquatic and terrestrial ecosystems for millennia[1,2]. Today, anthropogenic activities influence the majority of marine and terrestrial ecosystems[1,3]. Elevated biological resource availability (e.g., protein) within coastal regions relative to inland ecosystems has contributed to a concentration of human influences along coastlines[4]. While coastal communities have relied on mariculture for millennia, cultivating marine ecosystems has gained global importance over recent decades and has, for the first time, outpaced the amount of seafood extracted from wild populations[5,6]. This shift signals the emergence of a novel state in the history of human-marine ecosystem interactions. This expansion in cultivation has resulted in remarkable accomplishments for humanity, including advancements in infrastructure, emergent economies, and technology, but has also degraded many natural ecosystems[7,8]. Balancing food production with coastal resource management, ecosystem health, and population growth represents an emerging challenge facing 21st-century global conservation efforts.

Despite numerous human-ecosystem interactions leading to species loss, disrupted community dynamics, and environmental degradation, emerging research indicates that certain anthropogenic activities can create ecological states that foster robust biological communities[1,9,10]. These ecological states are predominantly associated with human communities that have developed management practices over dozens, if not hundreds of generations, and established an intergenerational understanding of the

ecosystem, often viewing themselves as an interconnected part of the whole, as opposed to a separate or superior entity[11,12]. The technologies and management strategies that Indigenous Peoples of the northeastern Pacific established to increase food production and ensure long-term sustenance, for example, have influenced ecosystems for millennia[11,13,14]. Along the coast of British Columbia, Indigenous Peoples have employed practices such as intentional successive landscape burnings and plant translocations to enhance forest productivity and plant species diversity[11,13,15]. Similarly, shellfish cultivation methods implemented over millennia increase the productivity of bivalve populations; a condition that persists despite colonial policies that have disrupted traditional bivalve management by Indigenous Peoples[16,17]. This spatial-temporal model of how humans alter their environment suggests that the legacy of these activities on ecological communities can persist for thousands of years, even if management frequency or intensity varies[9,17–19].

Coastal Indigenous populations have stewarded marine resources along the coastlines of the Pacific Northeast for generations[11,16,20,21]. The enhancement, management, and harvesting of bivalve populations are governed by complex socio-cultural systems within and among communities[16,17,22]. Beginning at least 3,800 years ago, Indigenous Peoples created and enhanced clam habitat by building "clam gardens"—low intertidal rock walls and associated soft-sediment terraces[16,23,24]. Clam gardens, also commonly called sea gardens owing to the diverse seafood they

[1]Department of Biology, University of Victoria, Victoria, BC V8P 5C2, Canada. [2]Hakai Institute, Heriot Bay, BC V0P 1H0, Canada. [3]Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC V9T 6N7, Canada. ✉e-mail: kieran_cox@sfu.ca

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cultivate, including clams, crabs, sea cucumbers, and seaweeds, have been observed from Alaska to Washington State[24–27]. Garden walls increase intertidal sedimentation rates by up to fourfold, creating a flattened terrace on the landward side of the wall that expands the amount of available clam habitat[28,29]. The soft-sediment terrace between the clam garden wall and the shoreline is maintained using a suite of tending practices, including adding gravel and broken shells to produce conditions that increase bivalve growth[16,18,21,23]. This ancestral mariculture practice increases clam abundance and productivity, providing predictable and stable shellfish populations adjacent to coastal communities[17,18,30]. Despite the extensive history of clam garden use, their existence and distribution have only recently come to the attention of Western science[16,22,25].

In contrast, contemporary commercial shellfish farming in the northeast Pacific has received considerable scientific attention[5,6,8]. Westernized shellfish farming began in the mid-1800s with the harvesting of Olympia oysters (*Ostrea lurida*). Overexploitation, foreshore modifications, and disrupted settlement cues collapsed this fishery by 1960[31]. The Pacific oyster (*Magallana gigas*), native to Japan, was introduced and cultivated by 1925[32]. The Manila clam (*Ruditapes philippinarum*), initially introduced accidentally with *M. gigas*, was integrated into the growing shellfish market in the 1980s[32]. Cultivating *M. gigas* and *R. philippinarum* involves establishing and maintaining populations within intertidal beaches (i.e., leased tenures) and subtidal shellfish rafts that allow farmers to seed, grow, and harvest shellfish while ensuring product quality and population viability[6,33,34]. Plastic fences, anti-predator netting, and other foreshore modifications (e.g., rock walls, cages) are also often used in the intertidal to section off outplants and increase habitat suitability[7,33,34]. The co-occurrence of western commercial shellfish and Indigenous clam gardens demonstrates the importance of bivalve cultivation within the northeast Pacific and provides an opportunity to assess how differing bivalve management systems influence local ecological conditions.

Here, we test the hypothesis that cultivating intertidal bivalves bolsters habitat complexity and alters substrate composition, fostering increased diversity in non-target communities (i.e., taxa that are not the primary cultivation target). For this investigation, we considered epifaunal (surface) invertebrates to be non-target communities but acknowledge that non-target communities will differ between cultivation methods due to broader resource use within clam gardens (i.e., sea gardens that cultivate and harvest a range of taxa) and the use of mono or co-culture approaches within shellfish farms. The co-occurrence of clam gardens, shellfish farms, and beaches lacking physical modifications along British Columbia's coast provides a natural experiment capable of testing this hypothesis. We quantified the diversity and density of the epifaunal communities within 24 intertidal sites (6 clam gardens, 6 shellfish farms, and 12 unmodified or non-walled beaches) within three regions along British Columbia's central and south coast (Fig. 1). We then evaluated the association of each site's epifaunal communities with the complexity of the physical habitat and substrate composition. To do so, we determined (1) the physical complexity of each intertidal site using structure-from-motion photogrammetry to generate and analyze three-dimensional habitat models, (2) if and how taxonomic diversity and community composition differ among cultivated and unmodified or non-walled sites, and (3) the extent to which alterations in habitat complexity and substrate composition influence biological communities within clam gardens and shellfish farms. The primary comparisons of interest were between shellfish farms and farm reference sites, and clam gardens and garden reference sites; however, differences between shellfish farms and clam gardens were also considered. Collectively, this novel study examines how intertidal resource cultivation practices engineered and implemented over decades, centuries, and millennia can shape contemporary ecosystems.

Results
Community composition
Distinct epifaunal communities were found within the mid-intertidal zones of clam gardens and shellfish farms relative to their respective reference beaches (Fig. 2). However, the extent to which observed communities differed varied among regions and according to cultivation method. Across all regions, clam gardens had elevated taxonomic richness. Of 60 total observed taxa, clam gardens contained 35 taxa, whereas shellfish farms contained 28 taxa, compared to the 27 and 26 taxa observed within garden and farm reference beaches, respectively (Fig. 2a, Table S1). Reduced diversity within garden reference beaches persisted when comparing Shannon diversity and inverse Simpson; both indices were considerably lower within reference sites (Fig. 2a). Comparatively, shellfish farms, clam gardens, and shellfish farm reference beaches exhibited relatively similar Shannon diversity and inverse Simpson values. Cultivated sites exhibited more even communities, as evident by the slope of the order q line stabilizing the Shannon diversity and inverse Simpson values (Fig. 2). Elevated taxonomic richness was more pronounced at clam gardens on Calvert Island and within shellfish farms in Baynes Sound (Fig. 2b, d). Across the site types, unique taxa were present within most of the ecological compartments considered (Fig. 2f, Table S2). Eight taxa were unique to clam gardens, four taxa were unique to shellfish farms, and fifteen taxa were common across all site types (Table S2).

There were significant differences in community composition between site types, years, and sites (Fig. 3, Table S4). These differences were present among and within regions. The non-Metric Multi-Dimensional Scaling (nMDS) plots stress ranged from 0.08 to 0.14, indicating an appropriate model fit between comparisons (Fig. 3). Among regions, the mid-intertidal communities observed within clam gardens, garden reference sites, shellfish farms, and farm reference sites differed (PERMANOVA, $F = 4.98$, $p = 0.018$, Fig. 3a), as did the communities observed annually and within each site (Table S4). Regionally, comparisons between the clam gardens on Calvert Island, Baynes Sound shellfish farms, and their respective reference beaches exhibited a high degree of divergence between communities (Clam Garden PERMANOVA, $F = 3.42$, $p = 0.029$; Shellfish Farm PERMANOVA, $F = 4.88$, $p = 0.005$; Fig. 3, Table S4). Year and site were different within all regional comparisons, except for the clam gardens and clam garden reference beaches on Calvert Island (Fig. 3; Table S4). Non-metric multidimensional scaling plots of mid-intertidal substrate composition display similar differences in community composition (Fig. S6).

Taxon-specific dissimilarity varied substantially between site types, with most taxa increasing in abundance within cultivated habitats (Fig. S7). The SIMPER analysis determined that clam garden and reference beach mid-intertidal communities were 67.66% dissimilar (Fig. 3f). This dissimilarity was driven primarily by increased densities of *Balanus glandula*, *Chthamalus dalli*, *Lottia persona*, *Balanus crenatus*, *Littorina scutulata*, and *Littorina sitkana* (Fig. 3f). Collectively, these taxa contributed over 90% of the cumulative dissimilarity, with numerous taxa (e.g., *Chthaamalus dalli*, *Balanus crenatus*, *Lottorina scutulata*) exhibiting up to a fourfold increase in abundance (Table S5). Although contributing considerably less to cumulative dissimilarity, clam gardens also displayed reduced abundances in several taxa, including *Mytilus* spp., *Haminoea vesicula*, and *Idotea* spp. (Fig. 3f, Table S5).

The SIMPER analysis of shellfish farms and reference sites determined that mid-intertidal communities were 74.86% dissimilar (Fig. 3g). Comparable to the analysis of clam gardens, this dissimilarity was driven primarily by increased abundances of *Balanus glandula*, *Chthamalus dalli*, *Lottia persona*, and *Littorina sitkana* (Fig. 3g). Additionally, *Hemigrapsus* spp. and Amphipoda abundances within shellfish farms increased by 1.5 and 2.4-fold, respectively, accounting for 4.63% and 2.61% of the observed dissimilarity (Table S5). A notable twofold increase in the introduced Japanese mud snail (*Batillaria attramentaria*) abundances was observed within reference sites (Fig. 3g). This increase accounted for 4.29% of the observed dissimilarity and was the only instance in which an increase in the density of a taxon within reference sites contributed more than 1% (Table S5). The comparison of Quadra Island shellfish farms and reference beaches resulted in 77.30% dissimilarity, whereas the Baynes Sound comparison resulted in 72.14% dissimilarity.
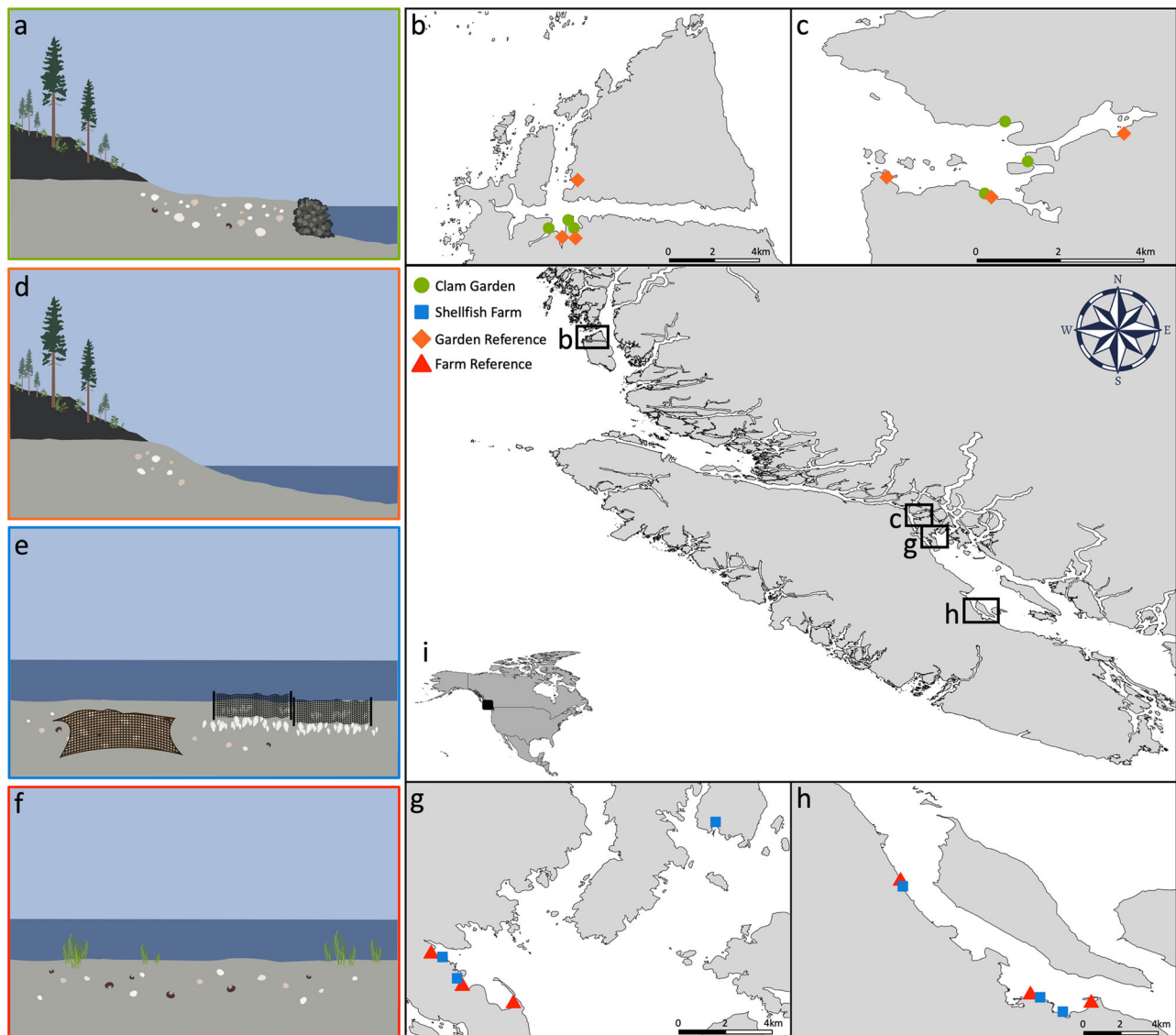
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Fig. 1 | Study locations along British Columbia's central and south coasts and illustrations of site types. Depictions of (**a**) clam garden, **d** unmodified clam garden reference beach, **e** shellfish farm, and (**f**) unmodified shellfish farm reference beach. Study sites within (**b**) Calvert Island and Hecate Island, **c** Northern Quadra Island, **g** Southern Quadra Island, and (**h**) Baynes Sound. **i** Location of British Columbia coastline.

Substrate-epifaunal community associations

The MRT analysis considering all sites and intertidal zones illustrated that the diversity and density of the 24 higher-level taxonomic classifications were primarily associated with gravel, oyster shell, cobble, and *Mastocarpus* spp. (Fig. 4a, Table S3). The root node of this tree identified gravel as the substrate type most closely associated with the epifaunal communities. Littorinidae, Lottiidae, and Sessilia were the discrimination taxa informing this split, all of which had higher right split mean values due to their association with gravel percentages above 7.31% (Table S6). In habitats that met this gravel condition, the subsequent decision node was dictated by the amount of cobble present. The co-occurrence of relatively high gravel and cobble forms a terminal or "leaf" node with a community comprised of the discrimination taxa Decapoda, Mytilidae, and Batillariidae (Fig. 4a). In habitats with relatively low amounts of cobble, the abundance of Pacific oyster shells and gravel dictated community composition. Specifically, an abundance of oyster shells promotes a terminal node community comprised of discrimination taxa Decapoda, Sessilia, Ostreidae, Lottiidae, and Asteriidae. The other terminal nodes were structured by combinations of gravel, oyster shells, and *Mastocarpus* spp. (Fig. 4a).

The MRF variable importance analysis determined the extent to which each substrate type and spatial factor (e.g., region, site) contributed to the resulting epifaunal communities. Average variable importance, a measure of change in the mean squared error, ranged from 0.08 to 17.15% (Fig. 4b), with region, gravel, *Mastocarpus* spp., site type, *Ulva* spp., and oyster shell being the most important factors averaged across taxa. However, variable importance differed considerably when considering taxa independently (Fig. S8), with several robust taxa-variable associations evident. For example, the importance of the associations between *Mastocarpus* spp., region, and gravel for Amphilepidida, were 77.15%, 68.52%, and 42.46%, respectively (Fig. S8, Table S7). The variance explained by the MRF model differed considerably among taxa, and as such, so did the model's ability to predict taxonomic variability (Table S7). Explained model variance was the highest in taxa that were consistently observed across the study sites or exhibited a high degree of site type fidelity. For example, the random forest model explained 48.64%, 46.43%, and 43.35% of the variability observed in Batillariidae, Decapoda, and Sessilia abundances, respectively. The predictive capabilities of the trained model mirrored this trend, with variance explained by the testing dataset proportional to the performance of the full model (Table S7).
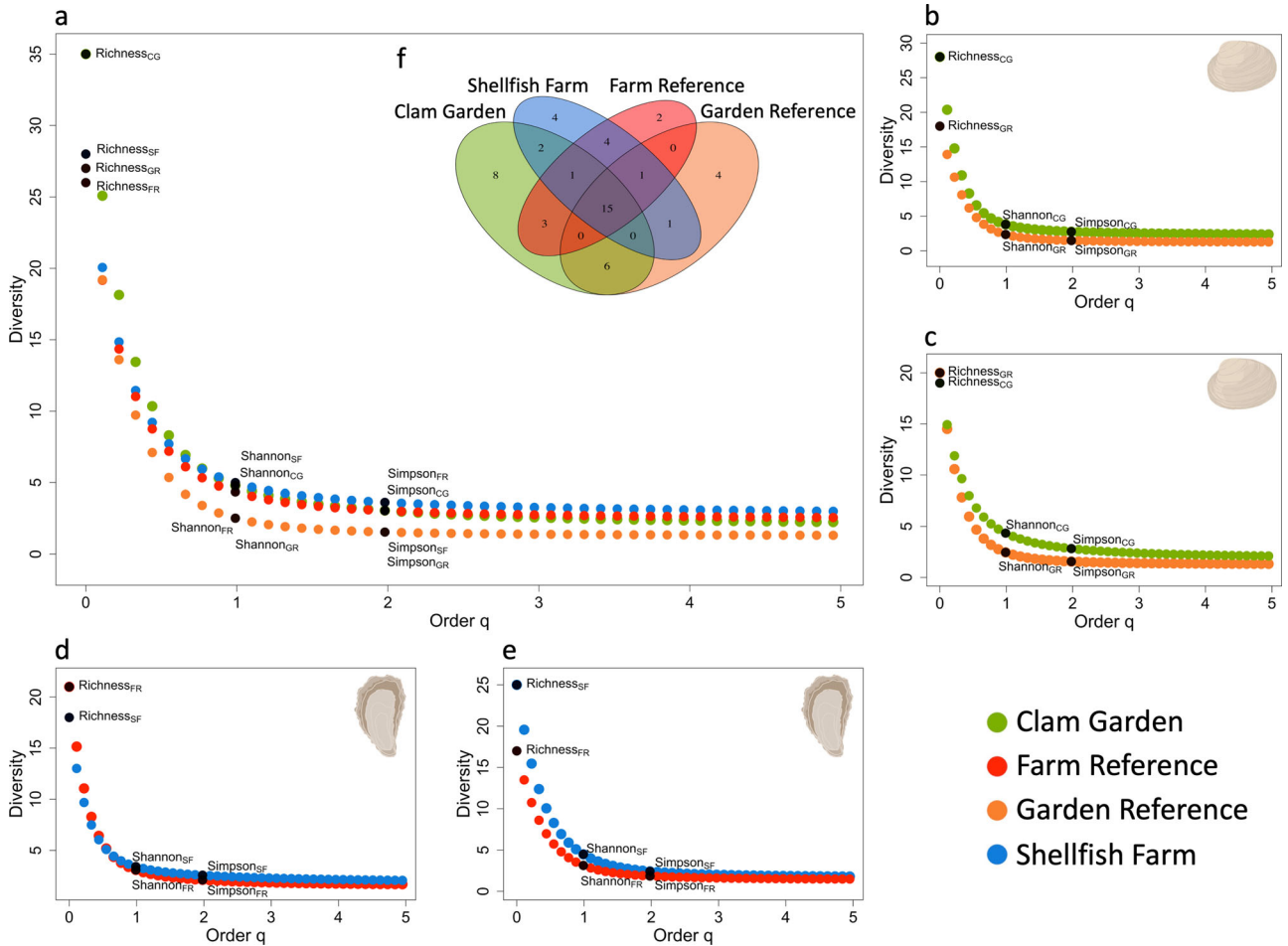
Fig. 2 | Diversity profile curves illustrating mid-intertidal diversity as a function of order q values. Black dots denote Hill numbers: species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson inverse diversity ($q = 2$). The slope of the curve reflects community evenness. **a** Diversity pooled across regions. **b–e** Diversity within (**b**) Calvert Island, **c** Northern Quadra Island, **d** Southern Quadra Island, and **e** Baynes Sound. **f** Venn diagram of taxa unique to each possible comparison. **b–e** Illustrations depict a species cultivated within each site type (**b**, **c**) Butter clams (*Saxidomus gigantea*), **d**, **e** Pacific oysters (*Magallana gigas*).

The MRT analyses conducted on each site type separately identified unique associations between epifaunal communities and the substrate variables. The MRT analysis of reference beaches illustrated that gravel, *Dendraster* shells, *Gracilaria*, and intertidal zone (i.e., tide height) structure these biological communities (Fig. 4c). The root node identified gravel as the most influential substrate type. Low gravel percentages interacted with a *Dendraster* based decision node, with increases in *Dendraster* generating the more diverse terminal node. Substrates within high percentages of gravel were further structured by *Gracilaria*, which, if abundant, interacted with intertidal zone to produce two terminal nodes. Within shellfish farms, *Mastocarpus* spp. structured the root node with gravel, mud and silt forming subsequent branches (Fig. 4d). Higher *Mastocarpus* spp. abundances produced a diverse terminal node with increases in Amphipoda, Batillariidae, Decapoda, Littorinidae, Lottiidae, Mytilidae, and Sessilia. Low amounts of *Mastocarpus* spp. produced a decision node based on mud and silt, which, at lower mud and silt percentages, interacted with gravel to form two terminal nodes—the more taxonomically diverse and dense of these nodes corresponded to increases in the amounts of gravel present. Within clam gardens, the root node of the MRT identified gravel at a relatively high percentage of 60.67% as the substrate type most influential for community composition (Fig. 4e). Habitats with amounts of gravel above this were structured by intertidal zone and *Ulva* spp. Under the root node condition of lower gravel, bivalve shells structure communities. If bivalve shells were abundant, gravel and bivalve shells function in combination to structure communities with gravel constrained by the initial root condition. This interaction generates

four-terminal nodes exhibiting considerable taxonomic diversity and densities. Of these nodes, the co-occurrence of gravel between 45.29 to 60.67%, and less than 31.19% bivalve shell, produced the most diverse and abundant community, comprised of Amphipoda, Cerithiidae, Decapoda, Lottiidae, Polychaeta, and Venerida.

Habitat complexity-epifaunal community associations
Analyzing three-dimensional reconstructions of the 24 sites quantified multiple aspects of each site's structural complexity and determined the importance of habitat structure for the resident epifaunal communities (Fig. 5). The reconstructions were more similar within than among site types, although considerable variability was evident within each site type (Fig. S9). Linear rugosity was elevated within clam gardens and shellfish farms relative to the corresponding reference sites, with clam gardens exhibiting the most rugged substrate (Figs. 5e and S10). Fractal dimension (D) among the site types exhibited a similar trend as linear rugosity; complexity was elevated within clam gardens and shellfish farms (Figs. 5F and S10). These increases in complexity were more prominent within clam gardens than shellfish farms. Unmodified garden and farm reference sites had similar levels of complexity (Fig. 5F). Within each site type, most of the site's D complexity was highest at fine-scale resolutions and declined with increasing resolution (Fig. 5F). Clam gardens deviated from this trend the most as 5–25 and 25–50 cm resolutions exhibited the highest complexity of the four spatial scales considered.
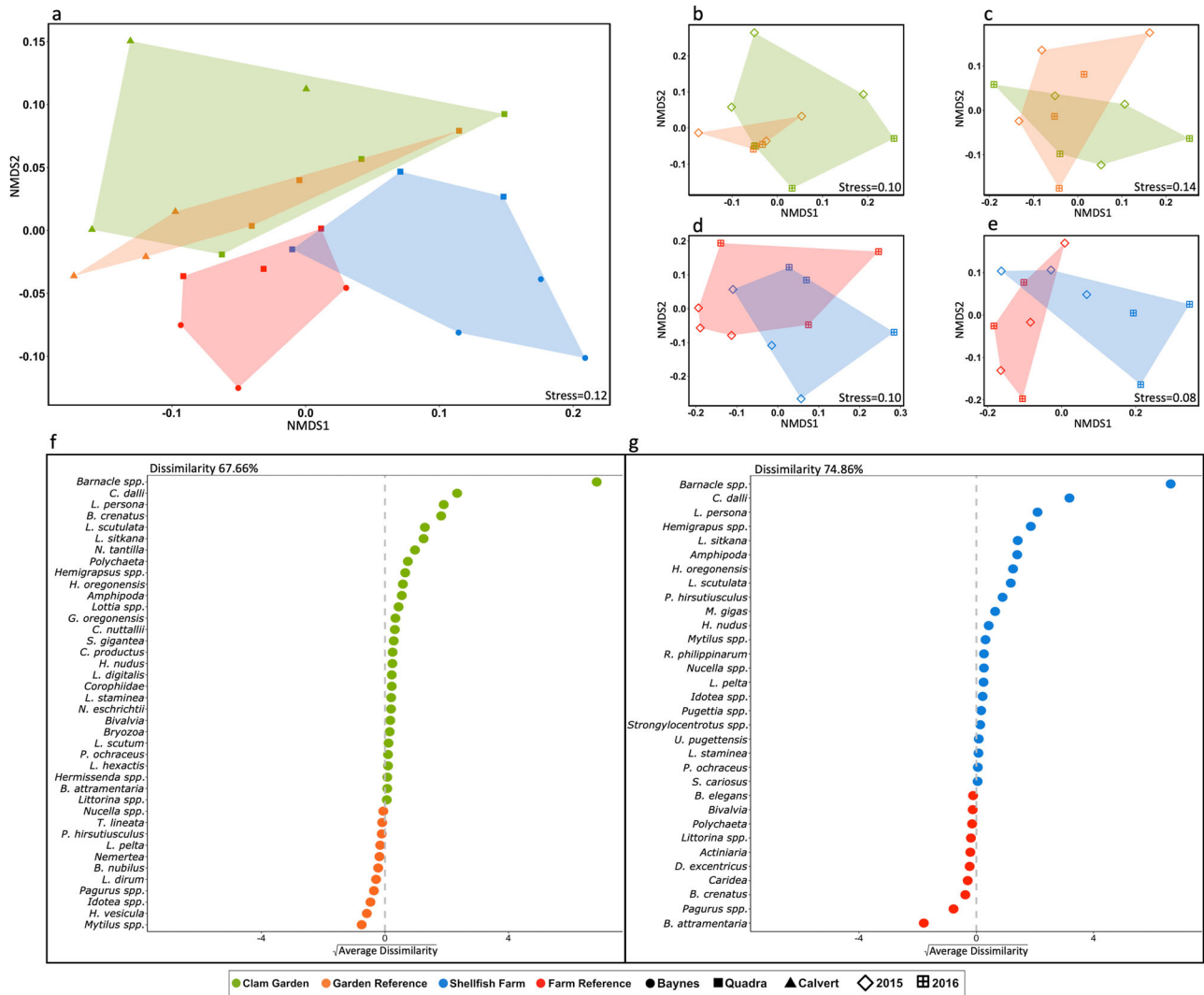
Fig. 3 | Non-metric multidimensional scaling plots and taxa-specific dissimilarity. a Community composition pooled across regions, with shapes denoting the study regions. Community composition within (**b**) Calvert Island, **c** Northern Quadra Island, **d** Southern Quadra Island, and (**e**) Baynes Sound, with fill type denoting years. **f**, **g** The average taxa-specific dissimilarity between cultivated and reference sites, with the square root of average dissimilarity plotted to improve visualization. **f** Clam gardens and clam garden reference beaches. **g** Shellfish farms and shellfish farm reference beaches. **f**, **g** Color denotes if the density of a species increases in clam gardens (green), garden reference sites (orange), shellfish farms (blue), or farm reference sites (red).

The MRF variable importance analysis determined that of the complexity metrics considered, D 25–50, D 50–100, and D 5–25 cm had the most notable impact on epifaunal community structure (Fig. 5g). However, variable order differed considerably for each taxon (Fig. S11), illuminating the unique combination of structural metrics that support each group. Similarly, the variability explained by the MRF model and the model's predictive accuracy also varied among taxa (Table S8). Model quality was strongly linked with population abundance, whereby the MRF model explained more variability for taxa consistently observed across most sites or exhibited a high degree of site type fidelity. Generally, high-quality models generated the most accurate predictions. The MRF model was able to explain up to 39% of the variability in taxonomic abundance and was relatively robust in predicting Decapoda, Batillariidae, Venerida, and Cerithiidae (Table S8).

Discussion

We add to the growing body of evidence that the coastal ecosystems of the northeast Pacific are shaped by intertidal resource cultivation practices engineered and implemented over decades, centuries, and millennia. Evidence that contemporary ecological communities are a function of human-

ecosystem interactions is becoming increasingly vital to global conservation efforts[12,35,36]. Our examination demonstrates that clam gardens and shellfish farms restructure epifaunal communities at several ecological (e.g., populations, communities) and spatial scales, with community responses proportional to how each cultivation practice alters the habitat. This work supports the supposition that traditional and contemporary intertidal resource cultivation practices create distinct nearshore communities[9,17,18,37].

Shellfish cultivation alters the diversity and composition of intertidal epifaunal communities, with clam gardens and shellfish farms producing distinct communities relative to reference beaches. Several taxa, namely *Balanus glandula*, *Chthamalus dalli*, *Lottia persona*, and *Littorina sitkana*, exhibited similar increases in abundance in response to both cultivation methods. Conversely, numerous taxonomic responses were divergent. Convergent and divergent responses were linked to the unique conditions created by each cultivation practice. Notably, altered tidal heights within clam gardens are known to increase bivalve productivity[18,30], and conceivably promote the proliferation of certain species. Altered tidal heights likely also exclude taxa that occupy intertidal zones that are above or below optimal clam habitat (e.g., *Mytilus* spp.) or occur within a habitat that would otherwise occupy the area (e.g., rocky intertidal). Clam gardens further
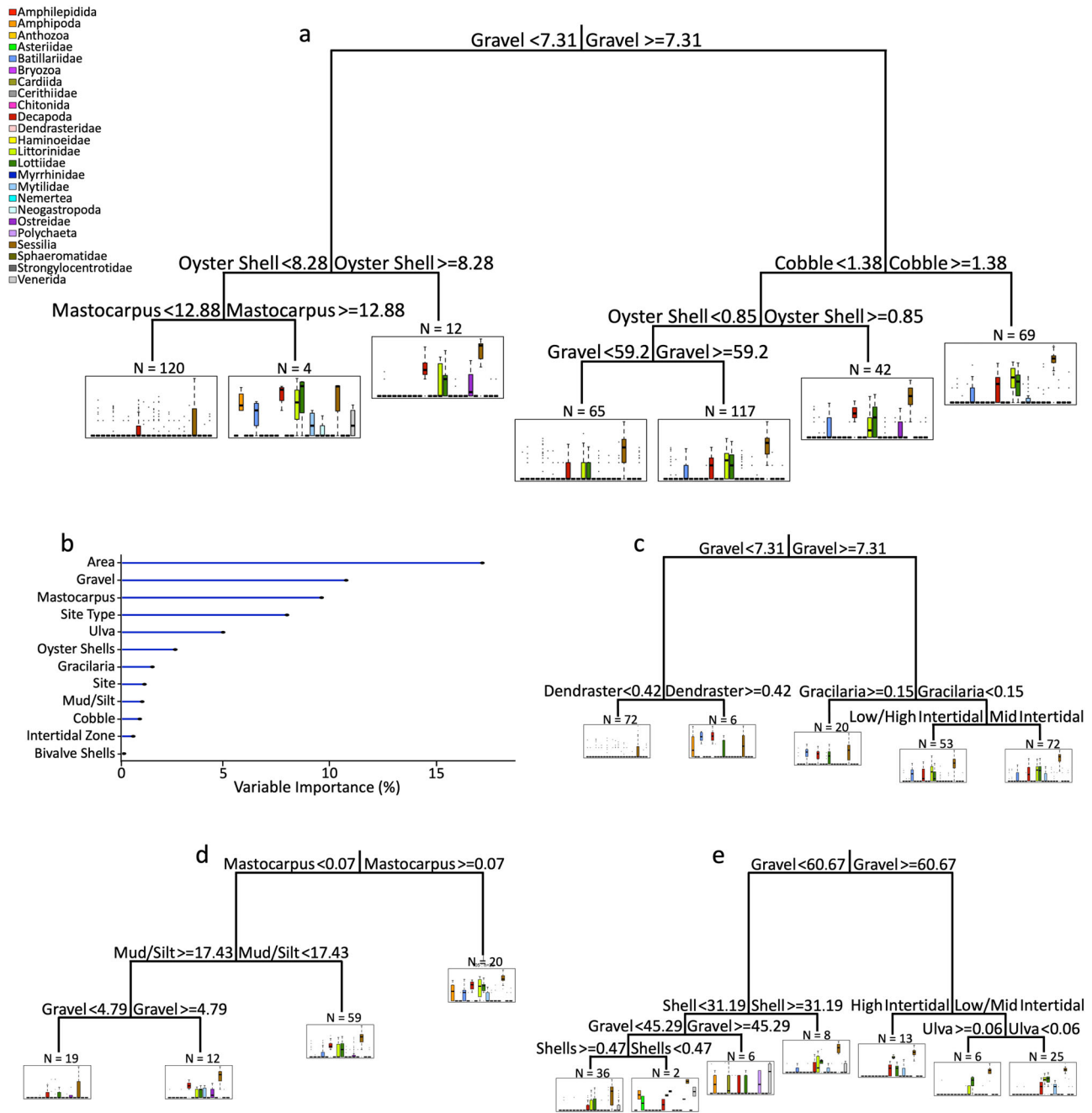
Fig. 4 | Multivariate regression trees (MRT) and multivariate random forest (MRF) variable importance analyses of the interaction between epifaunal communities and substrate composition. Each MRT's decision node denotes the split value for each respective substrate type. The MRT terminal node box plots 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.

promote unique intertidal communities through the emergence of two substrate compositions: elevated amounts of gravel and either abundant bivalve shells or growth of macroalgae (e.g., *Ulva* spp.)[18,21,23,28]. Although our analysis determined that bivalve shells and macroalgae growth support diverse communities, bivalve shells are known to be more ecologically beneficial than macroalgae. Specifically, the oral history of coastal Indigenous Peoples, communicated by Kwakwaka'wakw Clan Chief Kwaxistalla Wathl'thla Adam Dick in Deur et al.[16], states that garden tending practices involve seaweed removal from the beach surface and aerating the sediments through clam digging and increasing the density of shell fragments[21,22]. The MRT and MRF analyses reinforce this knowledge by illustrating that the combination of 45–60% gravel and less than 31% bivalve shells promotes the most biologically diverse communities observed within clam gardens.

Within shellfish farms, *Mastocarpus* spp., a common seaweed that grows on predator-exclusion nets, fostered diverse communities that varied depending on the amount of gravel, mud, and silt present. The role of sediment in this relationship is well-established. Broadly, species diversity and density correlate positively with mud and silt percentages until increases in fine-grain sediments facilitate oxygen depletion, resulting in toxic by-product accumulation and organic loading that cause diversity to decline[38]. Therefore, under optimal conditions, increased niche space provided by *Mastocarpus* spp. elevates biological diversity beyond the capacity of
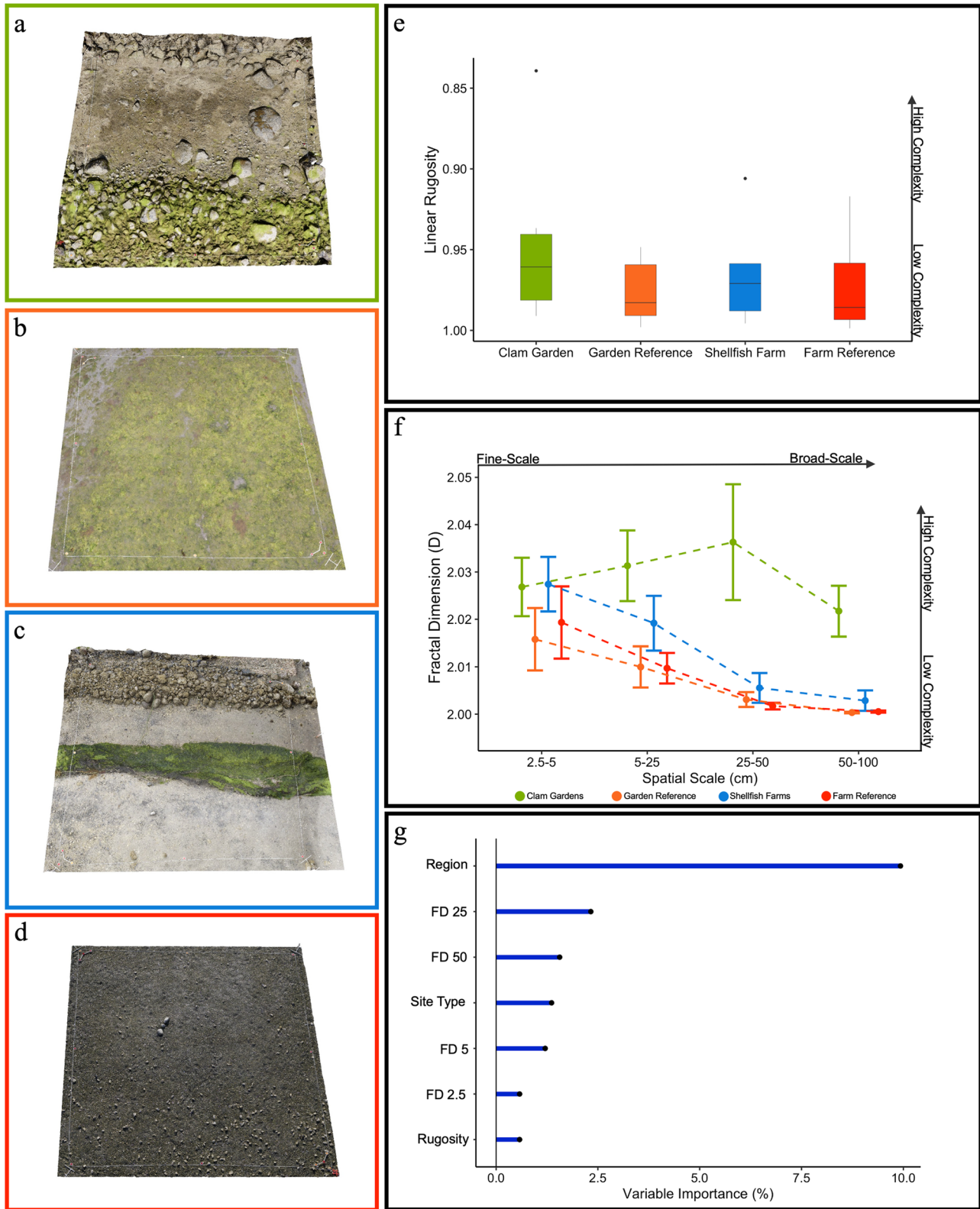
Fig. 5 | Habitat complexity analysis and the association between epifaunal communities and three-dimensional complexity. a–d Example three-dimensional reconstructions of the site types: **a** clam garden, **b** garden reference, **c** shellfish farm, **d** farm reference. **e** Site type's mean linear rugosity. **f** Fractal dimension of each site type at four spatial resolutions. Bar plots are mean and standard error values. **g** Multivariate random forest 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).

reference beaches. Optimal conditions conceivably persist until density-dependent effects or reduced water flow increase organic loading[7,33,39].

Elevated taxonomic richness within clam gardens relative to shellfish farms may be due to the increased structural complexity observed at several spatial scales. Clam garden construction can involve considerable foreshore modifications, including the input of large cobbles and boulders to establish rock walls that alter the beach slope, increase sedimentation rates, and stabilize shorelines[23,28]. These cobble and boulders inputs are within the 25–50 and 50–100 cm spatial scales that coincide with the observed increased complexity. The intertidal rock wall and associated soft-sediment terrace are then managed for generations and adapted to meet changing environmental conditions and community requirements[11,16,22]. Enhanced habitat complexity and ongoing management interact to transform substrate composition by increasing bivalve shells and gravel while removing excess algal growth. This process can transform a range of intertidal habitats into clam gardens, including bedrock, otherwise lacking an established clam population[23]. Alternatively, shellfish farming, a practice that began more recently, usually occurs on beaches with existing bivalve populations and involves the addition of predator exclusion nets, cages, and other low-lying structures into which shellfish broodstock and juvenile non-native shellfish seeds are introduced[32,34]. Therefore, shellfish farming involves comparatively fewer structural inputs within the 25–50 and 50–100 cm spatial scales, cultivation occurs across a less dynamic range of intertidal habitats, and habitat alternations are limited to recent decades.

Distinct physical features and biological communities within clam gardens and shellfish farms benefit these ecosystems. Increases in habitat complexity provide available niche space, offering refuge from adverse conditions and a range of exploitable resources[40]. The interaction between increased complexity and altered substrate composition likely produces more heterogeneous habitats. Specifically, structural inputs associated with clam garden or shellfish farm construction and maintenance directly influence substrate composition (e.g., abundance of boulders, cobble, and soft sediments) but also occur independently of management practices that alter the substrate (e.g., seaweed removal, added shell). Therefore, the taxa residing within these ecosystems respond to structural inputs, modified substrates, or the resulting habitat heterogeneity. The extent to which clam gardens and shellfish farms benefit from this process varies by cultivation method. Broadly, enhanced habitat complexity and altered substrate composition prompted proportional responses within biological communities. These increases in diversity and abundance suggest that the communities within clam gardens and shellfish farms exhibit more functional redundancy and ecological resilience than their respective reference beaches[41]. Consequently, these communities may have an increased capacity to resist and recover from disturbances, which increases the probability that these ecosystems maintain their function (i.e., bivalve production) despite increases in the severity and frequency of perturbations[41,42].

Ecological communities generally responded proportionally to cultivation intensity. However, the prevalence of regional stressors may alter the magnitude of diversity responses. For example, taxonomic richness was elevated at clam gardens on Calvert Island and shellfish farms within Baynes Sound relative to the reference and cultivated beaches surrounding Quadra Island. Calvert Island's nearshore ecosystems are less influenced by anthropogenic activities, with minimal shoreline modifications, overwater structures, and industrial logging relative to more southern regions[43,44]. This difference suggests that the comparatively weaker ecological responses within the Quadra Island sites may be due to anthropogenic stressors, specifically industrial logging[17]. Conversely, the scale and magnitude of shellfish farming within Baynes Sound surpasses northern counterparts, creating a novel ecosystem that maximizes ecological responses to cultivation[7,34,39].

A considerable portion of the examinations of aquaculture focus on environmental degradation, mismanaged introduced species, and declining ecosystem health[7,39,45]. Shellfish cultivation, however, is unique relative to finfish aquaculture in that shellfish require fewer nutrient inputs, occupy a lower trophic position, and introduce fewer infectious agents[39]. These characteristics may explain, in part, why ecological responses to shellfish cultivation persist despite variability in frequency and intensity of management. Ecological responses may lessen over time, but limited feed inputs or broodstock maintenance allows niche alterations attributed to construction to persist. This is a particularly evident situation within clam gardens as the primary cultivation species, *Saxidomus gigantea* and *Leukoma staminea*, occupy surrounding habitats, allowing broadcast spawn to continue to seed beaches[18,30,37]. Ecological responses to shellfish cultivation may cause less degradation than other aquaculture systems, but environmental impacts still occur. *Batillaria attramentaria*, introduced into the northeast Pacific as early as 1928 alongside *M. gigas*[46], exhibits a 2-fold increase within reference sites. Proliferation adjacent to the introduction site implies an invasion model in which the vector distributes the invader into a suboptimal habitat. The introduced taxa then flourish once they reach a more suitable habitat, in this instance, nearby mudflats. Functionally, this implies invasive species management requires surveying beyond the site of introduction and that numerous introduced taxa may be moving towards habitats that will support proliferation. Still, biological communities' responses to shellfish farming and clam gardening indicate that of the existing approaches to harvesting marine resources, shellfish cultivation represents a sustainable balance between human-ecosystem interactions capable of providing access to protein for millennia.

A series of local and global stressors threaten the cultivation of intertidal resources, many of which have become increasingly predominant in recent decades. Warming ocean temperatures, rising sea levels, increasing acidity, and lack of societal engagement in food security threaten shellfish aquaculture[34,45]. Humanity's ability to mitigate these ecological challenges will improve significantly if Indigenous knowledge is at the forefront of management plans[11,12,34,35]. As exemplified by clam gardens and other Indigenous management systems, traditional mariculture practices can be sustainable for millennia and withstand adapting to changing climatic conditions[17,21,47]. Therefore, the knowledge necessary to endure pending disasters has been well-established by coastal Peoples. The cultural, economic, and environmental knowledge developed during 3,800 years of clam garden construction and management and the lessons gained over the last 200 years of shellfish farming pose an opportunity to enhance local food security and mitigate environmental challenges[17,18,24]. This process is ongoing throughout the northeast Pacific, led by Indigenous shellfish farm ownership, Nation-directed clam garden restoration projects, and the expansion of commercial shellfish farming[2,21,32,34]. For example, the Clam Garden Restoration project led by the Hul'q'umi'num and WSÁNEĆ Nations, in partnership with Parks Canada, has restored gardens within the Gulf Islands National Park Reserve using traditional practices guided by Elders and knowledge holders[20,21,48]. Our findings support the notion that these restoration and cultivation efforts restore bivalve populations while creating biologically diverse seascapes that are evident at several ecological and spatial scales.

Conclusions

Scientific evidence that the robust and dynamic history of human-ecosystem interactions structures ecological communities is mounting[9,17,19,49]. A fact well-known by many coastal First Peoples, these interactions are not limited to the ecological communities and cultivation methods described here, as fish weirs, root gardens, forest gardens, landscape terracing, and shellfish cultivation are spatially and temporally abundant throughout the northeast Pacific[9,11,14,29]. Here, we show that intertidal resource management practices engineered and implemented over decades, centuries, and millennia structure contemporary intertidal ecosystems. We propose that the addition of habitat structural complexity and alterations to substrate composition that occur as part of clam garden or shellfish farm construction and maintenance provide the increases in available niche space required to foster distinct and diverse biological communities. Ecological responses can be maintained with continual harvesting and management, elevated through further intervention (e.g., introducing broodstock, excluding predators), and may persist even if reductions in management intensity occur. Understanding the

robust history of enduring intertidal resource cultivation practices is vital to facilitating resource management and conservation strategies that can contribute to achieving balanced human-ecosystem interactions. Shellfish cultivation exemplifies practices that can address diminishing marine resources and declining marine biodiversity while achieving local and global food security.

Materials and methods
Positionality of authors
Research carries the biases, personal history, and motivations of the researchers. The importance of this acknowledgment is amplified as the research questions examined here are at the nexus of Indigenous and settler societies. This positionality statement aims to help readers identify our strengths and weaknesses and any nuances in interpretation related to our social, experiential, or cultural biases. K.D.C is now a Liber Ero and NSERC Postdoctoral Fellow at Simon Fraser University and was a graduate student at the University of Victoria while this research was conducted. H.L.D. and M.B. are graduate students at the University of Victoria. B.M.M. is a graduate student at McGill University. M.H.L. is a marine scientist at the Hakai Institute. N.F.S. is a coastal archaeologist with the Hakai Institute. S.E.D. is a Research Scientist at Fisheries and Ocean Canada and an Adjunct Professor at the University of Victoria. F.J. is a Professor and Liber Ero Chair at the University of Victoria. Our research interests stem from our eagerness to better understand the management practices that have shaped coastal ecosystems for millennia. To us, clam gardens and shellfish farms exemplify a framework for mitigating environmental impacts while enhancing food production and increasing awareness of longstanding management strategies. We recognize that several aspects of these narratives, especially those within the study of clam gardens, are not ours to tell. We have strived for our contributions to this field to be grounded in our expertise as marine community ecologists and archaeologists. While doing so, we recognize that we still have much learning and unlearning to do and are grateful to those who have contributed to our understanding of the spaces we occupy.

Survey locations
This study was conducted within three regions along British Columbia's central and south coast: the Hakai Lúxvbálís Conservancy "Calvert Island" (51.65606°N, −128.13427°W), Quadra Island (50.21033°N, −125.26871°W) and Baynes Sound (49.52371° N, −124.82457° W) (Fig. 1). The 14,000-year continuous occupation of Calvert Island and the surrounding area by Indigenous Peoples established expansive settlements, clam gardens, and other marine resource harvesting sites[9,30]. Further south on northern Quadra Island, extensive clam garden construction has enhanced bivalve populations and increased settlement density in recent millennia[18,24,26]. Clam garden construction in the region began at least 3800 years ago, with gardens built continuously and used to the present day[23,24]. Garden walls are found along 35% of the shoreline, creating 113,000 m² of terrace beaches[26,29]. Shellfish farms on Quadra Island mainly cultivate *M. gigas* and *R. philippinarum*, and are predominantly located on the south end of the island[34]. On eastern Vancouver Island, Baynes Sound supports abundant shellfish farms, producing over half of all shellfish cultured in British Columbia[32,34].

Twenty-four intertidal sites were surveyed in 2015, 2016, and 2017. The four site types examined were clam gardens, non-walled clam garden reference beaches (hereafter, "garden references"), shellfish farms, and unmodified shellfish farm reference beaches ("farm references") (Fig. 1). The sites were distributed across the three study regions: three clam gardens and three garden reference sites on Calvert Island; three clam gardens, three garden reference sites, three shellfish farms, and three farm reference sites surrounding Quadra Island; and three shellfish farms and three farm reference sites within Baynes Sound (Fig. 1). The reference sites used in both comparisons were beaches that could support either a clam garden or a shellfish farm, respectively. Surveys of the biological communities and substrate composition occurred in 2015 and 2016. Habitat complexity surveys occurred in 2017. Long-term monitoring of several sites indicated habitat complexity is conserved year to year. All surveys occurred between May and July, and each regional comparison was surveyed over 5–8-day tidal windows to minimize seasonal effects (e.g., Baynes Sound shellfish farms and reference sites).

Field surveys
Surveys were conducted in a similar manner to previous examinations of regions' intertidal communities[50]. In 2015, site assessments involved running 40-m parallel transects along the 3.0, 2.2, 1.5, and 0.8 m tidelines (above MLLW), and a perpendicular transect from 3.0 to 0.8 m tidelines through the start of each parallel transect (Fig. S1). These transect lines 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 specific tidelines could not be accessed, transects were laid as close to these tidal heights as possible. Within each tidal zone, lines were extended at predetermined distances along the perpendicular and parallel transects. Distances along the perpendicular transects were chosen a priori using a random number generator, while parallel transect distances increased in increments of ten meters to ensure the entire horizontal distance was covered. Assessments occurred at the intersection of these extended lines, with each quantifying the biological community and substrate composition (Fig. S1). Five assessments within each zone were attempted, but only three assessments occurred in some cases due to limited access to each intertidal zone. In 2016, the same methodology was followed; however, based on the results of the previous year's surveys, only the mid-zone was surveyed.

Biodiversity surveys
Biodiversity surveys evaluated the epifaunal (surface) communities present at each of the assessment locations. Assessments were done using a 0.5 × 0.5 m quadrat strung vertically and horizontally every 5 cm to create 100 equal squares. Ten randomly selected 5 × 5 cm squares were chosen from the 100 squares formed by the strung quadrat (Fig. S2). All organisms within each square were counted and identified. If multiple layers (i.e., predator-exclusion nets, oysters) were present, the top and bottom layers were assessed separately and combined, representing the total epifaunal diversity present in the quadrat. The occurrence of multiple layers was low (11 of 435 surveys). Sixty taxa (e.g., species, genera) were observed across the study sites (Table S1). Abundances were multiplied by ten to estimate the total abundance within the quadrat. Despite extrapolation, this subsampling method accurately detects species diversity, reduces assessment effort, and results in reliable species abundance estimates[50]. Pacific oysters (*M. gigas*) were the only species not subsampled as their densities are easily assessed and respond poorly to extrapolation; thus, all oysters in each quadrat were counted. The resulting biodiversity data were denoted as species diversity and abundances within the 0.25 m² area.

Substrate composition
Percent cover of the substrate types observed within the 0.5 × 0.5 m quadrats was determined to evaluate ecological covariates of the associated intertidal substrate. Each quadrat was photographed before the biodiversity survey using a Nikon AW120 camera held 1 m above the quadrat (resolution: 2832 × 2832 pixels). Substrate photos were analyzed using ImageJ to derive surface cover metrics[51]. Quadrat photos were processed in an unordered fashion to avoid observer bias. Percent cover was determined by dividing each substrate's area by the total quadrat area. Algal taxa were primarily denoted by genera, with *Gracilaria* spp., *Fucus* spp., *Mastocarpus* spp., Phaeophyceae (Brown Algae), *Sargassum muticum*, *Ulva* spp., and *Zostera* spp. (eelgrasses) being observed. Habitat-forming calcareous shells and skeletons (tests) were denoted as clam shells, Pacific oyster shells, and *Dendraster* (sand dollar) shells. Sediments were classified using the Wentworth scale to identify the boulder, cobble, gravel, sand, and mud/silt composition of each quadrat.

Habitat complexity models
The structural characteristics of the 24 clam gardens, shellfish farms, and reference beaches were quantified using structure-from-motion (SfM) photogrammetry in 2017. This method generates high-resolution

georeferenced 3D reconstructions of the physical environments using 2D images[52,53]. A 10 × 10 m assessment area was established in the mid-intertidal region at each site, with the top corners at the 2.2 m tideline (Fig. S3). A detailed description of this process is included within the supplemental material (Supplemental Text). Briefly, image acquisition used a Canon SL1 digital SLR camera to photograph the 100 m² survey areas. Three-dimensional reconstructions of the 24 sites were generated using Agisoft Metashape Standard Edition (v1.7.4). The four key stages were: aligning photos, dense point cloud construction, mesh construction, and building texture (Fig. S4). The rendered 3D models of each of the 24 sites were exported as wavefront files for further analysis.

The habitat models were analyzed using Rhinoceros 3D[54]. The structural metrics measured were rugosity and fractal dimension (D). Rugosity (R) uses an extendible chain method to measure the topographic distance covered by a theoretical straight-line distance. Consequently, linear R measurements are between 1 and 0, with lower values denoting more complex surfaces. To avoid confusion, R was considered on an inverted scale (i.e., 0–1), to allow increases in R to reflect increases in complexity. Triplicate 9-m linear R measurements were taken in both directions (6 total) using a virtual chain with a 2 cm link length (Fig. S4B). The mean linear R for each site was determined by averaging the six measurements. Fractal dimension (D) measures how surface area changes with resolution by quantifying the slope of a model's resolution relative to the surface area on a logarithmic scale (i.e., how complexity varies with scale). Measurements of D are between 2 and 3, with higher values signifying increased heterogeneity. Fractal dimension was measured at four spatial resolutions, 2.5–5, 5–25, 25–50, and 50–100 cm; effectively, this measures habitat complexity within these size ranges. Five D measurements at the four spatial resolutions were taken for each model, one in each corner and one in the middle (Fig. S4C). These measurements were averaged to determine mean D at the four spatial resolutions.

Statistical analyses

All data analyses were conducted in RStudio version 3.6.1[55]. Data visualizations and analyses utilized the "ggplot2," "vegan," "mvpart," and "randomForestSRC" packages[55–59].

Community composition. Epifaunal communities were characterized using Hill numbers (i.e., richness, Shannon diversity, and inverse Simpson) to examine the variability between the taxonomic diversity and abundances at clam gardens, shellfish farms, and reference sites. The three indices were represented by a q-value, which denotes the sensitivity of the measurement to the taxa's relative abundances where $q = 0$ is richness, $q = 1$ is Shannon diversity, and $q = 2$ is inverse Simpson[50,60]. A function of order q (i.e., q value) until a maximum of five was generated for each site type and regional comparison (e.g., Quadra Island clam gardens and reference sites). The values were plotted as diversity profile curves, illustrating diversity as a function of order q. The resulting curve's slope reflects community evenness, with steeper curves denoting uneven abundances. Taxa unique to each site type, co-occurring between comparisons, and those present among all habitats were examined using a Venn diagram, illustrating the allocation of landscape species richness (gamma diversity) into the various ecological compartments. These analyses considered only the 2015 and 2016 biodiversity surveys conducted within the mid-intertidal zone to ensure a balanced sampling effort and minimize the confounding effect of tidal height ($N = 235$ 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" package[58], 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 between site types[61]. *Balanus glandula* and Barnacle Spp. (i.e., unidentifiable barnacle species) were merged during this analysis due to taxonomic resemblances; the majority of Barnacle Spp. were likely juvenile *B. glandula* that could not be differentiated from juvenile *Chthamalus dalli*.

Substrate-epifaunal community associations. Multivariate regression trees (MRTs) were used to analyze the association between the abundances of epifaunal taxa and substrate composition. The MRTs were fitted in R-Studio using the package 'mvpart'[56]. The 60 taxa observed during the biodiversity surveys were amalgamated into 24 higher-level taxonomic classifications to improve pattern visualization (e.g., family, order; Table S3). Densities were log-plus-one-transformed, following the addition of a dummy variable of 1. Multivariate regression trees analyzed taxonomic densities within and among site types. Garden and shellfish reference sites were pooled for this analysis to improve the description of the substrate types that structure the ecological communities within these habitats. Therefore, four separate MRTs were constructed: all sites combined, clam gardens, shellfish farms, and reference sites. This approach identified the environmental characteristics that predict taxonomic diversity within site types and among intertidal ecosystems. It also allowed the high, mid, and low intertidal zone surveys ($N = 435$ quadrats) to be considered without influencing the validity of comparisons (e.g., creating an unbalanced sample comparison).

Each MRT evaluated epifaunal taxonomic density as the response variable, and intertidal zone, percent boulder, cobble, gravel, sand, mud/silt, clam shells, oyster shell, *Dendraster* (sand dollar) shells, *Gracilaria* spp., *Fucus* spp., *Mastocarpus* spp., Phaeophyceae (Brown Algae), *Sargassum muticum*, *Ulva* spp., and *Zostera* spp. as explanatory variables. The optimal tree size for each MRT was determined following one-hundred-fold cross-validation. The three MRTs considering each site type separately were pruned to the lowest cross-validation error rate. The MRT with sites combined was pruned according to the one standard error rule, which states that the most parsimonious model is one with an error rate within one standard error of the best model[62]. This multi-method approach to pruning provided a more informative description of the substrate features important within each site type and a more conservative estimate of the substrate features relevant across intertidal sites. The tree's splits were chosen using a sum of squares criteria that minimizes each node's sums of squared distances. The four MTR trees were pruned to 4-7 'leaves' to avoid overfitting. The taxa that contributed the most to each split in the MTR with sites combined were determined using a discrimination analysis. This identified the taxa that explain the most variance at each node, the directionality (i.e.,

left versus right split) of their contribution, and the probability that the contributed variance was non-random.

Substrate variable importance. A multivariate random forest (MRF) was constructed using survey data from all habitats, intertidal zones, and the 'randomForestSRC' package to determine which of the substrate types identified by the previous MRTs were the most important to epifaunal taxa[59]. The MRF considered the importance of percent cobble, gravel, clam shells, *Mastocarpus* spp., *Ulva* spp., oyster shell, mud/silt, *Dendraster* shells, and *Gracilaria* spp., for the surveyed 24 taxa (Table S3). Site type, region, site, and intertidal zone were included in this investigation to identify the extent to which features not captured in the substrate survey may be contributing to diversity patterns. The MRF consisted of 6000 trees grown to a maximum node depth of six to avoid overfitting (Fig. S5). The number of candidate variables randomly selected for splitting a node was 4, following the default p/3 recommendation for regression, where p equals the number of variables. The minimum terminal node size was 5, again, following the regression default. The implications of different node sizes, number of trees, node depth, and candidate variables were explored and had minimal influence on the outcomes. Variable importance was calculated by randomly permuting values of the variables, running them through the model, and evaluating the change in mean squared error (MSE). Variable importance was determined for each of the 24 taxa and averaged among taxa.

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

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

An MRF analysis determined which of the habitat complexity measurements were the most important to epifaunal communities. The analysis used the 2015 and 2016 mid-intertidal zone epifaunal survey data to increase the spatial overlap between the measurements of the rendered models and the surveys while ensuring a balanced sampling effort. Epifaunal survey values were averaged according to the site's mid-intertidal zone for each year, then the 2015 and 2016 values were averaged for each site. Epifaunal data were log10 transformed following the addition of a plus one dummy variable. The MRF considered site type, region, average R, and D2.5, D5, D25, and D50 for the surveyed 24 taxa. The "site" term was not included in the MRF as the biodiversity and complexity data were determined at the site level. The MRF consisted of 6000 trees grown to a maximum node depth of six to avoid overfitting. The minimum terminal node size was 3, which deviated from the default setting for regression based on the 'tune node' functions recommendation. In keeping with previous MRFs, the importance of each variable was calculated by randomly permuting the values of the variables, running them through the model, and evaluating the change in mean squared error. Variable importance was determined for each of the 24 taxa and averaged among the taxa. A subsequent analysis examined the extent to which the MRF could predict species occurrences based on observed habitat complexity. The predictive accuracy of the MRF was determined using 80% of the data to train a model and the remaining 20% of the data to evaluate the model's predictions. Model construction used identical parameters as the previous variable importance analysis.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data required to interpret the results of this study are available in the supplemental. All data and code are available to any members of the Indigenous Nations whose territory this research was conducted within or shellfish farmers who lease the intertidal land where the research was conducted. Portions of these data are culturally sensitive in nature, restricting their open-access release. These data can be requested through Figshare with the identifier https://doi.org/10.6084/m9.figshare.25904917. Data and code that are not culturally sensitive in nature can be assessed through Figshare identifier https://doi.org/10.6084/m9.figshare.26044897.

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Author contributions
S.E.D. conceptualized the project. K.D.C., M.H.L., F.J., and S.E.D. designed the project; K.D.C., H.L.D., B.M.M., M.B., M.H.L., and S.E.D. performed the field surveys; K.D.C. analyzed the data; H.L.D. created the illustrations; K.D.C., H.L.D., B.M.M., M.B., M.H.L., N.F.S., F.J., and S.E.D. wrote the paper; M.H.L., N.F.S., F.J. and S.E.D provided supervision and funding acquisition.

Competing interests
The authors declare no competing interests.

Additional information
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Correspondence and requests for materials should be addressed to Kieran D. Cox.