Predicting the influence of stochastic and deterministic variables on hydrothermal vent communities after eruptions

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Identifying the factors influencing ecological succession is a central pursuit in ecology. Modern studies of succession disentangle stochastic and deterministic processes that influence the predictability of community assemblages (Chesson 2000; Fargione et al. 2003; Dumbrell et al. 2010; Måren et al. 2018). Recent decades have seen development of methods for characterizing microbial community composition and succession via metagenomics (Venter et al. 2004; reviewed in Handelsman 2005). This is promising for oceanic microbial ecology, where many microbes remain uncharacterized and disperse with ease (Müller et al. 2014; Brum et al. 2015; Sunagawa et al. 2015). Microbial biofilms are major contributors to biomass and ecological function in aquatic ecosystems (Battin et al. 2003) and pioneer re-colonization after primary disturbances (Gulmann et al. 2015). Efforts are ongoing to resolve the factors influencing microbial community assemblage and to adapt successional theories to oceanic microbiomes (Woodcock and Sloan 2017; Zhou and Ning 2017).

Succession in microbial hydrothermal vent ecosystems is not well understood due to the recent discovery and extreme depth of these habitats (Corliss et al. 1979; German et al. 2010). Hydrothermal microbial communities are diverse and exist in a disturbance-prone environment (Reveillaud et al. 2016; Fortunato et al. 2018). This environment provides myriad opportunities to study succession in microbe-dominated ecosystems (Marcus et al. 2009; Sylvan et al. 2012; Gulmann et al. 2015). I use the framework proposed by Zhou et al. (2014) for predicting compositional stochasticity after disturbance in a generalized fluidic ecosystem. I expand the considerations of this model to assess hydrothermal system succession. With an updated model, I predict that the magnitude of deterministic influences immediately post-disturbance may serve as predictors of compositional stochasticity as succession progresses. Regardless of initial deterministic selection, differences in pre- and post-disturbance geochemistry will lead to communities that do not resemble pre-disturbance communities (Figure 3).

Stochastic and deterministic models for community assembly

Zhou et al. (2014) propose a framework for predicting compositional stochasticity (CS) in fluid microbial ecosystems under different disturbance types and ecosystem fluidities (Figure 1). This framework compares antithetical deterministic and stochastic influences on community assemblage during succession. Deterministic (or “niche”) factors shape niches and species interactions to produce predictable community compositions under stable environmental conditions (Cowles 1899; Schoener 1974; Buss and Jackson 1979; Harrison 1979; Brändle and Brandl 2001). Purely deterministic models (for example, Tilman, 1990) use abiotic and biotic interactions to predict community assembly.

Stochastic community assemblage is associated with removal of competitive or selective interactions (Sale and Dybdahl 1975; Birch 1979; Grossman 1982). Stochastic models represent unpredictable population trajectories as a product of random disturbances, dispersal, ecological drift, and speciation (see Vellend (2010), Chesson (1991) and Grossman et al. (1982) for precise definitions of these processes). Neutral theory (Hubbell 2001) hypothesizes that community assemblage of ecosystems occurs via the above stochastic processes. In stochastic (or “neutral”) assemblage, ecological interactions are disregarded. The stochastic mechanisms of neutral theory have since been integrated into predictive theories for community assemblage (Tilman 2004), but many theories of community assemblage use neutral theory as a null condition to prove that deterministic factors are causes decreases in assemblage stochasticity (Dini-Andreote et al. 2015). Succession studies attempt to relate the magnitude of niche and neutral processes to succession trajectories (Ofiteru et al. 2010; Kreyling et al. 2011; Langenheder and Székely 2011).

The frameworks of Zhou et al. (2014) and others (Ferrenberg et al. 2013; Dini-Andreote et al. 2015) claim that disturbances may increase compositional stochasticity (CS) by relaxing competitive interaction (Figure 1A,1C) or decrease CS by removing species and reducing biomass (Figure 1B,1D). Zhou et al. additionally identify dispersal via fluidity as the primary distinction between fluidic ecosystems and non-fluidic ecosystems after disturbance. Increased fluidity in aquatic ecosystems increases dispersal of marine microbes and resources, modifying CS by distributing limiting nutrients and dispersing colonizing members of regional populations (Elderfield and Schultz 1996; Marsh et al. 2001; Lennon and Jones 2011; Müller et al. 2014).

This model must be revised to reflect environmental, microbial, and successional dynamics unique to hydrothermal ecosystems. Zhou et al. present a flawed argument for changes in CS after deterministic disturbance, contradicting the trend observed by studies on microbiome succession. The corrected prediction is applied to hydrothermal eruptions, which impact both nutrient input and deterministic disturbance to predict post-disturbance stochastic potential. I consider specific ecological and stochastic dynamics in hydrothermal vents, and integrate these considerations to predict several trajectories for hypothetical hydrothermal ecosystems after disturbances.

Correction to fluidic ecosystem succession model

Zhou et al. (2014) predict compositional stochasticity (CS) shifts in the post-disturbance phase based on how various disturbances differentially alter competitive and environmental selection (Houseman et al. 2008; Kreyling et al. 2011) (Figure 1). Nutrient inputs increase CS by relaxing competition for limiting resources (Bik et al. 2012; Werner et al. 2014) (Figure 1A,1C). Disturbances that intensify resource limitation (i.e. drought) or increase mortality (i.e. fire) are predicted to decrease CS (Figure 1B, 1D). This untested prediction conflicts with observed stochastic community assemblage during succession (Ferrenberg et al. 2013; Jurburg et al. 2017; Måren et al. 2018). Zhou et al. failed to identify that disturbances decrease competition by lowering biomass and reducing species richness (Grime 1977), facilitating stochastic recruitment from regional species pools. This creates a net stochastic community composition post-disturbance, despite deterministic influences and contrary to the predicted trend (Chase and Myers 2011; Woodcock and Sloan 2017) (Figure 1B).

Influences on succession in hydrothermal vents

Hydrothermal vents form when heat and pressure in crustal rocks facilitate geochemical reactions with seawater (Elderfield and Schultz 1996) (Figure 2). Dynamic seafloor geology produces frequent intense disturbances (German et al. 2010; Kinsey and German 2013) as a result of hydrothermal interactions and variable tectonic pressures fracturing seafloor rock, extruding large amounts of lava and chemical-enriched fluid trapped within the crust (Haymon et al. 1991, 1993; Tolstoy et al. 2006; Chadwick et al. 2013; Zahirovic et al. 2015). Trapped hydrothermal fluids are released, diminishing selection imposed by resource limitation and facilitating transient blooms of regional species (Butterfield et al. 1997). Rock surface formation during eruption reduces deterministic selection by reducing biomass and competition (Grime 1977). In conjunction with increased dispersal in fluid ecosystems, the removal of deterministic influences by eruption increases potential for regional colonization in the post-disruption environment (Mullineaux et al. 2010).

Deterministic influences diminish the potential for stochastic community assemblage after hydrothermal eruptions. These influences alter CS immediately post-disturbance and persist into ecosystem recovery. For example, hydrothermal communities often reflect vent geochemistry (Connelly et al. 2012; Akerman et al. 2013; Reveillaud et al. 2016; Anderson et al. 2017). Reactions between percolating seawater and minerals at high temperature produce hydrothermal fluids enriched with metallic, sulfuric, and organic species (Jannasch and Mottl 1985) (Figure 2). Hydrothermal fluid composition is influenced by specific geological contexts (German et al. 2010) and impacts the metabolic substrates available to coincident microorganisms and macrofauna populations (Brazelton et al. 2010; Vrijenhoek 2010). Geochemical moderation of colonization and community composition is found in mature communities (Flores et al. 2011), and in early succession, where *Epsilonproteobacteria* often dominate due to their fitness in sulfur-rich post-eruption environments (Gulmann et al. 2015; O'Brien et al. 2015). Competition-communities are capable of inhibiting community structure shifts via competitive exclusion of colonists in terrestrial and hydrothermal systems (Fargione et al. 2003; Gulmann et al. 2015). Hydrothermal microbes driving biogeochemical cycle mediation can further prevent ecosystem invasion by controlling resource availability (Marcus et al. 2009; Fortunato et al. 2018). Deterministic geochemical controls limiting colonization and invasion from regional pools decrease stochasticity following disturbance.

Specific variation in dispersal ability exists among species (Vrijenhoek 2010; Anderson et al. 2015), and is deterministically related to species traits, interactions with macrofauna, and vent site connectivity. High endemicity is found when species disfavor endospore formation (Anderson et al. 2015), communities have low connectivity (Opatkiewicz et al. 2009), or lack of macrofauna capable of facilitating microbial movement and colonization (Klose et al. 2015; O'Brien et al. 2015; Troussellier et al. 2017). High endemicity indicates deterministic interactions selecting local species to dominate colonization (Opatkiewicz et al. 2009; Mino et al. 2017). The combined magnitude of early deterministic geochemical, macrofaunal, and hydrological interactions in specific vent contexts determines the degree of deviation from a stochastic community of early colonizers. Some of these deterministic controls on succession also operate to decrease CS over time, particularly if a community is capable of biogeochemically or competitively excluding colonizers.

In post-disturbance hydrothermal sites, stochastic processes associated with geochemistry and dispersal work to increase CS in the manner predicted by neutral theory (Chave 2004). Hydrothermal fluids evolve after hydrothermal eruptions to reflect stochastic geochemical processes in the subseafloor (Von Damm et al. 1995; Butterfield et al. 1997). Stochastic evolution of fluid geochemistry and introduction of opportunistic species will act against long-term deterministic variables to increase CS if the existing community is unable to competitively exclude invaders. The large initial potential for stochastic community assembly and influence of stochastic factors indicate hydrothermal ecosystems will enter alternate states rather than return to pre-disturbance communities.

Updating predictive framework for hydrothermal systems

My updated model predicts compositional stochasticity after hydrothermal eruption in two phases: immediately post-disturbance and during community formation over time (Figure 3). In the immediate post-disturbance phase, potential maximum stochasticity (S_M) is large due to ecosystem fluidity and hydrothermal eruptions reducing deterministic influence. The actual compositional stochasticity (S_A) is diminished by site-specific deterministic influences of geochemistry on colonization, the site's hydrological connectivity, and interspecific relationships of microbes with macrofauna capable of facilitating recolonization. The difference between S_M and S_A (ΔS) is the degree to which deterministic influences diminish compositional stochasticity. In a highly connected ecosystem with diverse post-eruption geochemistry and low macrofaunal community, we would predict a relatively small ΔS and therefore a relatively stochastic initial community. For an isolated community, ΔS is large as lack of hydraulic distribution selects locally endemic species for colonization. The extent to which initial communities are deterministic may influence development of the later post-disturbance communities.

The second phase of the model predicts the dominant influence on community composition (stochastic or deterministic) from the magnitude of ΔS. I hypothesize that a deterministic initial community is better able to engage in competition, resource partitioning, and metabolic cycling in selective geochemical conditions. This stable community diminishes CS over time by buffering stochastic fluid evolution, mediating biogeochemical cycling and preventing opportunistic colonization. This prediction uses geochemical selection, but a large ΔS from poor hydrological connectivity will also diminish the stochastic effect of dispersal and prevent colonization. A stochastically assembled initial community (small ΔS) is not selected based on competitive ability and thus is unstable over time. Finally, because post-eruption geochemistry does not resemble pre-disturbance geochemistry, it is probable that neither deterministic nor stochastic assemblage will lead to convergence on pre-eruption assemblages.

Figures

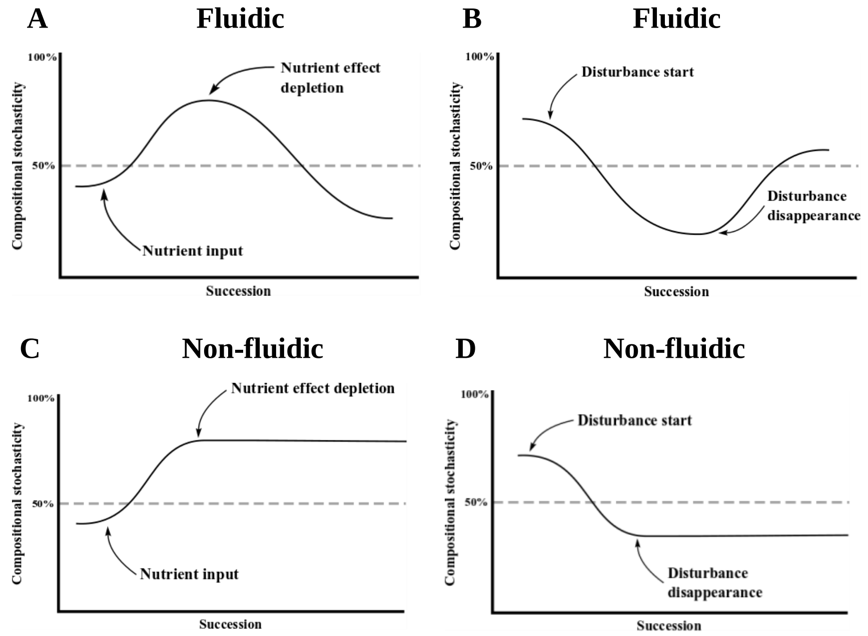

Figure 1 – From Zhou et al. (2014). A conceptual framework for modeling the relationship between stochasticity and succession with differences in ecosystem characteristics and disturbance types. Four models are depicted: (A) fluidic ecosystems with nutrient inputs, (B) fluidic ecosystems with biomass-reducing disturbance, (C) non-fluidic ecosystems with nutrient inputs, and (D) non-fluidic ecosystems with biomass-reducing disturbance. Initial compositional stochasticity is arbitrary. Plot x-axes correspond to a context-specific successional timescale. Nutrient inputs increase compositional stochasticity and biomass-reducing disturbance reduce compositional stochasticity in both ecosystem types. Fluidic ecosystems recover initial stochasticity and composition due to increased dispersal and resource fluidity.

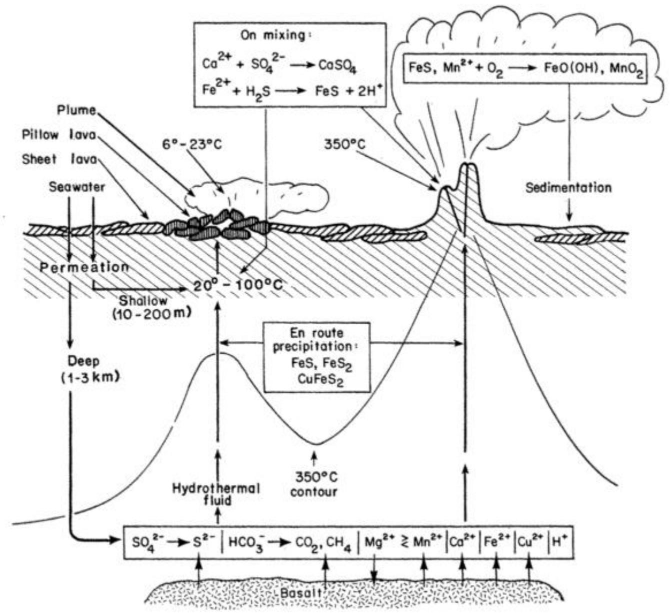

Figure 2 – From Jannasch and Motl (1985): an overview of the geochemical processes leading to hydrothermal vent formation and fluid ejection at the seafloor.

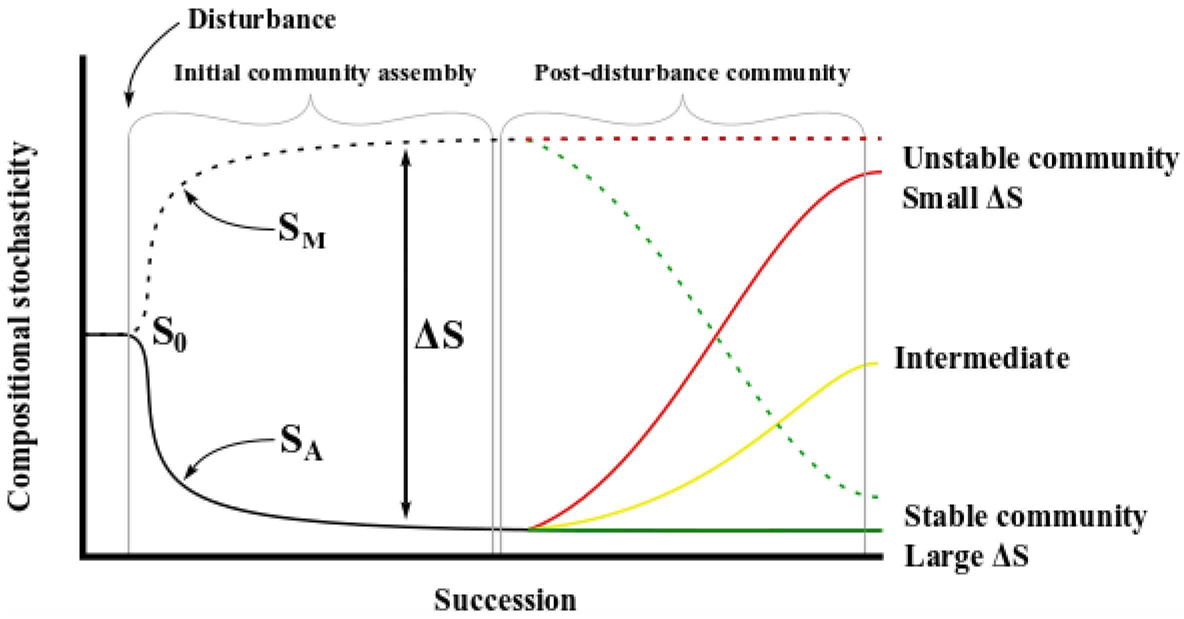

Figure 3 – Updated model for compositional stochasticity. Initial compositional stochasticity (S_0) is arbitrary. Maximum potential compositional stochasticity (S_M) is generated by a combination nutrient inputs and disturbance during hydrothermal eruption. Actual compositional stochasticity (S_A) reflects the diminished compositional stochasticity as a result of context-specific deterministic influences, including geochemistry, connectivity, and macrofaunal relationships. $\Delta S = S_M - S_A$, and is analogous to the extent of deterministic influence during initial succession. I predict a large ΔS will lead to a stable community capable of diminishing S_M over time through exclusion of colonizers and negation of geochemical shifts. A moderate to small ΔS community will not exhibit similar stable, and may change according to shifts in geochemistry, colonization, or other stochastic processes.

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