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ARTICLE

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Topographic heterogeneity triggers complementary cascades that enhance ecosystem multifunctionality

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Abstract

Topographic heterogeneity sets the stage for community assembly, but its effects on ecosystem functioning remain poorly understood. Here, we test the hypothesis that topographic heterogeneity underpins multiple cascading species interactions and functional pathways that indirectly control multifunctionality. To do so, we combined experimental manipulation of a form of topographic heterogeneity on rocky shores (holes of various sizes) with a comprehensive assessment of naturally assembled communities and multifunctionality. Structural equation modeling indicated that heterogeneity: (1) enhanced biodiversity by supporting filter feeder richness; (2) triggered a facilitation cascade via reef-forming (polychaete) and biomass-dominant (macroalga) foundation species, which in turn broadly supported functionally diverse epibiotic and understory assemblages; and (3) inhibited a key consumer (limpet). The model supported that these mechanisms exerted complementary positive effects on individual functions (e.g., water filtration, ecosystem metabolism, nutrient uptake) and, in turn, collectively enhanced multifunctionality. Topographic heterogeneity may therefore serve as a cornerstone physical attribute by initiating multiple cascades that propagate through ecological communities via foundation species, ultimately manifesting disproportionate effects on ecosystem multifunctionality.

KEYWORDS

biodiversity, ecosystem functioning, facilitation, foundation species, *Fucus serratus*, habitat complexity, substrate heterogeneity

INTRODUCTION

Across terrestrial, freshwater, and marine systems, experiments have revealed that declines in biodiversity reduce rates of both individual ecosystem functions and multifunctionality (Cui et al., 2022; Naeem et al., 1994; Rodil et al., 2022; Tilman et al., 1996; Wolf et al., 2021). Yet, levels of biodiversity are not extrinsic or independent to ecological systems but are instead controlled by the environment and species interactions. For instance, outside of controlled experiments, biodiversity loss is often attributed to the erosion of habitat heterogeneity and complexity (Graham, 2014; St. Pierre & Kovalenko, 2014) or declines in major habitat-forming foundation species such as trees, corals, or kelps (e.g., Dayton, 1972; Ellison et al., 2005; Sorte et al., 2017). Accordingly, a new generation of studies is emerging that consider biodiversity as part of a causal network, where biodiversity both responds to environmental and/or anthropogenic factors and mediates ecosystem functions and processes (e.g., Hong et al., 2022; Ratcliffe et al., 2017). Physical topographic heterogeneity is a key environmental factor that has been linked to both habitat-forming species and biodiversity (Liu et al., 2019; Loke & Todd, 2016; Munguía-Rosas & Sosa, 2008) and may have essential cascading effects on ecosystem multifunctionality.

Generated by geological features, biotic modification, and weathering, topographic substrate heterogeneity determines spatial variation in biologically relevant factors across both terrestrial (e.g., soil texture, nutrient status, water content) and aquatic systems (e.g., rivers: water flow rate; rocky intertidal: water retention) (Agra et al., 2024; Stein et al., 2014). Topographic substrate heterogeneity, which may be related to substrate or habitat complexity (Tokeshi & Arakaki, 2012), is especially evident as fissures, cracks, and holes in exposed rock, which is a prominent substrate during early primary succession in extreme (e.g., high altitude; do Carmo et al., 2016; Nowak et al., 2014) or built (e.g., heritage walls; Jim & Chen, 2010; Lundholm & Marlin, 2006) environments. Across systems, topographic and resulting environmental heterogeneity enhance microhabitat and niche diversity (Chesson, 2000; Tews et al., 2004), and provide refugia from consumers (Jernakoff, 1983) and physical stress (Thompson et al., 1996; Thomsen et al., 2022), ultimately promoting biodiversity and biomass (Figure 1A, path *i*). Topographic heterogeneity may also promote biodiversity via facilitation cascades, by providing suitable conditions for, and mitigating consumer pressure on, habitat-forming species such as cacti, trees, and kelps (Figure 1A, path *ii*). In turn, these foundation species facilitate other organisms, including potentially other foundation species, by creating additional habitat or modifying environmental conditions (Figure 1A, path *iii*; Benes & Carpenter, 2015; Thomsen et al., 2010). Thus habitat-forming species may

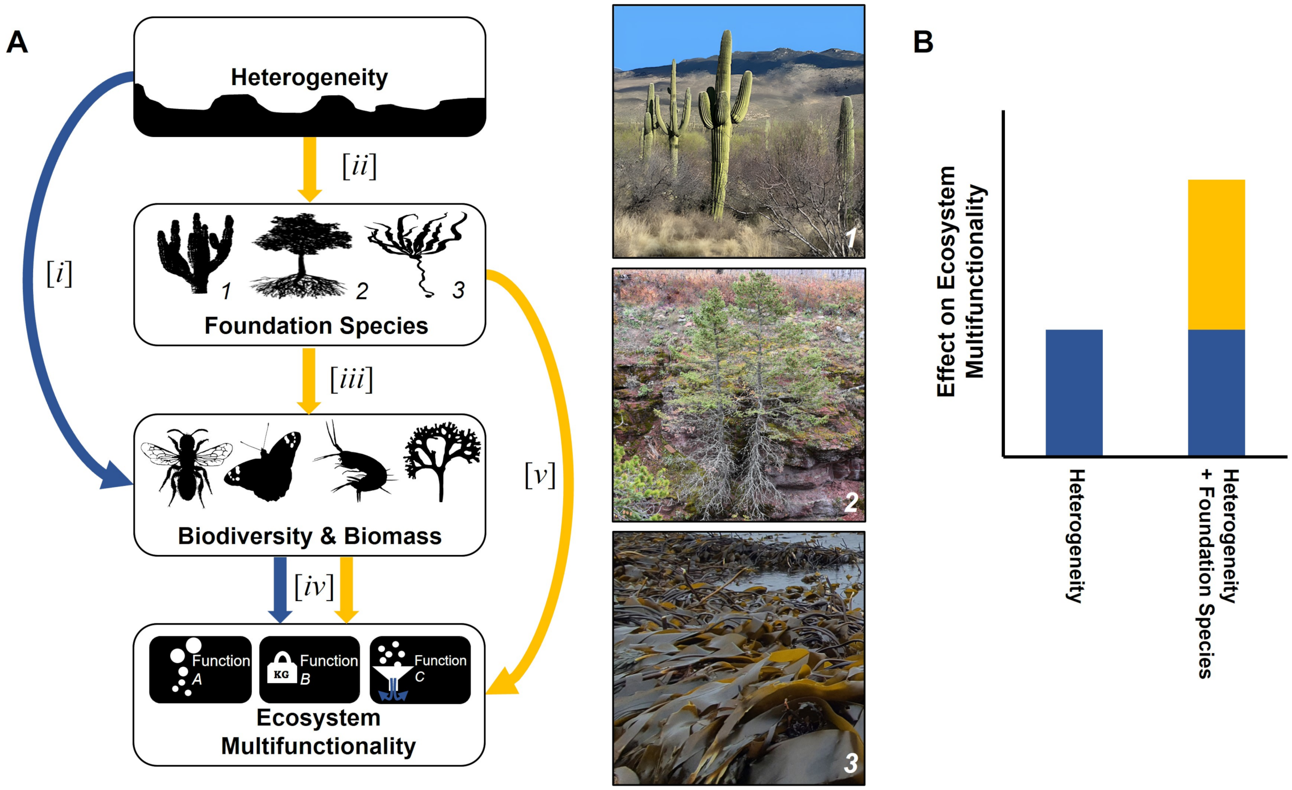

FIGURE 1 Multiple pathways potentially link abiotic topographic heterogeneity and ecosystem multifunctionality. Our conceptual model (A) holds that heterogeneity drives colonization of diverse communities both through direct provisioning of niche space (path *i*, blue) and by promoting foundation species (path *ii*, orange), which, in turn, provide secondary habitat for epibiotic and free-living species (path *iii*). Collectively, these biodiverse communities, driven directly by heterogeneity (path *iv*) and indirectly (paths *iv*, *v*) via foundation species (e.g., in cacti [top image; Munguía-Rosas & Sosa, 2008; Winkler et al., 2018]; trees [middle image; Frouz et al., 2018; Resler et al., 2005]; and kelps [bottom image; Azzarello et al., 2014; Randell et al., 2022]), support a wide diversity of other organisms, and are expected to provide a high level of ecosystem multifunctionality. Through these multiple pathways, heterogeneity is expected to enhance multifunctionality and do so more strongly where foundation species effects are in play (B). Image credit (panel A, photographs 1–3): Tom P. Fairchild.

effectively channel—or even amplify—effects of topographic heterogeneity on biodiversity (Figure 1A).

Direct and indirect biodiversity enhancement from high topographic heterogeneity may, in turn, enhance ecosystem functioning. Biodiversity, supported by heterogeneity and foundation species, is expected to boost individual ecosystem functions through mechanisms including niche complementarity (Cadotte et al., 2011; Cardinale, 2011), and facilitation (Cardinale et al., 2002; Navarro-Cano et al., 2019), and sustain multiple functions simultaneously (multifunctionality, sensu Hector & Bagchi, 2007; e.g., Pasari et al., 2013; Zavaleta et al., 2010) through the inclusion and enhanced biomass of species and groups with different capacities to drive distinct ecosystem functions (Figure 1A path *iv*; multivariate complementarity, sensu Duffy et al., 2003). Furthermore, foundation species alone, by virtue of their large individual size and biomass, often strongly and directly influence ecosystem functions (Figure 1A, path *v*; Ellison et al., 2005; Grime, 1998). Thus, foundation species have the potential to greatly amplify heterogeneity's effects on communities and yield disproportionate impacts on multifunctionality (Figure 1B).

Rocky shore intertidal systems have long been a testbed for ecological concepts due to their steep environmental gradients, relatively rapid community turnover and interactions, and tractable assemblages (Connell, 1972; Dayton, 1975). Heterogenous or complex substrates have been shown to enhance biodiversity (Loke & Todd, 2016; Stein et al., 2014; Tokeshi & Arakaki, 2012), and diversity deficits on anthropogenic coastal structures have been attributed to their reduced complexity or heterogeneity (Bishop et al., 2022; Bulleri & Chapman, 2010; Lawrence et al., 2021). Heterogeneity directly facilitates recruitment of various foundation species, including barnacles, mussels, reef-forming worms, and fucoid macroalgae, in part by reducing their vulnerability to consumers such as limpets (Jenkins et al., 1999) and forming refugia from environmental stress (Krück et al., 2009). On temperate shores, fucoid macroalgae, in particular, commonly dominate standing biomass and habitat structure, while strongly facilitating biodiversity and biomass of associated organisms (Benes & Carpenter, 2015; Jenkins et al., 1999). Foundation species themselves often interact, such as through amelioration of consumer pressure or provision of secondary habitat (Duggins & Dethier, 1985; Teagle et al., 2017), with "primary" supporting "secondary" foundation species which in turn support diverse communities (Angelini et al., 2011). The resulting species-rich assemblages often include phylogenetically and functionally differentiated organisms, from filter-feeding bivalves to grazing mollusks, and predatory polychaete worms (Loke & Todd, 2016; Teagle et al., 2017). Given their experimental tractability and comparatively well-understood species interaction networks, rocky shores provide an ideal system to investigate the cascading effects of topographic heterogeneity on multifunctionality.

Here, we report an experiment designed to determine how a form of abiotic substrate heterogeneity affects multifunctionality and to explore the mechanistic pathways. To do so, we manipulated the topographic heterogeneity (substrate holes of various sizes) of intertidal rock substrates and quantified foundation species and keystone grazer biomass, associated community structure (biomass and biodiversity), and ecosystem multifunctionality following long-term natural community assembly. Then, we investigated the role of cascading species interactions arising from heterogeneity using structural equation modeling (SEM). We hypothesized that heterogeneity would enhance multifunctionality both via its provision of varied niches and via its support for foundation species (i.e., reef-forming worms and fucoid macroalgae), with their structural complexity and varied microhabitats in turn further elevating biodiversity and biomass across diverse functional groups. Our results show that topographic heterogeneity can drive ecosystem multifunctionality and indicates that it may do so by initiating multiple, complementary, cascading interactions in which foundation species play a critical mediating role.

MATERIALS AND METHODS

Along rocky shores in South Wales (UK) (Figure 2A), we used natural rock tiles (low vs. high heterogeneity; Figure 2B,C), to manipulate substrate heterogeneity and allowed communities to naturally assemble over 30 months (Figure 2D,E). Upon retrieval of tiles from the field, we measured eight key ecosystem functions and exhaustively censused each community, before analyzing the effect of heterogeneity on multifunctionality, using SEM to explore the underlying causal pathways.

Experimental setup

To create the replicated low and high heterogeneity tile treatments, we cut 144 limestone tiles measuring 150 mm × 150 mm × 20 mm (±10 mm tolerance) from unfinished carboniferous limestone slabs, the same rock type as naturally found at the study sites. Tiles such as these allow manipulation of substrate heterogeneity while standardizing for other factors (e.g., location on the shore, rock type, area) and can be removed to assess ecosystem multifunctionality under controlled conditions.

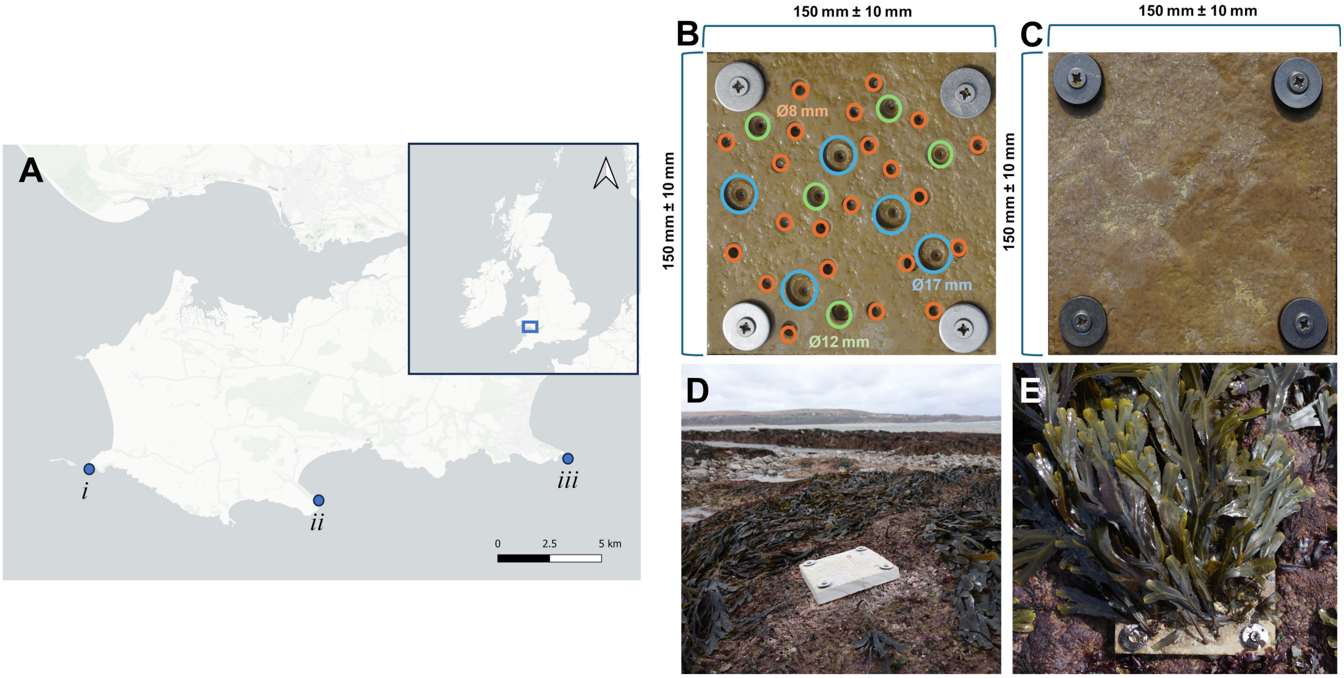

FIGURE 2 Overview of the field experimental setup to test effects of topographic heterogeneity. Tiles were deployed in blocks at three limestone rocky shores ([*i*]: Worm's Head, [*ii*]: Oxwich, [*iii*]: Mumbles Head) along the Gower Peninsula, South Wales UK (A). Heterogeneity was manipulated by drilling various-sized holes (blue: Ø17 mm, green: Ø12 mm, orange: Ø8 mm) in the surface of limestone tiles (B), contrasted to smooth tiles (C). Tiles were deployed in the mid-shore, *Fucus serratus*, zone (D) and retrieved after 30 months (E) for ecosystem multifunctionality measurements under controlled conditions. Image credit (photographs in panels B–E): Tom P. Fairchild.

Tiles have been used in various studies on rocky shores and analogous artificial structures to manipulate substrate conditions (Kosová et al., 2023; Loke & Todd, 2016). We manipulated half (72) to increase the heterogeneity of the substrate through standardized drilling of holes (or "pits") of various sizes (see Appendix S1: Section S1.2 for further details on hole sizes and tile design) (Figure 2B) and assigned the other half (72) to the low heterogeneity treatment where the only heterogeneity arose from natural cleavage in the rock surface (Figure 2C, Appendix S1: Figure S1). These drilled pits and holes have been used widely across intertidal biodiversity experiments (Firth et al., 2014; Hall et al., 2018), providing heterogeneity in surface texture and moisture retention, which are important features on natural shores (e.g., Loke & Todd, 2016; Skov et al., 2011), while mimicking small-scale depressions in the rock formed by weathering processes and engineering by grazing species (Kázmér & Taborosi, 2012; Naylor et al., 2012). Due to the variation in planar area resulting from manual cutting of the rock into tiles, combined with the limited additional surface area created from shallow holes and pits (which typically were less than variability from tile size differences), there was no detectable difference in the realized surface area between the high (21021.4 mm^2 ± 714.6 [SD]) and low (20938.9 mm^2 ± 639.3 [SD]) heterogeneity tiles (*t*-test: $t_{87.9} = 11.08$, $p = 0.29$, Appendix S1: Figure S2; based on 3D photogrammetry models).

To increase generality across locations, we selected three sites spanning ~20 km of coastline in South Wales, UK, for their extensive rocky shorelines and varied environmental contexts; Mumbles Head and Worms Head are along moderately exposed open coastlines, while Oxwich Point is in a moderately wave-sheltered embayment. Along an ~100 m stretch of shore at each site, we affixed tiles to the natural rock substrate in a narrow elevation band within the *Fucus serratus* zone (constrained to ~+2.6 to +3.6 m elevation in Chart Datum, <10% of the total tidal range at the sites) (Figure 2E); at each site, tiles were deployed in 6 groups of 8 (4 high topographic heterogeneity, 4 low heterogeneity, 48 in total) within 5 m diameter blocks to account for any residual variation in environmental conditions.

We deployed tiles in March 2016, at the beginning of many species' reproductive periods (e.g., *Fucus serratus*—Knight & Parke, 1950; *Mytilus edulis*—Myint & Tyler, 1982; *Palmaria palmata*—Pang & Lüning, 2006), to promote colonization of the tiles. We then recovered tiles from the field at peak biomass in late summer (September 2019) after 30 months of deployment, allowing adequate time for community development and establishment of foundation species such as fucoid algae (Jenkins et al., 2004; Speidel et al., 2001), and brought them back to the laboratory, individually sealed in chilled clip-lock containers to retain mobile fauna, for ecosystem function assays and destructive sampling of communities (Geert Hiddink et al., 2009; Ieno et al., 2006). Over the 30 months, 38 tiles had been damaged by winter storms, and equipment issues during functional assays meant a further 15 tiles did not have full associated functional data, giving a sample size of 91 tile communities—46 high heterogeneity and 45 low heterogeneity—used in this study.

Community sampling and functional categorization

Following assessment of ecosystem process rates (see below), we destructively sampled tiles for community composition. Organisms, including a diverse array of both sessile and mobile fauna and macroalgal species, were identified to species level using morphological features using an 80× magnification stereo microscope (minimum organism size ~0.1–0.3 mm), then dried and combusted to quantify biomass (see biomass methods in "*Quantifying ecosystem functions and multifunctionality*" section). To aid with analysis, species were condensed from 236 species to functional groups, based on principal component analysis (PCA) of comparable single species–ecosystem function relationships (Appendix S1: Table S1; Figure S3, Section S1.3). For macroalgae, these groupings aligned well with phylogenetic groups, consistent with recent multi-trait approaches (Fong et al., 2023; Mauffrey et al., 2020). In contrast, traditional morpho-functional groups (e.g., Littler & Littler, 1980) performed poorly, which may be related to their inability to capture diverse functions (Padilla & Allen, 2000). We also separated out three habitat-defining taxa due to their hypothesized strong structuring roles in intertidal communities and large biomasses in our tile communities (Figure 2): the canopy-forming macroalgal species *Fucus serratus*, key limpet grazers in the genus *Patella*, and the reef-forming worm *Sabellaria alveolata*. Note that, although a mobile grazer, limpet densities were largely consistent across tiles through time following initial colonization of tiles (Appendix S1: Figure S4, Table S2) and so measured abundances at 30 months should largely reflect the grazing pressures during community establishment. We observed similar limpet coverage at 9 months ($R^2 = 0.77$), 12 months ($R^2 = 0.83$), and 18 months post-deployment ($R^2 = 0.87$), when compared with the final sampling point (30 months) used in this study.

Quantifying ecosystem functions and multifunctionality

We removed tiles from the field after 30 months and relocated them to laboratory mesocosms where we measured key functions that indicate metabolic activities and contributions to water quality maintenance in the coastal zone (Troell et al., 1999; van den Burg et al., 2022). As some species within intertidal communities are known to remain metabolically active during tidal emersion ("low tide" conditions) (Ji & Tanaka, 2002; Levitt & Bolton, 1991), we measured relevant functions under both immersed and emersed conditions. We used custom-built 14-L gas-tight mesocosms subjected to standardized light, temperature, nutrient, and turbulence conditions (see Appendix S1: Section S1.5 for details). Immersed gross primary productivity (GPP; 1) and community respiration (CR; 2) were calculated based on measured changes in dissolved oxygen concentrations under light and artificially darkened conditions (Littler & Murray, 1974; Noël et al., 2010). Uptake rates of total oxidized nitrogen (TON; 3) and phosphate (PO_4;4) were calculated from extracted 10-mL water samples taken at regular intervals and analyzed using a segmented flow nutrient analyzer. Filtration rate (5) was measured based on the clearance of inoculated microalgal species of differing size, determined using fluorescence-based estimates of CHL-α (Attivissimo et al., 2015), providing an approximation of filtration rates (see Appendix S1: Section S1.5.3 for caveats of CHL-α based approaches). Emersed GPP (6) and CR (7) were measured using the same oxygen flux methods as (1) and (2), but utilizing high-speed axial fans to promote exchange in air. Finally, biomass (8), representing the net accumulation of biological material, and relating to habitat provision, carbon storage, and wave attenuation (Tano et al., 2016; Yong et al., 2022; Zhu et al., 2021), was measured by quantifying and summing the ash-free dry weight (AFDW) of each species within the tile community after destructive sampling.

We calculated a multifunctionality index using PCA based on z-standardized values of the eight individual ecosystem functions (rda function in the vegan package; Oksanen et al., 2017) to reduce the dimensionality of the functional space and account for colinearity in metabolic ecosystem functions (Antiqueira et al., 2017; Dooley et al., 2015). We summed PCA axis scores for the first 5 PCA axes, which accounted for 98% of the total variability, for each individual tile, weighted by the axis eigenvalue (Meyer et al., 2018). The PCA-derived and alternative multi-threshold approaches (Byrnes et al., 2014) gave generally comparable results ($R^2 \sim 0.72$–0.89 for thresholds from 10% to 60%, Appendix S1: Figure S5). See Appendix S1: Section S1.5.5 for more information.

Structural equation modeling

We analyzed all data using R statistical software (R 3.6.1—R Core Team, 2013). We initially identified the net effects of heterogeneity on total community biodiversity and multifunctionality, using linear mixed models, fitted using lme from the nlme package (Pinheiro et al., 2007), and including site and block as random effects. We then conducted two SEM analyses with different degrees of complexity. The first (aggregated SEM) aimed to explore associations between major components in our hypothesized cascade: heterogeneity, multiple foundation species, the biodiversity (species richness) and biomass of supported species, and ecosystem multifunctionality. It also allowed us to identify and compare pathways indicated as connecting heterogeneity and multifunctionality. The second, more complex, model (resolved SEM) aimed to elucidate the cascading pathways by including the richness and biomass of individual functional groups and their influences on individual ecosystem functions. The conceptual meta-model used to design our SEMs can be found in Appendix S1: Figure S6.

Two piecewise structural equation models (pSEM) were created using the PiecewiseSEM package (Lefcheck, 2016). Within the pSEM function, linear mixed models (as detailed above) were populated for each environmental, functional group, or ecosystem function node (Appendix S1: Tables S2 and S3). Model fits were assessed using visual assessment of residuals, and tests of directed separation (Lefcheck, 2016). Missing paths were identified and subsequently included where relationships had ecological relevance or were treated as correlated variables where they did not. From these SEM models, we calculated the total effects of different indirect pathways to multifunctionality as the product of connecting paths (Lefcheck, 2016; Sobel, 1987), termed here Standardized Multifunctionality Estimate (SME; Appendix S1: Section S1.7). To further explore multivariate complementarity, we visualized functional group-specific standardized effects across the full set of ecosystem functions, and calculated between-group Bray–Curtis dissimilarities (see Isbell et al., 2011 for a similar approach).

RESULTS

Net effects and the aggregated SEM

The tile communities comprised a total of 236 species and ~150,000 individuals (species list available in Fairchild & Griffin, 2024). Initial analysis evidenced that heterogeneity markedly enhanced species richness—doing so from initial sampling following deployment (Appendix S1: Figure S4, Table S2) through to the end of the experiment (Figure 3A; $t_{74.81} = 6.68$, $p < 0.001$, $R^2 = 0.59$)—and increased multifunctionality (Figure 3B; $t_{77.52} = 3.00$, $p = 0.003$, $R^2 = 0.38$).

The SEM indicated that these effects of heterogeneity were being driven through multiple pathways that ultimately differentially contributed to multifunctionality (Figure 4). The model suggested that heterogeneity directly increased supported biodiversity (species richness), increased the biomass of a reef-forming polychaete *Sabellaria*, and inhibited key grazers (limpets), patterns that were observed throughout the 30 months of the experiment

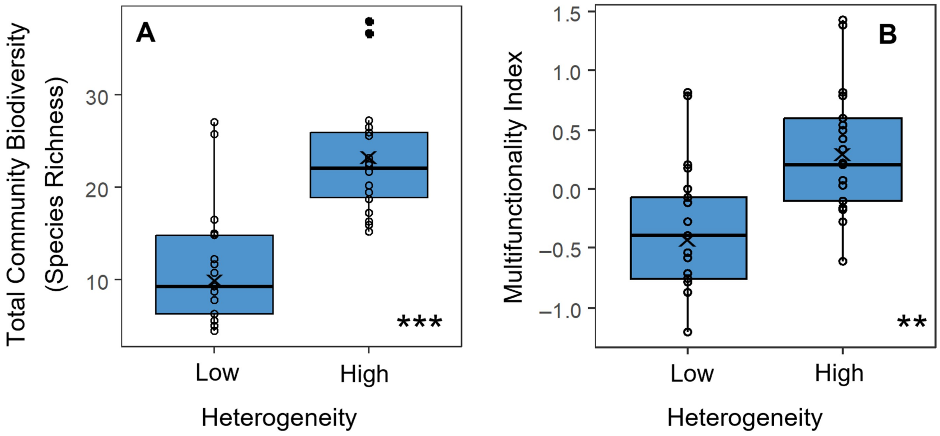

FIGURE 3 Topographic heterogeneity enhances (A) biodiversity (species richness) and (B) multifunctionality of rocky shore assemblages. Boxes on box plots represent data between 25th and 75th percentiles, whiskers indicate the largest values within 1.5 times the interquartile range, central lines represent median values, and X's indicate mean values. Across box and scatter plots, dots represent model partials (predicted values) from linear mixed-effects models. Asterisks indicate significance at α = 0.01 (**) and α = 0.001 (***).

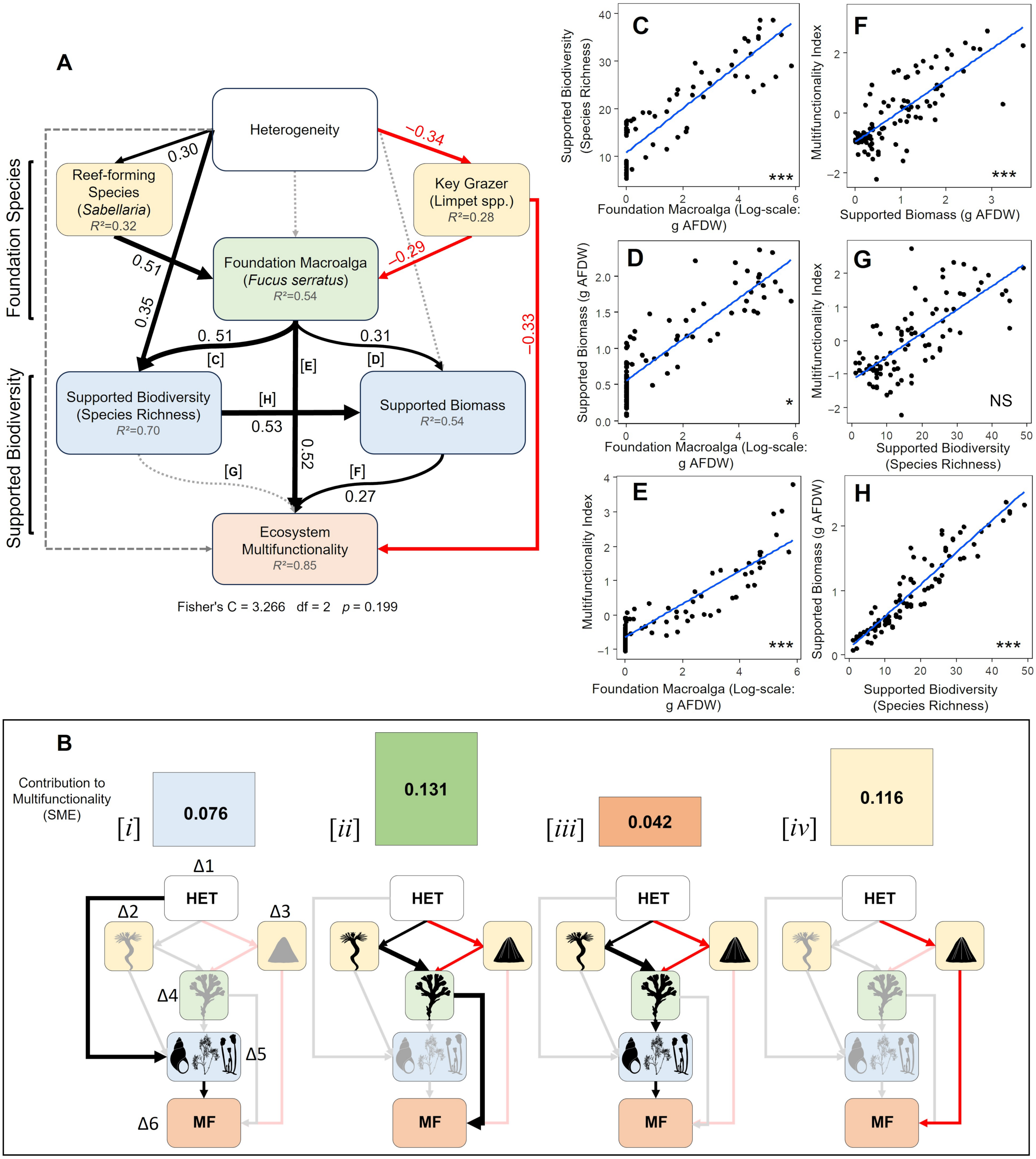

FIGURE 4 Cascading effects of heterogeneity on multifunctionality in intertidal rocky reef systems as revealed by the aggregated structural equation model. Displayed are the flow of effects from heterogeneity (HET in bottom panel) to ecosystem multifunctionality (MF in bottom panel) through foundation species and their associated communities (A), a summary of the four cascades connecting heterogeneity to multifunctionality (B), and biplots of individual connections between biodiversity, biomass, and multifunctionality (C–H). In A and B, black arrows indicate significant positive—and red significant negative—paths ($\alpha < 0.05$); in A, paths include standardized effect sizes and letters (C–H) corresponding to paths visualized in adjacent panels. Gray dashed lines indicate nonsignificant pathways. In B, colored bars and numbers indicate the strength of each pathway's contribution to multifunctionality, and boxes represent heterogeneity$^{\Delta 1}$, reef-forming *Sabellaria*$^{\Delta 2}$, key limpet grazers$^{\Delta 3}$, foundation macroalgae$^{\Delta 4}$, supported species$^{\Delta 5}$, and multifunctionality$^{\Delta 6}$. Across scatter plots, dots represent model partials (predicted values) from linear mixed-effects models. Asterisks represent significance at $\alpha = 0.05$ (*), $\alpha = 0.01$ (**), $\alpha = 0.001$ (***), and "NS" indicates nonsignificant trends. Model summaries can be found in Appendix S1: Table S3. AFDW, ash-free dry weight.

(Appendix S1: Figure S4). These interactions between heterogeneity and foundation species, in turn, cascaded through multiple channels to increase multifunctionality (Figure 4A–C). Four major cascading pathways are supported by the model and are shown in Figure 4B. Through the first pathway (pathway *i*) heterogeneity's enhancement of biodiversity led to greater supported biomass, ultimately leading to multifunctionality (SME = 0.076). The second and third pathways channeled, as hypothesized, through foundation species. Specifically, heterogeneity's positive effect on *Sabellaria* and inhibition of limpets both supported the foundation macroalga. In turn, these effects on the foundation macroalga propagated to multifunctionality in two ways: through the macroalga's direct effect on multifunctionality (pathway *ii*; SME = 0.131) and through the macroalga's indirect effect via its enhancement of biodiversity and biomass through habitat-provisioning (pathway *iii*; SME = 0.042). Finally, heterogeneity's inhibitory effect on limpets also cascaded, as limpets had a direct negative influence on ecosystem multifunctionality (pathway *v*; SME = 0.116). After accounting for these pathways, there was no support for an additional direct effect of heterogeneity on multifunctionality. Notably, the more direct pathway from heterogeneity to biodiversity and multifunctionality (pathway *i*) was substantially outweighed by pathways channeled through the foundation macroalga (*ii* and *iii*).

The resolved SEM

The resolved SEM (Figure 5A) echoed the above highlighted pathways while exposing a complex network of interactions and complementarity between functional groups. The model first indicated that the direct heterogeneity–biodiversity connection (Figure 5A) is explained by its positive effect on filter feeder richness and grazer/predator richness, suggesting that these species-rich groups (~71% of overall species pool) benefited from enhanced variability of the primary substrate. Heterogeneity's indirect enhancement of the foundation macroalga (Figure 5A, level *i*), in turn, appears to have directly influenced a suite of functions (detailed below) and facilitated a diverse range of functional groups (filter feeders, red macroalgae, and grazing and predatory animals), which was reinforced by richness-biomass enhancement effects across several groups (Figure 5A, interaction level *ii*). Furthermore, unlike the aggregated model, the resolved model supported an effect of the primary foundation species (*Sabellaria*) on biodiversity, indicating that it directly enhanced macroalgal species richness (Figure 5A; Appendix S1: Figure S7, pathway *v*).

Multivariate complementarity revealed by the resolved SEM

Heterogeneity's effects that appear to have channeled through multiple cascades, involving diverse functional groups, are further indicated to have propagated via the functional groups' complementary effects on distinct ecosystem functions, and thus on to multifunctionality. Filter feeder richness and biomass (Figure 5A) uniquely enhanced water clearance rates. Meanwhile, the foundation macroalga contributed directly and substantially to emersed GPP and respiration, immersed GPP, and total biomass (Figure 5A, interaction levels *ii/iii*). Macroalgal richness increased emersed GPP, and the biomass of red macroalgae increased uptake rates of total oxidized nitrogen (TON) and phosphate (PO_4), as well as contributing significantly to overall community biomass (Figure 5A, interaction level *iii*). Finally, the resolved model also suggests that heterogeneity's inhibition of limpets indirectly enhanced net removal of key nutrients (TON and PO_4), presumably by reducing the presence of this high biomass excreting grazer. Thus, the richness and biomass of multiple groups—themselves differentially influenced by multiple cascading interactions emanating from heterogeneity—appear to have had complementary effects across the ecosystem functions that collectively drive multifunctionality (Figure 5A, interaction level *iv*, Figure 5B,C). Notably, by more fully explaining interactions between specific functional groups and ecosystem functions, the SMEs in the resolved model slightly reduced the contribution of the foundation macroalga in directly driving multifunctionality (Figures 4B and 5A; Appendix S1: Figure S7), while enhancing indirect foundation macroalga contributions to multifunctionality via increases in biodiversity and biomass within supported functional groups. Otherwise, the relative contributions of the pathways to multifunctionality remained largely comparable, with the effects of heterogeneity on function being substantially directed through foundation species (Appendix S1: Figure S7).

Countervailing effects evident within the resolved SEM

The resolved SEM also suggested that some groups were influenced by the foundation species in a manner that had negative functional consequences. For instance, grazers and predators, facilitated via habitat-provisioning by the foundation macroalga, led to decreases in the amount of net TON uptake by the community due to high nitrogen excretion rates. Furthermore, unlike for other species groups, both foundation species displaced

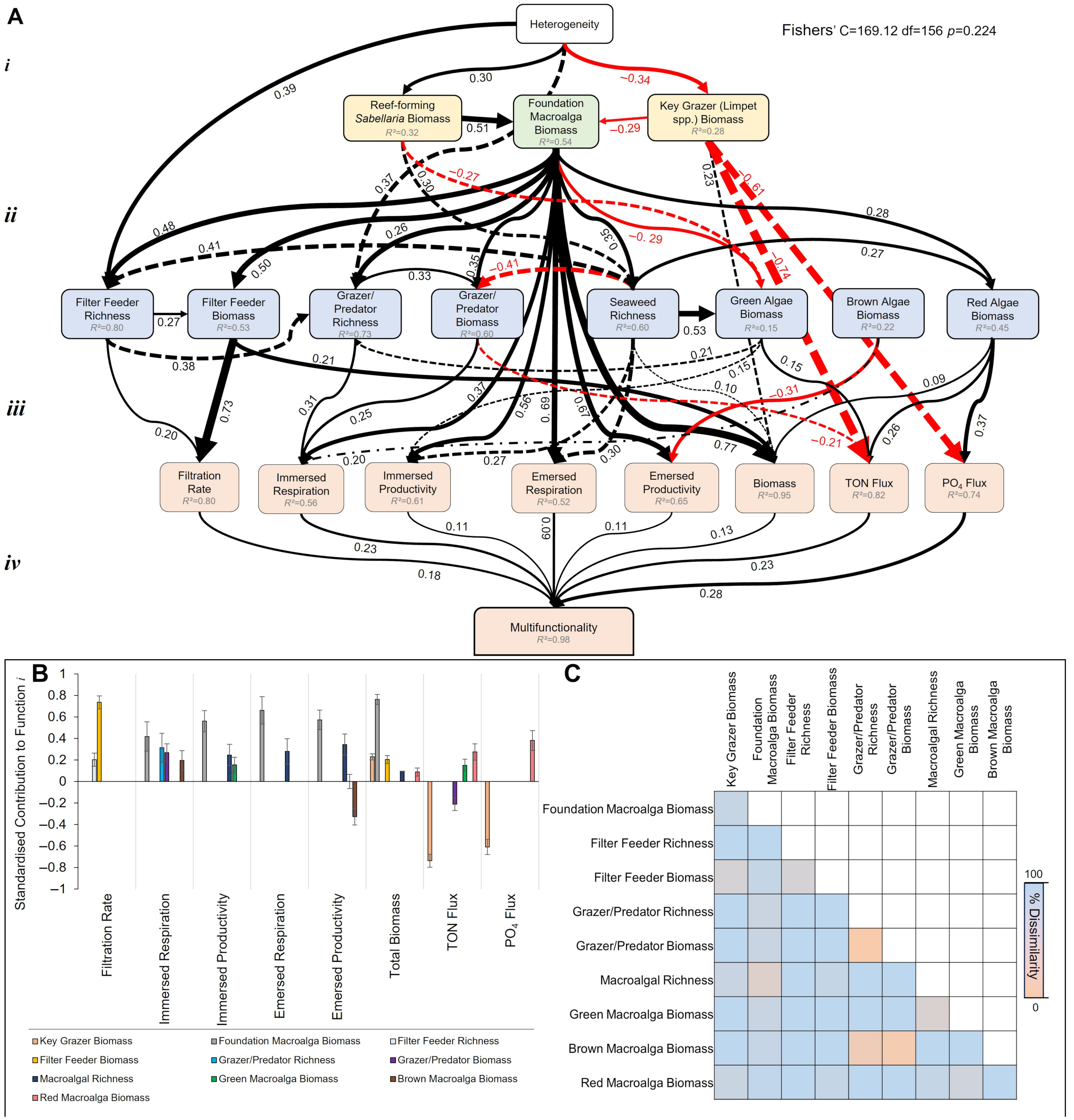

FIGURE 5 Resolved structural equation modeling (SEM) reveals specific cascading pathways from heterogeneity to function via foundation species and supported communities, as well as multivariate complementarity across supported functional groups. Topographic heterogeneity effects cascade to multifunctionality through specific functional groups and individual functions (A). Red lines indicate significant ($\alpha < 0.05$) negative effects, black lines represent significant ($\alpha < 0.05$) positive effects (including dashed lines for clarity). Numbers next to lines represent the standardized path coefficient, and R^2 values in boxes represent the proportion of variance explained. Y axis numerals denote interaction levels (see main text). Model summaries are available in Appendix S1: Table S4. Functional groups (richness and biomass) that were directly or indirectly supported by heterogeneity, in turn, showed evidence of multivariate complementarity (B, C). Ecosystem functions were differentially supported by specific functional groups (B), a phenomenon further reflected in the dissimilarity (Bray–Curtis index) of functional groups' effects across functions (C). In B, bars represent effects of functional groups that significantly contributed to each function ($\alpha < 0.05$), and error bars represent one standard error. Units are in standardized estimates from the SEM model in A–C, with high levels of turnover in functional groups' contributions to ecosystem functioning. Cells within the heatmap plot represent comparisons of dissimilarity in functioning between functional group pairs using Bray–Curtis dissimilarity. PO$_4$, phosphate; TON, total oxidized nitrogen.

green macroalgal biomass, likely by limiting light and available substrate for colonization. These fast-growing green species contributed to aerial primary productivity and were able to quickly take up nitrogenous nutrients, with exclusion by foundation canopy-forming species reducing these community functional rates. Notwithstanding these negative indirect effects on several ecosystem functions, the foundation species retained net positive indirect influences on ecosystem multifunctionality.

DISCUSSION

Our results provide direct experimental evidence that a form of abiotic topographic heterogeneity enhances biodiversity and ecosystem multifunctionality, and further suggests that it does so through multiple cascades. Our SEM analyses suggest that the cascading effects of topographic heterogeneity in our system are channeled through enhancement of foundation species and show complementarity in their support of diverse organismal groups and a breadth of associated functions. These findings extend our understanding of how heterogeneity influences ecosystems by demonstrating its effects can cascade beyond biodiversity to ecosystem multifunctionality, and therefore connects hitherto separate core areas of inquiry in ecology that relate heterogeneity to biodiversity (Kadmon & Allouche, 2007; Lundholm & Larson, 2003) and link biodiversity to ecosystem multifunctionality (Hector & Bagchi, 2007; Pasari et al., 2013).

Our results provide new evidence that foundation species—through their direct effects on functions, interactions with each other, and broad community facilitation—can serve as dominant conduits of heterogeneity's effects on multifunctionality (*Results*, Figure 4: pathways *iii–iv*). Our analyses indicate that heterogeneity, by supporting a primary foundation species (*Sabellaria*) while inhibiting a key grazer (*Patella*, limpets), enhanced the system's biomass-dominant secondary foundation species (*Fucus*). The positive response of *Fucus* to heterogeneity, contrasted with the negative response of key grazers, is consistent with classic work on a New England, USA, rocky shore (Lubchenco, 1983), as well as recent observational evidence from an urban shoreline in the southwest of the UK (Bauer et al., 2024). Our results show that *Fucus*, in turn, drove several metabolism-related functions and, equally importantly, both foundation species (*Sabellaria* and *Fucus*) together generated a diversity of microhabitats that supported a range of groups, including small grazers, algal epiphytes, and understory species, which in turn drove a broad suite of functions in a complementary fashion to enhance multifunctionality. In our study, foundation species thus appear to have propagated heterogeneity effects to multifunctionality via multiple channels.

In other systems, foundation species such as trees, mosses, and kelps are supported by topographic heterogeneity (Greenwood et al., 2015; Randell et al., 2022; Strain et al., 2017). In turn, as we observed, their generally high biomass, and functionally unique attributes, together with the diverse microhabitats they create, are likely to both directly drive several ecosystem functions (Grime, 1998) and support a high functional diversity of associated species (Angelini & Silliman, 2014), reinforcing and broadening their effects on ecosystem functions and multifunctionality. In fact, facilitation of diverse groups is probably a key step in the cascade to multifunctionality, since individual foundation species are limited in the breadth of trait modalities they can express (Cappelatti et al., 2019) and thus functions they can mediate. In light of our results, and given the generally high relative biomass and structural complexity of foundation species, we suggest that they have the potential to be a critical and general bridge between heterogeneity, biodiversity, and multifunctionality.

Yet, heterogeneity's effects on biodiversity and functionality are unlikely to flow exclusively through foundation species, as some species settle directly on, or forage over, the primary substrate and thus are more likely to be directly influenced. Indeed, in our study, heterogeneity was indicated to have additionally driven multifunctionality by: (1) directly facilitating a richer assemblage of filter feeders, a guild that includes many species that directly attach to the substrate and show partitioning across different microtopographic niches (Bishop et al., 2022; Sedano et al., 2020), in turn driving water clearance rates (*Results*, Figure 4: pathway *i*); and (2) inhibiting limpets and thus their suppression of net nitrogen and phosphate uptake (an excretion effect; *Results*, pathway *iv*). While few, if any, previous studies have examined the consequences for multifunctionality, the positive influence of topographic heterogeneity or complexity on biodiversity has found previous support across systems (Agra et al., 2024; Stein et al., 2014; Tokeshi & Arakaki, 2012). Overall, as supported by our results, a suite of pathways potentially connect heterogeneity to different components of the community that in turn exert complementary effects on multifunctionality.

Although our finding of a substrate heterogeneity triggered cascade that reaches multifunctionality is novel, the long chain of cascading positive species interactions, or facilitation cascade, is reminiscent of several previously documented cases in marine and coastal systems. For example, in a New Zealand estuary, a six-level cascade increases biodiversity, involving a bivalve, green seaweeds, trochid snails, a bryozoan, and finally a red seaweed (Thomsen et al., 2016). Furthermore, in the

White Sea, Russia, another bivalve creates substrate for barnacles, which support ascidians, in turn, hosting discord mussels, and eventually red seaweed (Yakovis & Artemieva, 2017). Such previous findings, together with ours, underline that marine biodiversity is often supported by long interaction chains, often involving multiple foundation species (Angelini et al., 2011).

We suggest that our findings from rocky shores will be applicable across a range of systems, particularly where geological features and variation create marked heterogeneity and generate refugia—or accumulate resources—within otherwise hostile rocky environments. The capacity of topographic heterogeneity to drive multiple cascades, as shown here, likely stems from its ability to create diverse microenvironments (Meager et al., 2011; Nowak et al., 2014), shelter crucial early life stages, and modify consumer access (Griffin et al., 2009; Lubchenco, 1983; Wahl & Hoppe, 2002), ultimately supporting the establishment of a broad range of species, including, crucially, foundation species. Moreover, the abiotic substrate and foundation species are likely to provide contrasting sources of microhabitat diversity and thus support different components of functionally diverse assemblages and thus multifunctionality (Thomsen et al., 2022).

It must be noted that, in our study, to achieve replication needed to decipher a complex web of cascading interactions, we were limited to a single form of substrate topographic heterogeneity (holes of various sizes) that is commonly found on rocky shores. Combined with previous evidence (e.g., Bauer et al., 2024; Lubchenco, 1983), we suggest that its influence likely did not arise from holes per se, but from the topographic heterogeneity that these features create. Other sources of substrate heterogeneity such as cracks, crevices, or geological intrusions may trigger similar mechanisms as those described in our study. While it would be premature to claim generality beyond the specific form of heterogeneity studied here, ecology progresses toward generality through the collective results of many studies that individually represent general concepts (e.g., keystone species) in specific ways (e.g., focal species). Future experimental work and syntheses should aim to test the generality of our findings by including different sources and scales of topographic heterogeneity and examining how this influences the cascading effects to multifunctionality. We suggest that topographic heterogeneity effects will be most prominent across systems where: (1) scales of variability and resulting refugia match foundation species' vulnerable establishment stages, while limiting consumer access; (2) primary substrates (e.g., rock) are exposed, thus generating sharp small-scale topographic variation; and (3) stress from both environmental factors and consumers, and thus the value of stress mitigation on heterogenous substrates is high (Bertness & Callaway, 1994).

There may also be applications of our findings in ecologically sensitive engineering of coastal—and other—environments, as we demonstrate heterogeneity can be linked to greater diversity, functionality, and potentially service provision. Importantly, our work shows how subtle—and thus cost effective—enhancements in heterogeneity can have disproportionate effects on diversity and functionality where they support establishment of foundation species. This strengthens growing evidence for the benefits of including ecologically sensitive design on marine artificial structures to help mitigate the often negative biodiversity outcomes (Evans et al., 2016; Firth et al., 2014; Hall et al., 2019). Our study demonstrates that, once accounting for cascading effects of heterogeneity via foundation species, ecological enhancement of substrates may lead to greater biodiversity and multifunctionality benefits than previously assumed. Our results support recent work in indicating the potential to use heterogeneity and naturally recruiting—or even seeded—foundation species as a material-efficient and cost-effective tool to functionally restore and enhance natural and managed systems (Bishop et al., 2022; Mayer-Pinto et al., 2024; Vozzo et al., 2023).

In conclusion, we have shown how subtle changes to the heterogeneity of substrates can lead to marked consequences for ecosystem multifunctionality. We provide support for a novel mechanism underpinning multifunctionality, whereby heterogeneity triggers multiple, complementary, cascades, predominantly channeling through foundation species to affect a broad suite of ecosystem functions. In this way, analogous to the top-down effects of keystone predators (Paine, 1966), topographic heterogeneity exerts disproportionate cornerstone effects (sensu Bracken & Low, 2012) from the base of the system. Cornerstone effects of heterogeneity are likely to be widespread, and we encourage others to investigate how the effects of heterogeneity of primary substrates, in systems from riverbeds to coral reefs and alpine rock fields, propagate through communities to determine ecosystem multifunctionality.

AUTHOR CONTRIBUTIONS

Tom P. Fairchild and John N. Griffin designed the experiment, did the statistical analysis, and wrote the manuscript. Tom P. Fairchild, Bettina Walter, and Joshua J. Mutter developed methodologies for the assessment of ecosystem functions on tile communities and carried out the experiment.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Fairchild & Griffin, 2024) are available in figshare at https://doi.org/10.6084/m9.figshare.24460123.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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