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SPECIAL TOPIC

# The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity

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## Abstract

Cold seeps are among the most heterogeneous of all continental margin habitats. Abiotic sources of heterogeneity in these systems include local variability in fluid flow, geochemistry, and substrate type, which give rise to different sets of microbial communities, microbial symbiont-bearing foundation species, and associated heterotrophic species. Biogenic habitats created by microbial mats and the symbiotic species including vesicomyid clams, bathymodiolin mussels, and siboglinid tubeworms add an additional layer of complexity to seep habitats. These forms of habitat heterogeneity result in a variety of macrofaunal and meiofaunal communities that respond to changes in structural complexity, habitat geochemistry, nutrient sources, and interspecific interactions in different ways and at different scales. These responses are predicted by a set of theoretical metacommunity models, the most appropriate of which for seep systems appears to be the 'species sorting' concept, an extension of niche theory. This concept is demonstrated through predictable patterns of community assembly, succession, and beta-level diversity. These processes are described using a newly developed analytical technique examining the change in the slope of the species accumulation curve with the number of habitats examined. The diversity response to heterogeneity has a consistent form, but quantitatively changes at different seep sites around the world as the types of habitats present and the size-classes of fauna analyzed change. The increase in beta diversity across seep habitat types demonstrates that cold seeps and associated biogenic habitats are significant sources of heterogeneity on continental margins globally.

## Problem

While it has long been known that the ocean margins are a mixture of rugged mountainous terrain and sediment-covered slopes, it is only during the last 30 years that the true heterogeneity of the continental margins has been realized. By using high resolution swath-bathymetry, side-scan sonar and seismic data, a great variety of sea floor structures and biological habitats linked to methane, oil and gas seeps have been identified (Sibuet & Olu 1998; Pinheiro *et al.* 2003; Fisher *et al.* 2007; Rathburn *et al.* 2009; Sibuet & Vangriesheim 2009). *In situ* observations with towed cameras, ROVs, and submersibles have revealed a particular suite of species adapted to utilize the chemosynthetic productivity in these habitats, and novel mechanisms that maintain biodiversity both at the local and regional scales. In this paper, we review existing data obtained from around the world and introduce new analyses pertaining to the patterns and drivers of biodiversity in deep seeps, placing particular attention on the sources of habitat heterogeneity and their role in shaping the biodiversity of cold-seep habitats.

## Sources of heterogeneity

Cold-seep ecosystems have been discovered in almost all of the world's oceans in different geological settings of passive and active margins (Sibuet & Olu 1998), and contain a variety of geomorphic and biological features that are sources of heterogeneity (Table 1). These ecosystems are formed where subsurface fluids become rich in reduced chemicals (most notably methane and sulfide) and 'seep' out at the sediment surface. Conduits for water extrusion result from a variety of processes including (i) tectonic activity, (ii) differential compaction of organic-rich sediments, (iii) gas hydrate dissociation and (iv) subsurface salt migration. These sites are often apparent using remote sensing technologies that detect the presence of bottom simulating reflectors (BSR) or where structure is conspicuously absent in seismic profiles, where bubble plumes appear on echo sounders, or as sites of organic matter deposition in deep canyons or channels seen on multibeam bathymetry.

There are numerous types of geologic features created by seepage on the seafloor that occur at a variety of spatial scales, from a few meters to several kilometers (Table 1). Mud volcanoes created by mud circulation and fluid escape are large structures which can be several kilometers in diameter (Prior *et al.* 1989; Vogt *et al.* 1999; Grevemeyer *et al.* 2004). Pockmarks are caused by the escape of gas from the sea floor (Hovland & Judd 1988) and are often associated with gas hydrate accumulations (MacDonald *et al.* 1990; Olu-Le Roy *et al.* 2007a). Gas hydrate outcrops of various sizes are the surface manifestations of BSRs and can occur as small nodules, large vein-filling structures or massive mounds (Sassen *et al.* 1999, 2001). Brine lakes associated with the migration of hypersaline fluids from the subsurface can also occur as small pools or flows or large features hundreds of meters across (MacDonald *et al.* 1990; MEDINAUT/MEDINETH, S.S.P. 2000; Joye *et al.* 2005; Roberts *et al.* 2007). Carbonate concretions resulting from anaerobic hydrocarbon oxidation also appear in areas of active fluid seepage through the seabed (Aharon & Fu 2000; Aloisi *et al.* 2000; Luff *et al.* 2004) and may eventually serve to slow the flux of fluid to the sea floor (Roberts 2001). All of these features may be present within a single seep site and provide a highly diverse suite of potential habitats for both endemic seep organisms and more opportunistic colonists (Fig. 1).

The geologic conditions at a seep site can result in different potential biogeochemical pathways, while the geochemical conditions are greatly affected by the microbial processes occurring within surface sediments. Microbial consortia (aggregates of archaea and bacteria) produce sulfide by the reduction of sulfate coupled to anaerobic methane oxidation in the upper sediment column (Aharon & Fu 2000; Boetius *et al.* 2000). Other processes are aerobic, such as carbon fixation through oxidation of methane or sulfide. This can be carried out by free-living microbes, but may be particularly efficient in the context of symbiosis between specialized bacteria and the habitat-forming invertebrate taxa (review by Dubilier *et al.* 2008). These processes create the conditions necessary for the symbiont-bearing species utilizing methane, sulfide, or occasionally both to inhabit and flourish in the seep environment.

The species richness and density of the symbiont-bearing megafauna communities are highly variable among different sites and may be explained not only by the depth and age of the geologic features but also by habitat heterogeneity. These forms of heterogeneity, including the geometry of seeps, the intensity and volume of fluid flow (Henry *et al.* 1992), the occurrence of gas hydrates, the methane and sulfide concentrations and their fluxes through the underlying sediment (Fig. 2) are manifested as differences among sites, areas within a site, or even in the variability in biogeochemical processes within the top sediment layers (MacDonald *et al.* 1989; Goffredi & Barry 2002; Levin *et al.* 2003; Treude *et al.* 2003; Olu-Le Roy *et al.* 2007a). Locally, the presence of bacterial mats and numerous large animals belonging to a limited number of phyla and families have been considered as one of the best indicators of active seeps marked by the existence of high levels of localized, chemosynthesis-based, primary productivity (Fig. 1). Typical symbiotic seep organisms include siboglinid polychaetes (vestimentiferan tubeworms and frenulate and monoliferan pogonophorans), bivalves (bathymodiolin mussels, and vesicomyid, lucinid, solemyid, and thyasirid clams), and sponges (Cladorhizidae) (reviews by Sibuet & Olu 1998; Sibuet & Olu-Le Roy 2002; Levin 2005; Cordes *et al.* 2009). The habitats that these various symbiotic species create supplement the geologic heterogeneity at various cold seeps (Fig. 2).

## Perception of habitat heterogeneity

A habitat corresponds to a delimited spatial domain with characteristic environmental conditions in which particular species may exist, forming a distinctive community or assemblage. The definition of habitat is scale-dependent because relatively homogeneous parameters measured at a given scale may appear heterogeneous at different

**Table 1.** Sources of habitat heterogeneity at known cold seeps.

| | Geological | | | | | | | | Biological | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Region | Oil seeps | Mud volcanoes | Salt diapirs | Brine pools | Gas hydrates | Pockmarks | Carbonates | Organic rich | Vestimentiferans | Frenulates | Bathymodiolins | Vesicomyids | Other bivalves | Microbial mats |
| East Pacific | | | | | | | | | | | | | | |
| Aleutian Margin/Trench | | | | | | | x | | | | | | | |
| Hydrate Ridge, OR | | | | | x | | x | | | | | x | | x |
| Eel River, CA | | | | | | | x | x | | | | x | x | x |
| Monterey Bay, CA | | | | | | | x | x | x | x | | x | x | x |
| Southern California | x | x | | | x | | x | x | | | | x | x | x |
| Guyamas, Mexico | x | | | | | | | x | x | | | x | | x |
| Costa Rica Margin | | x | | | x | | x | | x | | x | x | x | x |
| Peru Margin/Trench | | | | | | | | x | | | | x | | |
| Chile margin | | | | | x | | x | x | x | | | x | x | |
| West Pacific | | | | | | | | | | | | | | |
| Sea of Okhotsk | | | | | | | x | | | x | | x | | x |
| Kurile Trench | | | | | x | | x | | | | | | | |
| Japan Margin | | | | | x | | x | x | x | | x | | | |
| Japan Trench | | | | | | | x | | | | | x | x | |
| Edison Seamount | | | | | | | x | | x | | x | | | |
| New Zealand | | | | | x | | x | | x | x | x | x | x | x |
| Indian Ocean | | | | | | | | | | | | | | |
| Makran, Pakistan | | x | | | x | | x | | | x | | x | | x |
| Sunda Arc | | | | | x | | x | | | x | | x | x | |
| East Atlantic | | | | | | | | | | | | | | |
| Haakon Mosby | | x | | | x | | | | | x | | x | | x |
| Storega | | | | | | x | | | | | x | | x | x |
| Gulf of Cadiz | | x | x | | x | | x | | | x | x | x | x | |
| Mediterranean | | x | | x | | x | | | x | | x | x | | x |
| Gulf of Guinea | | | | | x | x | | | x | | | | | |
| Angola Basin | x | | x | | x | x | x | | x | | x | x | | x |
| West Atlantic | | | | | | | | | | | | | | |
| Laurentian Fan | | | | | | | | x | | | | x | | x |
| Blake Ridge | | | x | | x | | | | | | x | x | | x |
| Gulf of Mexico | x | x | x | x | x | x | x | | x | x | x | x | x | x |
| Barbados | | x | | | | | x | | x | | x | | | x |
| Brazil | x | | | | | | | x | | | | | | |

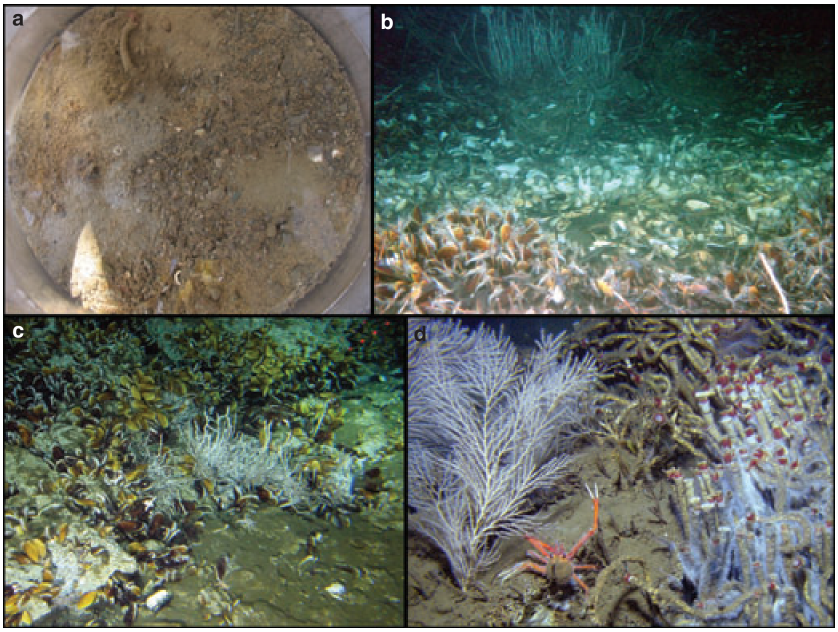

**Fig. 1.** Examples of habitat heterogeneity from various seep sites around the world. (a) Small-scale heterogeneity in a core sample from the Captain Arutyunov mud volcano at approximately 1300 m depth in the Gulf of Cadiz. (b) Overlapping vestimentiferan tubeworm, vesicomyid clam, and bathymodioline mussel habitats at the seeps from the Regab pockmark at approximately 3150 m depth on the Congo-Angola Margin. Abundant alvinocarid shrimp and galatheid crabs are seen in the foreground associated with the mussel bed habitat. (c) Co-occurring bathymodiolin mussels and vestimentiferan tubeworms on authigenic carbonates and soft sediments from the cold seeps at approximately 1000 m depth on the Costa Rica Margin. (d) Adjacent gorgonian coral and vestimentiferan tubeworm habitats (some with epibiotic bacteria) at approximately 500 m depth in the Gulf of Mexico.

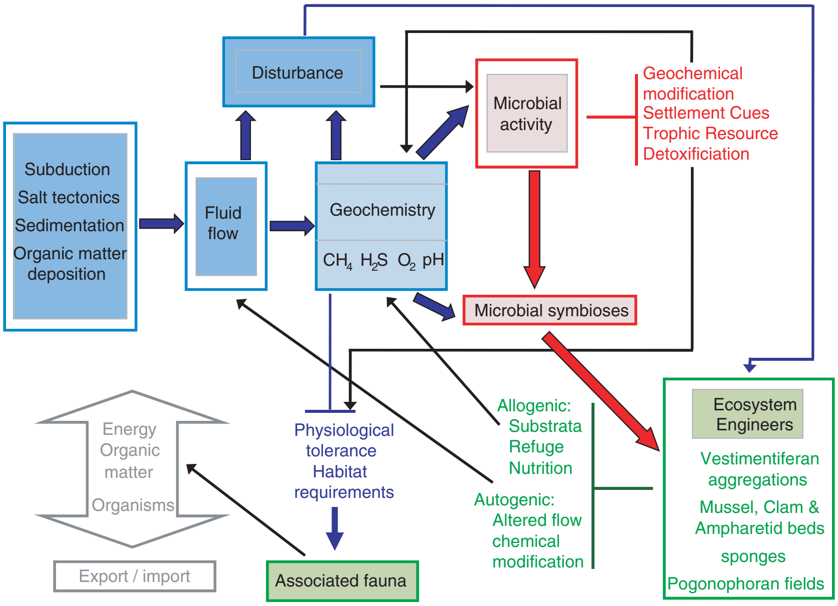

**Fig. 2.** Biological, biogeochemical, and geological processes creating habitat heterogeneity at cold seeps. Boxes represent abiotic (blue), microbial (red) and faunal (green) components of the seep ecosystem. Colored arrows and text reflect heterogeneity-generating interactions among system components and the mechanisms involved. Black lines and arrows reflect biotic feedback to abiotic and other biotic ecosystem components, generating additional heterogeneity. Gray indicates external (non-seep) properties of the continental margin influenced by interaction with seeps.

observational scales (Levin 1992). The perception of habitat and habitat heterogeneity by different taxa is dependent on their size, mobility and dispersal capability (Morris 1987). The habitat heterogeneity hypothesis assumes that structurally complex habitats lead to an increase in species diversity by providing a higher number of distinct niche dimensions and diverse ways of exploiting resources (MacArthur & Wilson 1967). At some point, depending on scale and the organism's perception, habitat heterogeneity may become habitat fragmentation and negative effects on species diversity may occur as a consequence of the disruption of key biological processes such as dispersal and resource acquisition (Saunders *et al.* 1991).

At the smallest scales, microbial distribution will be determined largely by the availability of reductants and oxidants to drive biogeochemical transformations. Microbially influenced biogeochemical processes in turn contribute to habitat heterogeneity at spatial scales relevant for all faunal groups. Methane and sulfide flux rates may primarily determine the distribution of specialized symbiont-bearing megafauna such as tubeworms, mussels and clams (MacDonald *et al.* 1989). This can lead to high turnover of symbiont-bearing foundation species among habitats within a seep site (Olu-Le Roy *et al.* 2007a). The most active areas exhibit sediment instability in the form of fluid or mud flows, which will favor the occurrence of foraging mobile organisms (*e.g.* gastropods, echinoids) over sessile megafaunal species (Fisher *et al.* 2007). As fluid flow slows, high rates of carbonate precipitation resulting as a by-product of hydrocarbon oxidation provide hard substrata for sessile seep fauna, and also filter/suspension feeders such as sponges, soft corals and stony corals (Cordes *et al.* 2008). The presence of habitat-forming megafaunal organisms will add structural complexity that may be perceived by smaller organisms (macro- and meiofauna) as habitat heterogeneity. Symbiotic species may also alter fluid flux and biogeochemical processes and increase small-scale habitat heterogeneity for smaller size classes of fauna (Treude *et al.* 2003; Cordes *et al.* 2005a).

There are usually lower rates of associated megafauna, macrofauna, and meiofauna species turnover between areas of different fluid flow intensity and geochemistry (Olu-Le Roy *et al.* 2009) with similar communities occasionally found in tubeworm aggregations and mussel beds at the same site (Cordes *et al.* 2009). Rather than complete species replacement and exclusion, turnover is normally manifested as shifts in dominance at the genus or family level (*e.g.* the REGAB seeps, Menot *et al.* 2010, Olu-Le Roy *et al.* 2009; Van Gaever *et al.* in press). Turnover may occur among different habitat types as defined by the foundation species present, or may also be evident in successional shifts in community composition over the course of the long life-span of the seep foundation species (Bergquist *et al.* 2003; Cordes *et al.* 2005b).

### Measuring habitat heterogeneity

Generally, habitat heterogeneity has been defined in relation to the number, extent (percentage cover, height/volume, patch size) and variety of physically structuring elements within a given habitat. In addition to physical structure, spatial and temporal variability in fluid flux may add a component of heterogeneity (Henry *et al.* 1992) that is less well constrained in the seep environment but has obvious biological consequences (Levin *et al.* 2003). The definition and meaning of habitat heterogeneity varies considerably depending on the taxonomic group and spatial resolution under consideration. The scale of observation may range from the architecture of a single organism (Bradshaw *et al.* 2003), to landscape patterns (Lawrie & McQuaid 2001; Le Hir & Hily 2005), to topographic heterogeneity at the continental-margin scale. Multibeam bathymetry provides a detailed image of the terrain of the seafloor, and may be complimented by an examination of acoustic backscatter providing information on the location of hard substrata and sub-bottom seismic reflectivity used to locate potential conduits for fluid migration (Roberts *et al.* 2007; Klauke *et al.* 2008).

At a more local scale, textural analysis of sidescan sonar images is useful for mapping marine benthic habitats but visual ground-truthing is required to establish the relationship between texture, bottom type, and animal distributions (Cochrane & Lafferty 2002; Roberts *et al.* 2007; Sahling *et al.* 2008; Schlacher *et al.* 2010). This may be accomplished by using video mosaic analysis to map biogenic habitats defined by structuring megafaunal species (Jerosch *et al.* 2007, Olu-Le Roy *et al.* 2007a; Lessard-Pilon *et al.* in press). Even though they are called 'cold seeps,' thermal gradients may be used to define the fluid flow variability of active sites at an even finer scale (Olu *et al.* 1997; Grevemeyer *et al.* 2004; Niemann *et al.* 2006).

### Measuring faunal diversity

Patterns of species diversity change over multiple scales (Levin 1992). On large spatial and temporal scales, species diversity depends on evolutionary history and the size of the regional species pool. At smaller scales, biotic interactions, habitat selection, disturbance, and colonization result in the patterns of diversity that are most often observed and measured. However, the local mechanisms that influence diversity interact on broader scales that result in regional patterns of diversity and establish a relationship between regional and local diversity (Ricklefs 2004).

Widely used diversity indices combine the richness of component species with their relative abundance at a defined point in space and time (*e.g.* Washington 1984) but the number of species (species richness) is the simplest measure of local and regional diversity (Magurran 1988). Species richness of different samples or sites (alpha diversity) may be examined using analysis of variance of diversity indices or by comparing the shapes of species accumulation and rarefaction curves (Colwell *et al.* 2004; Hurlbert 1971; Ugland *et al.* 2003), whereas species turnover among habitats (beta diversity) usually involves dimensionless metrics (Magurran 1988). Rarefaction scales down species richness to compare the same number of individuals across samples, largely avoiding some (but not all) common pitfalls in the measurement and comparison of species richness across different types of samples (Gotelli & Colwell 2001).

### Examining the response of diversity to habitat heterogeneity

Sampling species turnover within and among habitats generates a predictable response of diversity to habitat heterogeneity. Species accumulation curves (number of new species added per individual sampled) take a log form, with the rate of species additions declining with the number of samples added (Colwell & Coddington 1994; Gotelli & Colwell 2001; Mora *et al.* 2008). The initial slope of this curve is estimated as the slope of the relationship between log-transformed number of individuals on the $x$-axis and cumulative number of species on the $y$-axis. Within a single habitat, this examines species turnover among samples and will increase in diverse or heterogeneous habitats. Among multiple habitats, the slope of this curve is an estimate of beta diversity or the dissimilarity among habitats, with higher values for habitats with fewer species in common. As the number of habitats increases, the slope of this line should theoretically increase as additional samples from different species pools are added to the dataset. This relationship between the slope of the species accumulation curve and the number of habitats sampled will also be saturating, and will approach an asymptote as the habitats included begin to contain all of the species from the regional species pool.

## Methods

In this study, we gathered data on the presence of species in samples obtained from different deep-sea seep and adjacent habitats around the world. Accumulation curves were generated for each possible combination of habitats within a region. Curves were rarefied by quantifying the number of species present in an increasing number of individuals, randomly selected without replacement, from the available pool of samples to avoid distortions in the curves due to variations in species abundance and sampling effort (Gotelli & Colwell 2001). Randomizations were repeated 100 times and the number of species for each number of individuals averaged over all iterations. Once a curve was generated, it was linearized with a log transformation of the number of individuals and the slope of the line was calculated. Curves were generated for each habitat within a region, then curves were generated for a successively higher number of habitats within a region until all habitats present in the region were contained in a single curve. This hierarchal creation of curves allows the determination of which habitats add relatively more new species to the regional pool of species and how the emerging pattern compares to other regions. This method was automated with a VISUAL BASIC SCRIPT run from EXCEL that is provided with this article (Appendix S1).

This analysis was carried out on macrofauna sampled from the seeps of the Pacific coast of California (CA) and Oregon (OR) and the Gulf of Mexico as well as meiofauna from the Gulf of Guinea and Håkon Mosby mud volcano on the Norwegian Margin. The macrofauna datasets were generated at the species level and meiofauna datasets were provided at the genus level. The Gulf of Mexico data include communities sampled with vestimentiferan tubeworm aggregations, bathymodiolin mussel beds, and *Lophelia pertusa* coral structure and were sieved to 2 mm (Bergquist *et al.* 2003, 2005, Cordes *et al.* 2005b, 2006, 2008). The CA and OR macrofaunal samples were from near-seep (transition) sediments, vesicomyid clam beds, oxygen minimum zones, bacterial mats, and background non-seep sediments collected in sediment cores and sieved to 300 $\mu$m (Levin *et al.* 2010). Gulf of Guinea and Håkon Mosby nematode communities were sampled with a multicorer outside the seep and ROV pushcores inside the active seep area, and sieved on a 32-$\mu$m sieve. Gulf of Guinea habitats included seep, transition zone adjacent to the seep, canyon, and control sediments (Van Gaever *et al.* 2010). The Håkon Mosby samples were from bacterial mats, siboglinid-associated sediments from the outer rim of the volcano, and control sediments (Van Gaever *et al.* 2006).

## Results and Discussion

The highest within-habitat diversity from all of these samples (slope of the curve within a single habitat) was found in the nematode communities from Håkon Mosby, followed by Gulf of Guinea (Fig. 3). In fact, the steepest slope of the curves generated from the Håkon Mosby data was found among the single-habitat group of replicate samples. These results suggest that the alpha diversity in meiofaunal communities at seeps may be greater than macrofaunal diversity, even though the nematode communities were only identified to the genus level and therefore contain an even greater diversity at the species level. The high level of variability in the slopes of the single-habitat curves for both the nematode genera (Fig. 3) and the meiofauna orders (Fig. 4) from this mud volcano is likely due to the variability in the habitat types with highly heterogeneous control and tubeworm sediments on one hand and strongly nematode-dominated center and reduced-sediment habitats on the other hand. The meiofaunal communities may be responding to small-scale heterogeneity within each habitat, and the use of broad habitat characterizations based on the visual assessment of the communities may mask the microhabitat heterogeneity to which the meiofauna respond. Indeed, nematode assemblages exhibit distinct vertical profiles in the sediment with different taxa in the surface sediments compared to the subsurface sediment fauna, pointing to species-specific distribution patterns at the millimeter to centimeter scales. Similar observations also apply to the macrofauna from CA seep sediments (Levin *et al.* 2003).

When additional habitats are added to this analysis, the greatest rate of increase in the accumulation of species is

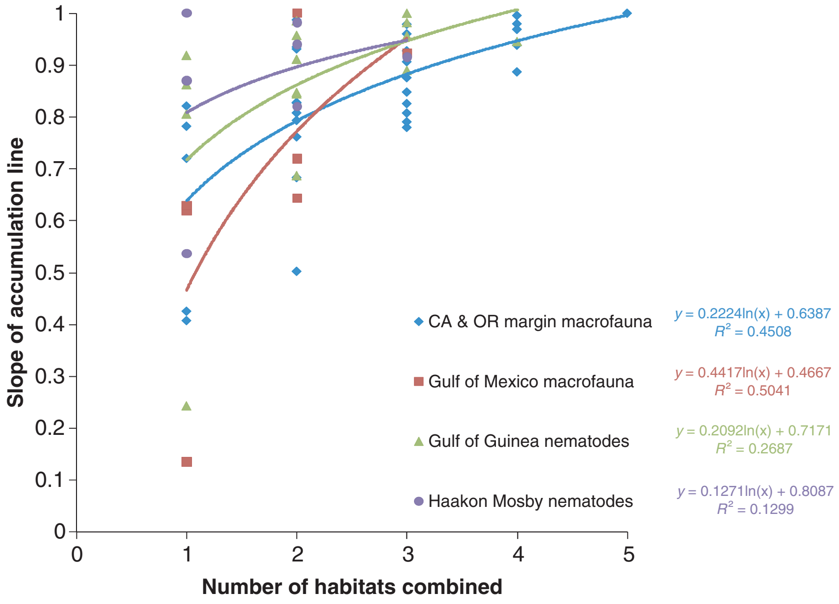

**Fig. 3.** Rate of taxon accumulation across habitats. CA & OR margin macrofauna include species-level data from near-seep sediments, vesicomyid clam beds, oxygen minimum zones, bacterial mats, and background sediments. Gulf of Mexico macrofauna include species-level data from vestimentiferan tubeworm aggregations, mussel beds, and scleractinian coral habitats. Gulf of Guinea nematodes are genus-level data from seep, transition, canyon, and control sediments. Haakon Mosby mud volcano samples are also genus-level nematode meiofauna from bacterial mats, siboglinid-associated sediments from the outer rim of the volcano, and non-seep influenced sediments. The greatest relative diversity response to habitat heterogeneity was found in Gulf of Mexico habitats, and the slowest increase in the rate of species accumulation with increased habitat heterogeneity was found in the nematode fauna of the Haakon Mosby mud volcano.

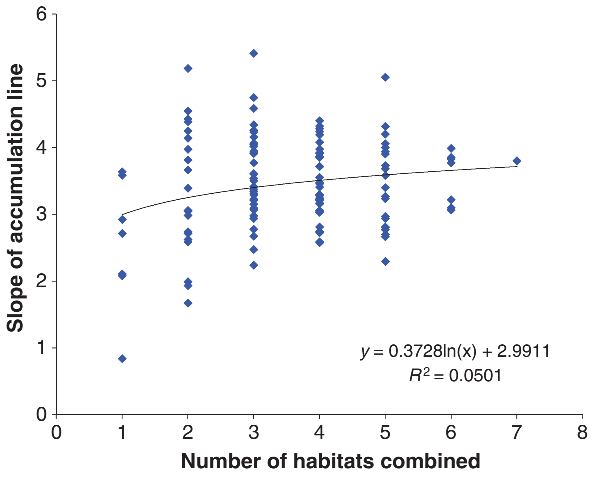

**Fig. 4.** Rate of species accumulation across habitats for meiofaunal orders sampled from the Norwegian Margin and Gulf of Guinea. Habitats include seep sediments, siboglinid sediments, bacterial mats, canyon sediments, seep-canyon transition, and control sediments from both regions. This figure demonstrates that at higher levels of taxonomic resolution, the majority of the diversity of the community may be captured by sampling across only two of these habitat types, and adding additional habitats only slightly increases the rate at which orders are accumulated.

found in the Gulf of Mexico habitats (Fig. 3). The high level of beta diversity among the mussel, tubeworm, and coral-associated communities is likely due to the strong differences in habitat chemistry as well as the differences in the structure of the biogenic habitats themselves (Cordes *et al.* 2008; Buhl-Mortensen *et al.* 2010). In addition, interspecific interactions (both positive and negative) among the foundation species and the communities they host will contribute to these patterns in diversity (Bergquist *et al.* 2003; Cordes *et al.* 2008). These interactions may account for the greater level of species turnover in this example where biogenic habitats exhibit higher rates of species turnover than do habitats from other systems that are primarily defined by geological habitat characteristics.

Following the Gulf of Mexico habitats, both the macrofaunal communities of the Pacific seeps and the meiofaunal nematode communities of the Gulf of Guinea exhibited similar rates of species accumulation as different habitats are added to the analysis. Gulf of Guinea nematode diversity was higher than CA and OR margin macrofaunal diversity, possibly due to the presence of an oxygen minimum zone off of CA and OR, but the slopes of the two relationships were very similar. The similarity in the size fractions of the fauna sampled and the habitat types contained in the investigations likely contributed to the similarity in these patterns.

To examine broader changes in diversity with habitat heterogeneity, the full meiofaunal datasets from Håkon Mosby and Gulf of Guinea were combined and examined at the order level (lowest level of taxonomic resolution). At this broad level, the relationship between diversity and habitat heterogeneity begins to fall off (Fig. 4). Even though these communities are from two locations separated by over 6000 km, the orders capable of colonizing deep-sea seep-related habitats appear to be limited and shared among these communities world-wide, and also appear to include other non-reducing deep-sea communities. Therefore, samples from only two or three habitats can represent a large proportion of the gamma diversity of seep meiofaunal communities at the order level.

### Ecological underpinnings of the habitat heterogeneity–diversity relationship

Different sources of heterogeneity can act to shape the path of community assembly in different ways. Recent work in ecology has identified a series of theoretical models to address how communities are assembled as metacommunities and how habitat heterogeneity, as patches of distinct habitat types, might influence this process (Leibold *et al.* 2004). The four models, species sorting, patch dynamics, mass effect, and neutral theory, all may play a role in the assembly of seep communities, but in different ways and with different intensities.

The species sorting model describes a strong effect of niche specialization where communities are largely structured by habitat characteristics. Habitat patches are theoretically distributed along a gradient of one or more environmental factors and the species are sorted along this gradient into the habitats to which they are best adapted. This form of community assembly has been demonstrated in the clam beds surrounding point-sources of fluids in Monterey Bay, where '*Calyptogena*' *kilmeri* inhabits areas of high porewater sulfide concentrations and *Calyptogena pacifica* (*sensu* Krylova & Sahling 2006) beds surround the periphery of the '*C.*' *kilmeri* zone where sulfide concentrations are lower (Barry *et al.* 1997; Goffredi & Barry 2002). Infaunal communities of Hydrate Ridge off the coast of Oregon also show a significant response to gradients in sulfide concentration where sulfide increases from background sediments to *Acharax* beds, *Calyptogena* beds, and *Beggiatoa* mats (Sahling *et al.* 2002). These community changes were related to the dynamics of fluid flow and sulfide concentration, but are also influenced by the seep fauna themselves through sediment irrigation (Treude *et al.* 2003). Similar changes in clam bed-, bacterial mat-, near seep- and background sediments are reported on the California and Oregon margins (Levin *et al.* 2010).

Species sorting along geochemical gradients is also demonstrated in the Gulf of Mexico vestimentiferan aggregations, where the distribution of many of the associated species exhibited significant correlations, both positive and negative, with epibenthic sulfide levels (Cordes *et al.* 2005b). Some of these species appeared to be functionally redundant (similar trophic niches), but were found in different aggregations according to the sulfide levels (different realized niches). More broadly, this concept is demonstrated in the differences among communities sampled in mussel beds consisting of *Bathymodiolus childressi* with methanotrophic symbionts, tubeworm aggregations of *Lamellibrachia luymesi* and *Seepiophila jonesi* with sulfide-oxidizing symbionts, and the deep-water coral *Lophelia pertusa* without symbionts (Bergquist *et al.* 2005; Cordes *et al.* 2008, 2009). Theoretically, the co-occurrence of habitat patches that select for specific communities within a single seep site should lead to increased beta diversity at the site scale as observed for the Gulf of Mexico communities (Fig. 2).

Patch dynamics considers a relatively homogeneous environment where the relative importance of competition and dispersal explain the composition of the community in any one habitat patch. Regional coexistence of species is provided by a tradeoff between competitive ability and dispersal capacity. The weaker competitor may be able to colonize a patch first, but eventually the poor disperser will arrive in the patch and outcompete the first. This theory explains community dynamics where successional processes dominate. An example of this form of temporal dynamics comes from the vestimentiferan aggregations of the Gulf of Mexico. In this system, young tubeworm habitats are colonized by endemic seep species from families common to seeps around the world and are slowly replaced by species common to the surrounding benthos of the Gulf of Mexico (Bergquist *et al.* 2003; Cordes *et al.* 2005b). There is also evidence that this pattern of seep succession occurs on geologic time scales. On the Barbados Accretionary Prism, the series of diapiric structures exhibits a variety of different fluid-flow patterns and correspondingly disparate community composition in terms of the relative abundance of vesicomyid and bathymodioline bivalves (Olu *et al.* 1996). A similar pattern was documented on the mud volcanoes of the eastern Mediterranean where active sites exhibited high methane and particulate flux and slower-flux sites contained greater areas of carbonate crusts (Olu-Le Roy *et al.* 2004). The relative age of the carbonate build-ups on mound structures in the Gulf of Mexico also greatly influences the types of seep (and non-seep) communities that develop at those sites (Roberts & Carney 1997; Fisher *et al.* 2007).

The mass effect describes a pattern of species abundance involving source and sink populations. At large or particularly suitable habitats, the population size of a given species will be quite high. This site will serve as a source of propagules dispersing into relatively small habitats where the probability of local extinction is high, or in marginal habitats where recruitment success or adult survivorship is relatively low. A series of localized, marginal habitats could also potentially link widely distributed sources populations. These interspersed 'sink' populations could account for the low level of genetic divergence among widely distributed populations of bathymodiolin mussels in the Atlantic basin (Cordes *et al.* 2007; Olu-Le Roy *et al.* 2007b; Génio *et al.* 2008) and vestimentiferan siboglinids on the Atlantic and Pacific sides of the Isthmus of Panama (McMullin 2003). For the meiofauna, the mass effect could explain source-sink exchange between shallow-water and deep-sea reduced environments but does not seem to account for exchange between seeps or reduced environments along adjacent continental margin sites. Indeed, different seeps consist of the same orders of meiofauna (Fig. 3) but only rarely share the same dominant species; rather, these species seem to be primarily derived from more abundant assemblages in shallow-water, organic-rich sediments (Van Gaever *et al.* 2006, 2010, in press).

Neutral theory predicts that random effects of colonization and extinction will produce observed species distribution patterns, assuming that species and habitat patches are all similar (but not necessarily identical). Because of the relatively strong influence of habitat chemistry on community composition that has been demonstrated in numerous settings, this theory appears to be less applicable to seep ecosystems. However, this theory could apply within certain taxonomic groups if they are assumed to have a certain degree of functional redundancy and similar habitat requirements or environmental tolerances. This model could account for some of the variability in community structure seen in young tubeworm aggregations at the more isolated seep sites in the Gulf of Mexico (Cordes *et al.* 2006). These vestimentiferan-associated communities did not strictly adhere to the model of community succession and appeared to be a more random accumulation of a subset of the potential pool of seep-endemic species commonly inhabiting the more extensive seep sites in the region. This theory could also apply to the background species that begin to colonize a seep following the reduction in seepage along with concentrations of sulfide and methane. These are often megafaunal predators that may be taking advantage of the elevated biomass at the seeps and potentially transporting seep productivity off site (MacAvoy *et al.* 2003; Sellanes *et al.* 2008). This component of the community would be a random accumulation of background species that happened to wander into the seep site and be observed or sampled while they were there. Again, neutral theory would only apply to a subset of the community (non-endemic vagrant species) and a subset of the habitat patches (early successional stages in isolated habitats).

These four models do not represent mutually exclusive hypotheses and could all contribute to our understanding of diversity and its response to habitat heterogeneity (Gravel *et al.* 2006). The species sorting model appears to most accurately represent the situation found at the seeps and explains a large portion of the previously demonstrated seep species distributions, particularly for the symbiont-bearing species. The patch dynamics model could help explain the successional patterns observed at some sites and the potential for high beta diversity where there were groups of habitat patches in different stages of succession. The mass effect may apply to some areas where sufficient high-density and low-density sites are spread over a large area such as the Gulf of Mexico or the entire Atlantic Basin, but examples of this situation are more rare. The neutral theory, although seemingly diametrically opposed to the species sorting (niche) theory, may also explain the distribution patterns observed at seeps, particularly for the vagrant species (*sensu* Carney 1994) that colonize the seeps and potentially utilize the increased productivity at those sites. However, we note that assemblages may appear to fit the neutral theory if the appropriate space and time scales or resource dimensions causing species sorting or creating patches are not investigated.

### Underlying mechanisms of the diversity response to habitat heterogeneity

If we assume that the most applicable theory of community assembly at seeps is the species sorting model, we may further examine the mechanisms by which species are sorted along environmental gradients. The mechanisms underlying the relationship between habitat heterogeneity and animal biodiversity at seeps are as complex as the seep habitats themselves. Geochemical, geological, and microbial drivers as well as biological interactions are all known to play critical roles in determining species distributions. The processes at play operate over a broad range of space and time scales from cm to many km, and from hours to MY (Fig. 5). On small scales they interact with one another to dictate biological activities as diverse as attraction to settlement, physiological tolerances, feeding mode and diet, life history, and symbioses. In addition, the abiotic factors that enable or inhibit the presence of prey, predator, competitor or symbiont will in turn affect the synecological interactions that determine animal distributions at seeps.

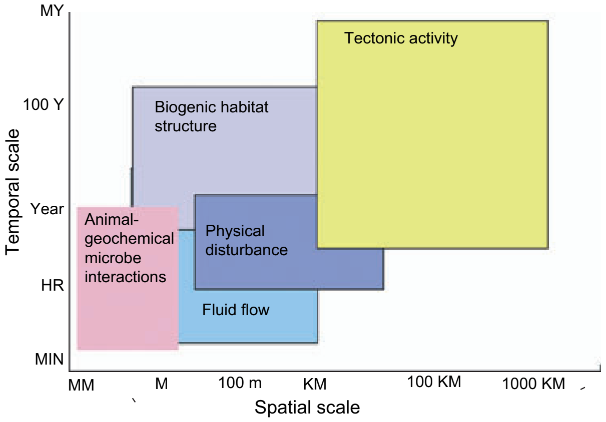

**Fig. 5.** Temporal and spatial scales of factors that influence habitat heterogeneity at cold seep sites.

Much of the habitat heterogeneity that we observe at seeps, regardless of its form, is driven by the patchy availability of methane and sulfide. While the geochemical conditions and availability of reduced compounds dictate the suitability of the habitat for the C fixation activities of bacterial symbionts, and thus the nutritional condition of the host invertebrates, they also establish a physiological realm that includes sulfide-tolerant species and excludes intolerant animal species (MacDonald *et al.* 1990; Barry *et al.* 1997; Sahling *et al.* 2002; Levin *et al.* 2003; Olu *et al.* 1996, 1997; Olu-Le Roy *et al.* 2007a). Sulfide gradients appear to affect the spatial distribution of animals horizontally and vertically within the sediment column (*e.g.* Levin *et al.* 2003), and to select evolutionarily for the radiation of taxa with sulfide (and low-oxygen) tolerance or detoxification capabilities (Hourdez *et al.* 2002; Hourdez & Lallier 2007). Sulfide, methane, or the microbes that utilize and produce them, may provide cues for settlement of some species and act as settlement inhibitors of others (Levin *et al.* 2006). Reduced compounds such as methane and sulfide also fuel a free-living microbial community that provides nutrition (and possibly settlement cues) for a wide array of smaller grazing, deposit feeding and suspension feeding taxa, as well as for bacterivores that may specialize on microbes with specific metabolic pathways or morphologies (Van Dover & Fry 1994; Robinson *et al.* 2004).

Many of the mechanisms linking heterogeneity to diversity are facilitative. Microbial mats of sulfide oxidizers have been proposed to transform sulfide into inert, non-toxic forms, creating a more favorable microhabitat that facilitates eukaryotic organisms (Gallardo *et al.* 1994; Brüchert *et al.* 2003). In addition, microbial consortia of anaerobic methane oxidizers precipitate carbonate, which provides a complex, often extensive hard substrate habitat for seep fauna. Aggregating megafauna form biogenic bushes (tubeworms), beds (bathymodiolin mussels, vesicomyid clams, ampharetid tubes, sponges) or fields (frenulate pogonophorans) that diversify available ecological niches by providing substrate, refuge, and food to a host of small invertebrates that live parasitically, commensally as epifauna, or in loose association (Bergquist et al. 2003, 2005; Turnipseed *et al.* 2004; Cordes *et al.* 2005b, 2006). In addition, some of these taxa further act as autogenic habitat engineers through irrigation, burrowing, and symbiont uptake of sulfide, all of which modify chemical conditions in ways that may benefit the free-living chemoautotrophic microbes that feed associated invertebrates and detoxify the habitat for metazoans (Sahling *et al.* 2002; Treude *et al.* 2003; Cordes *et al.* 2003, 2005a; Boetius 2005). The REGAB pockmark site at 3000 m water depth in the Guinea basin near the Congo canyon is one of the few sites where the mechanism underlying the diversity response may be examined in all three size classes of fauna (Sibuet & Vangriesheim 2009). At the pockmark scale, assemblages of vesicomyid and mytilid bivalves and siboglinid tube worms are sorted along gradients in methane fluid flow and substratum variability from the center to the periphery of the pockmark. However, in the central, active area there is also a high level of smaller-scale geochemical heterogeneity driving the distribution of the symbiont-bearing taxa (Ondréas *et al.* 2005; Olu-Le Roy *et al.* 2007a). In the central area, the distribution of the foundation species largely controls the relative abundance of the associated megafauna, while larger-scale patterns are generated by gradients in fluid flow and substratum type (Olu-Le Roy *et al.* 2009). The relative abundance of the macrofauna and meiofauna appear to be greatly influenced by the type of biogenic habitat (Menot *et al.* 2010, Van Gaever *et al.* 2009), with the vertical distribution of the infaunal species strongly impacted by the influence of the tubeworms and mussels on the sediment biogeochemistry (Menot *et al.* 2010). At the seeps along the Nordic Margin, meiofauna communities also show shifts in the proportions of the dominant genera from the siboglinid fields to background sediments (Van Gaever *et al.* 2006, 2009). Although most of these taxa show a continuous distribution over both habitats (Figs 2 and 3), the increase in abundance suggests that some taxa are better adapted to the more reduced conditions of the siboglinid patches, while others prefer the adjacent control sediments. These investigations suggest that while there are subtle differences in the mechanism underlying the patterns, the response of diversity to habitat heterogeneity is consistent among the different size classes of fauna at seeps as well as in other habitats.

## Summary

There are numerous sources of heterogeneity in seep ecosystems, and a variety of responses to this heterogeneity. Differences in geological drivers, fluid flux, and biogeochemical processes, as well as the influence of symbiont-hosting foundation species on these processes, provide one of the highest levels of local and regional habitat heterogeneity in any continental margin or deep-sea habitat. The diversity response appears to be strongest at the local (alpha level) in meiofaunal communities, whereas the beta level diversity response of the macrofaunal communities is greater when different types of biogenic habitats are investigated. These differences among the communities are most likely attributable to the influence of niche differentiation among these habitats and the fauna that inhabit them. The strong influence of habitat chemistry on the seep fauna is apparent in these analyses, and is the basis of the conclusion that the species sorting concept is the most applicable to seep systems. It is our hope that these findings and techniques will inform future studies of the diversity response to habitat heterogeneity and that some general principles of ecological theory might arise from future research in this field.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1**. This file is an Excel spreadsheet containing a macro program that will generate the accumulation curves presented in the manuscript (see manuscript for details of the method). The user selects the number of iterations for the model run and whether the habitats are sampled at an equal level of replication during the model run. The names of the different habitats are listed in column C, sample designations in column D, the species in row #12, and the presence/absence of the species (as "0" or "1") listed in the table. Once the data are entered, the user simply presses the "Run Calculations" button in cell 12 and the initial slope of the accumulations lines generated will be available in sheet 5. These data will allow the user to create the accumulation curves as presented in this manuscript.