In review

RUNNING TITLE: Community assembly and ecosystem function

Coupling spatiotemporal community assembly processes to ecosystem function

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Abstract

Community assembly processes govern shifts in species abundances in response to environmental change, yet our understanding of assembly remains largely decoupled from ecosystem function. Here, we test hypotheses regarding assembly and function across space and time using hyporheic microbial communities as a model system. We pair sampling of two habitat types (*e.g.*, attached and unattached) through seasonal and sub-hourly hydrologic fluctuation with null modeling and temporally-explicit multivariate statistics. We demonstrate that dual selective pressures assimilate to generate compositional changes at distinct timescales among habitat types, resulting in contrasting associations of *Betaproteobacteria* and *Thaumarchaeota* with selection and with seasonal changes in aerobic metabolism. Our results culminate in a conceptual model in which selection from contrasting environments regulates taxon abundance and ecosystem function through time, with increases in function when oscillating selection opposes stable selective pressures. Our model is applicable within both macrobial and microbial ecology and presents an avenue for assimilating community assembly processes into predictions of ecosystem function.

Introduction

Ecosystem function is strongly influenced by community membership at a given point in time and space, but links between assembly processes that govern community composition and ecosystem metabolism remain unclear. The extent to which community assembly processes regulate ecosystem function is contingent on myriad spatiotemporal factors (Foster *et al.* 2004, Graham *et al.* 2014, Graham *et al.* 2016, Kardol *et al.* 2013, Nemergut *et al.* 2014), and assembly processes themselves vary through space and time. A plethora of research has demonstrated the influence of historical community assembly processes and abiotic conditions on ecosystem function (Evans and Wallenstein 2012, Fukami *et al.* 2010, Hawkes and Keitt 2015, Kardol *et al.* 2013, Ulrich *et al.* 2015). Selection can enhance ecosystem function via species sorting mechanisms that optimize community composition for a given environment (Lindström and Langenheder 2012, Van der Gucht *et al.* 2007), whereas dispersal limitation can lead to a dominance of species that are poorly adapted to prevailing environmental conditions with resultant decreases in productivity (Hanson *et al.* 2012, Lindström and Östman 2011, Peres *et al.* 2016, Telford *et al.* 2006). As such, selection and dispersal aggregate across various spatiotemporal intervals to impact species composition, yet we lack a conceptual basis for how these processes collectively influence ecosystem function (Gonzalez *et al.* 2012, Prosser *et al.* 2007, Shade *et al.* 2013).

Community assembly processes intrinsically interact with disturbance history and biogeography to effect changes in community composition and ecosystem metabolism. For example, communities experiencing a history of strong, homogeneous selective pressures may contain taxa that are optimized for environmental conditions and maintain high rates of ecosystem function (Grime 1998, Knelman and Nemergut 2014). In contrast, such a history may exclude taxa that are able to utilize alternative resource pools relative to communities experiencing higher rates of dispersal or more variable selection (Cardinale 2011, Hooper *et al.* 2012, Loreau and Hector 2001). Spatial assembly processes (*e.g.*, dispersal) can result in an influx of diverse organisms that mediate ecosystem functioning, including species that are sub-optimal in present environmental conditions, and/or limit the ability of organisms with high fitness to reach an environment. Thus, we hypothesize that community assembly processes act through long timescales across a history of abiotic conditions and impose short-term controls over community composition at a given point in time and space. These assembly dynamics culminate in distinct community membership at every point in a spatiotemporal domain, impacting the efficiency of ecosystem function via changes in species distributions.

Environmental transition zones present a unique opportunity for examining interactions between ecosystem function and both long- and short-term assembly processes, as they experience extreme spatiotemporal variation in physicochemical characteristics and microbial community turnover across tractable spatial and temporal scales. In particular, hyporheic zones, with dynamic groundwater-surface water mixing, exhibit elevated rates of microbially-mediated biogeochemical cycling and strongly influence watershed-scale biogeochemistry (Hedin *et al.* 1998, McClain *et al.* 2003). The hyporheic zone of the Columbia River experiences geographic variation in groundwater-surface water mixing, porewater geochemistry, and microbial community composition on sub-hourly to annual timescales (Arntzen *et al.* 2006, Lin *et al.* 2012, Peterson and Connelly 2004, Slater *et al.* 2010, Stegen *et al.* 2012, Stegen *et al.* 2016, Zachara *et al.* 2013). Accordingly, the Hanford Reach of the Columbia River embodies a model system to facilitate the integration of community ecology and ecosystem function.

Here, we leverage inherent variation in hydrology, habitat heterogeneity, and aerobic respiration to examine the interplay of community assembly processes and systemic changes in ecosystem function. We employ null modeling in conjunction with temporally-explicit multivariate statistics to characterize assembly processes driving functional shifts in microbial communities and the efficiency of ecosystem function in the Columbia River hyporheic zone. Our results culminate in a broadly-applicable conceptual model coupling changes in selective environments, trait abundance, and ecosystem function through time.

Materials and Methods

Study Design

This study was conducted in Hanford Reach of the Columbia River adjacent to the Hanford 300A (approximately 46^{o} 22' 15.80"N, 119^{o} 16' 31.52"W) in eastern Washington, as described elsewhere (Slater *et al.* 2010, Stegen *et al.* 2016, Zachara *et al.* 2013). We monitored physicochemical conditions for three hydrologically connected geographic zones (nearshore, inland, river) via aqueous sampling (Table S1). The inland environment is characterized by an unconfined aquifer within the Hanford formation and more recent illuvial deposits and maintains a distinct hydrologic environment with stable temperatures (~15^{o}C) and high concentrations of anions and inorganic carbon relative to the river. River water contains high concentrations of organic material and low concentrations of ions with seasonally variable temperatures. The waters from these discrete hydrologic environments experience dynamic mixing in a nearshore zone that is regulated by fluctuations in river stage across sub-hourly (dam controlled) to seasonal (winter snowpack melt) variation in river stage; we focus on ecological dynamics within this zone. To monitor groundwater-surface water mixing across space and time, we utilize

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Cl^- as a conservative tracer for groundwater contributions to hyporheic porewater chemistry as employed by Stegen *et al.* (2016).

Detailed sampling and analytical methods are in the Supplemental Material. Attached and unattached communities were obtained from deployed colonization substrate and aqueous samples. These samples were collected at three-week intervals from March through November 2014, with the first unattached samples collected in March and the first attached samples collected after a six-week incubation period, from piezometers installed to 1.2m depth near the riverbed. Aqueous samples were obtained via pumping water from piezometers adjacent to colonization substrates and used to derive physicochemical conditions as well as to sample unattached communities. Attached microbial communities were sampled by deploying mesh stainless steel incubators of locally-sourced colonization substrate in piezometers within one meter of piezometers from which aqueous samples were obtained. All incubators were deployed six weeks prior to removal. Samples to construct the regional species pool for null models were simultaneously obtained at three inland wells and at one location in the Columbia River.

Null Modeling Approach.

We implemented null modeling methodology developed by Stegen et al. (2013, 2015) using *R* software (http://cran.r-project.org/) to disentangle community assembly processes (Supplemental Material). The approach uses turnover pairwise phylogenetic turnover between communities, calculated using the mean-nearest-taxon-distance (βMNTD) metric (Fine and Kembel 2011, Webb *et al.* 2008), to infer the strength of selection. Communities were evaluated for significantly less turnover than expected (βNTI < -2, homogeneous selection) or more turnover than expected (βNTI > 2, variable selection) by comparing observed βMNTD values to the mean of a null distribution of βMNTD values—and normalizing by its standard deviation—to yield βNTI (Stegen *et al.* 2012). Pairwise community comparisons that did not deviate from the null βMNTD distribution were evaluated for the influences of dispersal limitation and homogenizing dispersal by calculating the Raup-Crick metric extended to account for species relative abundances (RC_{bray}), as per Stegen *et al.* (2013, 2015). Observed Bray-Curtis dissimilarities were compared to the null distribution to derive RC_{bray}. RC_{bray} values > 0.95, > -0.95 and < 0.95, or < -0.95 were assumed to indicate dispersal limitation, no dominant assembly process, or homogenizing dispersal, respectively. Inferences derived from both βNTI and RC_{bray} have previously been shown to be robust (Dini-Andreote *et al.* 2015, Stegen *et al.* 2015).

Statistical Methods

Regressions and one-sided Mann Whitney *U* tests were conducted using the base statistics package in *R*. Variation in community composition was assessed with PERMANOVA in QIIME (Caporaso *et al.* 2010). The contribution of nestedness versus turnover to community differences was determined using the 'betapart' package in *R* (Baselga and Orme 2012). We conducted variance partitioning (ADONIS) and fit porewater characteristics to NMDS plots of Bray-Curtis dissimilarities with and without stratifying by time within attached and unattached communities using the 'vegan' package in *R* (999 permutations, Oksanen *et al.* 2013). Further details are available in the Supplemental Material.

Because we observed large seasonal differences in species richness in both attached and unattached communities, we performed similarity percentage (SIMPER) analysis to identify individual species driving community dissimilarity between time periods of high and low richness in each environment (Clarke 1993). SIMPER was conducted across all attached and unattached communities and within attached and unattached communities across time periods of high and low species richness, defined by time rather than species numbers to control for seasonal effects (Supplemental Material). We extracted taxonomic groups of organisms at the class-level containing at least one species identified as having a significant impact on community composition by SIMPER ($P < 0.05$) for subsequent analyses. Organisms were grouped at the class-level to provide sufficient statistical power for analysis. Mantel tests were used to compare the average relative abundance of taxonomic groups identified by SIMPER across samples to associated βNTI and RC_{bray} values ('vegan', 999 permutations). Finally, we compared dissimilarity in species richness between samples within and across attached and unattached communities to βNTI and further, if $-2 < \beta NTI < 2$, to RC_{bray} using Mantel tests to infer community assembly processes generating species turnover between samples.

Results

Hydrologic shifts through time

We observed distinct temporal trends in groundwater-surface water mixing, characterized by an abrupt increase in Cl^- concentration (Figure 1A) and decrease in NPOC (Figure 1B) associated with a seasonal shift in water stage (Figure S1, Table S1). Temperature peaked during August and followed a smooth temporal trend (Figure 1C). Species richness in both attached and unattached communities mirrored the trend in temperature, with the highest number of species observed during the warmest summer months (Figure 1D). Further, species richness was more tightly correlated with temperature (Figure S2, regression, attached: $R^2 = 0.25$, $P = 0.001$, unattached: $R^2 = 0.22$, $P = 0.002$) than Cl^- (regression, attached: $P = 0.01$, $R^2 = 0.14$, unattached: $P > 0.05$) and NPOC (regression, attached: $P = 0.04$, $R^2 = 0.10$, unattached: $P > 0.05$). Finally, average species richness between two samples was positively associated with Bray-Curtis dissimilarity within attached and unattached communities, even when constraining analysis by sampling time to remove confounding effects from temperature, suggesting richness as a driver of community divergences in our system (Figure 2A).

Spatiotemporal assembly processes

Attached and unattached communities remained taxonomically distinct through time (PERMANOVA, R^2 = 0.19, P = 0.001), driven by species turnover rather than nestedness (avg. dissimilarity due to turnover, 96.4%). The composition of both attached (PERMANOVA, R^2 = 0.44, P = 0.001) and unattached (PERMANOVA, R^2 = 0.44, P = 0.001) communities changed across our sampling period. Assembly processes governing variation in community composition varied by environment type (Figure 2B and C). βNTI was positively correlated with differences in species richness in unattached samples (Mantel, P = 0.001, r = 0.41, Figure 2C), with weaker correlations in attached communities (Mantel, P = 0.02, r = 0.24, Figure 2B) and between attached and unattached communities (Mantel, P = 0.006, r = -0.26, Figure 2D).

When examining selective processes at discrete timescales, unattached communities were correlated to more environmental variables than attached communities at a sub-hourly timescale (stratified NMDS, Figure 3A and B, Table S2). Conversely, attached communities correlated more tightly with physicochemical attributes over a seasonal timescale (unstratified NMDS, Figure 3A and B). Temperature and dissolved oxygen were significant predictors of community composition over a seasonal but not sub-hourly timescale in both unattached and attached communities.

Phylogenetic variability in assembly and functional outcomes

SIMPER analysis revealed species driving differences among attached and unattached communities during periods of high versus low species richness (Table S3). In separate analyses of attached and unattached communities, 231 species were identified as significant drivers of community composition, while 863 species were identified as drivers of community composition across unattached versus attached environments. We extracted phylogenetic classes of organisms containing species identified by SIMPER and examined them for relationships with βNTI and $RC_{bray.}$ All significant correlations with *r* values greater than +/- 0.30 are listed in Table S4. In particular, taxa within unattached communities exhibited no relationships with βNTI, but the mean relative abundance (across two samples) of many taxa, including *Thaumarchaeota* (positive, Figure 4A), a class of *Acidobacteria* (positive, Figure 4B), *Actinobacteria* (negative, Figure 4C), and *Alphaproteobacteria* (negative, Figure 4D), displayed correlations with RC_{bray}. The mean relative abundance of *Parvarcheota* and a class of candidate phyla OP3 (*koll11*) were positively correlated with βNTI derived from comparisons across attached and unattached communities (Figure 4E and F). Finally, within attached communities, βNTI was correlated with the mean relative abundance of *Thaumarchaeota* (positive, Figure 4G) and *Betaproteobacteria* (negative, Figure 4H).

We also observed a seasonal increase in the abundance of *Thaumarchaeota* in attached communities with a decrease in *Betaproteobacteria* (Figure 5A) that corresponded with shifts in hydrology (Figure 5B). Oxygenated conditions persisted throughout our sampling period, and aerobic metabolic activity normalized to active biomass (Raz:ATP) also increased seasonally within attached communities, an effect that correlated with day of year (Figure 5C) but not temperature, NPOC concentration, or hydrology (regression: temperature P = 0.10, NPOC P =

0.21, log(Cl^-) P = 0.15). The relative abundance of *Thaumarchaeota* and *Betaproteobacteria* in attached communities also correlated positively and negatively, respectively, with Raz:ATP (Figure 5D) and exhibited contrasting responses to porewater physicochemical properties (Table S5).

Discussion

Microbial responses to hydrologic change

Hydrology, organic carbon concentration, and temperature each explained some variation in community dissimilarity within attached and unattached communities, potentially indicating the influence of selection and dispersal on microbial community composition (Table S6). Indeed, both selection by the geochemical environment and/or dispersal from local sediment communities have been demonstrated within the groundwater aquifer in our system (Stegen *et al.* 2012). While dispersal potential within hyporheic zones remains unclear (Bärlocher *et al.* 2006, Cornut *et al.* 2014), physical filtering of particulates can inhibit microbial dispersal at relatively small spatial scales zone (Brunke 1999, Hartwig and Borchardt 2014). Further, variation in selective environments and/or dispersal limitation should enhance rates of turnover relative to nestedness, and species turnover governed almost all dissimilarity between community types. Other studies have demonstrated little overlap between porewater and sediment microbial community composition in hyporheic zones (Febria *et al.* 2012), as well as the importance of organic carbon concentration and temperature within aquatic systems (Docherty *et al.* 2006, Findlay *et al.* 2003, Hullar *et al.* 2006), effects that may be prevalent within our system.

To assess the extent to which selection versus dispersal governed the addition of new species to communities, we employed null modeling to infer the importance of these processes across differences in richness between samples. Our results indicate stronger selection imposed by the physical environment than by aqueous chemistry, an inference supported by lower absolute βNTI values in unattached communities relative to attached communities. Homogeneous selection (*e.g.*, selection for consistent traits) appears to be the dominant assembly process in attached communities, while unattached communities are influenced by a combination of homogeneous selection, variable selection (*e.g.*, selective pressures for a of mixture traits), and spatial processes (*e.g.*, dispersal). Homogenous selection remained dominant in attached communities as differences in species richness increased (Figure 2B), indicating strong and consistent selective pressures imposed by a relatively stable environment.

As such, the physical substrate may inherently contain a limited number of ecological niches—potentially related to mineralogy or physical structure—with slow changes in available niche space through time, whereby species added with increases in richness were ecologically similar to existing taxa. Conversely, relative to attached communities, we observed greater seasonal changes richness in unattached communities (Figure 1D) and differences in richness that were positively correlated with βNTI (Figure 2C), as would be expected if differences in richness were due to expansion of available niche space.

Variation in assembly processes between attached and unattached communities may be due to inherent differences among these environments, such as influences of mineralogy (Carson *et al.* 2007, Jorgensen *et al.* 2012), physical matrix composition (Breulmann *et al.* 2014, Vos *et al.* 2013), and/or relative rates of change in environment characteristics (discussed below). Deviations in assembly processes and niche dynamics between environments may furthermore induce differential responses to both sub-hourly and seasonal fluctuations in environmental conditions.

Timescales of selection

The timescales at which selection imposes constraints on microbial community composition are poorly understood (Nemergut *et al.* 2013, Shade *et al.* 2012). Here, we provide new insights into these timescales, showing that selection on unattached communities operates at the timescales of shifting porewater conditions (sub-hourly to seasonal), while selection on attached communities operates primarily at seasonal timescales. Rapid microbial turnover in unattached communities may be the result of oscillating selective pressures in the aqueous environment and enhanced rates of dispersal relative to attached communities. Further, our results indicated that temperature and dissolved oxygen impacted community composition only at seasonal timescales. These factors are less variable over sub-hourly periods relative to seasonal changes and may exert cumulative effects on community composition only when large changes are sustained over seasonal timescales.

Selection on attached communities operated at the seasonal timescale, and these communities were therefore resistant to short-term hydrologic variation. Short-term stability could be facilitated by a number of mechanisms. Attached microbial communities can have adhesion mechanisms (Hori and Matsumoto 2010) that confer stability in concert with priority effects that slow rates of turnover in these communities relative to unattached communities (Fukami 2004, Fukami *et al.* 2010). Biofilms, whereby microbial cells are imbedded within a matrix of extracellular polymeric substances, are prevalent in aquatic systems and buffer communities against fluctuations in the hydrologic environment (Battin *et al.* 2016). Temporal stability may also be conferred by high species richness, in which the propensity for a community to contain a range of organisms with complementary traits/metabolisms as well as physiologically plastic organisms is enhanced and turnover is diminished by metabolic flexibility (Evans and Hofmann 2012), niche construction (Kylafis and Loreau 2011), and/or reduced susceptibility to invasion (Stachowicz *et al.* 2002). Indeed, in our system, attached communities contained more species on average than unattached communities (Figure 1D).

Conceptual basis for taxon-specific assembly processes

Community assembly processes, by definition, describe community-level dynamics, but taxa may respond differentially to prevailing environmental conditions. For instance, only some taxa contain traits that are under selection in given conditions (Knelman and Nemergut 2014, Krause *et al.* 2014, Lebrija-Trejos *et al.* 2010, Poff 1997), and traits that facilitate dispersal (*e.g.*, winged or waterproof seeds, spore formation) are preferentially contained within certain taxa (Martiny *et al.* 2006, Tremlová and Münzbergová 2007). These taxon-specific effects are obscured when examining βNTI and RC_{bray} values that reflect community-level processes. To address this issue, we compared the relative abundance of key microbial taxa to βNTI values.

An increase in the abundance of a particular taxon as βNTI increases implies that a reduction in selection enhances successful colonization of that taxon, and hence, that predominate selective pressures target traits outside of that taxon. This effect is more probable for organisms occupying narrow niche spaces, as wider niche breadths are characterized by a greater variety of environmental attributes. In contrast, βNTI decreasing with increases in the relative abundance of a taxon should indicate that the primary selective pressure is for traits contained within that taxon. In both cases, changes in βNTI may be induced either by a change in the magnitude and/or direction of a single selective pressure (*e.g.*, sediment chemistry) or by an introduction of a secondary source of selection (*e.g.*, a shift in a hydrology overlaying selection that is consistently imposed by physical habitat features).

Relationships between RC_{bray}, after removing selection, and taxon abundance also suggest taxa-specific assembly dynamics, indicating the role of spatial processes. A given taxon's dispersal ability can, however, manifest in differing relationships with RC_{bray}. For instance, a positive relationship between RC_{bray} and taxon abundance (*i.e.*, high abundance under dispersal limitation) may provide evidence for traits that diminish dispersal ability such as non-motility or a lack of appendages in macroinvertebrates, large propagule size in vascular plants, or substrate attachment in microorganisms; or for traits that are governed by a combination of ecological drift and selection in the environment (Nemergut *et al.* 2013), as they are able to persist despite community-level dispersal limitation. Alternatively, these organisms may possess traits that facilitate dispersal, allowing for immigration and conveying a competitive advantage despite community-level dispersal limitation. Likewise, negative relationships with RC_{bray} (*i.e.*, high abundance under homogenizing dispersal) may indicate the propensity for a taxon to disperse, thereby enhancing their probability of successful immigration relative to other organisms. Such organisms may be at a competitive disadvantage when lower dispersal rates require organisms to persist locally over longer periods of time. Conversely, these organisms may have poorer dispersal abilities relative to other community members, and therefore, may increase in abundance when the abiotic environment facilitates dispersal (*e.g.*, advective hydrologic transport).

Taxon-specific dispersal between unattached communities

In light of rapid hydrologic-induced changes in the porewater environment, relationships in our dataset provide evidence for a role of taxa-specific dispersal mechanisms in regulating microbial community composition over short timescales (Table S4). In particular, positive relationships of *Thaumarchaeota* (Figure 3A) and a class of *Acidobacteria* (Figure 3B) with RC_{bray} and negative relationships of *Actinobacteria* (Figure 3C) and *Alphaproteobacteria* (Figure 3D) with RC_{bray} were among the strongest correlations (Table S4). Although we cannot be certain of the mechanisms responsible for the relationships in our study system, the trends we observed may aid in elucidating the ecological dynamics that govern the abundance of key microbial taxa within hyporheic zones. For example, *Acidobacteria* (Fierer and Jackson 2006, Jones *et al.* 2009) and *Thaumarchaeota* (Francis *et al.* 2005, Pester *et al.* 2011) are widely distributed globally, suggesting that positive relationships between RC_{bray} and these taxa in our dataset may denote the ability for these organisms to disperse under community-level dispersal limitation. Conversely, *Alphaproteobacteria* can produce filaments that aid in attachment (Jones *et al.* 2007, Kragelund *et al.* 2006), and dispersal limitation has been demonstrated in soil *Actinobacteria* (Eisenlord *et al.* 2012). Thus, negative relationships between these taxa and RC_{bray} may reflect an enhanced ability of these organisms to persist locally relative to other community members.

Selective environment of attached versus unattached communities

Examining assembly processes governing differences between attached and unattached communities revealed selection for microbial taxa with unique ecological properties in the porewater environment (Table S4). We identified linear positive relationships between βNTI and the average relative abundance of two classes of organisms—a candidate class of archaea

(*Parvarchaeota*, Figure 3D) and a class of the candidate phyla *OP3* (*koll11*, Figure 3E). Here, *Parvarchaeota* and *koll11* were almost exclusively found in unattached communities. Although the specific selective pressures regulating the abundance of these organisms are unknown, archaea and members of the PVC superphyla to which *OP3* belongs have a cell membrane lacking peptidoglycan that conveys resistance to common antibiotics and have the genetic potential to metabolize C1 compounds such as methane (Fuerst and Sagulenko 2011). The distinctive features of these organisms and abundance within our system merits future investigating into their role in carbon cycling in hyporheic environments.

Selection in attached communities and functional effects through time

Within attached communities, we observed changes in the abundance of two major taxa—*Betaproteobacteria and Thaumarchaeota*—that correlated with changes in βNTI, porewater conditions, and aerobic metabolism; potentially indicating the emergence of a secondary fitness peak introduced by a change in selective pressures levied by porewater conditions. Members of *Betaproteobacteria* increased in relative abundance in concert with increases in the strength of homogeneous selection (Figure 4H), while members of *Thaumarchaeota* (Figure 4G) increased as homogeneous selection waned.

Betaproteobacteria is a metabolically diverse taxon, exhibiting a range of aerobic and facultative metabolisms including methylotrophy (Kalyuzhnaya *et al.* 2006), ammonia-oxidation (Freitag *et al.* 2006), nitrogen fixation (Rees *et al.* 2009), phototrophy (Gifford *et al.* 2013), and a variety of heterotrophic metabolisms (Amakata *et al.* 2005, Sato *et al.* 2009, Yang *et al.* 2005). Although we cannot be certain of the primary metabolic role(s) of these organisms, a positive correlation between their abundance and NPOC concentration coincident with negative correlations with nitrate, sulfate, and inorganic carbon supports their important contribution to heterotrophy in this system. Evidence for preferential selection of *Betaproteobacteria* in attached communities that are stable across short timescales may also suggest niche overlap, trait complementarity, functional redundancy, and/or generalist life strategies within this group, all of which have been demonstrated to enhance community stability (Gonzalez and Bell 2013, Hawkes and Keitt 2015, Needham *et al.* 2013, Shade *et al.* 2012).

In contrast, metabolic activity of *Thaumarchaeota* is primarily constrained to ammonia-oxidation (Beam *et al.* 2014, Pester *et al.* 2011, Weber *et al.* 2015). These ammonia-oxidizing organisms increased as homogeneous selection decreased, suggesting an important role for a second set of selective pressures that effectively add a viable niche dimension. Our results are consistent with recent work investigating timescales of environmental variability and species-level physiological plasticity across globally-distributed macroecological systems (Chan *et al.* 2016) and provide evidence for universal ecological principles across microbial and microbial systems. Chan *et al.* (2016) demonstrated that specialist organisms thrive under variable conditions at sub-daily timescales, while long-term variability in the environment selects for organisms with broad tolerances. Correspondingly, we observed overarching selective pressures favoring more generalist *Betaproteobacteria*, while more specialized *Thaumarchaeota* increased in abundance during periods with pronounced variation in the physicochemical environment (Figure 1A-B, Figure 5A). Thus, we propose that community composition in dynamic environments is often the product of multiple selective pressures that operate across different timescales, resulting an increase of specialist organisms during periods in which selection by an oscillating environment opposes that of a temporally-stable environment. In our system, we infer that consistent selective pressures for heterotrophs—putatively imposed by stable sediment features, such as mineralogy— in particular those within *Betaproteobacteria*, work alongside seasonally fluctuating porewater selective pressures that select for autotrophs during groundwater discharge conditions.

Importantly, we also observed seasonal increases in aerobic activity that positively correlated with the relative abundance of *Thaumarchaeota* (Figure 5D) and negatively correlated with the relative abundance of *Betaproteobacteria* (Figure 5D). *Thaumarchaeota* abundance also positively correlated with nitrate concentration and particulate organic nitrogen and negatively correlated with NPOC (Table S5), suggesting a heightened importance of *Thaumarchaeota*-mediated nitrification when organic carbon concentrations are limiting (Taylor and Townsend 2010). Thus, temporally consistent selective pressures may favor heterotrophs within *Betaproteobacteria* that are outcompeted by nitrifiers as NPOC concentrations drop with groundwater intrusion into the nearshore environment. As a whole, our results suggest that the realized niche space of ammonia-oxidizing archaea widens when with a shift to groundwater discharging conditions causes a decrease in carbon availability that, in turn, decreases homogeneous selection. These dynamics contribute to an observable functional response at the community level and are consistent with work in both micro- and macroecology demonstrating that productivity increases with niche diversification (Cardinale *et al.* 2007, Cardinale 2011, Gravel *et al.* 2011, Hooper *et al.* 2005, Hunting *et al.* 2015).

Ecological Implications

Our findings suggest a conceptual model describing relationships between trait selection, organismal fitness, and ecosystem function for communities experiencing dual selective pressures that result from a combination of stable and oscillating environments (Figure 6). Our model furthers ecology theory by providing a mechanistic basis for changes in species composition in response to environmental variability and provides support for the applicability of Connell's intermediate disturbance hypothesis both within and beyond microbial systems (Connell 1978, Griffiths and Philippot 2013, Hawkes and Keitt 2015), as most terrestrial and aquatic ecosystems experience dual selection at system-relevant timescales. For example, in terrestrial ecosystems, physical soil properties and soil water content are relatively stable and oscillating, respectively, from the perspective of associated plant communities. Likewise in subsurface systems (such as the example presented here), sediment geochemistry is relatively stable over monthly timescales and hydrologic conditions are continuously fluctuating generating dual selective pressures for benthic organisms. Furthermore, across most ecosystems physical habitat structure and prey abundance are relatively stable and oscillating, respectively, from the perspective of predator communities.

In this context, selection imposed by a stable feature of the environment can favor organisms possessing traits that oppose traits selected for by the oscillating environment (Figure 6A). Because the stable environment applies consistent selective pressures, shifts in the strength of homogeneous selection are driven by changes in the oscillating environment. Provided selection in the stable environment is sufficiently large, stable selection nonetheless dictates the overarching direction of selection. For example, given a stable environment represented by the black dot in Figure 6A, the strength of homogeneous selection in Figure 6B is determined by selection imparted by the oscillating environment, denoted as a gradient from blue to red. In this scenario, selection from the oscillating environment causes a decrease in homogeneous selection that results in niche diversification and enhanced efficiency of ecosystem function (Figure 6B-C).

In our system, this model manifests in observed relationships with βNTI, which represents the summation of selective processes generating dissimilarity across samples. βNTI was consistently negative (homogeneous selection) across attached communities but oscillated from -7 to +10 (Figure 2B) across unattached communities. Indeed, unattached communities appeared to be influenced by selection from porewater conditions at shorter timescales than attached communities (Figure 4). We also observed seasonal shifts in the composition of attached communities as well as relationships between taxa putatively involved in aerobic respiration and changes in the magnitude of homogeneous selection. These results suggest that unattached microbial communities in our system are primarily affected by an oscillating selective pressure, and thus are able to rapidly respond to changes in the porewater environment, while dual selective pressures on attached communities generate shifts in community composition at longer timescales. Consequently, we find that community assembly processes assimilate through time to impact ecosystem function, an effect that generates distinct timescales of compositional shifts among habitat types.

Our work represents a key step forward in spatiotemporal ecological research by assimilating shifts in community composition, assembly processes, and ecosystem function across two spatially connected habitat types experiencing pronounced temporal variation in environmental conditions. We postulate that ecosystem function is enhanced when the direction of selection imposed by an oscillating environment opposes that of the stable environment, allowing for niche diversification and for specialist organisms to increase the efficiency of ecosystem function. Our model represents an advancement in the integration of individual and community-level ecology theory with ecosystem functioning and develops a conceptual framework for coordinating assembly processes, changes in species abundance, and predictions of ecosystem function in response environmental change.

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FIGURES

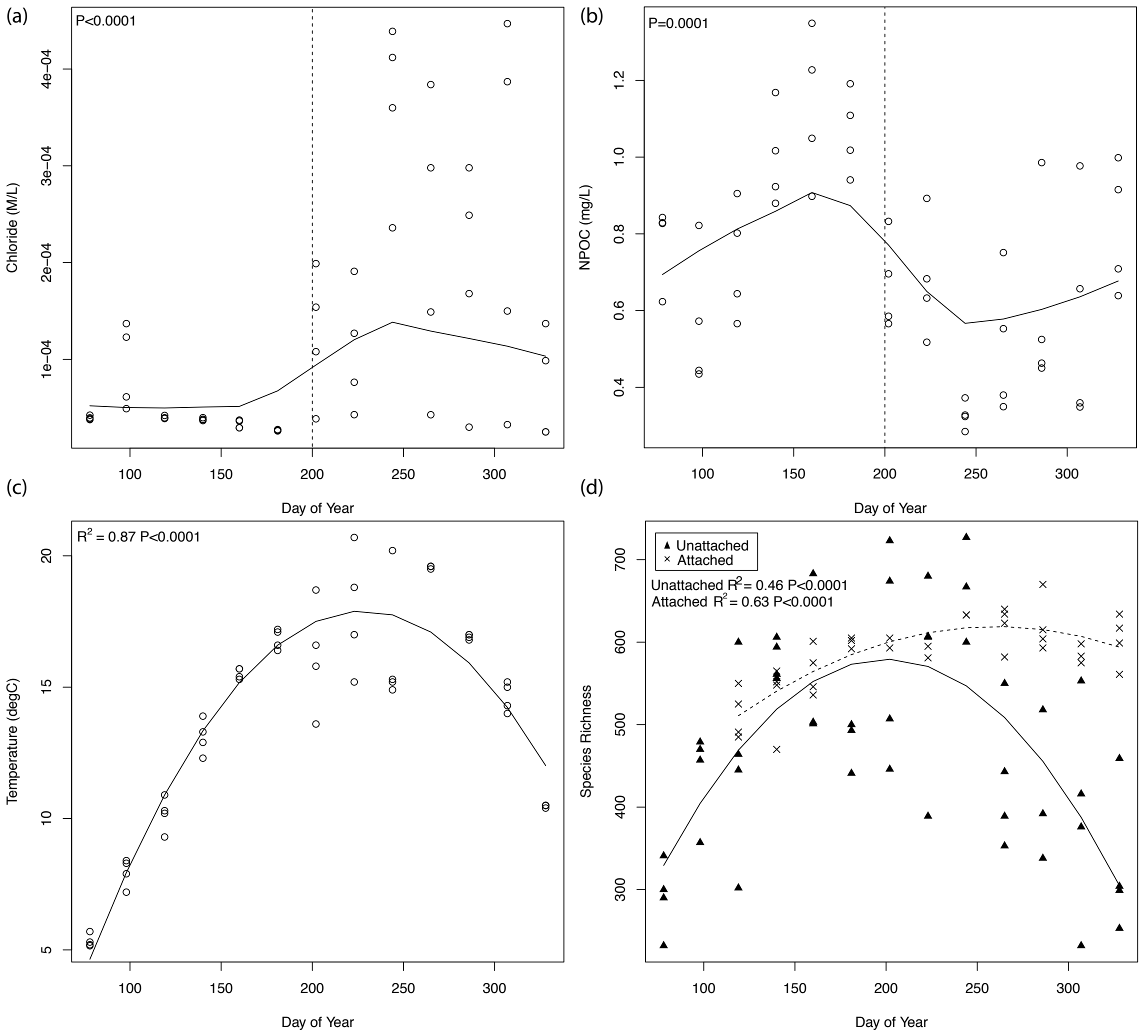

Figure 1 Changes in (A) chloride concentration, (B) NPOC concentration, (C) temperature, and (D) species richness across our sampling period are depicted in Figure 1. Chloride and NPOC concentration show abrupt shifts beginning at our July 22 sampling point (vertical dashed lines). P-values in (A) and (B) denote one-sided Mann-Whitney *U* test results of samples taken before versus on or after July 22, while trends through time in (A) and (B) are displayed using locally weighted scatterplot smoothing (LOWESS). Quadratic polynomials were fit to temperature and

species richness data and plotted in (C) and (D). Triangles in (D) represent unattached communities; X's represent attached communities.

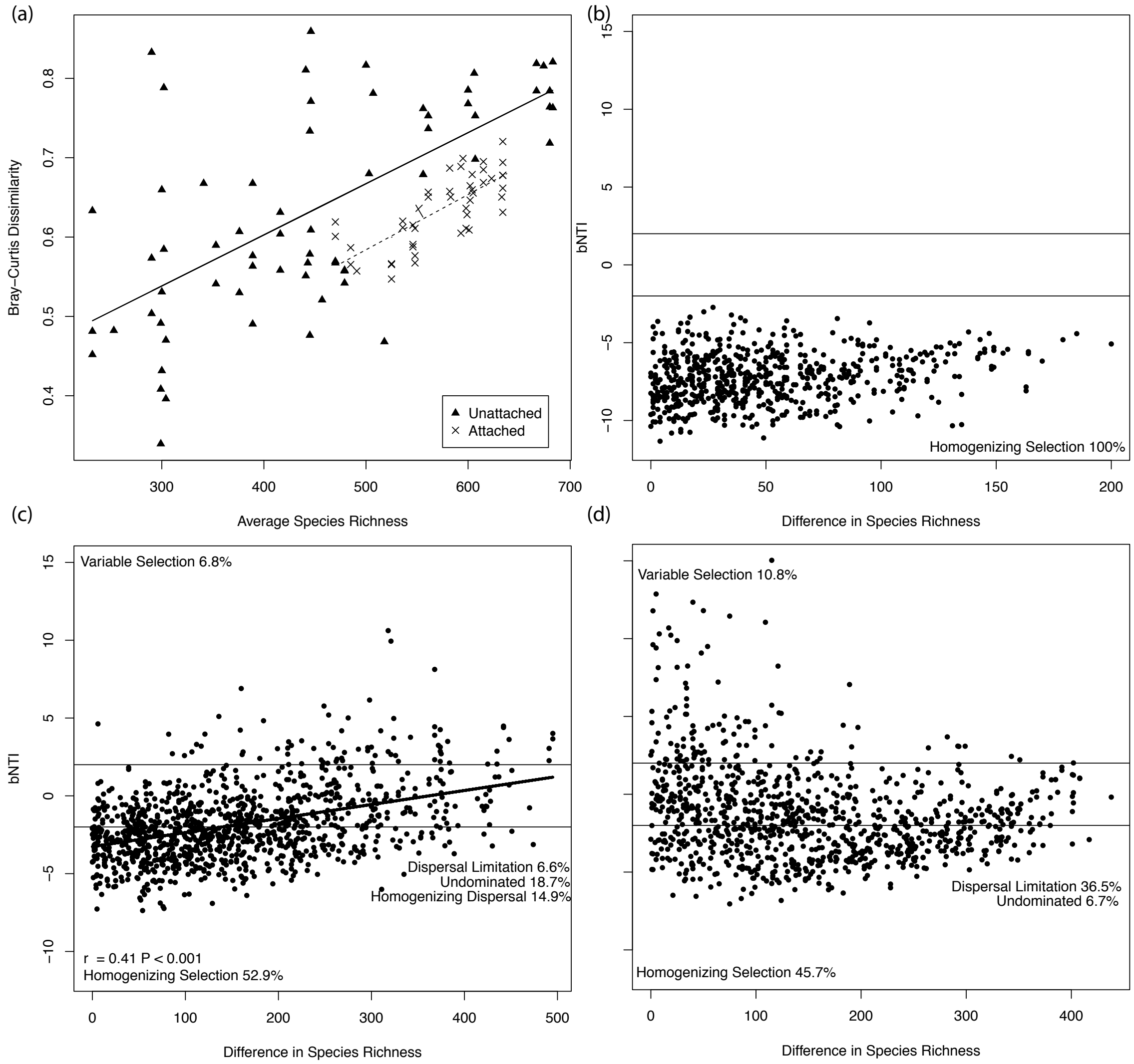

Figure 2 (A) Bray-Curtis dissimilarity within each sampling time point increased as mean species richness increased in attached (X's) and unattached (triangles) communities. In addition, βNTI values across differences in species richness are shown for (B) attached, (C) unattached, and (D) attached vs. unattached communities. Horizontal lines at βNTI = -2 and βNTI = 2 denote thresholds for assembly processes. βNTI values less than -2 suggest assembly is governed by homogeneous selection, while values greater than 2 suggest assembly is governed by variable selection. Stochastic assembly processes (dispersal limitation, homogenizing dispersal) and

undominated assembly processes lie between βNTI -2 and 2. The proportion of βNTI values within each category are listed as text in (B), (C), and (D). A linear regression trend line is depicted in (C) with significance assessed via Mantel test.

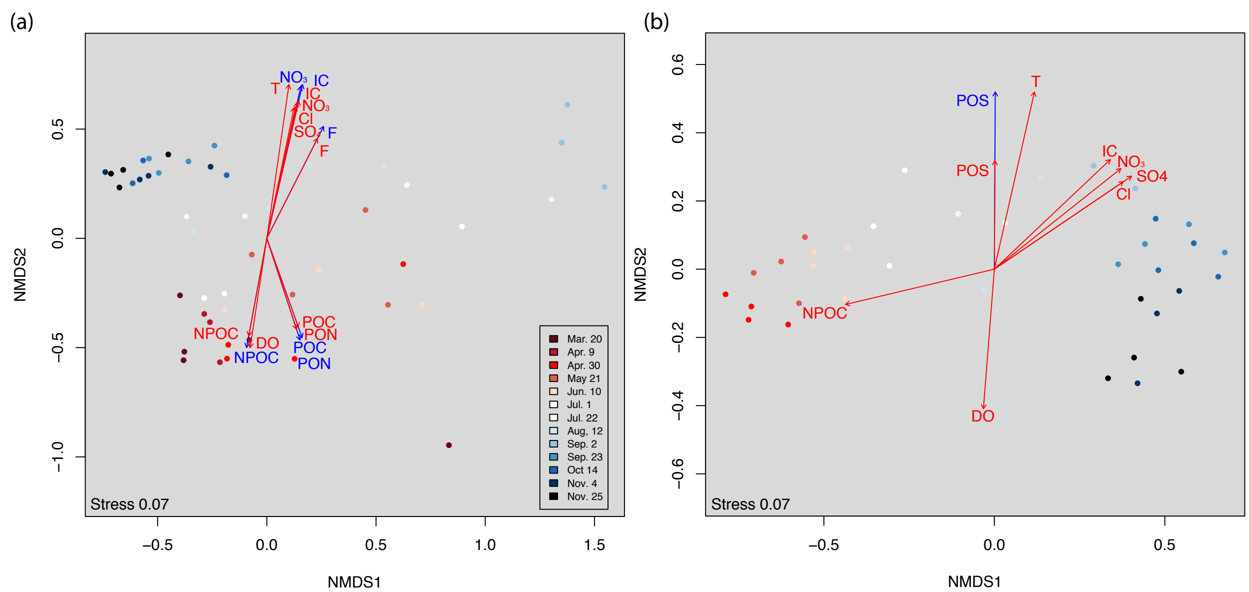

Figure 3 Non-metric multidimensional scaling (NMDS) analysis was conducted on Bray-Curtis distances within (A) unattached and (B) attached communities. Colors denote seasonal shifts in community structure along a gradient from March (red) to November (blue). Physicochemical characteristics were fit to each plot with (blue arrows) and without (red arrows) stratifying permutations by sampling time to assess short- and long-term community responses, respectively, to the aqueous environment.

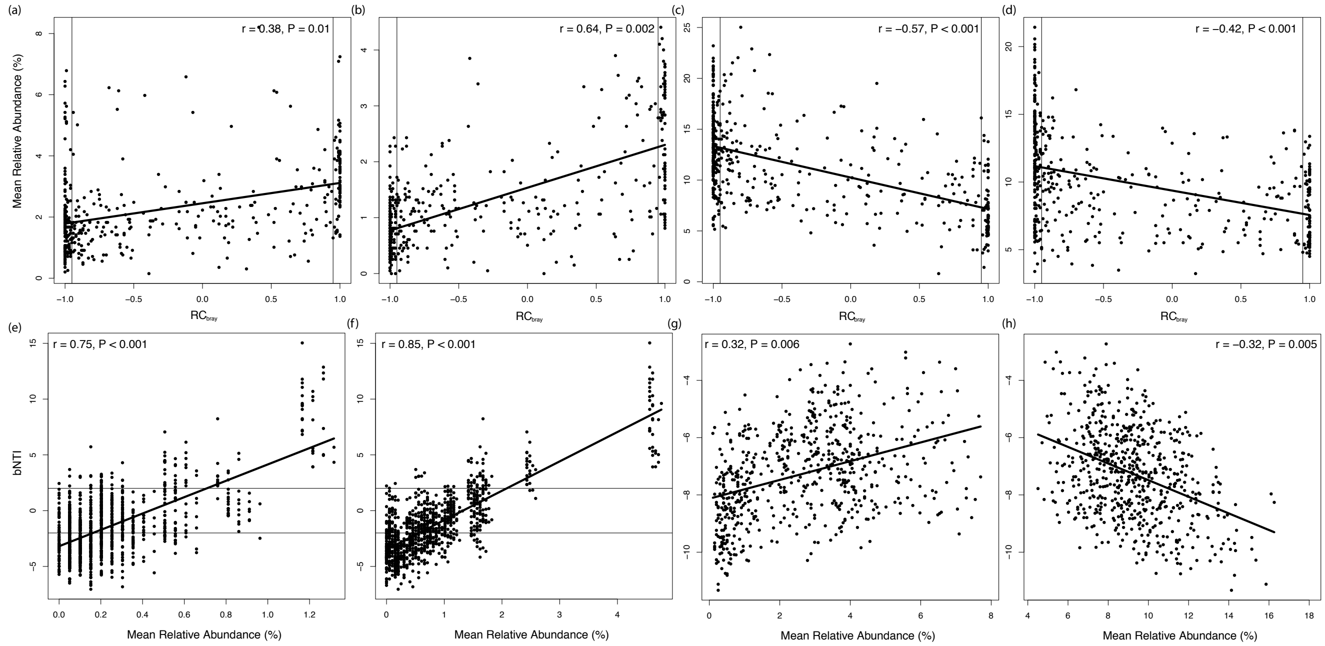

Figure 4 Relationships between βNTI or RC_{bray} and the mean abundance (across samples) of selected taxa identified by SIMPER analysis are depicted in Figure 4. (A-D) demonstrate relationships of *Thaumarchaeota*, *Acidobacteria-6*, *Actinobacteria*, and *Alphaproteobacteria*, respectively, versus RC_{bray} in unattached communities. Horizontal lines at βNTI = -2 (homogeneous selection) and βNTI = 2 (variable selection) and vertical lines at RC_{bray} = -0.95 (homogenizing dispersal) and 0.95 (dispersal limitation) denote thresholds for assembly processes. Trend lines in all panels were derived from linear regressions and significance was assessed via Mantel test. (E) and (F) show relationships of βNTI with *Parvarchaeota* and *koll11* in attached vs. unattached communities; while (G) and (H) denote relationships of βNTI with *Thaumarchaeota* and *Betaproteobacteria* within attached communities, respectively.

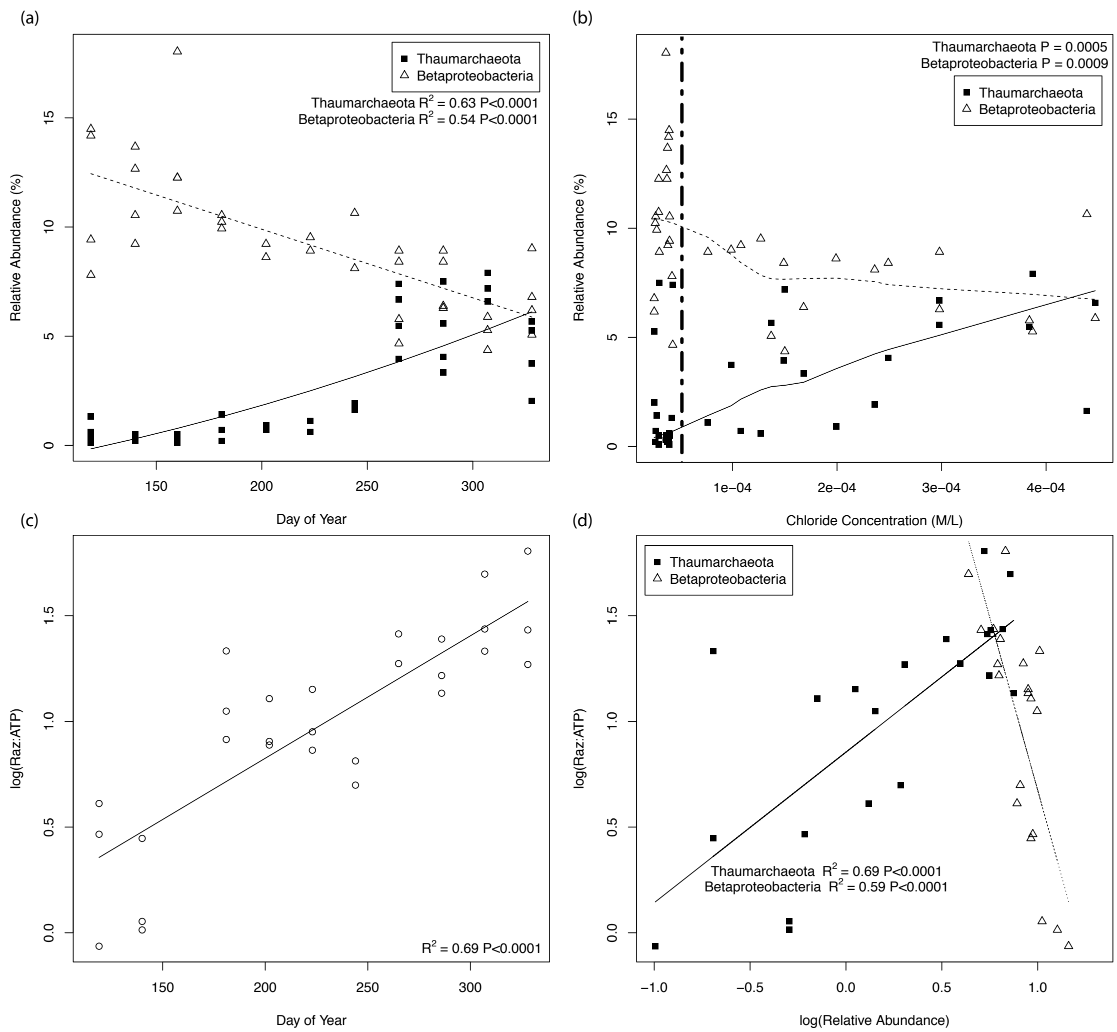

Figure 5 Figure 5 (A) and (B) show changes in *Thaumarchaeota* and *Betaproteobacteria* across changes in time (A) and chloride concentration (B). Trend lines in (A) denote linear (*Betaproteobacteria*) and quadratic (*Thaumarchaeota*) regressions. The vertical line and statistics in (B) denote one-sided Mann-Whitney *U* test results of *Betaproteobacteria* and *Thaumarchaeota* when chloride concentrations are above or below the maximum Cl^- concentration in the Columbia River (5.16e-05 M/L). Panel (C) shows increases in aerobic

respiration normalized to active biomass (Raz:ATP) through time. Finally, (D) shows relationships of *Betaproteobacteria* and *Thaumarchaeota* with Raz:ATP. Trend lines and associated statistics in (C) and (D) were derived with linear regressions. *Thaumarchaeota* and *Betaproteobacteria* are shown as closed squares and open triangles, respectively, in (A), (B), and (D) with trends for each group shown with a solid (*Thaumarchaeota*) or dashed (*Betaproteobacteria*) line.

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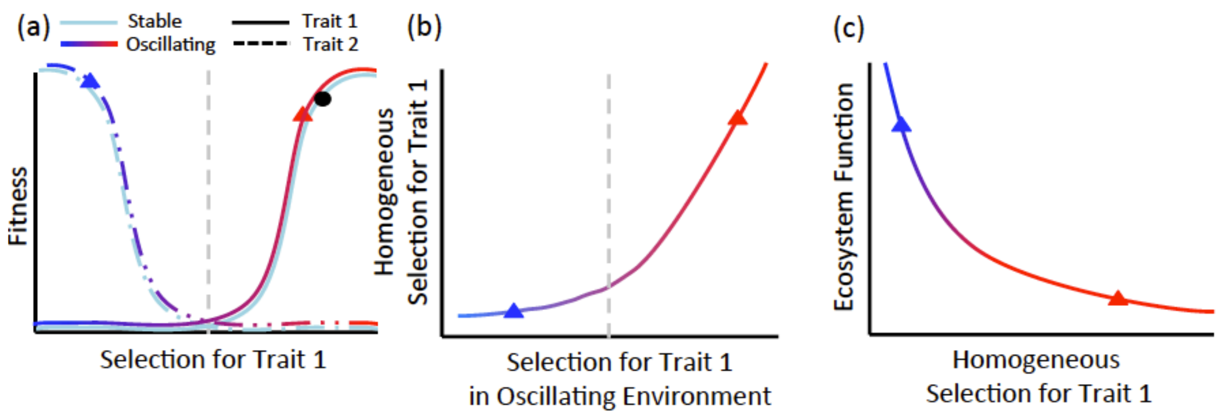

Figure 6 Figure 6 depicts a conceptual model describing relationships between trait selection, organismal fitness, and ecosystem function for communities experiencing dual selective pressures. (A) Selection for a trait follows a continuous gradient within a stable environment (light blue) and oscillating environment (blue to red gradient). Organisms that contain opposing traits (dashed vs. solid lines) are favored at each end of the spectrum, delineated here as to the left (selection against trait 1 and for trait 2) or right (selection for trait 1 and against trait 2) of the vertical gray line. Given selection in a stable environment denoted by the black dot in (A), variation in homogeneous selection (B) is driven by the magnitude and direction of selection in the oscillating environment. When selection in the oscillating environment opposes selection in the stable environment, homogeneous selection decreases (B) and ecosystem function increases (C) due to an increase in realized niche space and biodiversity. Blue and red triangles in (B) and (C) correspond to oscillating selection locations on the fitness landscape in (A).