

Research Article

Ecosystem engineers and functional dominance: when species loss matters for ecosystem function

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Understanding when and why species loss affects community function in natural communities remains an open question in ecology. Recent cross-system analyses have shown that functional dominance is associated with whether species loss matters: in communities dominated by few high-performing species, lost species contribute little to function. But the question is what generates functional dominance in the first place. Here we examine whether an ecosystem engineer can generate it. Along a natural density gradient of the intertidal mussel *Mytilaster minimus* (202–2317 ind. m⁻², 54 samples, 93 associated taxa) in the Mediterranean Sea, we applied the extended Price equation to decompose between-site variation in community abundance into five additive components. Context dependence (CDE) – the inflation of shared species – is the largest component of the change in community function along the density gradient, accounting for ~46% of total absolute variation across Price components. Species loss is non-random: rare, low-functioning species are preferentially lost at low engineer density. Functional dominance increases with engineer density and the importance of species loss is lower where dominance is higher, replicating the cross-system dominance pattern within a single engineer-structured system. Each Price component correlates with the quantity and quality of organic matter trapped by the mussel matrix: the CDE tracks trapped organic matter ($\rho = -0.45$), non-random species identity tracks total biopolymeric carbon ($\rho = +0.44$) and species loss tracks microalgal biomass (partial $r = -0.52$ controlling for density). The ecosystem engineer thus generates a resource-mediated pathway: density drives trapping, trapping feeds the dominant species, dominance buffers function against species loss. This mechanism is consistent with species richness per se being a poor predictor of function in engineer-structured systems and points to engineer density as a highly informative conservation parameter.

Keywords: biodiversity-ecosystem functioning, ecosystem engineer, functional dominance, *Mytilaster minimus*, organic matter trapping, Price equation, resource-mediated pathway, species loss



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Introduction

A positive relationship between species richness and ecosystem function is among the most replicated results in ecology, particularly in experimental studies (Cardinale et al. 2012, Hooper et al. 2012, van der Plas 2019). Yet decades of experimental evidence have not resolved how species loss affects function in natural communities. Experiments that randomize species composition at varying richness levels consistently show strong richness effects (Hector et al. 1999) while observational studies in real communities find that richness, composition, dominant species or aggregate abundance variably drive function (Winfrey et al. 2015, Duffy et al. 2017, Genung et al. 2020). This discrepancy has been attributed to functional dominance: when communities are dominated by a few high-performing species, species richness is less important because lost species tend to be those contributing least to function (Grime 1998, Smith and Knapp 2003, Genung et al. 2020). Genung et al. (2020) formalized this insight using the ecological Price equation (Fox 2006, Fox and Kerr 2012) across 129 experimental and natural datasets, showing that higher functional dominance is associated with a weaker effect of species loss on function in nature but not in experiments. A key question left open by their analysis concerns the factors generating functional dominance in natural communities. If the mechanism generating dominance could be identified, then the conditions under which species loss matters for functioning would become predictable from first principles rather than measured post hoc.

Ecosystem engineers – organisms that modulate the availability of resources for other species by modifying the physical habitat (Jones et al. 1994) – could be strong candidates to answer this question. Engineers create biogenic habitats that determine the structural template within which associated communities assemble (Buschbaum et al. 2009, Koivisto and Westerborn 2010, Crotty et al. 2018, Bogdanski et al. 2024). Bivalve beds in particular trap organic matter (OM) within their interstitial matrix, providing a trophic resource that sustains deposit feeders, micrograzers and detritivores (Bégin et al. 2004, Norling and Kautsky 2007, O'Connor and Crowe 2008). If the density of the engineer controls OM availability and if OM availability selectively inflates certain trophic guilds, then engineer density should generate functional dominance and ultimately determine whether species loss translates into functional loss. The direction of this effect is not given a priori. An engineer that subsidises a narrow set of resource-dependent species will raise dominance and lower evenness, whereas one that adds habitat for many rare species without a dominant resource pathway could instead raise evenness and lower dominance; engineers can therefore in principle push communities either way. We state the prediction directionally – that in this system increasing engineer density raises functional dominance and thereby weakens the link between species loss and function – and let the data adjudicate.

Here we test this hypothesis in intertidal beds of the small mussel *Mytilaster minimus* along a natural density gradient

in a Mediterranean coastal area. We used the extended Price equation partition (Fox and Kerr 2012) – which distinguishes species loss from species gain and separates random from non-random components – to decompose variation in community function across patches with different engineer densities. We then correlated each Price component with measurements of trapped organic matter quantity (Trap DW) and quality (chlorophyll a [CHL-a] and lipids [LIP], proteins [PRT], carbohydrates [CHO] and their sum as expressed by biopolymeric carbon [BPC]) to identify the trophic mechanism linking engineer density to community structure. Finally, following Genung et al. (2020), we tested whether functional dominance – itself a product of engineer density – predicts the importance of species loss. Our prediction was that ecosystem engineers generate a resource-mediated pathway (density $\square$ trapping $\square$ dominance $\square$ buffered function) that highlights the importance of engineer density on community function and explains why species richness per se is often a poor predictor of community function in natural communities. To make the chain of reasoning explicit, the analysis proceeds in four mapped steps. We first characterise community structure along the density gradient (richness, evenness, beta diversity and species-density scaling) to test whether dominance rises with engineer density. We then partition functional change with the extended Price equation to test whether context dependence, rather than species loss, dominates. We next correlate each Price component with trapped-OM quantity and quality, using partial correlations on density as a mediation test, to identify the trophic mechanism. Finally, following Genung et al. (2020), we test whether functional dominance predicts the importance of species loss. Each hypothesis, the method used to test it and the corresponding result are summarised in the schematic roadmap.

Material and methods

Study system and sampling design

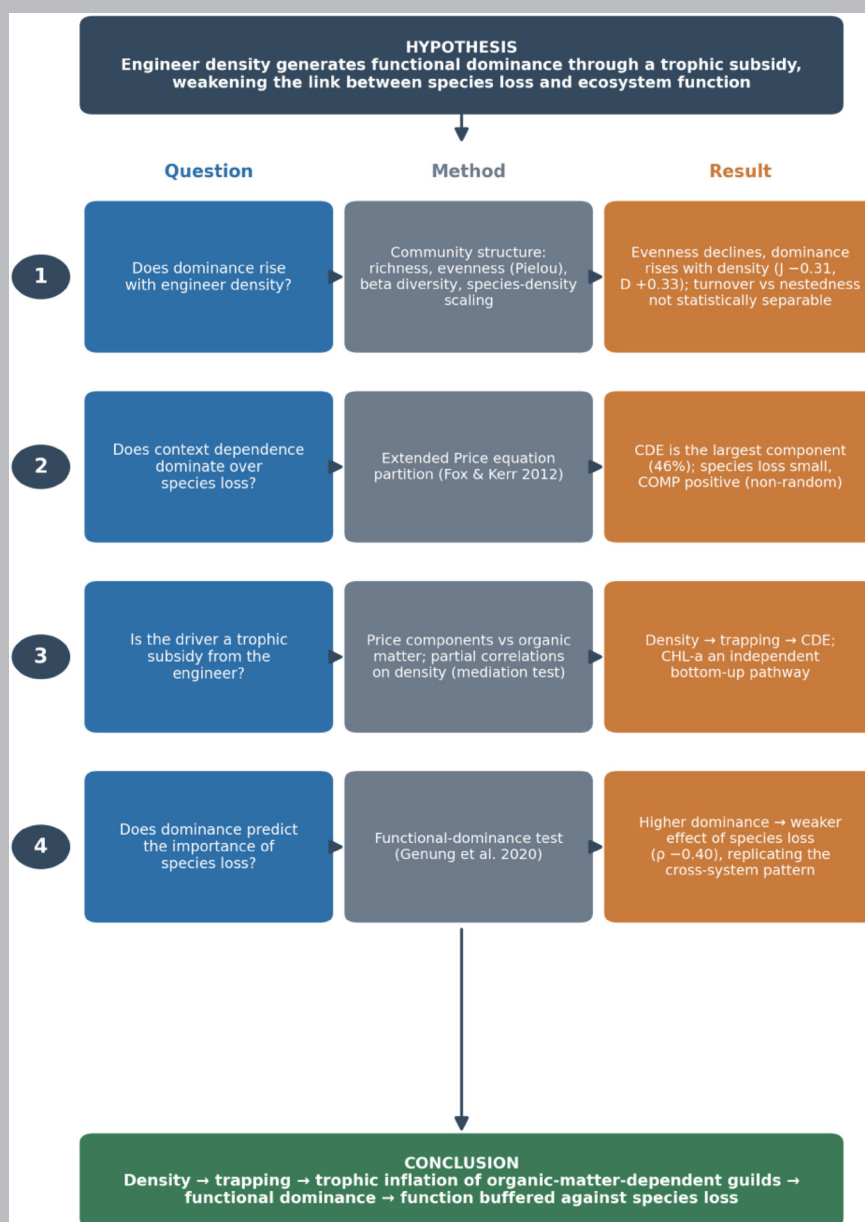
The study was conducted at two rocky intertidal sites along the north-western coast of Sicily, between Trapani and Palermo (Mediterranean Sea), hereafter referred to as site C and site A. The two sites showed similar wave exposure and tidal conditions, with a microtidal semidiurnal regime and a tidal amplitude of about 30 cm, typical of the southern Mediterranean Sea. At both sites, *Mytilaster minimus* forms continuous beds in the mid-intertidal zone with naturally varying density. *Mytilaster minimus* is a small Mytilid (adult shell length 5–12 mm; Sarà and De Pirro 2011) that creates three-dimensional biogenic habitats by attaching to the rocky substrate and to conspecifics via byssus threads. The interstitial matrix among living and dead shells traps sediment and organic matter (OM), providing substrate, refuge and trophic resources for a diverse community of associated invertebrates.

At each site, 27 quadrats (10 $\times$ 10 cm) were haphazardly placed within *M. minimus* beds, spanning the full range of

Box 1

Analytical roadmap.

Each of the four hypotheses tested in this study is linked to the method used to test it and to the corresponding result. The cascade runs from engineer density through organic-matter trapping and the trophic inflation of organic-matter-dependent guilds to functional dominance and the buffering of function against species loss.



naturally occurring densities (site C: 202–2184 ind. m^{-2} ; site A: 352–2317 ind. m^{-2} ; overall: 202–2317 ind. m^{-2} ; $n = 54$ quadrats total). All material within each quadrat was scraped from the rock surface and preserved in 4% buffered formalin. In the laboratory, *M. minimus* individuals were counted and reported as density (number of individuals per m^2) and all associated macrofauna were sorted, identified to the lowest

practicable taxonomic level (usually species) and counted. A total of 93 associated taxa were recorded across the 54 quadrats. Trapped material was separated from the biological fraction by wet sieving (0.5 mm mesh), dried at 60°C for 48 h and weighed (Trap DW, g dry weight). Shell fragments were similarly quantified (Frag DW). Biochemical composition of the trapped OM was determined on subsamples following

standard spectrophotometric protocols (Danovaro and Fabiano 1990, Sarà and Mazzola 1997): CHL-a (Lorenzen and Jeffrey 1980, $\mu\text{g g}^{-1}$), LIP (Bligh and Dyer 1959, Marsh and Weinstein 1966), PRT (Hartree 1972), CHO (DuBois et al. 1956) and BPC ($\text{BPC} = 0.49 \times \text{LIP} + 0.49 \times \text{PRT} + 0.40 \times \text{CHO}$; all in mg g^{-1}). BPC represents the fraction of sedimentary OM that is potentially available to benthic consumers (Graf et al. 1983, Grant and Hargrave 1987, Fabiano et al. 1995, Sarà 2006). Feeding guild assignments for each taxon were based on published literature (Hayward and Ryland 1995, Southward and Campbell 2006, Supporting information). All variables were measured at the individual quadrat level, yielding a fully crossed dataset of community composition, engineer density and OM quantity and quality.

Extended Price equation partition

We applied the five-term extended Price equation of Fox and Kerr (2012) to decompose between-site differences in total community function. For each pairwise comparison of a higher-function baseline site (s species, total function $T = \sum z_i$) and a lower-function comparison site (s' species, total function $T' = \sum z'_j$), the difference $\Delta T = T' - T$ is partitioned into five additive terms (see also Harrison et al. 2022 for an abundance-based extension):

$$\Delta T = \text{SREL} + \text{SREG} + \text{SCEL} + \text{SCEG} + \text{CDE}$$

where $\text{SREL} = (s - s') \bar{z}$ is the expected functional change from random species loss; $\text{SREG} = (s' - s) \bar{z}'$ is the expected change from random species gain; $\text{SCEL} = \text{Sp}(w_L, z)$ captures non-random loss of species with respect to their baseline function; $\text{SCEG} = -\text{Sp}(w_G, z')$ captures non-random gain; and $\text{CDE} = \sum \Delta z_i$ is the context-dependent change in function of species shared between both sites ($s = \text{number of shared species}$). Throughout, the subscripts L and G denote loss and gain, $\bar{z}$ and $\bar{z}'$ are the mean per-species function at the baseline and comparison site, w_L and w_G are the indicator vectors selecting the lost and gained species. $\text{Sp}(x, z)$ is the sum-of-products operator of Fox (2006), i.e. the summed cross-product of x and z over species, equivalent to a population covariance scaled by the number of species. Species functional contribution z_i was defined as the abundance (number of individuals per m^2) of species i at a given site. Total function $T = N$ (total abundance) is thus a summed function sensu Fox and Kerr (2012), satisfying the additivity requirement of the Price framework. Abundance as z_i is a structural proxy for community-level function rather than a direct ecosystem rate, this currency is consistent with several natural-community applications of the ecological Price equation (Winfree et al. 2015, Genung et al. 2020, Harrison et al. 2022, Ulrich et al. 2022). In those applications the per-species function is typically abundance multiplied by a per-capita function estimator (for example per capita pollen deposition in Winfree et al. 2015) that rescales function differently among species but is held constant across sites; using raw abundance here is the special case in which this per capita term equals one for every

species, so that between-site differences in function are driven by abundance alone. Two clarifications follow. First, in the Fox and Kerr (2012) partition z_i is the per species function and total function is its simple sum ($T = \sum z_i$); there is no separate relative-abundance weighting, so adopting abundance as z_i does not collapse the partition into an absolute-count identity but applies the framework with abundance as the function currency as in Winfree et al. (2015) and Harrison et al. (2022). Second, the partition does work that a direct comparison of dominance cannot: the composition terms (SCE_L , SCE_G and their sum COMP) isolate whether the species lost or gained are systematically higher- or lower-functioning than the community average, and it is exactly this non-random component that separates natural from experimental communities (Genung et al. 2020). We none the less treat abundance as a structural proxy and return to its limitations in the Discussion.

Following Genung et al. (2020), we defined species loss as $\text{RICH} + \text{COMP} = (\text{SRE}_L + \text{SRE}_G) + (\text{SCE}_L + \text{SCE}_G)$, capturing all functional changes attributable to changes in species number and identity. We quantified the non-randomness of species loss as COMP/RICH : values near zero indicated random loss; positive values indicated preferential loss of low-functioning species (the natural-community pattern in Genung et al. 2020) and finally negative values indicated preferential loss of high-functioning species. Throughout, species loss refers to compositional differences between assemblages along the spatial density gradient, not to temporal extinction events.

We conducted two complementary analyses. First, we pooled samples into five density quintiles (Q1–Q5) and computed the Price partition using Q1 (lowest density) as the baseline against each higher quintile. Second, following Genung et al. (2020), we computed the partition for all possible pairwise comparisons of individual samples ($n = 1429$ pairs where the baseline had higher total function). For each pair, all five terms were normalised by baseline function T to yield unitless effect sizes comparable across pairs and across ecosystem functions. The organisation of higher-function baseline against lower-function comparison sites follows Fox (2006) and Fox and Kerr (2012); each term is then standardised relative to baseline function. The two analyses serve different purposes and provide a robustness check on each other: the quintile partition gives an interpretable, pooled picture of the density extremes, whereas the all-pairwise analysis uses no binning at all and therefore does not depend on the arbitrary choice of quintiles. Because the two approaches yield the same qualitative conclusions, the dominance of context dependence and the sign of the composition term are not artefacts of how density classes are defined.

Functional dominance

Functional dominance was quantified for each sample using the Hill-number-based index of Chao and Ricotta (2019) at order $q = 1$, as implemented by Genung et al. (2020): $D = 1 - (e^H - 1)/(S - 1)$, where H is Shannon entropy computed on

species abundances and S is species richness. D ranges from 0 (all species contribute equally) to 1 (one species dominates). We tested whether functional dominance predicts the importance of species loss and the non-randomness of species loss by correlating D with the mean normalised Price components across all pairwise comparisons of each sample. This index is the complement of an abundance-based evenness and is therefore related to classical evenness measures (Pielou 1966); we use the Chao and Ricotta (2019) formulation at $q=1$ to remain directly comparable with Genung et al. (2020). As with any evenness or dominance metric, the relationship between species loss and the index is not fixed in sign: the loss of rare species can raise evenness and lower dominance, so the direction we report is an empirical property of this system rather than a built-in consequence of the metric.

Beta diversity decomposition

To characterise whether changes in community composition along the density gradient reflect species replacement (turnover) or ordered species loss (nestedness), we partitioned pairwise Sørensen dissimilarity into its turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) components following Baselga (2010). The partitioning was applied both to density quintile pools and to individual sample pairs.

Species–density relationship

We fitted a power-law species–area relationship treating engineer density as the analogue of island area: $\log(S) = \log(c) + z \times \log(\text{Density})$. The exponent z was estimated by ordinary least-squares regression on log-transformed data. Models were fitted for the full dataset and for each site separately. The canonical range for oceanic islands is $z=0.20\text{--}0.35$ (MacArthur and Wilson 1967). To derive a conservation-relevant prediction, we estimated the proportional species loss expected from a 50% reduction in engineer density as $1 - (0.5)^z$.

Price components and organic matter

To test whether the trophic resource generated by the ecosystem engineer explained variation in Price equation components, we correlated per-sample mean values of each Price component with sample-level OM variables: Trap DW (quantity of trapped material), BPC (biopolymeric carbon concentration), CHLa (benthic microalgal biomass) and OM_{total} ($= BPC \times \text{Trap DW}$, i.e. total biopolymeric carbon per sample). To assess whether OM effects were independent of engineer density, we computed partial correlations between Price components and OM variables controlling for density.

Statistical analysis

Because pairwise Price comparisons are not independent (each sample appears in multiple pairs), all inferential statistics were computed at the sample level rather than at the pair level. For each sample serving as baseline, we computed the mean of each normalised Price component across all its pairwise comparisons. The sample with the lowest total function never served as baseline, yielding $n=53$ samples with

valid baseline-perspective mean Price terms. These sample-level means were the units of analysis for all subsequent tests. Confidence intervals for mean Price components were obtained by bootstrap resampling of the 53 sample-level means (9999 replicates; percentile method). Effect sizes were quantified as Cohen's d (mean/SD) and as relative importance ($|\text{component}|/\Sigma|\text{all five components}|$). To test whether species loss was non-random ($COMP \neq 0$), we permuted species identity labels within samples (999 permutations), recomputing the Price partition after each permutation. Correlations between Price components and OM variables were tested by Spearman (ρ) rank correlation with significance assessed by permutation of sample labels (999 permutations), equivalent to a Mantel-like test. Partial correlations controlling for density were accompanied by bootstrap 95% confidence intervals (999 resamples of samples). The Genung et al. (2020) test of functional dominance as a predictor of species loss importance was conducted by Spearman correlation with permutation-based significance (999 permutations of dominance labels) and bootstrap 95% CI. Influential observations in bivariate correlations were identified using Cook's $D > 4/n$. All analyses were performed in Python 3.12 using NumPy, SciPy and pandas.

Results

Community structure along the engineer density gradient

A total of 93 taxa (17 472 individuals) were recorded across 54 quadrats spanning a tenfold range in *Mytilaster minimus* density (202–2317 ind. m^{-2}). Species richness (S) ranged from 7 to 34 and total abundance (N) from 20 to 1355 individuals per quadrat (Fig. 1a). N increased with density (Spearman $\rho=+0.52$, $p < 0.001$) but S increased weakly but significantly with density ($\rho=+0.27$, $p=0.043$) with a strong site effect: mean S was 23.1 at site C and 10.9 at site A across comparable density ranges (Fig. 1a). Shannon diversity H was unrelated to density ($\rho=+0.03$, $p=0.82$), while Pielou evenness J declined significantly ($\rho=-0.31$, $p=0.03$; Fig. 1b), indicating that increasing engineer density produced communities with more individuals but a more uneven distribution of abundances among species. Community composition between density extremes was predominantly nested: 92.5% of species present in the lowest density quintile also occurred in the highest quintile (37 of 40 species), whereas 25 species were unique to high density and only 3 to low density, though intermediate quintile comparisons were dominated by turnover (Supporting information). Beta diversity decomposition confirmed that dissimilarity between the extreme quintiles (Q1 versus Q5) was 74% nestedness-driven ($\beta_{SNE}=0.213$) and only 26% due to turnover ($\beta_{SIM}=0.075$), although the difference between the turnover and nestedness components was not statistically distinguishable in any Q1–Q k comparison, the bootstrap 95% confidence intervals of the two components overlapping in all cases (Fig. 1d), while the Q2 versus Q4 pair showed 97% turnover (Supporting

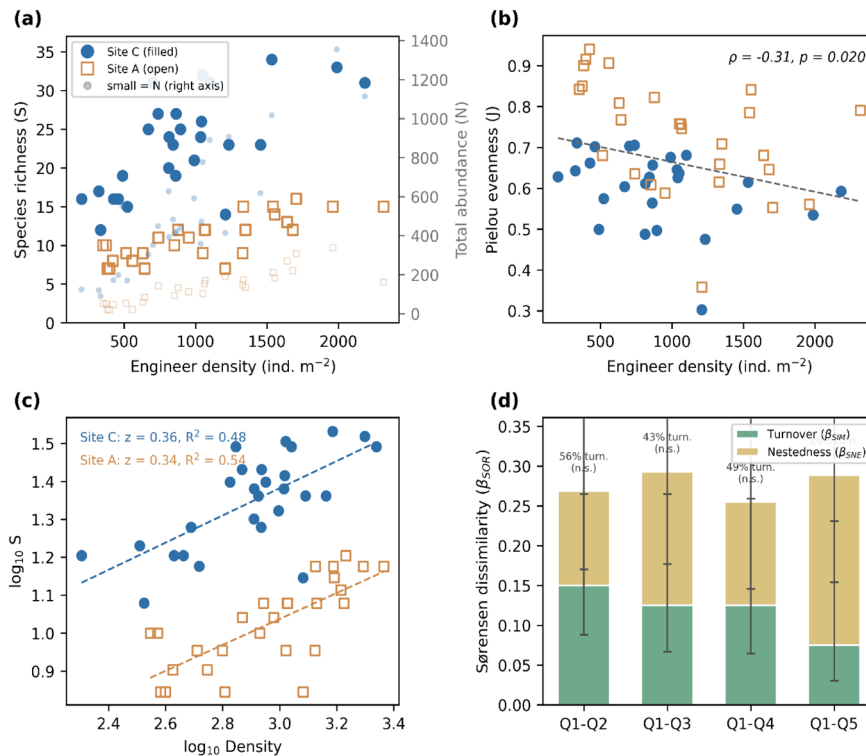


Figure 1. Community structure along the *Mytilaster minimus* density gradient. (a) Species richness S and total abundance N as a function of engineer density for site C (filled circles) and site A (open squares). Lines are LOESS smoothers. (b) Pielou evenness J as a function of density (Spearman $\rho = -0.31$, $p = 0.03$). (c) Power-law species–density relationship on log-log axes; dashed lines show separate fits for site C ($z = 0.36$) and site A ($z = 0.34$). (d) Turnover (β_{SIM}) and nestedness-resilient (β_{SNE}) components of Sørensen dissimilarity (β_{SOR}) between density quintiles, partitioned following Baselga (2010). Error bars are bootstrap 95% confidence intervals (999 resamples of samples within quintiles); the turnover and nestedness components were not statistically distinguishable in any comparison.

information). These two contrasts are reported as representative cases: Q1 versus Q5 is the maximal-density contrast and Q2 versus Q4 is a symmetric intermediate contrast; the full quintile matrix is given in the Supporting information. The power-law species–density relationship yielded $z = 0.264$ (± 0.109 SE; $R^2 = 0.10$, $p = 0.019$) for the full dataset and $z = 0.34$ – 0.36 within individual sites ($R^2 = 0.48$ – 0.54 ; $p < 0.001$), all within the canonical island biogeographic range of 0.20 – 0.35 (Fig. 1c–d). A 50% reduction in engineer density from the site-level means is estimated to cause approximately 17–22% species loss.

Price equation partition: context dependence dominates

The five-term extended Price equation (Fox and Kerr 2012) applied with Q1 as baseline revealed that the CDE was the single largest component of functional change along the density gradient, accounting for the largest relative importance (46%) among all five Price components (Fig. 2a, Supporting information). SRE_G was substantial (+222.3, reflecting the gain of 27 species at high density) but was almost entirely counterbalanced by SCE_G (−195.1), indicating that gained species had far below-average abundance – gain was strongly non-random. SRE_L was small (−9.8) because only 3 species were lost between extremes.

In the Genung-style all-pairwise analysis ($n = 1429$ comparisons normalised by baseline function), mean effect sizes were: $\Delta EF = -0.52$ [95% bootstrap CI: −0.57, −0.46], species loss ($RICH + COMP$) = −0.24 [−0.30, −0.18] and $CDE = -0.28$ [−0.32, −0.23] (Fig. 2b, Supporting information). All five individual components had 95% bootstrap CIs excluding zero. $RICH = -0.35$ [−0.39, −0.31] and $COMP = +0.11$ [+0.07, +0.14]: the positive $COMP$ indicates that species lost between higher- and lower-function sites had below-average functional contribution, the hallmark of natural (versus experimental) communities (Genung et al. 2020). The CDE had the second-largest relative importance (22.8%) among the five Fox and Kerr terms (Table 1), but accounted for the largest net contribution to total functional change. The relative importance (22.8%) and the mean normalised effect size (−0.28) are distinct quantities and are not directly comparable: the relative importance is the share of $|CDE|$ in the sum of the absolute values of all five components (Table 1), whereas the effect size is the mean across pairs of the CDE normalised by baseline function (Supporting information).

Five OM-dependent species dominate the CDE

Decomposing the CDE to individual species revealed that the CDE was concentrated in a few species. Five species accounted for 78.5% of the total CDE between the lowest

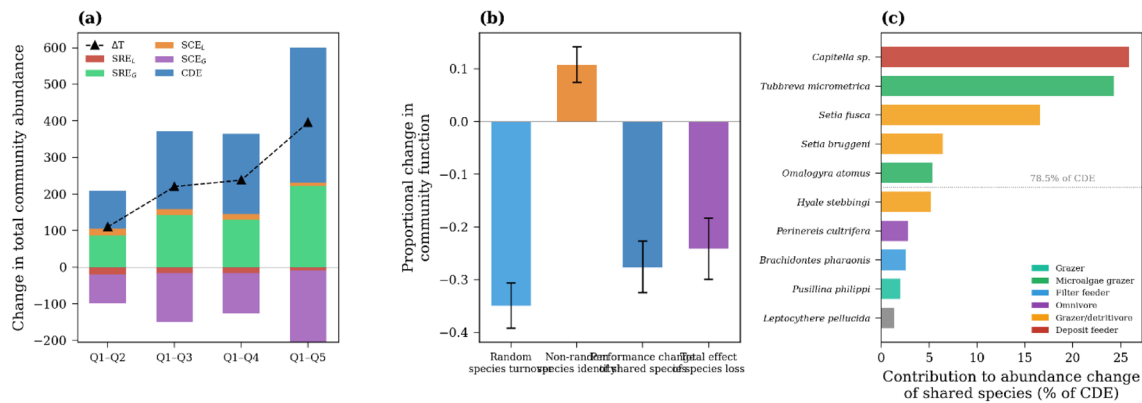


Figure 2. Extended Price equation partition (Fox and Kerr 2012). (a) Five-term partition for density quintile comparisons (Q1 as baseline). Bars show SRE_L , SRE_G , SCE_L , SCE_G and CDE; dashed line marks ΔT . (b) Mean normalised effect sizes across all 1429 pairwise comparisons (Genung-style; error bars=95% bootstrap CI from resampling $n=53$ samples). Grey horizontal line at zero. (c) Top 10 species ranked by CDE contribution (Q1 versus Q5); bars coloured by feeding guild. The five labelled species account for 78.5% of total CDE; 85.7% of the CDE budget comes from OM-dependent guilds.

and highest density quintiles (Fig. 2c, Table 2): *Capitella* sp. (deposit feeder; 25.9%), *Tubbreva micrometrica* (microalgae grazer; 24.3%), *Setia fusca* (grazer/detritivore; 16.6%), *Setia bruggeni* (grazer/detritivore; 6.4%) and *Omalogyra atomus* (microalgae grazer; 5.3%). Across all shared species, 85.7% of the CDE was attributable to trophic guilds directly dependent on organic matter (deposit feeders, microalgae grazers, grazer/detritivores). For reference, 40 of the 93 taxa (43.0%) belonged to these organic-matter-dependent guilds and accounted for 87.7% of all individuals recorded (Supporting information); the 85.7% share of the CDE is therefore close to the assemblage-level abundance share of the same guilds.

Functional dominance predicts the importance of species loss

Functional dominance ranged from 0.13 to 0.91 across samples (mean=0.61) and increased with engineer density ($\rho=+0.33$, $p=0.024$; Fig. 3a). Dominance was significantly negatively correlated with the importance of species loss ($\rho=-0.40$, permutation $p=0.006$, bootstrap 95% CI $[-0.60, -0.13]$; Fig. 3b) and positively correlated with the non-randomness of species loss (COMP/RICH: $\rho=+0.34$, permutation $p=0.016$; Fig. 3c): at high dominance COMP/RICH approached zero, indicating that the few species lost

were so functionally marginal that their loss was nearly indistinguishable from random expectation. The CDE was not correlated with dominance ($\rho=+0.04$, $p=0.77$; Fig. 3d).

Price components track organic matter quantity and quality

Each Price equation component correlated with OM variables consistently with the resource-mediated pathway hypothesis (Fig. 4, Table 3). The CDE correlated strongly with Trap DW ($\rho=-0.45$, permutation $p < 0.001$) and OMtotal ($\rho=-0.38$, $p=0.003$): where more organic matter was trapped, shared species inflated more (Fig. 4a). COMP correlated with Trap DW ($\rho=+0.44$, $p=0.001$) and OMtotal ($\rho=+0.44$, $p < 0.001$): where trapping was greater, species loss was more non-random (Fig. 4b). Among the OM variables, species loss was correlated only with CHL-a ($\rho=-0.44$, permutation $p=0.002$), the one OM variable that was independent of engineer density ($\rho=+0.10$, $p=0.49$ for CHL-a versus density). No other OM variable predicted species loss (all permutation $p > 0.55$; Fig. 4c). This identifies a second, bottom-up pathway: where benthic microalgal biomass (i.e. as expressed by CHL-a as a proxy) is higher (irrespective of engineering), the community retains more species.

Partial correlations controlling for density clarified the causal pathway. The CDE versus Trap DW association

Table 1. Effect sizes for normalised Price equation components. Mean and 95% bootstrap CI computed by resampling sample-level means ($n=53$ samples, 9999 replicates). Cohen's d is mean/SD, testing deviation from zero. Relative importance is $|\text{component}|/\Sigma|\text{five components}|$.

Component	Mean	95% CI lower	95% CI upper	Cohen's d	Rel. importance (%)
SRE_L	-0.527	-0.568	-0.485	-3.38	43.3
SRE_G	0.177	0.160	0.195	2.64	14.6
SCE_L	0.171	0.141	0.200	1.57	14.1
SCE_G	-0.063	-0.075	-0.050	-1.33	5.2
CDE	-0.277	-0.324	-0.228	-1.56	22.8
RICH	-0.350	-0.392	-0.306	-2.18	
COMP	0.108	0.074	0.141	0.87	
SpLoss	-0.242	-0.299	-0.182	-1.11	

Table 2. Species contributing to the CDE between the lowest (Q1) and highest (Q5) density quintiles. Shared species are ranked by CDE (= mean abundance at Q5–mean abundance at Q1). Feeding guild assignments from published literature. Cumulative % is the running total of |CDE| contributions. The five species above the dashed line account for 78.5% of total CDE. Species gained at high density and lost at high density are listed separately below.

Species	Feeding guild	Abundance Q1	Abundance Q5	CDE	% total CDE	Cumulative %
<i>Capitella</i> sp.	deposit feeder	18.7	114.3	95.5	25.9	25.9
<i>Tubbreva micrometrica</i>	microalgae grazer	16.3	105.9	89.6	24.3	50.2
<i>Setia fusca</i>	grazer/detritivore	55.0	116.1	61.1	16.6	66.8
<i>Setia bruggeni</i>	grazer/detritivore	2.1	25.8	23.7	6.4	73.2
<i>Omalogyra atomus</i>	microalgae grazer	5.9	25.5	19.6	5.3	78.5
<i>Hyale stebbingi</i>	grazer/detritivore	2.9	22.1	19.2	5.2	83.7
<i>Perinereis cultrifera</i>	omnivore	2.9	13.2	10.3	2.8	86.5
<i>Brachidontes pharaonis</i>	filter feeder	1.8	11.3	9.5	2.6	89.1
<i>Pusillina philippi</i>	grazer	2.8	10.2	7.4	2.0	91.1
<i>Leptocythere pellucida</i>	dDeposit feeder	0.1	5.0	4.9	1.3	92.4

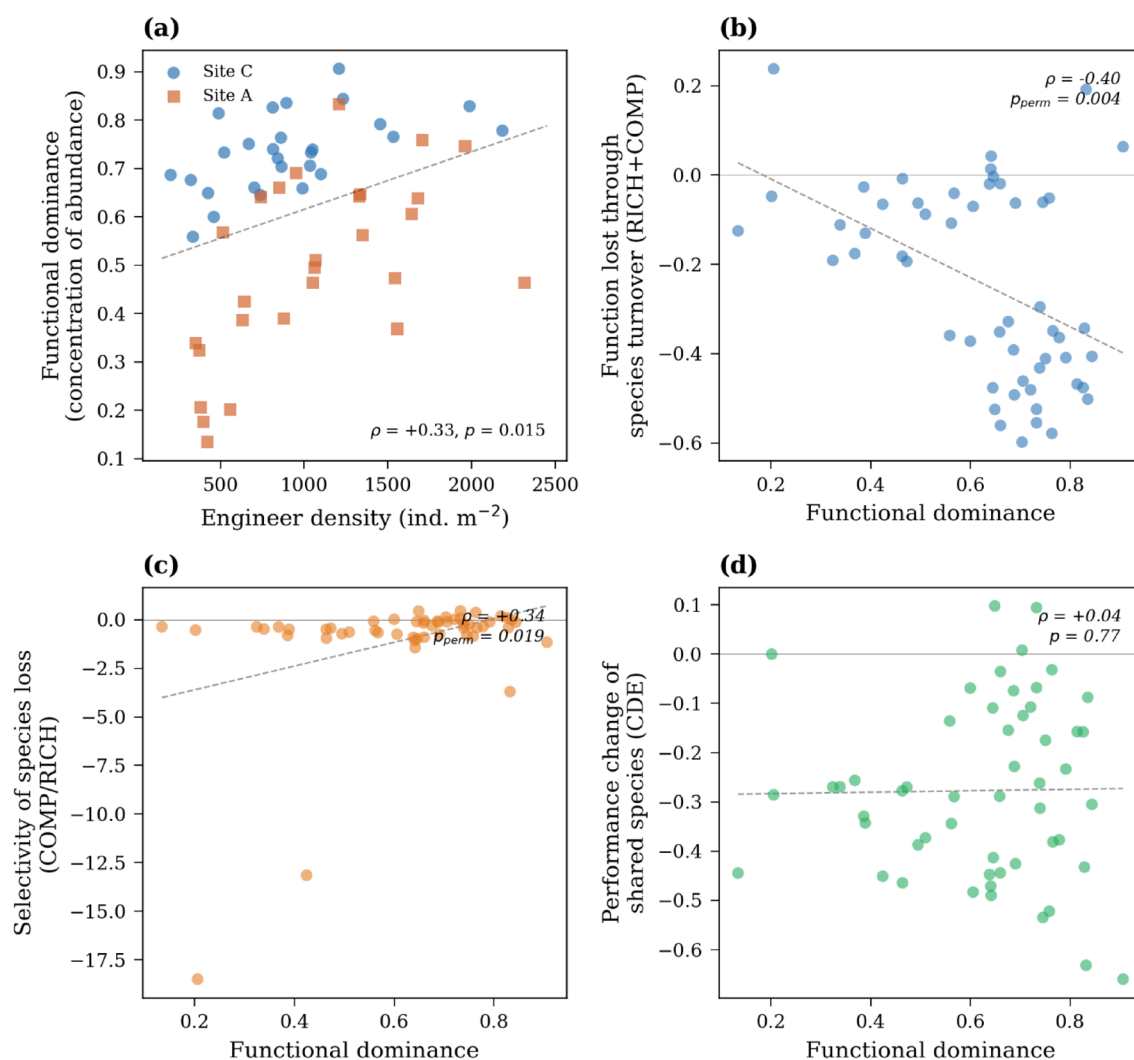


Figure 3. Functional dominance mediates the importance of species loss, replicating Genung et al. (2020). (a) Functional dominance (Chao and Ricotta 2019 at $q=1$) versus engineer density ($\rho=+0.33$, $p=0.024$). (b) Effect of species loss (RICH + COMP, normalised) versus functional dominance ($\rho=-0.40$, permutation $p=0.006$). (c) Selectivity of species loss (COMP/RICH) versus functional dominance ($\rho=+0.34$, permutation $p=0.016$). (d) CDE versus functional dominance ($\rho=+0.04$, $p=0.77$). Each point represents one sample, averaged across all pairwise comparisons in which it served as a baseline ($n=53$). (a) includes all 54 samples; (b–d) use the 53 samples with valid mean Price terms.

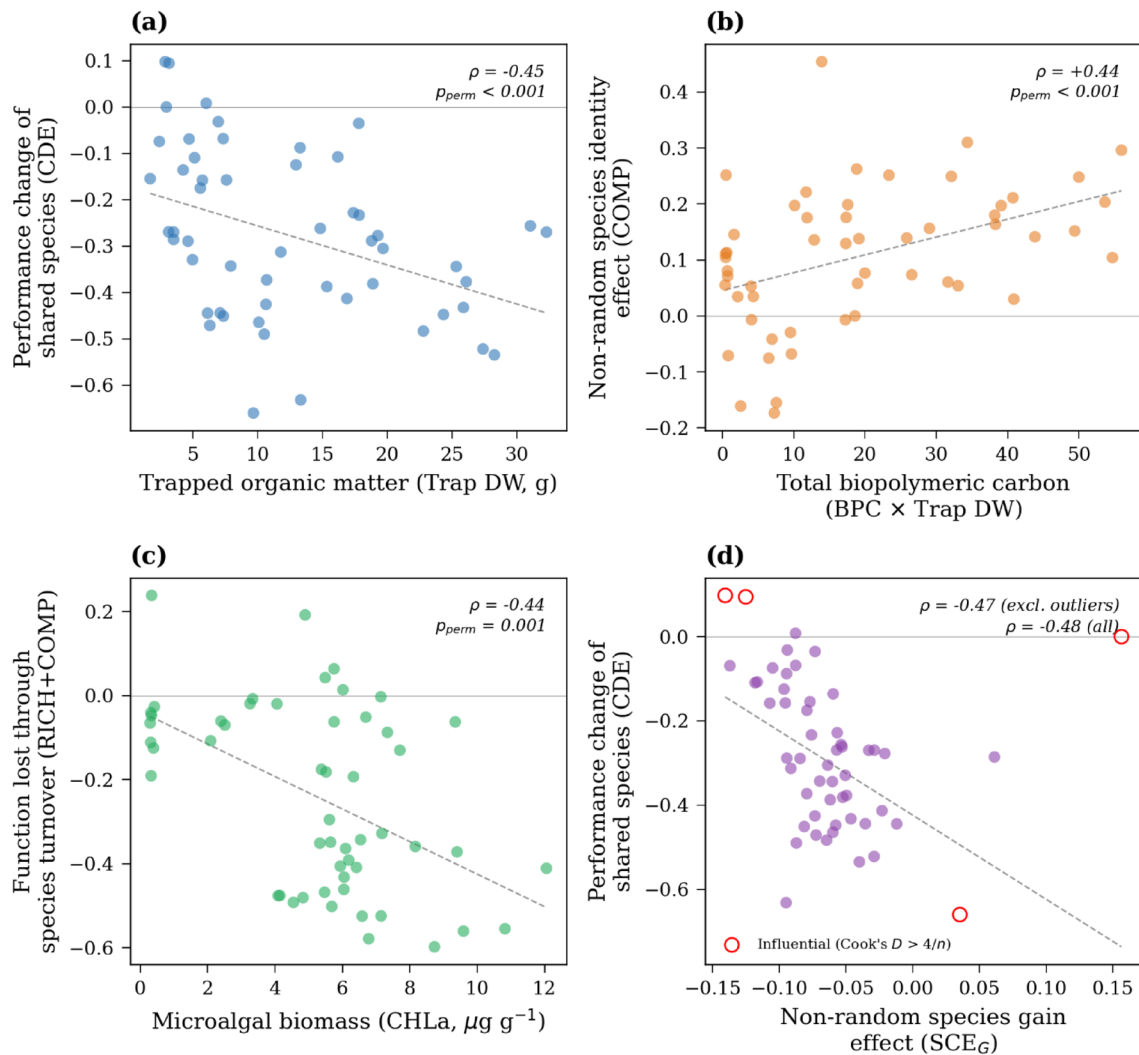


Figure 4. Price equation components correlate with organic matter variables. (a) CDE versus Trap DW per sample ($\rho = -0.45$, permutation $p < 0.001$). (b) COMP versus OMtotal (BPC $\times$ Trap DW; $\rho = +0.44$, permutation $p < 0.001$). (c) Species loss versus CHLa ($\rho = -0.44$, permutation $p = 0.002$). (d) CDE versus SCEG ($\rho = -0.48$, $n = 53$; points flagged by Cook's $D > 4/n$ are marked in red for transparency), paralleling Fox and Kerr (2012, their Fig. 5). All variables are sample-level means of normalised Price terms ($n = 53$). Dashed lines show linear fits; shaded bands are 95% CI.

disappeared entirely (partial $r = +0.04$, $p = 0.76$), confirming that trapping mediates the density effect on the CDE: density $\rightarrow$ Trap DW $\rightarrow$ CDE. However, CHLa retained significant partial correlations with both the CDE (partial $r = +0.42$, bootstrap CI $[+0.18, +0.62]$) and species loss (partial

$r = -0.52$, bootstrap CI $[-0.67, -0.34]$), demonstrating an effect independent of engineer density.

The CDE and SCEG were negatively correlated ($\rho = -0.48$, all 53 samples; Fig. 4d), paralleling the pattern found by Fox and Kerr (2012) in the Cedar Creek LTER grasslands. In their

Table 3. Spearman correlations between sample-level mean Price components and organic matter variables ($n = 53$ samples). Significance assessed by permutation of sample labels (999 permutations). Bold: permutation $p < 0.05$. CHLa is the only OM variable independent of engineer density ($\rho = +0.10$, $p = 0.49$). Partial correlations controlling for density are reported in the text for CDE and SpLoss versus CHLa (the only cases where the bootstrap 95% CI excludes zero).

Price comp.	Trap DW (ρ)	Trap DW (p)	BPC (ρ)	BPC (p)	CHLa (ρ)	CHLa (p)	OM_total (ρ)	OM_total (p)
CDE	-0.445	<0.001	-0.262	0.052	0.342	0.010	-0.38	0.003
RICH	-0.201	0.151	-0.073	0.575	-0.497	<0.001	-0.21	0.138
COMP	0.438	0.001	0.329	0.014	-0.138	0.331	0.441	<0.001
SpLoss	0.082	0.549	0.080	0.592	-0.445	0.002	0.065	0.658
SCE_G	0.291	0.036	0.082	0.543	-0.283	0.041	0.220	0.113

system, the correlation was attributed to competitive suppression of shared species by high-performing immigrants. In our system, the correlation arises from shared trophic dependence on trapped OM: both the species that gain (SCEG correlated with Trap DW, $\rho = +0.29$, $p = 0.036$; Table 3) and the shared species that inflate (CDE) respond to the same OM resource.

Discussion

Thirty years of biodiversity–ecosystem function experiments have shown that species loss often has a role in reducing ecosystem function, although the magnitude depends on which functional groups are lost and on the degree of redundancy among species – in our intertidal system the redundant taxa are the rare members of organic-matter-dependent guilds (Cardinale et al. 2012). This conclusion rests on the assumption that species richness causally drives function and has inspired three competing models for how that causal link operates: the rivet model (Ehrlich and Ehrlich 1981), in which species act like the rivets holding an aircraft together, so that initial losses are buffered by redundancy but function collapses once a critical number have been removed; the linear model, in which species contribute equally and proportionally and the redundancy model (Walker 1992, Lawton and Brown 1993), in which function saturates at low richness because many species are functionally interchangeable. Our results are not well described by the linear model, nor by the rivet model over the range of loss we observe. Losing species from high-density patches scarcely affected community function (species loss accounted for less than half of the total functional change and COMP was consistently positive, meaning lost species were those contributing least). This pattern may resemble the redundancy model in that function appears buffered against species loss because a few dominant species sustain most of it. Nevertheless, the underlying mechanism may be quite different. In the classical redundancy framework, buffering arises from functional overlap among species within the same trophic guild. In our system, buffering arises because the ecosystem engineer generates the trophic resource (trapped organic matter) that inflates a narrow set of species, making the rest functionally marginal regardless of their guild identity. The engineer does not create redundancy – it creates dominance. And dominance, not redundancy, is what buffers function, in line with the mass-ratio hypothesis that ecosystem properties are governed largely by the traits and abundance of the dominant species (Grime 1998).

This distinction has a deeper implication. Along the *Mytilaster minimus* density gradient, biodiversity and community function do not stand in a cause–effect relationship – they are co-consequences of the same upstream driver, i.e. the engineer density. Mussels create the physical habitat that sustains species and simultaneously generates the trophic resource that inflates the abundance of the few species dominating community function. Sites that differ in species richness but not in the presence of the engineer show very

similar function, whereas the loss of the engineer itself would be expected to reduce both biodiversity and function – not because species were lost but because the structural and trophic template that sustains them would be gone. The classical BEF question – how does richness affect function? – may be therefore the wrong question for these engineer-structured systems while the right question may be what generates the structure that sustains both richness and function. In our case, the answer is the density of the ecosystem engineer.

The engineer as generator of functional dominance

The extended Price equation (Fox and Kerr 2012) makes this pathway visible. Among-site differences in function are driven mostly by the set of shared species rather than by which species are gained or lost: context dependence – the change in performance of species present at both sites – accounts for the largest relative importance (46%) among all five Price components along the density gradient, dwarfing the direct effects of species gain or loss. The same shared species therefore perform more or less depending on the trophic context the engineer provides, rather than function depending on how many species are present. Five OM-dependent species alone account for 79% of the CDE (Table 2), confirming that the functional response is concentrated in a narrow trophic guild whose abundance tracks trapped organic matter. The mechanism is analogous to a fertilization effect in grasslands (Suding et al. 2005), but here the fertilizer is produced by the engineer itself, creating a positive feedback: more engineer density $\square$ more trapped OM $\square$ more trophic inflation $\square$ higher dominance $\square$ less sensitivity to species loss.

Functional dominance – the structural feature that Genung et al. (2020) identified as the key predictor of whether species loss matters – is itself a product of this trophic inflation. In our dataset, dominance increases with engineer density ($\rho = +0.33$) and the importance of species loss is lower where dominance is higher ($\rho = -0.40$, permutation $p = 0.004$), replicating the cross-system pattern of Genung et al. (2020) within a single engineer-structured system. This points to a possible mechanism generating the dominance-dependent species loss pattern that those authors documented across 129 datasets worldwide. The importance of species identity, and not richness alone, in shaping ecosystem function has long been recognised in this field (Loreau and Hector 2001, Hooper et al. 2005); our contribution is to identify a habitat-forming, resource-concentrating process that generates such identity-driven dominance in a natural community. Hopper et al. (2023) applied the Price equation to freshwater Unionidae mussel aggregations and similarly found that CDE dominated standing-stock biomass variation. However, they did not identify a trophic mechanism linking the engineer to the CDE. Zhang et al. (2025) showed that shrub encroachment on the Qinghai-Tibet Plateau increased plant biomass primarily through the CDE of persisting species (67% of total change) with species identity effects partially cancelling richness effects – a pattern that closely mirrors our result and suggests that CDE-dominated dynamics may be a general feature of facilitated communities.

Experiments versus natural communities

Experiments and natural communities differ not only in the non-randomness of species loss and gain but also in their initial evenness and in the scope for priority effects (Genung et al. 2020). Our system replicates the natural-community pattern exactly: COMP is positive, meaning lost species have below-average function. This pattern emerges because the trophic subsidy generated by the engineer concentrates abundance in a few resource-dependent species. The species absent from low-density patches are therefore predominantly the rare, low-abundance ones, which by construction contribute little to the abundance-based function, so their loss has a small functional effect (COMP positive). In experiments, species identity is usually randomized by design and this hierarchy cannot influence species loss. Our results identify a possible ecological mechanism for the experiment-nature discrepancy: in engineer-structured habitats, the same force that generates biodiversity (biogenic habitat creation, Stachowicz 2001, Crain and Bertness 2006) also generates the dominance that makes richness less predictive of function. This identity-driven stabilisation aligns with Genung and Winfree (2025), who showed that dominant species stabilise pollination services through response diversity rather than richness per se (i.e. the common feature is that function is carried by a few dominant species rather than by richness, although the stabilising agent differs - response diversity to land-use change in their pollinator system and a trophic subsidy in ours). Similarly, Navarro-Cano et al. (2021) applied the CAFE/Price framework to a nurse-plant system and found that facilitation enhanced ecosystem function via non-random species gains - species recruited under nurse canopies were disproportionately productive - a compositional mechanism analogous to our trophic subsidy pathway.

The role of organic matter

The correlations between Price components and OM variables (Table 3) are not merely descriptive - they strongly suggest the causal architecture of the cascade. Controlling for density eliminates the CDE-Trap DW correlation (partial $r = +0.04$, CI crossing zero), confirming that trapping is the mechanistic mediator of the density effect on CDE (pathway: density $\square$ Trap DW $\square$ CDE). The CDE-BPC correlation likewise disappears when conditioned on density (partial $r = +0.12$, CI crossing zero), indicating that both the quantity and the biochemical quality of trapped OM are density-driven. These partial correlations function as a mediation test: if trapping were merely correlated with density but not causally intermediate, removing density would not eliminate the CDE-Trap association.

CHL-a, the one OM variable independent of engineer density ($\rho = +0.10$, $p = 0.49$), is the only one to predict species loss (partial $r = -0.52$ controlling for density, bootstrap CI $[-0.67, -0.34]$). This identifies a second, bottom-up pathway operating through basal autotrophic resources rather than through engineering: where benthic microalgal biomass is higher, irrespective of mussel density, the community hosts more species. The coexistence of these two pathways

- one engineer-mediated (density $\square$ Trap $\square$ CDE) and one environment(trophic)-mediated (CHL-a $\square$ species loss) - underscores that engineer density is the dominant but not the sole determinant of community structure.

The negative CDE-SCE_G correlation ($\rho = -0.47$) mirrors the pattern found by Fox and Kerr (2012) in the Cedar Creek LTER grasslands, where it was attributed to competitive suppression of shared species by high-performing immigrants. In our system the mechanism is different: gained species and inflating shared species both depend on the same trapped OM resource. This shared trophic dependence, not competition, generates the correlation. More broadly, Yakovis and Artemieva (2021) demonstrated that trophic cascades can control facilitation cascades in bivalve-engineered communities, confirming that trophic and facilitation processes are deeply intertwined in engineer-structured habitats.

Conservation implications

The practical consequence of our findings is that engineer density is in this and similar engineer-structured systems, a highly informative metric for conservation of marine intertidal biodiversity and function. The power-law species-density relationship ($z = 0.26-0.36$) permits approximate prediction of species loss from density reduction: a 50% decline in engineer density predicts 17-22% species loss (pooled and per site estimates). But the Price equation reveals that the functional consequences exceed the species-level taxonomic consequences: the CDE - which reflects the performance of persistent species - collapses proportionally with OM availability. Species may still be present but function less because the trophic resource has diminished. For marine protected area management and in general for conservation purposes, monitoring engineer density provides a low-cost, taxonomically undemanding surrogate for the state of the entire associated community and its trophic functioning (Silliman et al. 2011, Rossi et al. 2017). The density of a dominant habitat-former has been advocated as a low-cost surrogate for the functional state of foundation-species systems (Sarà et al. 2021). A monitoring protocol based on ecosystem-engineer density in fixed quadrats would capture the state of the system more reliably than species inventories, which are expensive, require taxonomic expertise and - as our data show - may miss the functional changes that matter most.

Caveats and future directions

The observational nature of the density gradient precludes strong causal inference and this implies that manipulative experiments varying density and trapping independently would strengthen any mechanistic claim. In addition, the components of the Price partition are not mutually independent and their absolute and relative magnitudes are constrained by the underlying data structure (Ulrich et al. 2024); we therefore treat the relative importance of components as a descriptive ranking rather than as a set of independent effect sizes and rely on the all-pairwise, baseline-standardised analysis and on the consistency of each component's sign across comparisons to

guard against artefacts of this non-independence. The study is based on a single engineer species in a single region and two sites thereby generalization to other systems and engineers is needed (Castilla et al. 2004, Christie et al. 2009, Beadman et al. 2004). Functional contribution z_i was measured as abundance rather than biomass or a direct ecosystem rate; future work should quantify per capita processing rates of trapped OM by the dominant CDE species. The strong site effect (mean $S = 23.1$ versus 10.9 at equivalent densities) indicates that the regional species pool and local environmental conditions modulate the engineer's effect. Within-site analyses confirmed the core community structure relationships (density versus S , N , J and dominance) and the COMP-OM association at both sites, though the Genung dominance-species loss test and the CHL-a pathway operated primarily at the across-site scale (Supporting information). This interaction deserves explicit treatment across broader spatial scales (Kawatsu and Kondoh 2018, Landi et al. 2018). In addition to the resource-mediated pathway documented here, *Mytilaster* beds also help to maintain associated assemblages across intertidal stress gradients (Bogdanski et al. 2024) and may additionally buffer thermal extremes within the interstitial matrix, providing a second, microhabitat-mediated pathway by which engineer density may promote species retention. Field evidence from a Mediterranean lagoon shows that the loss of a foundation bivalve during a combined heatwave-hypoxia event propagates through the ecological hierarchy to community reorganisation and a collapse of organic-matter-mediated functioning (Sarà et al. 2021), consistent with the expectation that function tracks engineer density in these systems. Disentangling trophic from thermal effects requires dedicated thermal profiling across the density gradient and further research is needed to investigate the interactions between these biodiversity drivers.

Speculations

If functional dominance in this system is generated rather than intrinsic, engineer density may act as a single keystone factor predicting ecosystem function across biogenic habitat-formers more generally – mussel and oyster beds, tubeworm reefs, seagrass and coral frameworks – wherever the engineer both builds habitat and concentrates a trophic resource. Two consequences follow that we cannot yet test. First, function may decline ahead of species loss: as the engineer thins, the trophic subsidy contracts and the dominant species lose abundance while remaining present, so abundance-based function could fall before any species disappears, making engineer density an earlier warning than richness. Second, if biodiversity and function are co-outputs of one driver, restoration that re-establishes the engineer alone might recover both without species-level intervention and richness-based metrics could misdirect effort in these systems. More speculatively, the cross-system dominance pattern of Genung et al. (2020) may itself be, in part, a signature of unmeasured ecosystem engineering: where dominance predicts the irrelevance of species loss, a habitat-forming, resource-concentrating species may often be present in the background.

Alternative viewpoints

The dataset supports more than one interpretation of what these results imply for ecosystem function and the two are not separable with the evidence at hand. One line of reasoning holds that abundance is a legitimate community-level function currency: in the Fox and Kerr partition it is the per species function, the approach follows established natural-community applications and the partition isolates the non-random selectivity component that a dominance comparison cannot; on this reading the buffering of function by dominance holds. Another holds that abundance is a structural proxy and that function in the process sense – organic-matter processing, secondary production, nutrient turnover – is not measured; if the dominant species are not also the most efficient per capita, a buffering of abundance need not imply a buffering of process and the relationship could reverse. The data do not discriminate between these readings, because per capita process rates of the dominant CDE species were not quantified. Resolving which holds – whether abundance dominance and process dominance coincide in engineer-structured systems – is therefore an open empirical question rather than a matter of preference.

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Data availability statement

Data are available from Mendeley: doi: 10.17632/d3vg7hz4xr.2 (Sarà 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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