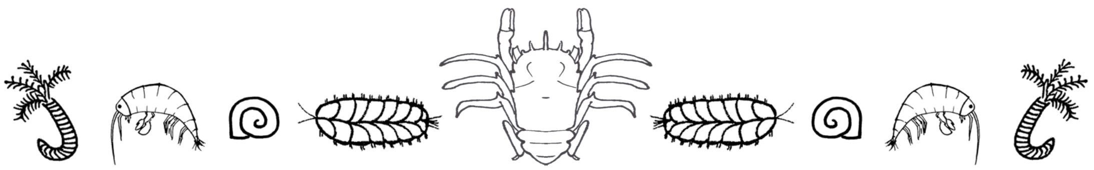


UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

SCHOOL OF OCEAN AND EARTH SCIENCE

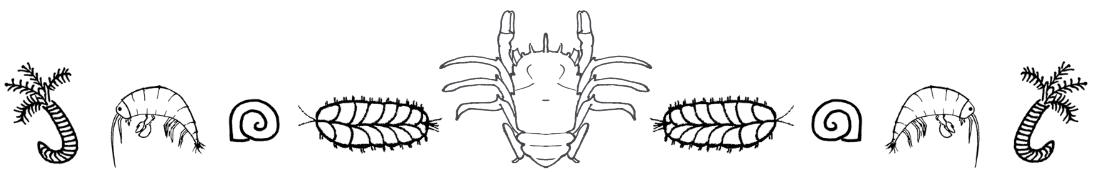
A TRAIT-BASED APPROACH TO THE BIODIVERSITY OF DEEP-SEA HYDROTHERMAL-VENT ECOSYSTEMS

by

ABBIE SARAH AMY CHAPMAN

Thesis for the degree of Doctor of Philosophy (PhD)

September 2018



UNIVERSITY OF SOUTHAMPTON

ABSTRACT

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A TRAIT-BASED APPROACH TO THE BIODIVERSITY OF DEEP-SEA HYDROTHERMAL-VENT ECOSYSTEMS

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Abbie Sarah Amy Chapman

The study of the functional component of biodiversity has experienced a recent resurgence in popularity because of its capacity to inform our understanding of the relationships between species and their environments for their conservation and management. Ecological traits, such as body size and trophic level, can be used to compare communities that differ taxonomically but share traits. Hydrothermal-vent communities are well suited to a trait-based approach because they are home to highly endemic species. To date, vent ecologists have instead focused on taxonomic and phylogenetic biodiversity patterns, grouping vents into distinct biogeographic provinces. The relative biodiversity of these provinces can be compared using traits as a common, cross-province 'currency'. Here, we use a trait-based approach to study the biodiversity of active deep-sea hydrothermal-vent ecosystems, gaining insights relevant for ecology and conservation science. First, we identify traits shaping the performance of a vent species within its physico-chemically extreme environment, as well as its influence on ecological processes. Of these traits, we score those for which relevant information is available for the majority of vent fauna, using available literature and expert advice. We first focus on the well-sampled vent fields of the Juan de Fuca Ridge region in the Northeast Pacific Ocean. Here, our investigations showcase hydrothermal vents as model, 'untouched' ecosystems for developing ecological theory for conservation. This potential leads us to create a global trait database for vent fauna with an international pool of expert contributors - 'sFDvent'. To accompany the trait, taxonomic, and occupancy information in sFDvent, we also extract, map, and analyse large-scale environmental data of potential influence on the ecology of vent communities. Finally, we use trait, taxonomic, and environmental characteristics of well-studied vent regions to quantify their relative uniqueness for conservation purposes. These dimensions of uniqueness are not spatially congruent, suggesting that a multidimensional approach is critical to ensure that priority areas for conservation and management are not missed. By 2020, deep-sea mining is expected to begin on a commercial scale, exploiting polymetallic sulfides formed from hydrothermal-vent precipitates. We hope that our investigations will inform hydrothermal-vent management policies and guidelines before the first human footprints are left on these unique, untouched ecosystems.

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Declaration Of Authorship

I, Abbie Sarah Amy Chapman, declare that this thesis, entitled "A trait-based approach to the biodiversity of deep-sea hydrothermal-vent ecosystems", and the work presented in it are my own and have been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

   Chapman, A. S. A., Tunnicliffe, V., and Bates, A. E. (2018). Both rare and common species make unique contributions to functional diversity in an ecosystem unaffected by human activities, *Diversity and Distributions*, 24, 5, pp. 568 - 578, doi: 10.1111/ddi.12712.

Signed:

Date:

Acknowledgements

I have been so lucky to have so many doors opened, so many life experiences, and so many learning opportunities during this PhD thanks to my supervisor, Amanda. Thank you, Amanda, for always making time for me, for teaching me how to 'talk science', and for helping me to lose my fear of statistics. Thank you for making me a scientist. Thank you for introducing me to great people, who have welcomed me into their research communities and helped to build my confidence. I will never forget my first Canadian rock climbing experience in Montréal, watching you hop up those rocks with ease, nor curry in buckets on the beach on the Isle of Wight. Thank you for creating a supportive, fun lab group. I know words will never do justice the many, many hours that you have given to help me get to this point. I'd like to thank you and also your family - Tom, Linnaea, Moana, and Loki - for the times that I've been on email, Skype, and Zoom and disrupting the flow at home. Thank you for sticking with me, Amanda. I hope I can do you proud.

Verena - thank you. Thank you for becoming, willingly, knowingly, or otherwise, my unofficial supervisor. Thank you for sharing your expert advice and sending me interesting ideas and papers throughout my PhD. Thank you for welcoming a very nervous me to your lab in Victoria, for welcoming Sam too, and for being so understanding on my first cruise - I was a rookie for sure but you were very patient with me - thank you. I am also grateful to you for the way you welcomed me to the deep-sea research community at conferences, introducing me to your friends and colleagues. I saw my first deep-sea hydrothermal vents in 'real life' with you and I will never forget my experiences on the *Tully*. Thank you for welcoming me aboard, and for all of your support since.

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I'd also like to thank vent fauna themselves. I am submitting this thesis when their future is uncertain. Many vent fauna have been sampled in an effort to understand and conserve vent ecosystems. Thus, to those fauna, I am grateful. Without them, we wouldn't have any of the work in this thesis. To the vents - beautiful and unusual - thank you for continuing to inspire and excite me after years of getting to know you better.

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To Colin - thank you for sharing your best boy Ben with us. Thank you, Ben, for the fresh air, ball games, and lots of fun walks together.

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This thesis is dedicated to the support team I will never have the words to be able to thank enough. My loving family - always there at the end of the phone or a relaxing drive in Bert and the ones who took me on my very first trip to the seaside. My Sam - who understands me in a way I never thought anyone other than my family could. And my Dogbert - Lettice - wiggling, playing, snoring, and always making a smile with her ever so fluffy face and gorgeous deep-brown eyes. Thank you all. Without you, I wouldn't be able to take on big challenges like this one. With you, I climb mountains. I am lucky to have you there with me on the winding journey up each one and to take the lift with me at the end to admire the view. You make me happy and calm just by being around and I feel so lucky to have you in my life. Thank you for coming on this PhD journey with me. To my smart, supportive Dad, Simon, I found coding to procrastinate productively at last! Thank you for always being there when I need advice. To my bro, Dominic, I 'just got it written'! I am so proud to have you as a brother. Thank you for welcoming me to your world of coding (albeit the rather rookie version!) and thank you for always being there for me, no matter how busy you are. To Sam - no more final pushes, it's done! Thank you for all the tea, hugs, long, long pep talks, and for looking after me - doing everything in your power to make life easier for me while I worked. To Lettice - I love you, little wiggler. And to my wonderful, fun Mum, who always has the perfect words and just gets me - this is my PhD!

Chapter One: Introduction

1. BACKGROUND

1.1 The unique characteristics of hydrothermal-vent ecosystems

Fascinating scientists and members of the public alike since their discovery around 40 years ago, deep-sea hydrothermal vents, and the fauna they sustain, are generally considered to be unusual, extreme, and productive ecosystems. Vent systems arise as a result of seawater percolating down through the Earth's crust. The water is superheated and chemically altered before rising and exiting the crust as hydrothermal fluid, laden in reduced metals and hydrogen sulfide, but reduced in pH and depleted of oxygen (**Figure 1**; Jannasch, 1985; Lutz and Kennish, 1993; Hessler and Kaharl, 1995). These individual emissions can cool to form precipitates, which accumulate to build chimneys (Jannasch, 1985). Vent fields are groups of these chimneys and fluid emissions and can span tens to hundreds of metres according to the underlying geology - the vent 'plumbing system' (Hessler and Kaharl, 1995). Hydrothermal-vent fluid typically flows out from hard, basalt-rock substrata, and fields are distributed across the globe along mid-ocean ridges, in back-arc basins, on arc volcanoes, and, less commonly, in other tectonic settings (**Figure 2**; **Figure 3**; Hessler and Kaharl, 1995; Ramirez-Llodra et al., 2010). The spatial configuration of vent systems is thus closely linked with volcanism and plate tectonics (**Figure 3**), including seafloor-spreading rate, which can vary from less than 20 millimetres per year to around 200 millimetres per year, shaping the relative isolation, oceanography, and geomorphology of venting regions (Hessler and Kaharl, 1995; Ramirez-Llodra et al., 2010).

Most vents are found in the deep sea, more than 200 metres below the sea surface, beyond the reach of sunlight (Beaulieu, 2015). Accordingly, the fauna found thriving in high-biomass communities at vents predominantly rely on chemosynthesis for energy (Tunnicliffe, 1992; McMullin et al., 2000). In fact, vent communities are the only ones on the planet not dependent on sunlight for energy (though oxygen for respiration is photosynthetic in origin; Hessler and Kaharl, 1995; Van Dover, 2000; Ramirez-Llodra et al., 2010). Instead, many vent animals depend on microbes capable of oxidising hydrogen sulfide, and other reduced chemicals, to make organic compounds (Jannasch, 1985; Fisher et al., 2007). Some vent animals host bacteria via special adaptations (e.g., *Riftia pachyptila,* a tubeworm without a mouth or digestive system, replaced by a bacteria-storing 'trophosome', and *Rimicaris exoculata* shrimp, which have bacteria in their large gill chambers and on their carapaces; **Figure 4**; Ramirez-Llodra et al., 2010). Others graze on energy-rich 'bacterial mat' (e.g., *Lepetodrilus* limpets feed on these accumulations of bacteria; **Figure 4**), organic matter from the surface and/or other fauna, or feed on other fauna directly, as carnivores (e.g., pycnogonids and anemones; **Figure 4**; Van Dover, 2000; Micheli et al., 2002).

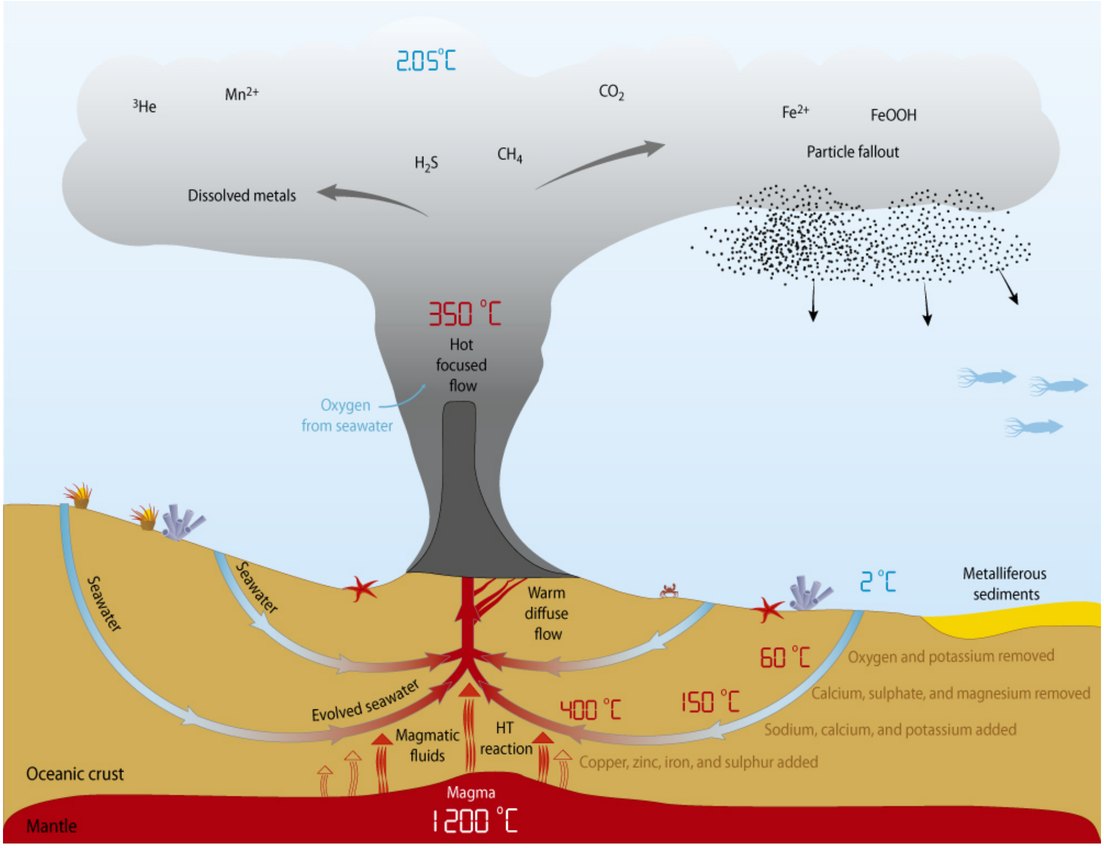
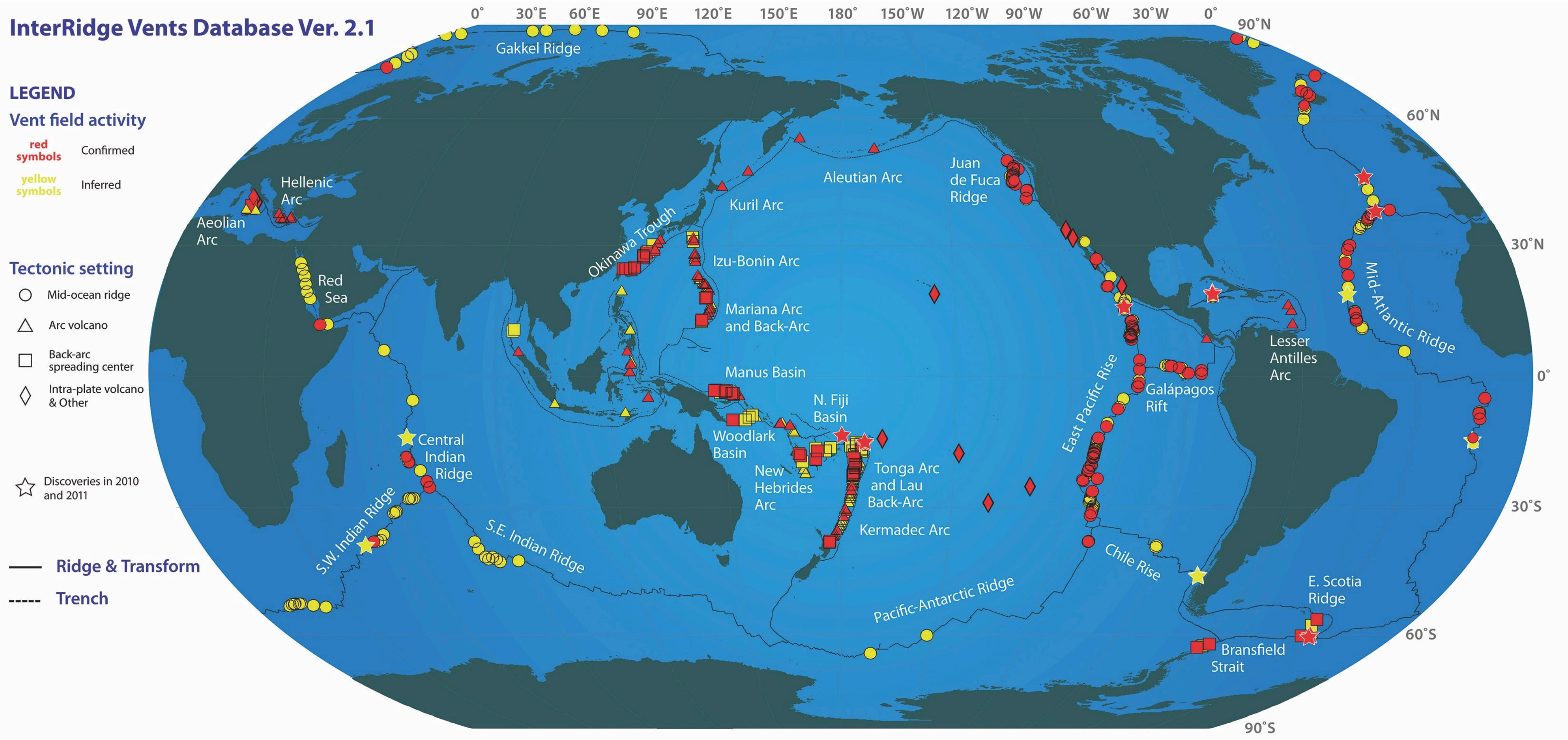


Figure 1: Diagram illustrating the processes involved in the formation of hydrothermal-vent fluid. Image source: GRID-Arendal (2014; www.grida.no/resources/8166).

Figure 2 (overleaf): Map of the global distribution of known vent fields (according to version 2.1 of the InterRidge Vents Database; Beaulieu et al., 2011). This map includes known vents, for which vent activity has been confirmed through seafloor observations, and inferred vents, for which vents are assumed to be present given signals measured from the sea surface. The tectonic setting for each vent field is delineated using symbols, as described in the legend. The total length of the Mid-Ocean Ridge system is estimated to be 60,000 kilometres (Ramirez-Llodra et al., 2010). Map source: Beaulieu et al. (2011).



InterRidge Vents Database Ver. 2.1

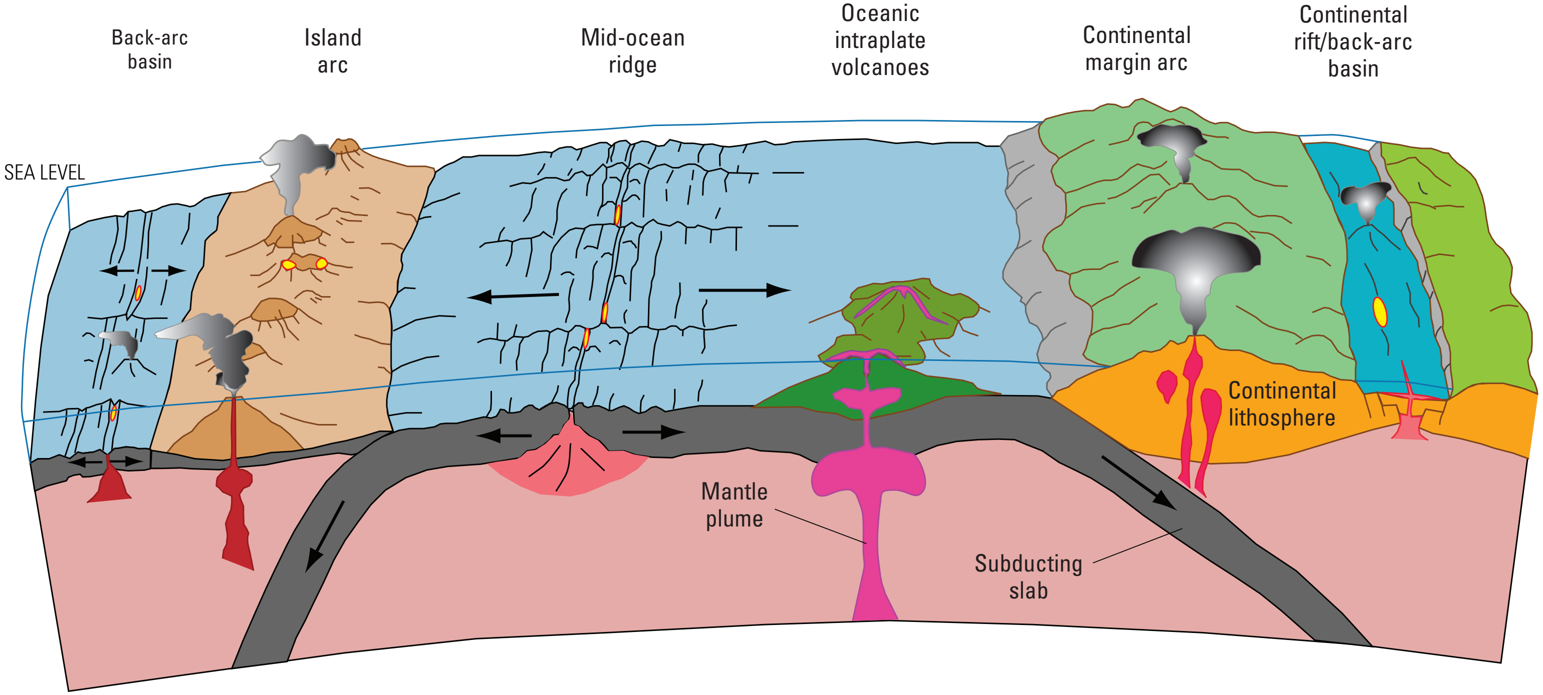


Figure 3: Diagram representing, among others, the different types of tectonic setting within which deep-sea hydrothermal vents are found. Here, the back-arc basin represents the 'back-arc spreading centers' shown in **Figure 2**. The island arc represents 'arc volcanoes' in **Figure 2**. The tectonic plates shown in grey are oceanic lithosphere, while orange plate is continental. Arrows represent the spreading movement of tectonic plates. Image source: Shanks and Thurston (2012, as made available by the U.S. Geological Survey).

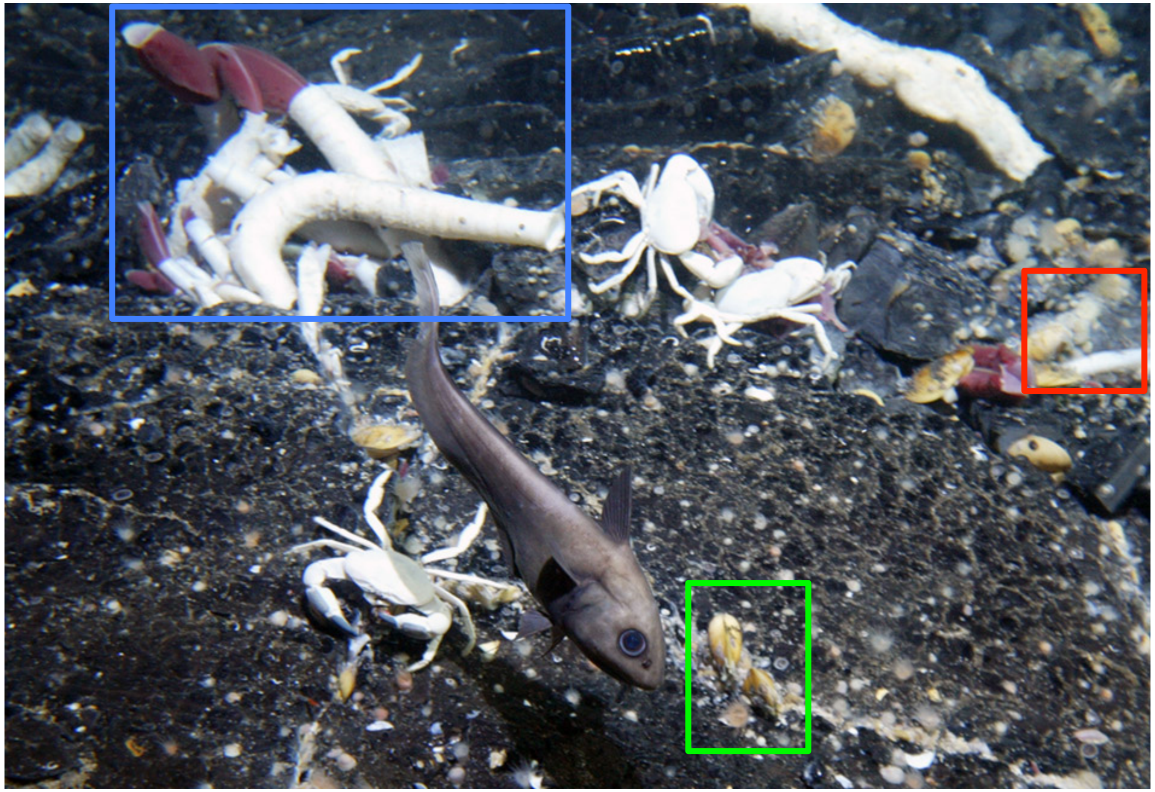


Figure 4: Photograph illustrating the different feeding modes of, and nutritional sources available to, vent fauna. This photo highlights the role of bacterial mat, or microbial mat, as a food source for grazers (e.g., gastropods, highlighted in the red box), as well as the symbiont hosts (e.g., tubeworms, as shown in a blue box), scavengers (e.g., fish), carnivores (e.g., crabs), suspension feeders (e.g., mussels, such as those in a green box) and detritivores (e.g., gastropods and scaleworms) feeding in vent ecosystems. Image source: © Woods Hole Oceanographic Institution (2013, reproduced with permission).

Vent communities are species-poor (e.g., 37 species have been recorded across well-sampled, basalt-hosted Juan de Fuca Ridge communities), relative to the hundreds of species found in terrestrial and shallow-marine systems, as well as non-chemosynthetic ecosystems of the wider deep sea (Grassle and Macioleck, 1992; Ramirez-Llodra et al., 2007, 2010). The low numbers of species do not limit the uniqueness of vent communities, which comprise endemic species, adapted to microhabitats across strong physico-chemical gradients (Jannasch and Wirsen, 1979; Hessler and Smithey, 1983; Sarrazin et al., 1999). Temperatures, for instance, can range from that of ambient seawater - generally a couple of degrees - to more than 400°C, within a centimetre of space (**Figure 5**; Chelvadonné et al., 1992; Haymon et al., 1993; McMullin et al., 2000). Therefore, there is plentiful, diverse niche space for invertebrates to exploit, producing a distinct set of well-adapted fauna, capable of thriving in physiologically extreme environments (Tunnicliffe, 1992; Tunnicliffe et al., 2003; Ramirez-Llodra et al., 2010).

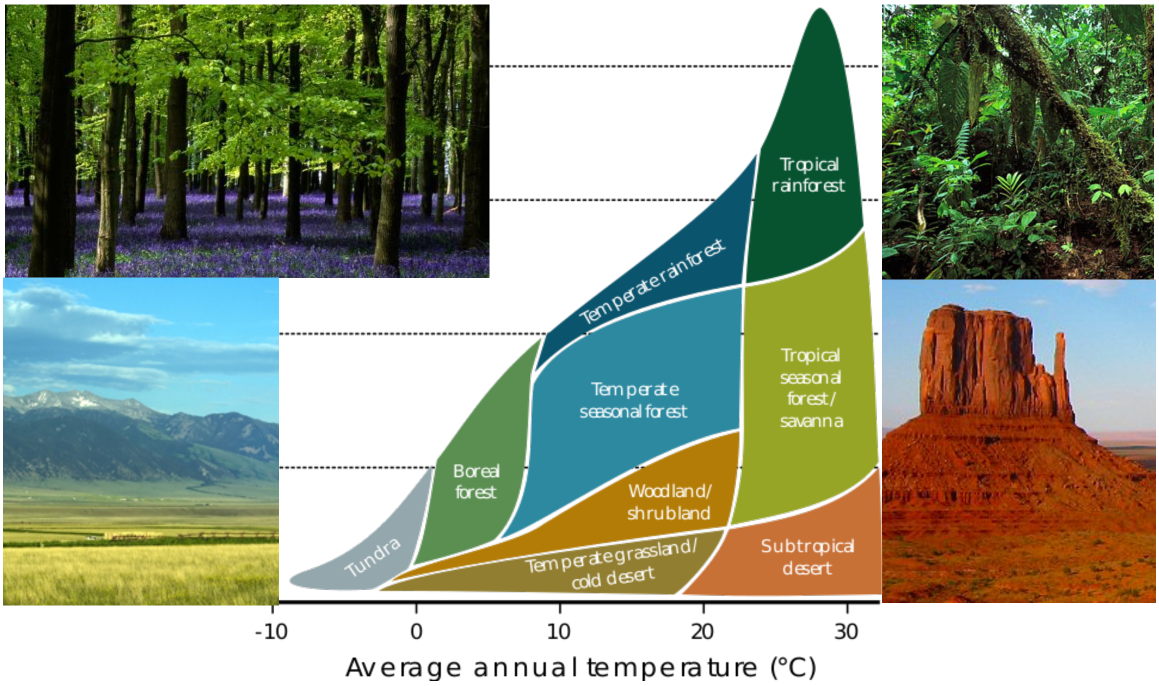


Figure 5: An illustration of the different ecosystems one would need to compare on land to see the same temperature gradient as that across several centimetres at many deep-sea hydrothermal vents. Image sources: rainforest (top right, Abyss, 2016); desert (bottom right, Mantel, 2016); woodland (top left, Spender, 2009); grassland (bottom left, Lee, 2002); and diagram (centre, Wikimedia Commons, 2017).

Vent communities are further shaped by the instability common in vent ecosystems (Hessler and Kaharl, 1995; Ramirez-Llodra et al., 2010); though, see Du Preez and Fisher (2018) for an example of a relatively stable system in the Lau Basin. Active vents are typically considered ephemeral environments, driven by volcanic activity that can cause vent flow to wane, change, or shut off completely, rendering a vent inactive (Hessler and Kaharl, 1995; Tsurumi and Tunnicliffe, 2001). Thus, vent fauna must be able to adapt to rapid environmental change, regularly reproducing and/or producing larvae that can travel the distances between active vent fields (Johnson et al., 1988; Lutz and Kennish, 1993; Van Dover and Trask, 2000). The unique geological and chemical settings of deep-sea hydrothermal vents make them compelling 'natural laboratories' for the study of biodiversity patterns on Earth.

1.2 Using traditional indices to study the biodiversity of hydrothermal-vent communities

Biodiversity describes the variety of life on Earth. First defined by E. O. Wilson in 1988, the definition of biodiversity is now used to refer to many different aspects of communities and ecosystems. The Convention on Biological Diversity (1992) suggests that biodiversity incorporates the variety of living things - terrestrial, marine, and aquatic - as well as the habitats and ecosystems of which they are part (Gray, 1997). Nonetheless, while diversity to a taxonomist may represent a number of species, it may to a community ecologist also incorporate the distribution of these species across different habitat types and the environmental factors influencing this distribution (Noss, 1990). At deep-sea hydrothermal vents, ecologists have characterised taxonomic diversity, focusing on traditional diversity indices like species richness (the number of species in community) to shape their studies (**Table 1**). However, higher taxonomic classifications are shared across the globe (e.g., bythograeid crabs are found across the Pacific and Atlantic oceans; Hessler and Kaharl, 1995). This suggests that there is an opportunity to move beyond taxonomic approaches for understanding and quantifying biodiversity patterns.

Much of what scientists have learnt about the diversity of hydrothermal-vent communities since their discovery in 1977 has been collated using specimens, photographs, microbiological samples, phylogenetic trees, and multivariate statistical analyses (Grassle, 1985; Tunnicliffe, 1992; Lutz and Kennish, 1993; Black et al., 1997; Cavanaugh et al., 2006; Vrijenhoek, 2010b). As sampling the deep sea depends on submersible equipment launched from research vessels, like Remotely Operated Vehicles and towed cameras, it is often considered to be more haphazard and less systematically planned than in terrestrial ecological studies (Lutz and Kennish, 1993; Morris et al., 2014). Many researchers therefore argue that species-richness data cannot be used to compare vent communities across large scales because of taxonomic constraints, uneven sampling efforts, and differing methods (Jollivet, 1996; Van Dover and Trask, 2000; Gotelli and Colwell, 2001; Tsurumi and Tunnicliffe, 2001). While some of these sampling issues can begin to be addressed using rarefaction techniques (e.g., **Figure 6**), standardised sampling (e.g., using standard ecological units, like mussel beds or tubeworm grabs (Van Dover and Trask, 2000; Van Dover and Doerries, 2005)), and other mathematical tools, the reliability of species richness as a diversity measure can still then be affected by sampling approach (Gotelli and Colwell, 2001). Sampling constraints have perhaps encouraged vent ecologists to limit their scope to taxonomic dissimilarity measures and richness-based indices (e.g. Shannon and Simpson - see **Table 1**) to inform cluster analyses, compare sites, define biogeographic provinces (**Figure 7**), and propose potential environmental drivers, rather than assessing the relative biodiversity of hydrothermal-vent communities (Desbruyères et al., 2000; Van Dover and Trask, 2000; Tsurumi and Tunnicliffe, 2001; Tsurumi, 2003; Bachraty et al., 2009; Rogers et al., 2012; Nakajima et al., 2014).

Table 1: Definitions of the traditional diversity indices typically used in hydrothermal-vent ecological research.

Diversity index	Definition	Examples of use in vent ecology
Species richness	The number of species in a community, which is widely accepted as a useful and important measure for conservation (Gotelli and Chao, 2013).	Sarrazin and Juniper, 1999; Van Dover and Trask, 2000; Marcus and Tunnicliffe, 2002; Tsurumi, 2003; Turnipseed et al., 2003; Van Dover and Doerries, 2005; Gollner et al., 2007; Kelly and Metaxas, 2008; Bernardino et al., 2012; Sarrazin et al., 2015
Pielou's Evenness Index	This diversity measure is commonly used to quantify the spread of abundance of species in a community (Magurran, 2004).	Van Dover and Trask, 2000; Turnipseed et al., 2003; Van Dover and Doerries, 2005; Gollner et al., 2007; Kelly and Metaxas, 2008; Bernardino et al., 2012
Shannon Index	Also known as the Shannon-Wiener Index, this is a well-used measure that combines evenness and richness to quantify diversity. This index is used under the assumption that species have been randomly sampled and that all species have been captured in the sample (Magurran, 2004).	Tsurumi, 2003; Turnipseed et al., 2003; Van Dover and Doerries, 2005; Gollner et al., 2007; Kelly and Metaxas, 2008; Sarrazin et al., 2015
Inverse Simpson Index	The Inverse Simpson Index is a more readily interpretable version of the Simpson Index, which represents the probability of two individuals being the same species when drawn at random from a sample (Magurran, 2004). It combines elements of richness and evenness.	Van Dover and Trask, 2000 (Simpson); Tsurumi, 2003 (Simpson); Galkin and Goroslavskaya, 2008 (Simpson); Sylvan et al., 2012

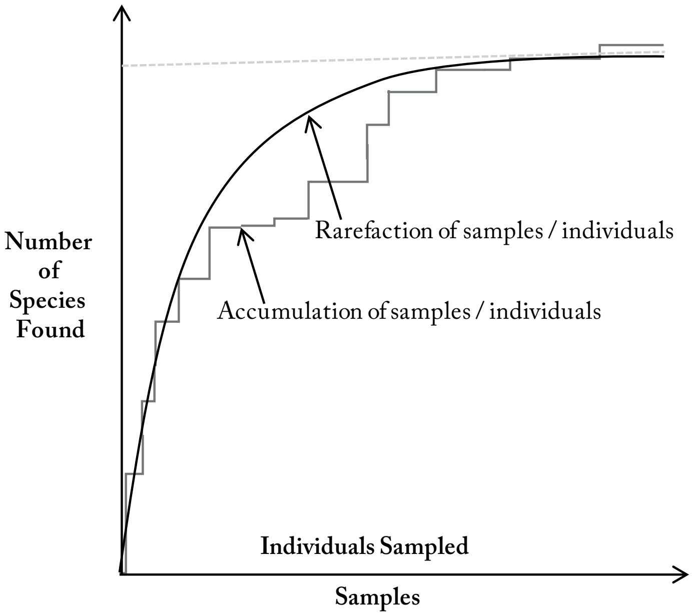
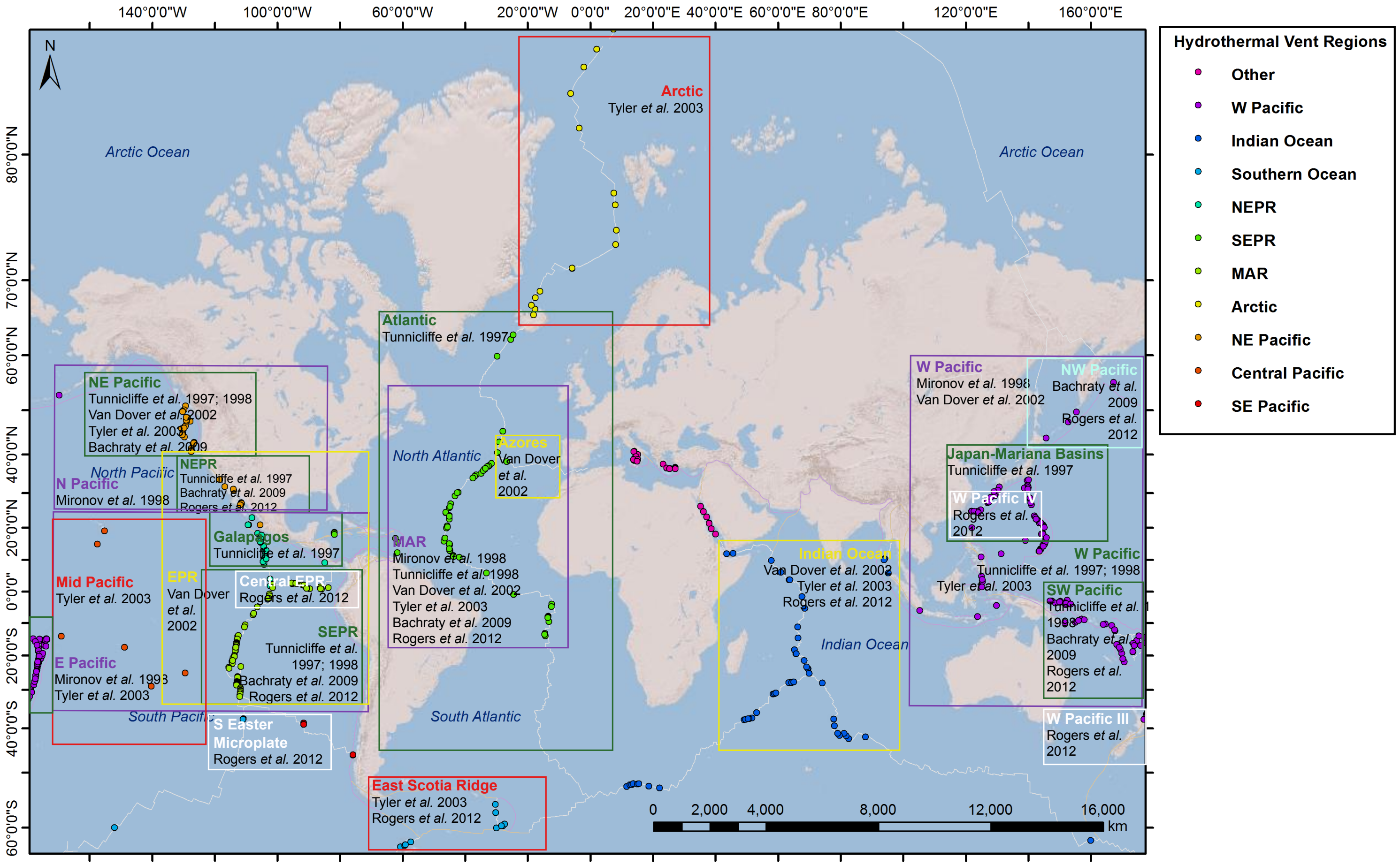


Figure 6: The main features of a rarefaction, or 'collector's' curve, used to show that increasing one's sample size increases the number of species found, until a plateau is reached whereby most, if not all, of the species in a sample area have been counted. Rarefaction curves are useful measures of how representative a species richness estimate is and abundance data are. This schematic is adapted from Gotelli and Colwell (2001).

Nevertheless, studies aiming to compare diversity across the globe have revealed interesting patterns. For instance, species richness tends to increase with productivity, consumption, and biogeochemical flux in many global ecosystems (Gotelli and Colwell, 2001; Gamfeldt et al., 2014); faunal hydrothermal-vent communities, however, have low richness, but maintain high levels of biomass (Jollivet, 1996; Vrijenhoek, 1997; Dubilier et al., 2008). In addition, the drivers of the formation of distinct provinces based on community composition (**Figure 7**) are well known and include: spreading rate, fluid chemistry, temperature, distance along ridge, and geological and oceanographic dispersal limitations, including vicariance events, ocean currents, and depth (Van Dover, 1990; Tunnicliffe et al., 1998; Van Dover et al., 2002; Tsurumi, 2003). It is likely that these drivers will also be important factors influencing diversity and the maintenance of biomass in these systems.

Figure 7 (overleaf): A map delineating vent biogeographic provinces, as they have been proposed, through time. This map was created using the vent location data available through InterRidge (Beaulieu, 2015) and vent biogeography papers published to date. It illustrates the changing view of vent biogeographic provinces through time, with each vent field exploration programme. The rectangles are colour-coded according to province model. Vents have been colour-coded according to the regions assigned to them by the majority of the province models and, in some cases, InterRidge.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● Arctic
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● SE Pacific

Quantifying and defining biodiversity has become increasingly important for conservation and management applications in a variety of environments (CBD, 1992, 2010; Gray, 1997; ITTO/IUCN, 2009). As scientists have been some of the only visitors to vents to date, adhering to voluntary codes to keep their impacts to a minimum (InterRidge, 2009), it has perhaps not been a high priority to plan to manage or conserve these relatively untouched, unexplored systems. We are still working to understand fundamental biological and ecological processes operating in vent ecosystems (Tunnicliffe, 1990; Tyler et al., 2005). However, commercial deep-sea polymetallic sulfide mining is expected to commence by 2020 and hydrothermal-vent ecosystems, previously relatively untouched by man, now need management plans based on quantifiable, definable diversity (Van Dover et al., 2018).

Overall, our current understanding of the biodiversity of hydrothermal-vent communities is generally shaped by traditional diversity indices (**Table 1**), based on taxonomic information that is still being updated and added to. For context, during the first thirty years of vent exploration, two species were being described every month (Van Dover et al., 2002; Ramirez-Llodra et al., 2010). To make management decisions concerning these environments with confidence, we need a deeper understanding of vent diversity, incorporating: the diverse forms and functions of its inhabitants (e.g., **Figure 8**); the different substrata; and environmental drivers, as for other ecosystems, such as forests and rivers (Petchey and Gaston, 2006; Hillebrand and Matthiessen, 2009; Menezes et al., 2010; Cadotte, 2011; Cadotte et al., 2011).

1.3 A trait-based approach to ecology

Across ecosystems, including vents, the majority of ecological and conservation-focused studies use species richness to represent biodiversity (Cadotte, 2011; Schmera et al., 2017). However, there is inherent importance in the variety in form and function present in an ecosystem (Cadotte, 2011), demonstrated in the long-term existence of functional ecology and its principles (Darwin, 1859; Calow, 1987; Laureto et al., 2015). A functional-trait approach (**Figure 9**) uses traits such as body size, trophic level, and habitat use to understand how species interact with their environment and to assess the contributions of species to ecosystem processes. Functional traits therefore offer a common 'currency' with which to compare taxonomically distinct species pools. Traits enable us to capture the differences among species known to influence the ecology of an ecosystem - important for conservation and management strategies (Cadotte, 2011; Cadotte et al., 2011). Most established in the study of plants, for which there is now a protocol for measuring traits (Pérez-Harguindeguy et al., 2013) and a global trait database (Kattge et al., 2011), it has been argued that traits can be used to predict productivity and to measure ecosystem functioning (Bremner et al., 2003; Petchey and Gaston 2006; Schmera et al., 2017) better than richness-based biodiversity measures (Flynn et al., 2011; Aguilar-Trigueros et al., 2015).

A trait-based approach has been used successfully and increasingly since the 1990s (**Figure 10**) in terrestrial, shallow-marine, and freshwater environments to complement traditional diversity measures when investigating: large-scale diversity patterns (Wright et al., 2005; Díaz et al., 2007); community composition (Wiescher et al., 2012; Wiedmann et al., 2014; van der Plas et al., 2015); ecosystem functioning and productivity (Clark et al., 2012; Greenfield et al., 2016); a community's potential resilience to future change (Belmaker et al., 2013; Buisson et al., 2013; Mori et al., 2013; Vandewalle et al., 2010); and the best areas to target for conservation (Stuart-Smith et al., 2013; Coleman et al., 2015). Scientists use a trait-based approach to biodiversity to account for the fact that not all species contribute to a system's productivity or function equally - the underlying assumption when quantifying diversity using species richness, for example (**Figure 8**; Petchey and Gaston, 2006; Lefcheck et al., 2014). Functional diversity measures also account for temporal plasticity in species traits in a way that diversity measures based on taxonomy alone, based on fixed traits, cannot (Zhang et al., 2012).

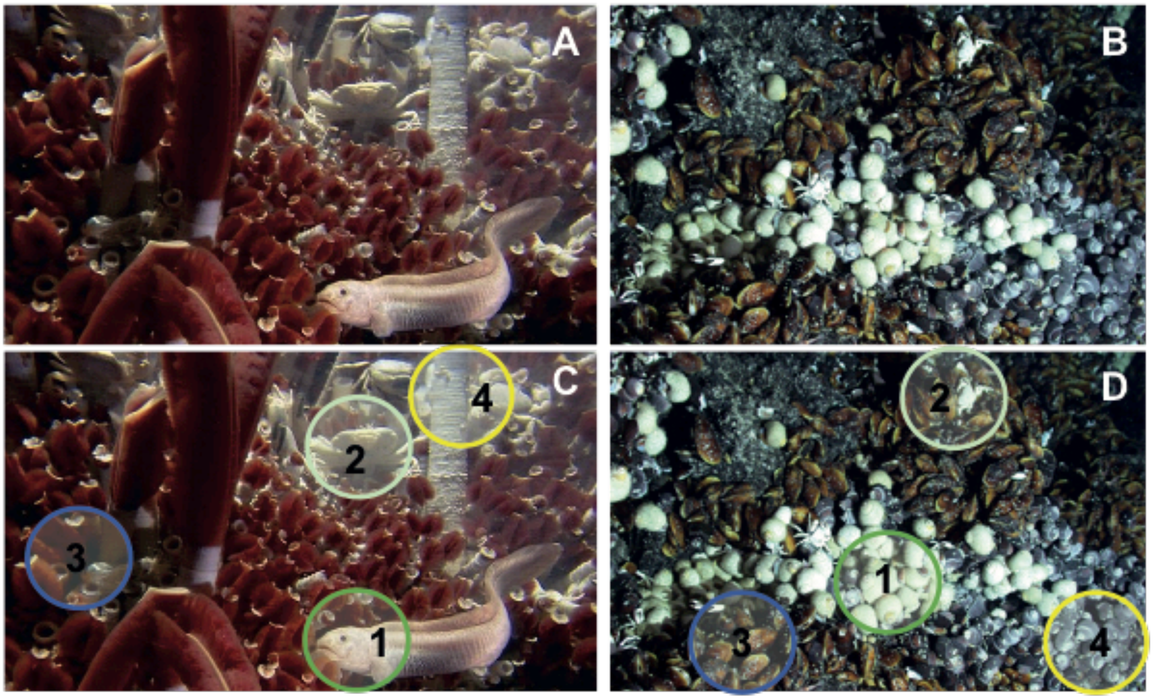

Figure 8: These images highlight the differences between perceived diversity (where A appears more diverse than B) and species richness (C and D have equal species richness, based on a superficial visual survey of each image). They illustrate the importance of functional diversity at hydrothermal-vent sites. For example, A and C show fauna of different body sizes, forms, and trophic levels (higher functional diversity), whereas B and D comprise mostly hard-shelled grazers of similar size (lower functional diversity). Image sources: A and C - Kristoff (n.d.) and B and D - FLEXE (n.d.). Figure adapted for vents from Lefcheck (2014).

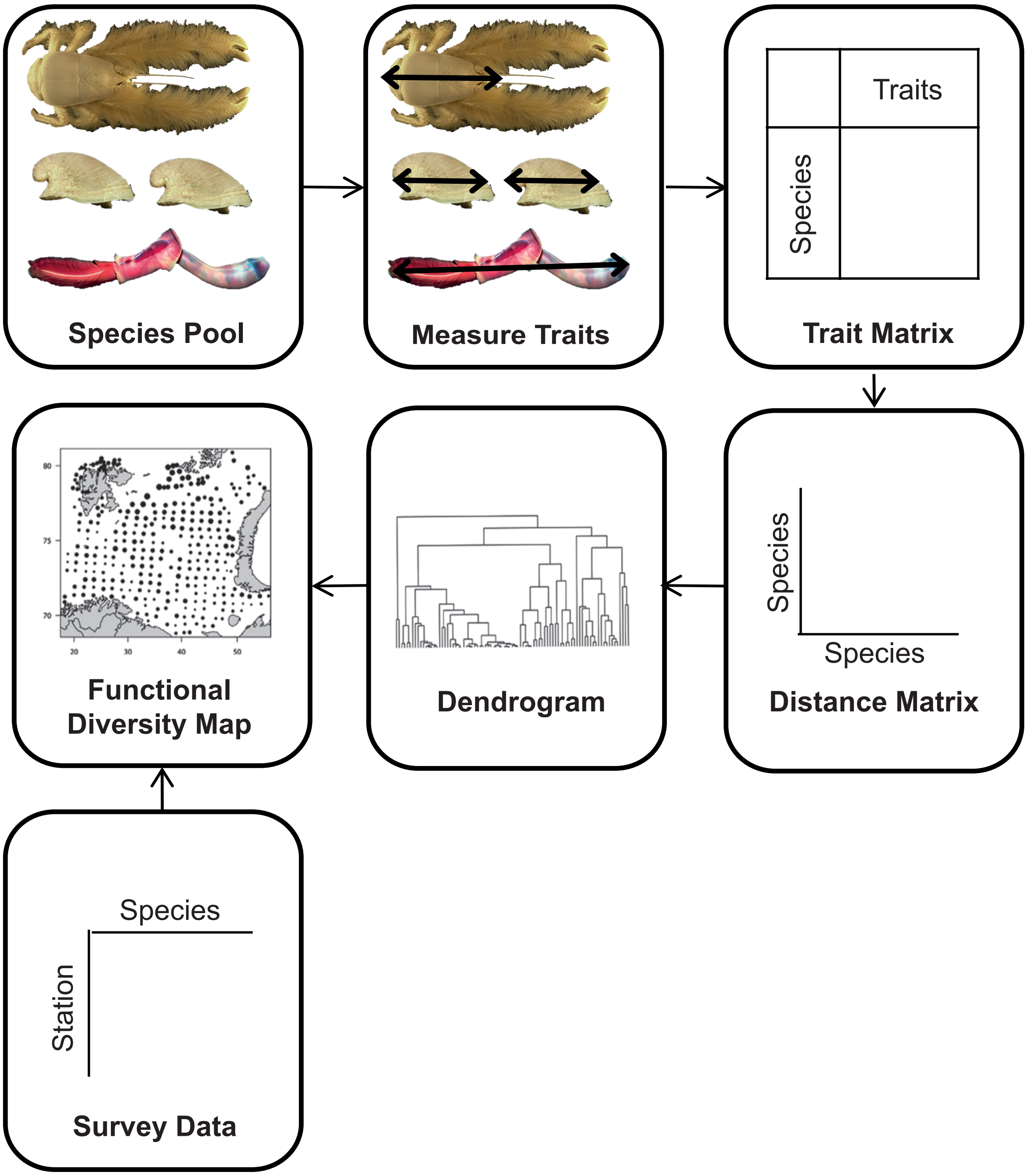

Figure 9: The functional-trait approach to biodiversity research. This schematic depicts the most commonly used functional-trait approach, whereby a species-trait matrix is used to quantify functional diversity for mapping and hypothesis testing. The schematic was created using parts of figures provided in Mouillot et al. (2013b), Lefcheck et al. (2014), and Wiedmann et al. (2014). Faunal images were sourced from: IFREMER (2005) - *Kiwa* crab, the WoRMS database (Boxshall et al., 2016) - *Lepetodrilus fucensis*, and Batson (n.d.) - *Riftia pachyptila*.

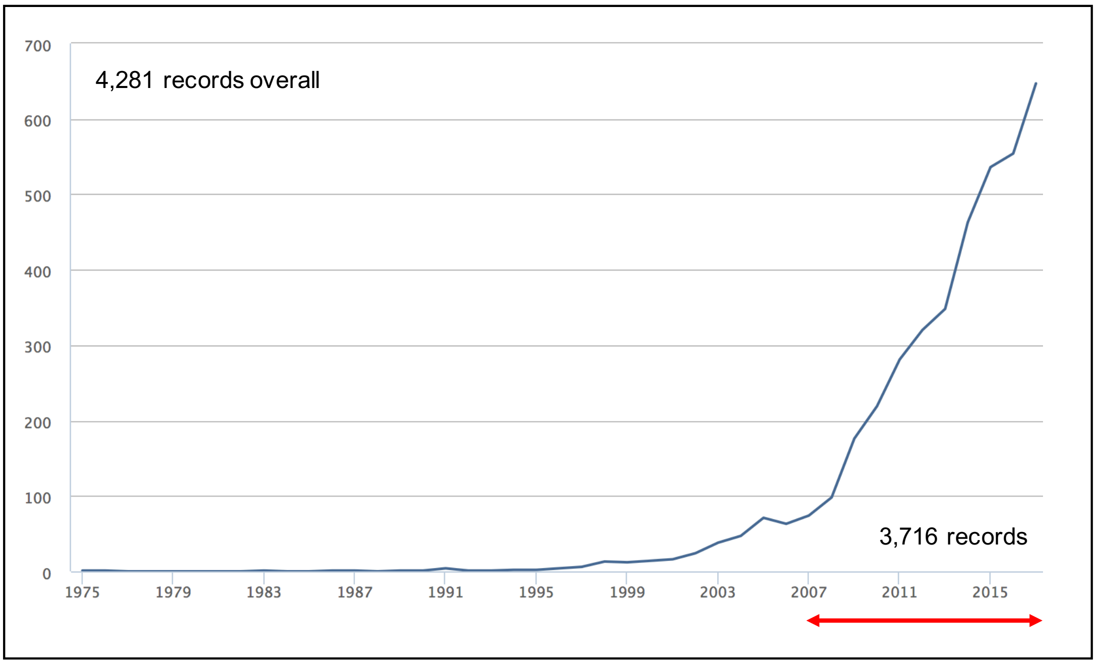

Figure 10: Graph representing the increasing use of a trait-based approach in biodiversity research, based on a Scopus.com search for publications containing 'functional trait' and 'diversity' up to the end of 2017.

There are, however, limitations to functional-diversity studies. For example, the quantification of functional diversity requires a matrix of species and traits (**Figure 9**). Traits may include: body size, feeding mode, morphology, adaptive strategy, or reproductive mode (Paganelli et al., 2012; Pérez-Harguindeguy et al., 2013; Lefcheck et al., 2014). Trait selection is often hampered by a lack of consensus on traits suitable for analysis (Lefcheck et al., 2014) and the very definition of a functional trait. For example, it is debated whether traits must be linked directly to ecosystem function, or whether they can be any physiological trait of an organism (Violle et al., 2007; Mlambo, 2014). Before a push towards a 'functional' definition of traits, though, traits were simply defined as characteristics of a species affecting its performance, or fitness, in an ecosystem (Violle et al., 2007; McGill et al., 2006), and this definition stands today (Cadotte et al., 2011; Schmera et al., 2017).

As many hydrothermal vents remain undiscovered, and others found relatively recently, a large proportion of vent fauna are still being formally described. Thus, using a trait-based approach with macrofauna from vents is limited by data availability. Deep-sea vents cannot be resampled as regularly or as easily as some terrestrial environments; therefore, a trait-based approach in vent ecosystems would be limited by a lack of trait data for some, or even many, organisms. A first step would be to incorporate species traits, rather than individual traits, and traits affecting species performance, rather than those linked directly to a measurable ecosystem function. Nevertheless, the quality of functional-diversity studies is often reduced by the inclusion of too many traits (Lefcheck et al., 2014). In using a large number of traits, one simply recreates a species list, rather than identifying functional groups; comparing the functional and taxonomic dimensions of diversity will therefore be uninformative. Accordingly, the absence of a ready-made database comprising many traits may facilitate targeted, informative studies of vent diversity, and may be a benefit, rather than a hindrance, of limited data availability.

1.4 Measuring functional diversity

Functional diversity represents the variety and spread of functions and/or traits in a given species pool. Measured using traits, functional diversity has been described using a plethora of metrics, graphics, and equations (Pavoine and Bonsall, 2011; De Bello et al., 2013). Its major components, however, are similar to those of traditional biodiversity metrics, incorporating richness and evenness, as well as a trait-specific measure - redundancy (De Bello et al., 2009). The number of indices used to measure different components of functional diversity continue to grow, though most depend on distance-based measures to compare traits within a multidimensional 'trait space'. This enables us to establish where species are similar in their characteristics and in their position in trait space relative to other species in a community. Trait metrics generally recommended for the measurement of functional diversity are summarised in **Table 2**. In addition to these indices, functional redundancy can be used to measure overlap within a species pool, or the number of species with shared combinations of traits (Fonseca and Ganade, 2001; Wellnitz and Poff, 2001; Rosenfeld, 2002). The relationship between functional richness and species richness can be used to identify functional redundancy, which is present when an increase in species richness does not increase functional richness (**Figure 11**; Micheli and Halpern, 2005; Mori et al., 2013). Functional redundancy is interpreted as a means of interchangeability, wherein two species sharing identical trait combinations could potentially replace one another should one be lost (Rosenfeld, 2002; Schmera et al., 2017), though this is controversial and does not account for differences in population density (Wellnitz and Poff, 2001).

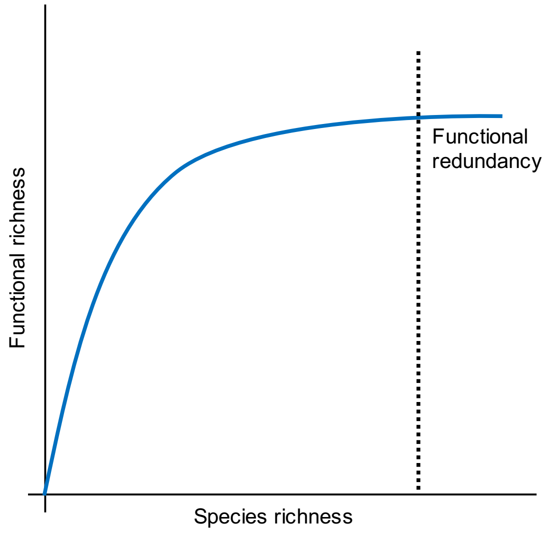

Figure 11: Diagram representing a relationship between species richness and functional richness wherein the point of saturation (adding species does not increase functional richness) is the point at which there is said to be functional redundancy in a species pool.

Functional diversity metrics are highly sensitive to the input data (i.e. traits and subcategories, or modalities) and the scoring method used (e.g., mixing categorical and continuous data, standardising trait scores, or fuzzy coding) (Chevenet et al., 1994; Poos et al., 2009; Lefcheck et al., 2014). It is therefore particularly important to: select traits relevant to the research question (Petchey and Gaston, 2006); weight traits in analyses so differing numbers of modalities do not inflate or deflate the relative importance of a given trait; check for, and manage, correlation among traits (Lefcheck et al., 2014); and select distance, correction, and diversity measures according to the types of trait data being used (e.g., the Gower distance matrix can handle both categorical and continuous trait data, where a Euclidean distance matrix would be inappropriate). If the relationship between the traits of species and the ecological process being studied is relatively well understood, traits can also be weighted according to functional importance (Walker et al., 1999; Petchey and Gaston 2002; Roscher et al., 2004; Petchey and Gaston, 2006). It is unlikely, however, that a first trait-based approach at vents could reliably weight traits in order of functional importance, unless a specific ecological process was being investigated (e.g., one might rank trophic level, mobility, and body size as more important traits than fecundity in a study of resource partitioning, or simply remove fecundity from said analysis).

Table 2[1]: Metrics commonly used to measure functional diversity. The calculation of these metrics is described in detail in the references cited in the 'Reference' column. Note that this table is split into two, to represent the R packages used to compute these indices (UTC and associated metrics are computed using 'multirich', while FRic and other indices are calculated using the 'FD' package).

Metric(s)	**Details**	**Strengths**	**Weaknesses**	**Similar traditional diversity metric**	**Reference**
Unique Trait Combinations (UTC); scaled UTC (sUTC); functional overlap	UTC represent the functional richness of a community in multivariate trait space, by looking at the trait combination of each species in a community and establishing whether it is unique, relative to all other species the species is found with. UTC measures the total number of unique trait combinations in a community, while sUTC is this number, divided by the maximum number of combinations that could have been possible, given the number of species and traits. Functional overlap represents the number of species that overlap in trait space by identifying duplicate trait combinations.	- Easy to calculate and interpret, without need for further multivariate analyses. - Identifies the amount of filled and unfilled trait space (the hypervolume containing all possible trait combinations), which can be interpreted as the amounts of niche space filled and unfulfilled.	- Sensitive to trait selection (e.g., level of binning, or number of trait categories). For example, if many traits were used to calculate this metric, the potential number of UTC would be larger. - Sensitive to missing values. - Trait space can be increased by ecologically impossible trait combinations.	Taxonomic dissimilarity, computed using a distance matrix.	Keyel and Weigand, 2016

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[1] Note that **Table 2** was produced by A. S. A. Chapman to support McClain et al. (2018). A. S. A. Chapman is a co-author on this publication. The table is presented here in an adapted form, with metrics added to support those used and referenced in this thesis.

Functional richness (FRic)	Functional richness is the amount of functional trait space (calculated as the minimum convex hull volume) that a community fills. FRic tends to increase with the number of species in a community (species richness), unless there is functional redundancy (i.e. a species in the community shares the same traits, and the same trait space, as another species).	- Higher values equate to higher values of this component of functional diversity (easy to interpret). - Can be combined with species richness information to assess functional redundancy.	- Cannot incorporate information on the relative abundances of species and is therefore sensitive to species with extreme trait values (e.g., rare, specialist species). - Often correlated with species richness. - Sensitive to trait selection (and scores).	Species richness	Mason et al., 2005; Cornwell et al., 2006;Villéger et al., 2008; Laliberté and Legendre, 2010; Laliberté et al., 2014
Functional evenness (FEve)	Functional evenness captures how the abundances of species are spread in the convex hull they occupy (e.g., where dominant and rare species are found, based on their relative abundances). FEve is 1 when species are equally distributed in the convex hull, based on their traits and abundances; it is 0 when species are clustered in a particular area of the convex hull, given their traits and abundances.	- Higher values equate to higher values of this component of functional diversity (easy to interpret). - Independent of species richness and functional richness.	- Does not look at the distribution in the convex hull with respect to its volume. - Sensitive to trait selection (and scores).	Pielou's evenness	Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010; Laliberté et al., 2014
Functional divergence (FDiv)	Functional divergence is similar to functional evenness, but accounts for dissimilarities in abundance distributions within the convex hull volume. It is calculated relative to the centre of trait space.	- Higher values equate to higher values of this component of functional diversity (easy to interpret). - Independent of species richness and functional richness.	- Does not look at the distribution in the convex hull with respect to its volume. - Sensitive to trait selection (and scores).	Simpson index (Simpson, 1949)	Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010; Laliberté et al., 2014

Functional dispersion (FDis)	This metric measures the mean distance of a species to the centroid of trait space. The centroid is calculated using all species in the community. FDis captures the dispersion of species within available trait space. The centroid and the mean distance are both weighted using species relative abundances.	- Independent of species richness. - Can have more traits than species. - Can incorporate abundance information. - Not strongly influenced by outliers.	- Not constrained between 0 and 1. - Sensitive to trait selection (and scores).	Simpson index (Simpson, 1949)	Laliberté and Legendre, 2010; Laliberté et al., 2014
Rao's quadratic entropy (Rao's Q)	Rao's Q is another measure of functional divergence. It incorporates information on the pairwise differences between species in terms of their traits and relative abundances.	- Independent of species richness. - Captures dissimilarity among species given abundance and/or traits.	- Sensitive to trait selection (and scores) through covariance.	Simpson index (Simpson, 1949)	Rao, 1982; Botta-Dukát, 2005; Laliberté and Legendre, 2010; Laliberté et al., 2014
Functional Group Richness (FGR)	This is the number of functional groups present in a community or species pool. It is typically computed by visually assessing the functional dendrogram that represents the dissimilarity among species based on their traits, though R packages also exist to compute the number of functional groups.	- Easy to compute and interpret. - Useful means of comparing and/or grouping species according to trait similarity for further analyses (e.g., as in trophic analyses, where species are grouped into categories such as 'insectivore' or 'frugivore').	- Sensitive to trait selection and dependent on user-defined cut height for, or number of groups to be selected from, a dendrogram.	This is similar to the assessment of species dissimilarity using cluster analysis.	Hooper et al., 2002; Laliberté and Legendre, 2010; Laliberté et al., 2014

Community Weighted Mean (CWM)	The CWM is calculated by taking the relative (based on abundance or frequency) contribution of a species to a community and multiplying this value by the trait value of the species. This is repeated for each species within the community to generate a CWM for a particular trait.	- Commonly presented in trait-based studies. - Easy to compute and interpret. - Summarises overall trends in trait values, so useful for large-scale studies.	- The modal value might be more appropriate for categorical traits and when abundance data are not available. - Sensitive to outliers.	-	Lavorel et al., 2008; Laliberté and Legendre, 2010; Laliberté et al., 2014
Number of functionally singular species	This is the number of species that have unique trait combinations relative to other species in the pool. If all species are functionally unique, the number of functionally singular species will be the same as the number of species.	- Easy to compute and interpret. - Can be computed at the same time as other metrics calculated using the 'FD' package.	- Similar to UTC, but potentially affected by the selection of parameters in the 'dbFD' function, whereas UTC is independent of the 'FD' package and its required inputs.	-	Laliberté and Legendre, 2010; Laliberté et al., 2014

2. RESEARCH AREAS THAT CAN BE EXPLORED USING A TRAIT-BASED APPROACH TO THE BIODIVERSITY OF VENT ECOSYSTEMS

2.1 Deep-sea hydrothermal vents as model systems for trait-based ecology

Despite the potential limitations of a functional-trait approach, and the debate surrounding the definitions of functional traits and functional diversity, hydrothermal vents are ideal systems for trait-based analyses. For instance, the relationship between species richness and functional richness should be weaker in these naturally unstable and extreme systems, where adaptation and plasticity are essential for survival. As an example, the polychaete *Nereis diversicolor* switches feeding mode depending on the nutritional sources available and thereby contributes one species to a richness-based measure of diversity but fulfills more than one functional role (Hooper et al., 2002). As endemism and evolutionary novelty are high at hydrothermal vents (Van Dover, 2000; Ramirez-Llodra et al., 2010), it is likely that vent communities will host a suite of traits whose plasticity can be better represented by a functional approach than a taxonomic one. Furthermore, as the vent ecosystem is, in many cases, unstable, disturbed by volcanic eruptions, seismic events, and fluctuations in hydrothermal fluid (Tsurumi, 2003), a functional approach will also be appropriate for assessing how communities change through time (de Juan et al., 2007; Mouillot et al., 2013b; Edwards et al., 2014; Flores et al., 2014).

A trait-based approach may also help to explain why well-established, productive communities thrive in unstable vent environments. For example, the 'insurance hypothesis' suggests that it is the variation in the responses of species to variability, determined by their traits, that enables them to buffer environmental change (Yachi and Loreau, 1999; Díaz and Cabido, 2001). In addition, multiple geological, biological, chemical, and physical processes affect vent communities, and the ecological impacts of these processes can be difficult to isolate using traditional, taxonomy-based methods. A trait-based approach facilitates the linking of environmental processes, species, and communities (Kleyer et al., 2012; Keck et al., 2014).

Looking to the future, when vent ecologists will be increasingly applying their knowledge to develop deep-sea mining strategies and reach conservation goals, a functional approach should provide more insight into which communities or areas should be protected to conserve ecosystem function (Stuart-Smith et al., 2015). Additionally, hydrothermal vents might be low in functional redundancy, with each species likely to have a unique functional role or set of functional traits, due to the high levels of endemism and adaptation in their fauna (Loreau, 2004). If this is the case, a trait-based approach might reveal a need to conserve biomass, rather than species, when developing conservation plans and protecting areas (Rosenfeld, 2002; Gosling et al., 2015).

In sum, it is the low richness and high levels of endemism in vent communities that might make hydrothermal vents useful model systems on which to test functional-trait methods. As described in **Section 1.1**, hydrothermal-vent species are typically well adapted to extreme and variable environmental conditions and display a high degree of endemism, often only found at a particular vent, within a biogeographic province, or within a particular area of an ocean (Tunnicliffe, 1992; Rogers et al., 2012). It is also this high level of endemism that makes hydrothermal vents an interesting ecosystem to approach from a trait-based perspective. Different vents and regions might not have common species, but all invertebrates share comparable functional traits, facilitating large-scale studies of vent biodiversity. While a functional-trait approach will likely complement current understanding of the diversity of hydrothermal-vent communities, studying vents in this way should also inform our knowledge of the power of functional-diversity indices themselves. Vents may become a 'testing ground' for the development of functional diversity tools, particularly given the low richness of these systems, which makes running tests less computationally demanding in relative terms.

2.2 Testing widely-applicable ecological principles in remote, unique ecosystems

As 'wilderness' systems (Ramirez-Llodra et al., 2011), presently untouched by human activities, and likely relatively unaffected by historic mass-extinction events (Tunnicliffe, 1992), vents might also prove useful testing grounds for ecological theories developed in human-impacted terrestrial, freshwater, and shallow-marine ecosystems. Their disturbed and ephemeral nature lends itself to studies of community assembly and succession, as many previous vent ecologists have shown (Fustec et al., 1987; Sarrazin et al., 1997; Tunnicliffe et al., 1997; Kelly et al., 2007; Marcus et al., 2009). If large-scale data were available for vents, however, the doors to macroecology would be opened, and, with these, investigations into theories concerning global species trends, such as those reviewed in Gaston (2000).

2.3 Building a case for the protection of deep-sea hydrothermal-vent ecosystems

Furthermore, studying vents in a conservation ecology context would likely broaden understanding for the conservation and management of wilderness areas on land and in the sea. Work like this is becoming increasingly important and urgent for vent ecosystems as a result of growing demand, and technological capacity, for deep-sea mining (Van Dover et al., 2018). Previously deemed unviable, commercial-scale mining of deep-sea resources is expected to commence by 2020, with hydrothermal vents at risk because of the value of the polymetallic sulfides, or seafloor massive sulfide (SMS) deposits, many of them form (**Figure 12**; Glover and Smith, 2003; Ramirez-Llodra et al., 2011; Boschen et al., 2013; Van Dover et al., 2018). The hot "black smokers", for which many vents are best known, emit metal-rich fluids that precipitate to form polymetallic sulfides

(Van Dover et al., 2018). These sulfides contain high levels of precious minerals and metals, including copper and zinc (Ramirez-Llodra et al., 2011; Van Dover et al., 2018). As computers and mobile phones become 'everyday' necessities, the global demand for rare earth elements and minerals grows, and prices rise, making the high concentrations of precious metals on the seafloor commercially viable, despite the difficulties associated with deep-sea extraction (Boschen et al., 2013).

International laws set out in the Convention on Biological Diversity (1992) dictate that biodiversity should be conserved, and environments exploited, in a way that ensures no long-term net loss of biodiversity or irreversible environmental damage. Discussions regarding the protection of hydrothermal vents proceed with this in mind, by designing systematic conservation-planning tools to identify conservation areas according to uniqueness, rarity, connectivity, 'naturalness', and 'representativeness', among other characteristics (Ardron et al., 2011; Van Dover, 2011; Van Dover et al., 2012, 2014). Biogeographic provinces and bioregions have been proposed as the focal spatial units for management, to maintain habitat heterogeneity and biodiversity (Ardron et al., 2011). However, if species richness is the only measure used to define these areas, it is unlikely that the regions will truly reflect and protect the variety of life in these systems. For instance, in a tropical rainforest, two sites could be equal richness, but one could host populations of the endangered Orangutan while the other does not, demonstrating a fundamental limitation of using taxonomic richness alone as a comparative measure.

Unusual, remote, and productive - hydrothermal-vent communities are both interesting and important to study for ecological and conservation-oriented understanding, termed 'living libraries' in Van Dover et al. (2018). In the one hundred most important questions for conservation biology, compiled by Sutherland et al. (2009), researchers asked: which strategies will be most effective for the conservation of marine biodiversity in areas beyond national jurisdiction, where many vents are located; what ecosystems looked like before human impact; and how this knowledge of untouched ecosystems can be used to improve management practice. Vent systems offer us a rare opportunity to study the wilderness before the first human footprints are left. Hydrothermal vents are far from human habitats, yet soon to be affected by humankind. We need to work to understand the diversity of life at vents to protect them and the wider ocean they likely support through productivity, energy supply, and ecological processes yet to be modeled, mapped, and understood. A group of scientists has recently made the case for the prohibition of mining on any active hydrothermal vents, given: the expected severity of environmental impact; the value of hydrothermal vents for ecology, medicine, arts, and the search for the origin of life; and the relatively low economic potential and small predicted yields (Van Dover et al., 2018). As widely accepted in ecological research across ecosystems (Cadotte, 2011), a trait-based approach could help to improve our understanding of vent ecology and ensure the successful management and conservation of these unique ecosystems if deep-sea mining continues as planned.

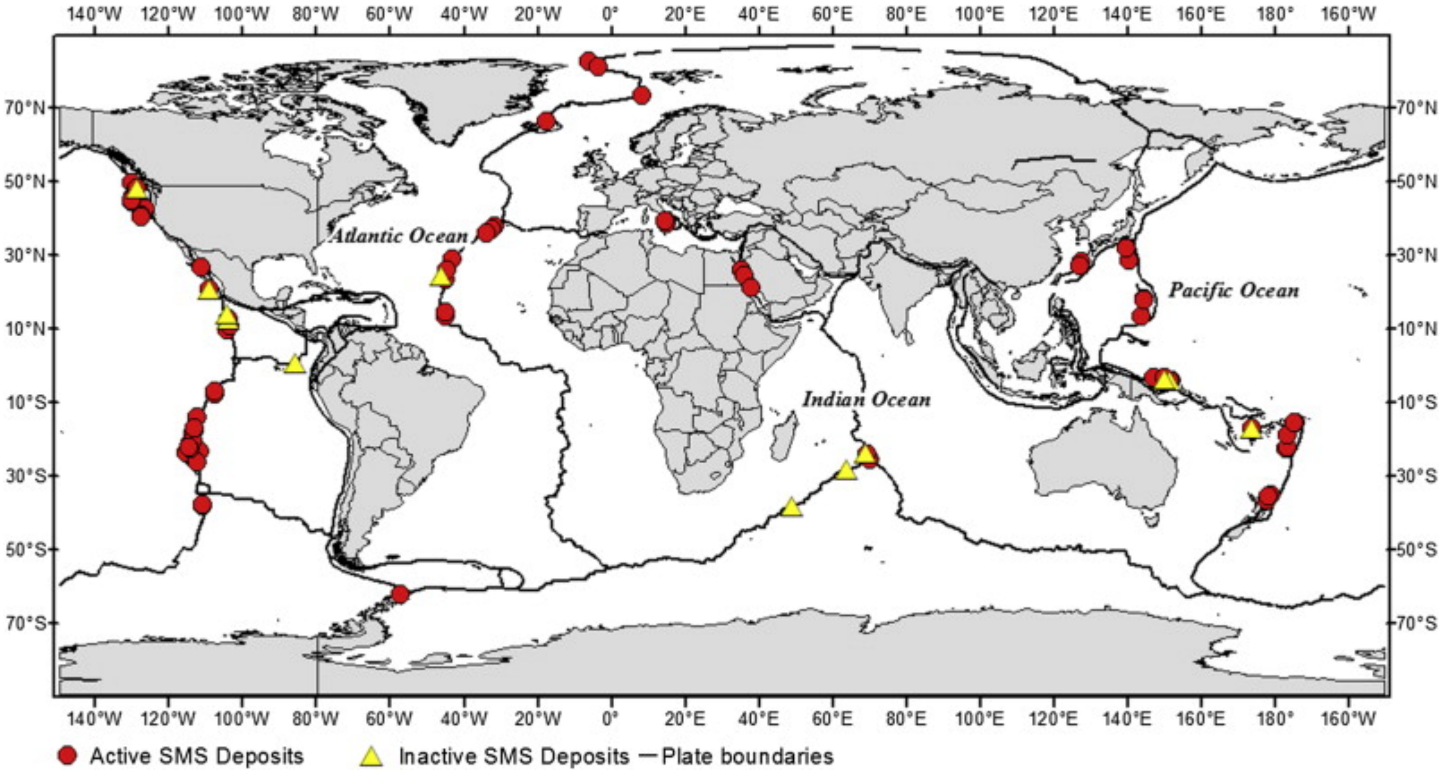

Figure 12: Global distribution of Seafloor Massive Sulfide (SMS) deposits, as discussed in Boschen et al. (2013). This map uses vent-field locations from the InterRidge Vents Database (Beaulieu, 2010), though more deposits have been found (Hannington et al., 2011). Map source: Boschen et al. (2013), reproduced with permission from Elsevier.

3. SUMMARY OF DATA CHAPTERS AND AIMS

3.1 Thesis aims

Following forty years of study, data on the variety of life at vent ecosystems is increasing in availability. We are therefore at a critical juncture in vent ecological research, wherein large-scale analyses comparing vent regions might be possible. Vent biogeographers have compared the taxonomic composition of vent fields and regions over several decades, with a new outcome resulting from each new system explored. Despite the well-established benefits of a trait-based approach to the biodiversity of ecosystems, this approach is yet to have been tested at vents. Furthermore, while data exist in article tables and laboratories of vent ecologists, they are rarely readily accessible and useable (e.g., see comments on the World Register of Marine Species and Ocean Biogeographic Information System in Ramirez-Llodra et al., 2010). Databases also need to be updated (e.g., the ChEss database on deep-sea species from chemosynthesis-based ecosystems, including vents, was last updated in 2010; Baker et al., 2010).

Thus, the aims of the work presented in this thesis are as follows:

- To identify traits for which relevant information is available for the majority of vent fauna (Chapters 2 and 3)
- To score the traits of fauna from one of the best-studied vent regions, using literature and expert knowledge (Chapter 2)
- To test, at these well-studied vents, an ecological theory developed as a result of trait-based investigations in other ecosystems (Chapter 2)
- To build a trait dataset for vent species across the globe, to update publicly available species lists for vents, to facilitate trait-based studies across vent ecosystems, and to ensure expert knowledge is recorded in a centralised format (Chapter 3)
- To identify and map environmental variables of potential influence on vent regions, as previous biogeographic models identify separate, but geographically constrained provinces, suggesting large-scale oceanographic and environmental processes might shape vent macroecology (Chapter 4)
- To conduct the first, trait-based, global-scale study of hydrothermal vents, involving a functional biogeographic analysis, incorporating environmental and taxonomic data, to establish the relative uniqueness of vent regions across the globe (Chapter 5)

3.2 Summary of data chapters

In Chapter Two, I present research published in *Diversity and Distributions* investigating whether rare species over-contribute to the functional diversity of vent ecosystems in the Northeast Pacific Ocean - a pattern identified in several terrestrial and shallow-marine environments. Chapter Three, in review in *Global Ecology and Biogeography*, summarises the production and contents of a trait database for vent species across the globe - sFDvent - produced through an international, collaborative process. In Chapter Four, I compare the environmental characteristics of vent fields across the globe by compiling large-scale environmental variables expected to influence vent ecology. Finally, in Chapter Five, I compare the taxonomic, functional, and environmental uniqueness of well-sampled vent regions through: updating the taxonomic biogeographic model for vents, given new data from the sFDvent database; grouping vent regions according to environmental characteristics; and analysing the functional diversity, functional-group distributions, and functional redundancy of vent regions, using sFDvent trait data. I conclude by emphasizing the importance of vents as untouched ecosystems, soon to be impacted by humans - ecosystems we need to study and, now, protect.

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Chapter Two: Both rare and common species make unique contributions to functional diversity in an ecosystem unaffected by human activities

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I designed this study, contributed trait data, undertook the analyses, and drafted the manuscript with lead supervisor Dr Amanda Bates. Prof. Verena Tunnicliffe provided sample data collected by herself and Dr Jean Marcus and Dr Maia Tsurumi (University of Victoria, Canada), as well as contributing trait scores and manuscript revisions, and verifying the study outcomes based on her expert experience working at the Juan de Fuca Ridge. The following experts provided trait-scoring advice, in addition to Dr Amanda Bates and Prof. Verena Tunnicliffe: S. Beaulieu, J. Copley, S. Hourdez, A. Metaxas, and A. Warén. Dr Tom Bird also provided valuable advice for this work.

Additional supporting information, as published with the article in *Diversity and Distributions*, is given in **Appendix A** of this thesis.

ABSTRACT

Aim Rare species typically contribute more to functional diversity than common species. However, humans have altered the occupancy and abundance patterns of many species - the basis upon which we define 'rarity'. Here, we use a globally unique dataset from hydrothermal vents - an untouched ecosystem - to test whether rare species over-contribute to functional diversity.

Location Juan de Fuca Ridge hydrothermal-vent fields, Northeast Pacific Ocean.

Methods We first conduct a comprehensive review to set up expectations for the relative contributions of rare and common species to functional diversity. We then quantify the rarity and commonness of 37 vent species with relevant trait information to assess the relationship between rarity and functional distinctiveness - a measure of the uniqueness of the traits of a species relative to traits of coexisting species. Next, we randomly assemble communities to test whether rare species over-contribute to functional diversity in artificial assemblages ranging in species richness. Then, we test whether biotic interactions influence functional diversity contributions by comparing the observed contribution of each species to a null expectation. Finally, we identify traits driving functional distinctiveness using a distance-based redundancy analysis.

Results Across functional diversity metrics and species richness levels, we find that both rare and common species can contribute functional uniqueness. Some species always offer unique trait combinations, and these species host bacterial symbionts and provide habitat complexity. Moreover, we find that contributions of species to functional diversity may be influenced by biotic interactions.

Main Conclusions Our findings show that many common species make persistent, unique contributions to functional diversity. Thus, it is key to consider whether the abundance and occupancy of species have been reduced, relative to historical baselines, when interpreting the contributions of rare species to functional diversity. Our work highlights the importance of testing ecological theory in ecosystems unaffected by human activities for the conservation of biodiversity.

Keywords: conservation, diversity, functional distinctiveness, biological trait, human impact, hydrothermal vent, rarity, review, species richness, unique trait combination.

1. INTRODUCTION

Rare species, in having small populations, restricted geographic ranges, and, often, narrow environmental niches, are more vulnerable than common species to disturbance, environmental change, and competitive exclusion (Rabinowitz, 1981; Gaston, 1994). These rare species are often considered unique, endemic, and threatened - a combination that puts them at a higher risk of extinction than their common counterparts (Pimm et al., 1988; Gaston, 1994, 2003; Margules and Pressey, 2000; Hartley and Kunin, 2003). Yet, in possessing the characteristics that define rarity (low occupancy, abundance, and biomass), rare species may also contribute less than common species to ecosystem functioning processes (Grime, 1998; Smith and Knapp, 2003).

Functional traits are characteristics of a species affecting its contribution to the functioning of, and fitness within, an ecosystem (e.g., body size, trophic level). They can support empirical approaches when evaluating the respective roles of rare and common species in communities (Violle et al., 2017). Studies assessing the contributions of rare species to functional diversity encompass numerous methods, scales, and systems, which we comprehensively review in **Table 15**, provided in **Appendix A**. Seven of the eight studies that focus on contributions of rare species to functional diversity (**Table 15**) showed that rare species contributed more to functional diversity than expected given small abundances, occupancies, or ranges. Thus, the majority of evidence suggests that rare species contribute disproportionately to communities by offering functional uniqueness and, therefore, supporting diverse ecosystem functions (Smith and Knapp, 2003; Ellingsen et al., 2007; Bracken and Low, 2012; Mouillot et al., 2013a; Jain et al., 2014; Leitão et al., 2016). Rare species introduce functional redundancy by sharing traits with other species (a phenomenon that becomes more likely as species richness increases) and, consequently, may provide insurance and resilience for an ecosystem under different, future environmental conditions (Walker et al., 1999; Yachi and Loreau, 1999; Mouillot et al., 2013a; Jain et al., 2014).

Most studies reporting over-contribution of rare species to functional diversity focus on ecosystems that humans have fundamentally altered (e.g., through fishing and aquaculture, tourism, and logging), including: coral reefs, rainforests, marine soft sediments, and alpine meadows (Vitousek et al., 1997; Mora et al., 2011; and see **Table 15**). By contrast, deep-sea hydrothermal-vent communities thrive thousands of metres below the sea surface, without light, in warm, mineral-rich fluids that emerge from the seafloor, supporting diverse microbial communities - the primary producers in this system - and fauna highly adapted to these environments (e.g., **Figure 13c**; Ramirez-Llodra et al., 2010). Energy in deep-ocean hydrothermal environments is provided via chemosynthesis, where microorganisms use the reduced compounds in vent fluid and inorganic carbon to form organic matter (e.g., Cavanaugh et al., 2006 and Ramirez-Llodra et al., 2010). Hydrothermal vents therefore provide a rare opportunity to assess the relative contributions of rare and common species to functional diversity in a chemosynthetic environment with which only scientists have interacted, and thus human impacts are minimal, relative to terrestrial and shallow-water systems (Ramirez-Llodra et al., 2011).

Here, we take advantage of a globally unique dataset of hydrothermal vent macrofaunal samples from one biogeographic region to test the hypothesis that rare species over-contribute to functional diversity. We focus on abundance, occupancy, and geographic extent as the main facets of rarity, in concordance with other rarity-oriented studies that use a functional-trait approach, based on Rabinowitz' forms of rarity (Rabinowitz, 1981; Hartley and Kunin, 2003; Jain et al., 2014; Violle et al., 2017). We artificially assemble communities ranging in species richness from four to thirty-seven. For this range in species richness, we test the relative contribution of each species to local functional diversity in both artificially assembled and observed communities. Next, for the species that are functionally redundant with increasing species richness, we test whether species contributions differ from our null expectation as a result of community-assembly processes. Finally, we identify the traits driving functional distinctiveness - a measure of the uniqueness of the trait values of a species, relative to the traits of all other species in a community (Grenié et al., 2017b; Violle et al., 2017). Our work highlights differences in how species contribute to functional diversity in ecosystems that have not yet been reshaped by humans and, henceforth, a need to develop and test ecological theory in unaltered systems.

2. METHODS

2.1 Measuring rarity and commonness using abundance, occupancy, and geographic extent

This study focused on invertebrate species assemblages (‘communities’) living more than 1,000 metres below the sea surface, at hydrothermal vents on basalt rocks along the Juan de Fuca Ridge tectonic plate boundary in the Northeast Pacific Ocean (**Figure 13**). Samples include sites in the Endeavour Marine Protected Area (**Figure 13b**). Sixty-three tubeworm samples (44 tubeworm grabs, 10 suction samples, and nine samples compiled from both) were taken from 47 basalt-hosted sites between 1986 and 2001 (as described in detail in: Tunnicliffe et al., 1997; Tunnicliffe 2000; Tsurumi and Tunnicliffe 2001, 2003; and Marcus et al., 2009). Based on these samples, and for each of 37 species, we quantified the: (i) maximum relative abundance, to capture dominance potential and to discount sampling variability inherent in grab and suction samples (see **Figure 13c**); (ii) occupancy (the number of samples within which a species occurred); and (iii) geographic extent (the number of vent fields where each species occurred). We also computed a combined rarity index for each species (calculated as outlined in Leitão et al. (2016) but without log transformation), to enable cross-ecosystem comparability. The values for all four rarity metrics, for each of the 37 species, are provided in **Table A.1.1** on the USB storage device that accompanies this thesis.

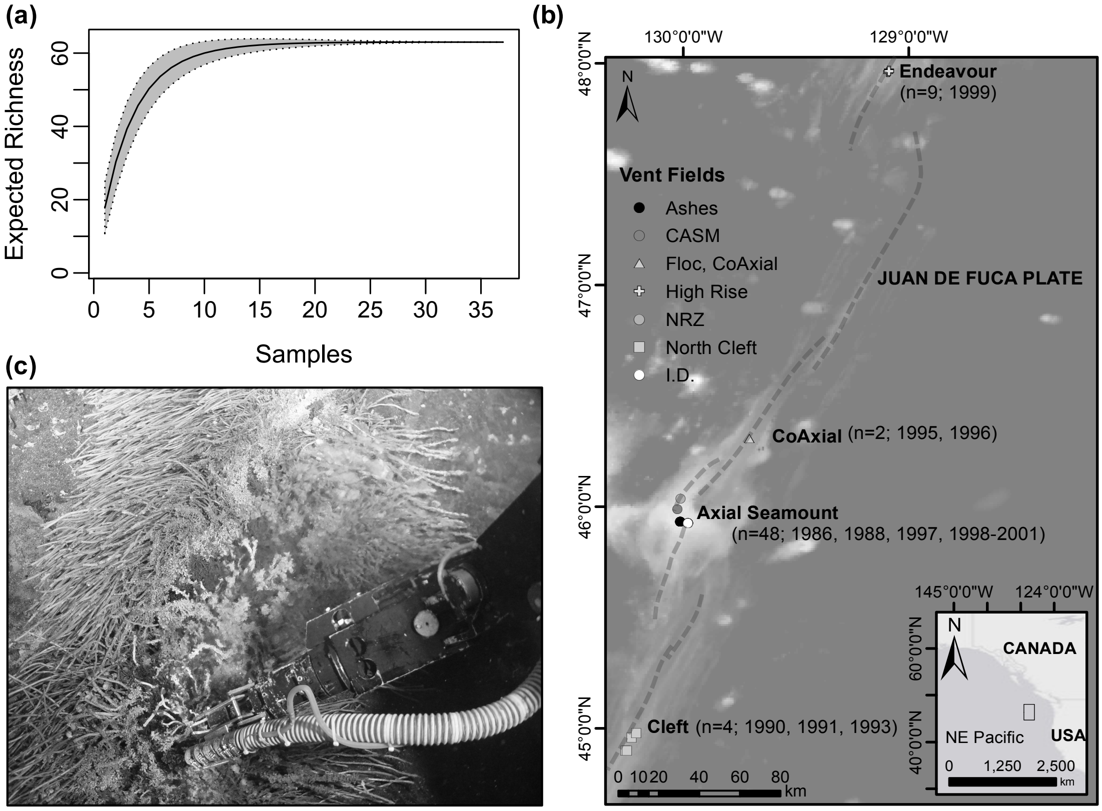


Figure 13: Overview of sampling effort and collection methods used to obtain macrofaunal data: (a) collector's curve (with 95% confidence intervals shown in grey) for the regional species pool compiled by combining all species sampled and using the Coleman et al. (1982) method; (b) location map, placing the hydrothermal vents ('sites') sampled along the Juan de Fuca Ridge (with 'n' the number of vents sampled at a particular vent field (labelled in bold), preceding the years of sampling, and the ridge marked with dashed lines); (c) image showing tubeworm grab sampling with a submersible claw - a method commonly used to sample communities hosted by tubeworms like *Ridgeia piscesae.* The suction sample hose supplements the grab to retrieve animals on the substratum under the bushes, and mobile species escaping the grab. Image about 120 cm across. Bathymetry in (a) was sourced from Esri et al. (2012), vent-field locations from sample records and the InterRidge Vents Database (Beaulieu, 2015) (note that I.D. is International District), and the Juan de Fuca Ridge was drawn using information in Newman et al. (2011), Chadwick et al. (2013), and VanderBeek et al. (2016).

We include all macrofauna (≥ 1 mm in size) with species-level taxonomic identities and, thus, with fully assigned trait information (see species list in **Table A.1.1**, verified using the World Register of Marine Species (Horton et al., 2017)). *Ridgeia piscesae* individuals (worms living inside tubes, aggregating to form bushes attached to the basalt rock substratum) were not included in this dataset, as they form the substratum for the sampled communities (e.g., see **Figure 13c**), in the same way that corals are often excluded from datasets as they provide habitat for reef fauna. The collector's curve in **Figure 13a** illustrates that sampling effort was sufficient to capture most of the

Juan de Fuca Ridge vent species pool.

2.2 Species traits

We assembled a matrix of species traits based on a comprehensive literature search and expert knowledge of these species (see **Table A.1.1**). We selected five species-level traits that should reflect adaptations to rarity or commonness, as well as the functional contribution of a species to an ecosystem: relative adult mobility, maximum (recorded) body size, trophic level indicator, nutritional symbionts (present or absent), and forms a three-dimensional structure (yes or no). The justification and description of our traits are provided in **Table A.1.1**.

2.3 Testing whether rare species over-contribute to functional diversity in vent ecosystems

To test the hypothesis that rare species over-contribute to functional diversity, we compared the functional distinctiveness of each of the 37 species to their rarity (abundance, occupancy, geographic extent, and a combined rarity index). Functional distinctiveness was computed using the 'funrar' and 'cluster' packages in R (Grenié et al., 2017a; Maechler et al., 2017; R Core Team, 2017; Violle et al., 2017). We also assessed whether functional distinctiveness was related to species richness, as functional diversity and taxonomic richness often have a strong linear relationship in other systems, detected using commonly used functional-diversity metrics (e.g., functional richness - FRic, functional dispersion - FDis, and Rao's quadratic entropy (Laliberté et al., 2014); see **Figure 48**). We then created artificial communities, applying a random subsampling approach, to test the hypothesis that rare species over-contribute to functional diversity in vent communities ranging from four species (the minimum observed species richness on the local scale) to 37 species (the maximum, regional-scale species pool). We assembled 1,000 communities per level of species richness (four to thirty-seven), sampling randomly without replacement to create a presence-absence matrix. This matrix was used to compute the proportion of artificially assembled communities within which each species would contribute a novel unique trait combination (UTC - i.e. the combination of traits a species possesses is not found in other species it coexists with; see equation below); this proportion was plotted against species richness using a LOESS line of best fit alongside the proportion calculated using observed (sampled) data (displayed as points). Supporting R (R Core Team, 2017) script is provided in **Appendix A.2** on the USB storage device that accompanies this thesis. For the full set of N species, we calculate the proportion of communities (artificially assembled or sampled) within which a species i ($i = 1, \ldots, N$) makes a unique trait combination contribution. This proportion, $p_{species\ i}$, is the number of UTCs in a community when species i is included (UTC_{total}) minus the number of UTCs when species i is excluded from the community (UTC_{-i}), divided by the total number of communities species i is present in, C:

$$p_{species\ i} = \frac{\Sigma\,(\mathrm{UTC_{total}} - \mathrm{UTC_{-i}})}{\mathrm{C}}$$

We used the Unique Trait Combination (UTC) metric to quantify species contributions to functional diversity to capture the redundancy and uniqueness of combinations of traits from a multifunctional perspective. This approach was selected as Mouillot et al. (2013) show that species with distinct trait combinations are more likely to support vulnerable ecosystem functions than species with commonly observed trait combinations. The UTC metric was computed using the 'mvfd' function of the 'multirich' R package (Keyel and Wiegand, 2016; R Core Team, 2017). This metric does not share limitations with the commonly used convex-hull based 'FRic' functional richness metric (of particular relevance, given the low richness of vent communities) (Cornwell et al., 2006; Villéger et al., 2008; Schmera et al., 2009; Laliberté et al., 2014); the UTC metric can accommodate the limited number of continuous measurements available for relatively inaccessible and expensive to sample deep-sea hydrothermal-vent species by incorporating categorical trait values (Keyel and Wiegand, 2016).

Species were placed in one of three groups ('always unique', 'redundant with richness', or 'rapidly redundant') according to the shape of the relationship between species richness and the proportion of communities within which their trait combination was unique in 1,000 randomly assembled artificial communities. We tested whether community-assembly processes and biotic interactions could be shaping the functional uniqueness of the species that we identified as becoming increasingly redundant with richness (for species observed in at least 10 samples - an arbitrary threshold selected to minimize sampling effort bias). We compared the proportion of sampled communities in which each of the species in the 'redundant with richness' group observed in at least 10 samples contributed a UTC to a null expectation established using our randomly assembled community data. We used a binomial test to determine whether the proportion contributed by sampled species differed significantly from the proportion species would be expected to contribute based on the outcomes of the randomly assembled samples. Richness levels were binned for the tests as, despite using one of the world's most complete hydrothermal-vent-sample datasets, we had insufficient samples to conduct the test for each richness level. Bins are highlighted as dotted boxes in **Figure 16** (with further details and binomial test results presented in **Table 16**). We selected the minimum probability value for the null expectation in each bin to be conservative.

Finally, to assess the trait similarity among the species in the 'always unique' group, we used a distance-based redundancy analysis (db-RDA; Legendre and Anderson, 1999). We adapted the db-RDA with an input of a species by trait matrix as our explanatory matrix and a species by functional distinctiveness matrix as our response. Given the nature of our functional-trait data (i.e. some semi-quantitative traits), we used the Gower distance metric for the db-RDA (Gower and

Legendre, 1986; Laliberté and Legendre, 2010). The db-RDA is appropriate because our data did not meet assumptions of Euclidean distances and normality (Legendre and Anderson, 1999; Legendre and Legendre, 1998).

3. RESULTS

In 63 hydrothermal-vent community samples, 27 species were relatively rare (if we consider a species with a rarity index value of < 0.5 to be rare, as the index is scaled from 0 to 1; **Figure 49**) and 10 relatively common (> 0.5 rarity index value; **Figure 49**). In these 63 samples, some of the most rare and common species contributed to functional distinctiveness. All three measures of rarity, as well as a combined rarity index, hold the same flat relationship with distinctiveness (**Figure 14**); therefore, this outcome does not support a hypothesis of increasing contribution with rarity (**Figure 14a**; **Table 17** contains the outputs of the linear models presented in **Figure 14b-e**). Nonetheless, as species richness increased in sampled communities, functional distinctiveness decreased (**Figure 15**), supporting the expected pattern of increasing functional redundancy with richness; when number of species increases, the probability of a new species contributing to functional distinctiveness decreases because there is a higher chance that the traits of a new species already exist in another species in the community. These results were not simply an outcome of trait selection or scoring methodology, as tested in **Appendix A.3**.

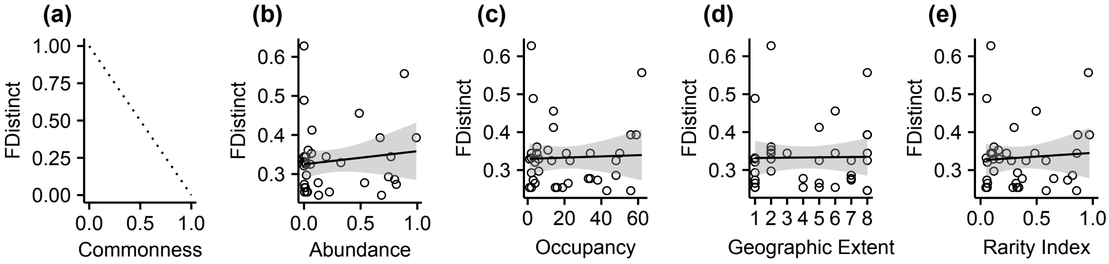


Figure 14: The relationship between rarity and functional distinctiveness in Juan de Fuca Ridge vent communities. (a) The expected linear relationship between rarity and distinctiveness, whereby more common species offer less functional distinctiveness than rare species. (b) The observed relationship between maximum relative abundance of each species and functional distinctiveness relative to all other species in the community. (c) The relationship between occupancy (number of samples within which the species occurs) and functional distinctiveness for each species. (d) The relationship between geographic extent (number of vent fields within which the species was observed) and functional distinctiveness of each species. (e) The relationship between the Rarity Index (per Leitão et al. (2016) without log transformation) and functional distinctiveness. Note that the relationships shown in (b), (c), (d), and (e) are relatively flat, contrary to the expectation presented in (a), suggesting that rare and common species contribute functional distinctiveness. Model outputs to support panels (b), (c), (d) and (e) are provided in **Table 17**.

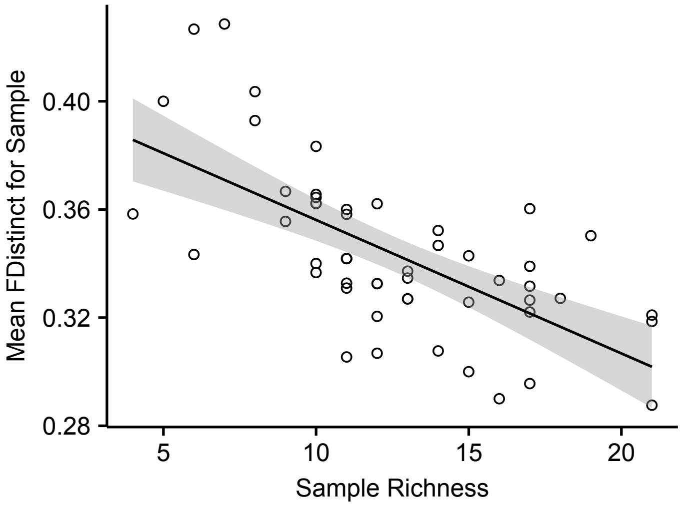
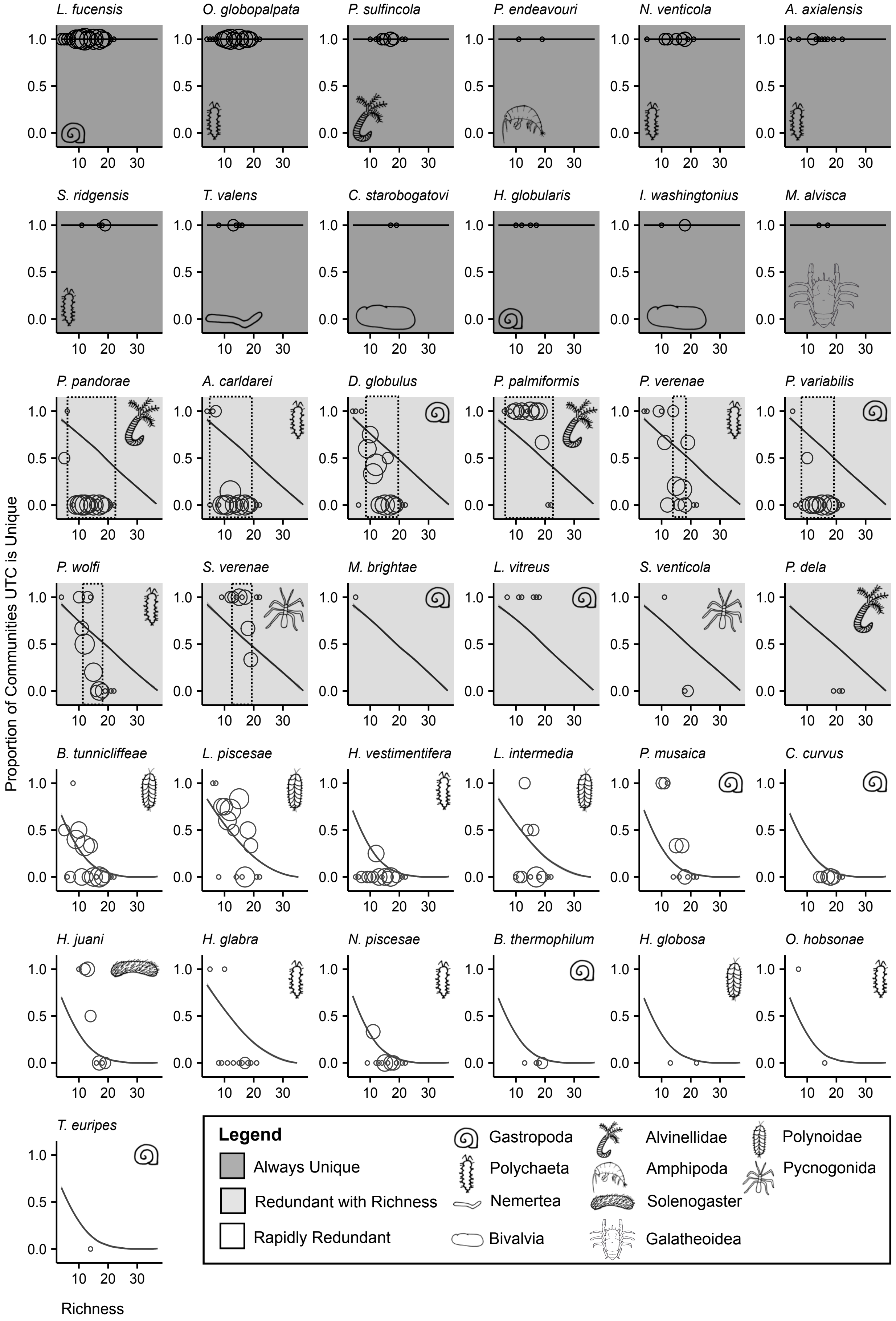


Figure 15: The relationship between taxonomic richness per sample and mean (across all species present in a sample) functional distinctiveness per sample, as computed using the 'distinctiveness' function of the 'funrar' functional rarity package (Grenié et al., 2017). The linear relationship was fitted using a linear model (formula: mean FDistinct ~ richness) and is a significant linear relationship, with slope -0.005 and p-value <0.05 (adjusted R-squared value: 0.4157; F-statistic: 37.29 on 1 and 50 degrees of freedom).

Figure 16 (overleaf)**:** The proportion of communities within which each species makes a unique trait combination (UTC) contribution. Each panel in this figure shows the proportion of communities to which a species (named at the top of each panel) makes a unique contribution (y-axis), relative to species richness (x-axis). Solid lines in each panel depict the relationships identified using artificial, randomly assembled communities of four to thirty-seven species in richness (mean values based on communities that were randomly assembled 1,000 times per level of richness - see Methods). Circles in each panel are observations from sample data, with circle size relative to the number of samples with the given result. Dotted boxes, shown on some central panels, encompass the richness bins used in the binomial tests to see whether the observed UTC contribution made by a species significantly differed from the null, random expectation (shown in the artificial community line). Each panel is shaded according to the groups listed in the legend that are assigned based on the shape of the relationship between species richness and UTC contributions revealed in the randomly assembled communities. Cartoon inserts illustrate the taxonomic group of each species, as outlined in the Legend. Species names have been shortened, but are given in full in **Table A.1.1**. The species presented on this figure combine to represent the regional species pool - the 37 taxa identified to species level for basalt samples from the Juan de Fuca Ridge.


L. fucensis
O. globopalpata
P. sulfincola
P. endeavouri
N. venticola
A. axialensis
S. ridgensis
T. valens
C. starobogatovi
H. globularis
I. washingtonius
M. alvisca
P. pandorae
A. carldarei
D. globulus
P. palmiformis
P. verenae
P. variabilis
P. wolfi
S. verenae
M. brightae
L. vitreus
S. venticola
P. dela
B. tunnicliffeae
L. piscesae
H. vestimentifera
L. intermedia
P. musaica
C. curvus
H. juani
H. glabra
N. piscesae
B. thermophilum
H. globosa
O. hobsonae
T. euripes
Proportion of Communities UTC is Unique
1.0
0.5
0.0
10
20
30
Richness
Legend
Always Unique
Redundant with Richness
Rapidly Redundant
Gastropoda
Polychaeta
Nemertea
Bivalvia
Alvinellidae
Amphipoda
Solenogaster
Galatheoidea
Polynoidae
Pycnogonida

Given the strong relationship between species richness and functional distinctiveness, we further tested whether rare and common species both contribute to functional distinctiveness across a range of species richness levels, spanning beyond the maximum sample richness (21) to that of the regional pool (37). We accounted for the contributions made by species given known co-occurrences, rather than contributions to the overall regional pool - which can include species that, in reality, never co-occur. Considering the independent contributions of each species (**Figure 16**), we found that 12 species, including eight rare and two very common species, contributed unique trait combinations at all levels of richness ('always unique'). Twelve species contributed uniqueness at low levels of richness but became increasingly redundant with richness ('redundant with richness'), while 13 became rapidly redundant at lower richness ('rapidly redundant'). For the most part, the groupings highlighted in **Figure 16** comprised a mix of taxonomic classes, but all the scaleworm polychaetes (in the phylum Annelida) fell only within the 'rapidly redundant' group. Each group is described in more detail in **Table 18**.

The proportion of communities in which eight, well-sampled species in the 'redundant with richness' group made unique contributions to the assemblages in which they were sampled was compared to the random expectation. The worms, *Paralvinella pandorae* and *Amphisamytha carldarei*, and snails, *Depressigyra globulus* and *Provanna variabilis,* contributed a unique trait combination (UTC) in fewer communities than would be expected by chance (**Figure 16** and **Table 16**). By contrast, the worm, *Paralvinella palmiformis*, and sea spider, *Sericosura verenae*, contributed a UTC in more communities than expected (**Figure 16** and **Table 16**). The contributions of two worms, *Protomystides verenae* and *Parougia wolfi,* did not differ significantly from random (see **Table 16**).

Two key traits emerged as driving functional distinctiveness in the 'always unique' group: hosting nutritional symbionts and forming a three-dimensional structure (**Figure 17**, and see **Table 19**). These two traits also shaped the functional distinctiveness of species in the 'redundant with richness' and 'rapidly redundant' groups, influencing the relative distances between all species (**Table 18** and **Table 19**). The direction of influence differs in these traits for species in the 'rapidly redundant' group, though, as these species do not form 3D structures or have nutritional symbionts (**Table 18**).

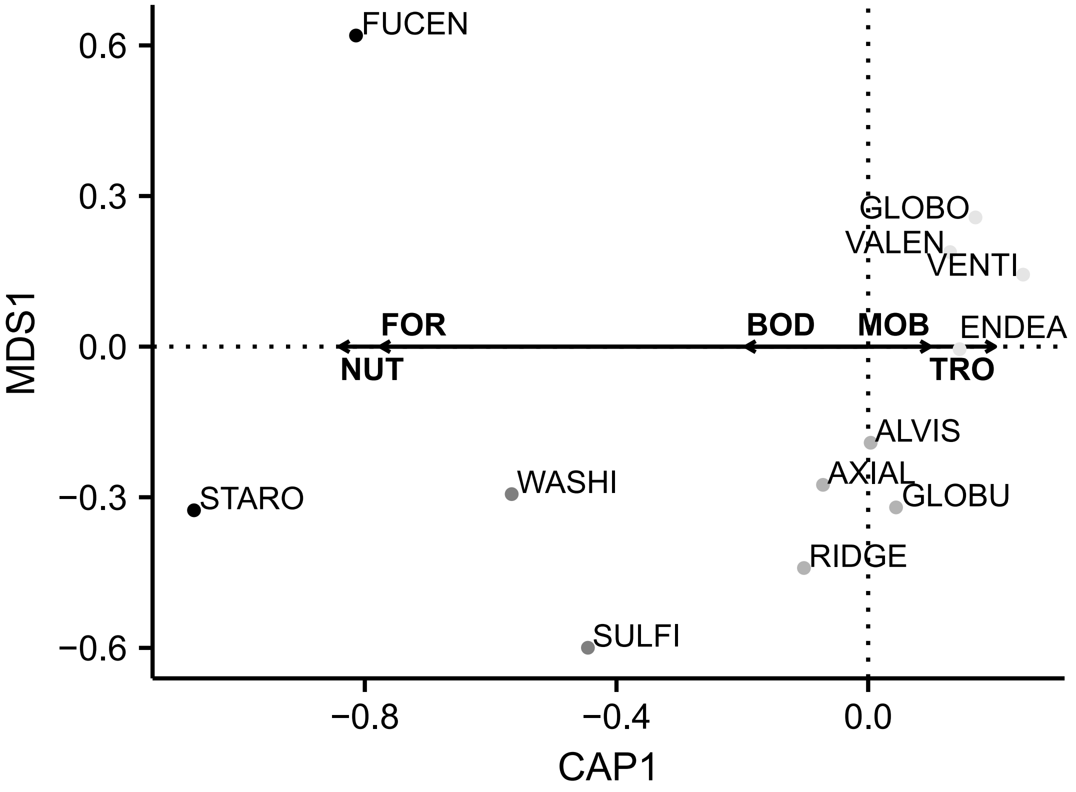


Figure 17: Distance-based redundancy analysis (db-RDA) of Gower distances showing the functional distinctiveness of each of the species relative to one another and the potential traits driving distinctiveness differences (labelled in bold next to arrows, with trait names shortened as follows: NUT - Nutritional Symbionts, FOR - Forms a 3D Structure, BOD - Maximum Body Size (mm), MOB - Relative Adult Mobility, and TRO - Trophic Level Indicator). 'Nutritional Symbionts' and 'Forms a 3D Structure' were significant traits in the db-RDA model, based on an ANOVA by terms with 200 permutations (a permutation test used to assess the significance of constraints for each trait separately (Oksanen et al., 2017); see **Table 19**). Functional distinctiveness is colour-coded, with the two most functionally distinct species (*Lepetodrilus fucensis* and *Calyptogena starobogatovi*) shown in black and the point colours becoming lighter with decreasing functional distinctiveness. The species labelled on this plot belong to the 'always unique' group (see **Figure 16**), though the functional distinctiveness of all 37 species was driven by the same traits. Species names shortened in this figure are: ALVIS - *Munidopsis alvisca*, AXIAL - *Amphiduropsis axialensis*, ENDEA - *Pardalisca endeavouri*, FUCEN - *Lepetodrilus fucensis*, GLOBO - *Ophryotrocha globopalpata*, GLOBU - *Hyalogyrina globularis*, RIDGE - *Sphaerosyllis ridgensis*, STARO - *Calyptogena starobogatovi*, SULFI - *Paralvinella sulfincola*, VALEN - *Thermanemertes valens*, VENTI - *Sericosura venticola*, and WASHI - *Idas washingtonius*.

4. DISCUSSION

Here, we show that rare species do not contribute significantly more to the functional distinctiveness of vent communities than more common species. This finding is supported at all levels of species richness (from the minimum sampled richness - four species - to the 37-species regional pool). Our results contradict those of most research into rarity-functional diversity relationships to date, which, instead, demonstrate that rare species over-contribute to functional diversity (a review of the research on this topic is presented in **Table 15**). For example, in coral reefs, tropical rainforests, and alpine meadows, the most distinct trait combinations are supported by rare species (Mouillot et al., 2013a). In addition, in a removal experiment conducted on a rocky shore community, rare species had bottom-up influences on the diversity and abundance of consumers (Bracken and Low, 2012).

Despite diverging from the expectation set in other trait-based studies, our findings are supported by ecological theory. If rare species are specialists, adapted to specific environmental conditions (hence their small geographic range, for example), we expect rarer species to have traits that reflect this specialisation. These specialist traits would be dissimilar to the traits of species occupying other habitats and niches, enabling specialist rare species to persist with low occupancy and abundance (Rabinowitz 1981; Gaston 1994). At the same time, common species are expected to thrive in a wider range of habitats and environmental conditions, and have more generalist traits enabling them to do so; yet, common species must also possess unique traits (or combinations of traits) to successfully outcompete other species for space and resources, attain high abundances, maintain broad geographic ranges, and occupy many habitats (Tilman, 1999; Gaston, 2010, 2011).

While our results are supported by ecological theory, there remain several explanations as to why our results differ from previous studies. These include: (1) trait selection (e.g., see Lefcheck et al., 2014) and scoring methodology (as the number of modalities per trait can influence trait space and, thus, indices computed using a multidimensional trait-space volume; Lefcheck et al., 2014); (2) sampling method (i.e., at vents, remotely operated equipment enables the retrieval of intact assemblages comprising diverse taxa, rather than the taxon-specific 'community' data collected for some studies described in **Table 15**); (3) species richness of the study system, which can shape functional diversity by influencing the potential for functional redundancy; and (4) the natural and anthropogenic processes affecting ecosystem stability and function.

First, the results of any trait-based study depend, in part, on the traits selected and on limited biological information on species (Lefcheck et al., 2014; Májeková et al., 2016). Given this issue, we selected traits that can be clearly linked to species rarity and commonness, community stability, and community-assembly processes. We did not include ecologically irrelevant information (for example, selecting a trait like 'body colour', even though vent ecosystems have no light and host many species without eyes). As such, while our species-specific findings depend on the traits selected (a problem also encountered in other fields of ecology - for example, when choosing to use genetic or morphologically based species information), the results provide a means to understand these traits and the processes with which they are associated. In addition, we explored whether our results were robust to inclusion of different ecologically relevant traits and different scoring schemes (see **Appendix A.3**, **Figures 50-54**, and **Table A.3.1** for the associated trait matrix) and found agreement in our main result with a different trait matrix. Our main result is thus not simply an outcome of the traits we selected for our analyses.

Second, it is possible that sampling methodology may also influence our understanding of common versus rare species contributions to functional diversity. To sample the communities included herein, remotely operated equipment (for example, a remotely operated vehicle controlled from a ship thousands of metres above a vent) can sample intact assemblages comprising diverse taxa, as opposed to collecting taxon-specific "community" data (e.g., as for dragonflies or trees). The sampling approach at vents therefore not only facilitates trait-based studies of whole communities, but also enables vent ecologists to incorporate traits that are intractable for specific taxa when investigated in isolation (e.g., forming a 3D structure would not be a trait included in a study of coral reef fish, but is likely a fundamental trait for reef communities that would be captured if coral species were also included). As our findings contrast with those presented in research focusing on single taxonomic groups (e.g., see **Table 15**), we propose that future trait-based studies might benefit from a broader taxonomic perspective.

Third, vents are species poor, relative to ecosystems like tropical coral reefs and rainforests. Yet, in other species-poor systems, studies have reported over-contributions in rare species only. For example, Bracken and Low (2012) found that rare species have disproportionately large impacts on the diversity and abundance of higher trophic levels in the rocky intertidal with a small species pool - around 30 species. Furthermore, while higher species richness could affect a trait-based study by increasing the probability of functional redundancy, it is also the number of generalists, specialists, and habitats that affect capacity for redundancy and uniqueness, through availability of functional space (Rosenfeld, 2002). Accordingly, the presence of functionally redundant species in our study system (e.g., in the 'rapidly redundant' group) highlights the availability of functional space, or plentiful niche space, at Juan de Fuca Ridge vents - potentially unexpected, given their low species richness. As such, it might not be appropriate to argue that our results diverge from others due to the low richness of vent communities. The more species in a community, the more likely functional redundancy is to occur, so the 'rapidly redundant' group seen in vents suggests that the vent communities, while species poor, represent a similar variety of life as present in higher richness communities. In addition, 12 species (including rare and common species) continue to contribute unique trait combinations (UTCs) when co-occurring in the regional pool of 37 species, suggesting that rare and common species cannot only be contributing to the functional diversity of Juan de Fuca Ridge communities because they are relatively species poor. Still, as trait-based rarity research has predominantly focused on speciose systems to date (**Table 15**), this richness argument requires further testing in other species-poor ecosystems - a priority area for future research.

Finally, hydrothermal-vent communities are considered fundamentally unique, given extreme variability, spatial isolation, chemolithoautotrophic primary production (in an otherwise food-poor deep sea), and complex habitat structure (Ramirez-Llodra et al., 2010). Hydrothermal vents are often portrayed as unusual, extreme environments with marked variability on small spatiotemporal scales (Chelvadonné et al., 1992; McMullin et al., 2000; Bates et al., 2010). Catastrophic eruptions and earthquakes can disturb vents in faster spreading, more geologically active, regions like the Juan de Fuca Ridge (Marcus et al., 2009). However, Earth has many extreme and disturbed environments (e.g., storms and tides impact the rocky intertidal communities studied by Bracken and Low (2012), and fires reshape vegetation such as that in the Sandhills region of North Carolina in Ames et al. (2017)). In addition, vents share fundamental ecosystem processes with many of the planet's systems, albeit with the processes taking place on smaller spatial and temporal scales. For example, epiphytes on forest trees add structure, and alter access to light by other plants in tropical rainforests in a manner similar to the gastropods living on tubeworms that form 3D structures at vents, and affect access to chemosynthetic energy sources (Tsurumi, 2003; Bates et al., 2005; Kelly and Metaxas, 2008).

After considering alternative explanations, we propose that our results may, instead, differ from the expectation set in shallow-marine and terrestrial ecosystems because vents are unique in being a relatively untouched ecosystem on Earth. Species abundance and occupancy patterns at vents have not yet been markedly altered by human activities (Ramirez-Llodra et al., 2011). For example, Juan de Fuca Ridge predator species *Buccinum thermophilum*, a snail, and *Nereis piscesae*, a worm, are redundant (in terms of the traits we selected) with other species in nearly every community in which they occur. It is likely that relatively large predatory species like these would be unique if incorporated in trait-based studies of ecosystems within which humans have removed many large, mobile predators (e.g., by hunting). Conversely, in Juan de Fuca vent communities, we find many relatively large predators that are mobile and carnivorous (Bergquist et al., 2007; Kelly et al., 2007), making these traits - and thus these snail and worm species - functionally redundant in these systems.

At vents and in other remote ecosystems, rarity and commonness are the result of various abiotic and biotic processes shaping abundance, occupancy, and geographic range extent. In contrast, in ecosystems such as coral reefs and tropical rainforests, human activities have caused species losses and gains, and have fundamentally altered species abundances, occupancies, and geographic range dimensions (e.g., see Inger et al., 2015). Thus, when we study 'rare' species in human-altered systems, we might be including species that were once common but appear low in abundance, extent, or occupancy at the time of study as a result of human action (Gaston, 2008; Gaston and Fuller, 2008); this would affect our perceived contributions of 'rare' species to functional diversity. For example, *Dipturus batis* (common skate) is a demersal marine species that has been reduced in number by human activities (Gaston and Fuller, 2008), and would be considered 'rare' if studied today, as opposed to several decades prior.

It could therefore be argued that ecological research more widely would benefit from studying undisturbed systems like hydrothermal vents, as results such as those presented here have conservation and management implications. Rare species are often the focus of conservation strategies because they may be more prone to extinction (e.g., a species low in abundance could be lost altogether with the loss of several individuals) (Kruckeberg and Rabinowitz, 1985; Gaston, 1994; Margules and Pressey, 2000). However, we have shown that common species also influence functional diversity in vent systems; thus, common species losses may also have important implications for ecosystem functioning and stability (e.g., see Lyons et al., 1997 for discussions of relationships between functional diversity and ecosystem functioning). For instance, if a common species facilitates a rare species, reducing the number of individuals of this common species will likely have a knock-on effect on the rare species (Gaston, 2011; Lindenmayer et al., 2011). For hydrothermal-vent communities specifically, as deep-sea mining is likely to affect these presently undisturbed assemblages, conservation approaches must move rapidly to assess effects of species loss (Van Dover et al., 2017). Given our findings at the Juan de Fuca Ridge, we propose that conservation planning incorporating functional assessments that include the roles of common species may be particularly effective at vents, as well as in other ecosystems, where rare species are more often the focus at present.

Furthermore, our work advances understanding of the ecology of hydrothermal-vent communities in identifying features of these communities that clarify assemblage structures and key species roles (summarised in **Table 20**). We identify two traits underpinning contributions to relative functional distinctiveness: 'possessing nutritional symbionts' and 'forming a three-dimensional (3D) structure'. Possessing nutritional, bacterial symbionts enables a host species to access chemical energy and accumulate biomass in the same way that corals rely on zooxanthellae to reach high biomass in a low-productivity tropical ocean. Common species hosting nutritional symbionts will have direct access to primary productivity (Stewart et al., 2005; Cavanaugh et al., 2006) and, as space can be limited at vents, this often translates to increased abundance and biomass. At the same time, rare species might also benefit from hosting nutritional symbionts, to thrive with limited resources or compete with common species, especially if the symbiont-host association requires conditions that differ from competitive dominants.

In addition to, or instead of, having nutritional symbionts, for some vent species that have limited access to tolerable conditions in high temperature or fluid flux gradients, the ability to form 3D structures may enable them to modulate flow and/or access specific habitats (Tsurumi and Tunnicliffe, 2003; Bates et al., 2005; Kelly and Metaxas, 2008; Bates et al., 2010). Common *Lepetodrilus fucensis* limpets access and alter fluid flow patterns by stacking vertically (see Bates et al., 2005), like epiphytes on forest trees. Such species that form 3D structures likely also play a key role as ecosystem engineers, increasing habitat complexity and facilitating colonisation by other species. In other ecosystems, common species are typically the engineers (Gaston, 2011). Also common are the limpets and tube-forming polychaetes that form 3D structures at Juan de Fuca Ridge vents, enabling other species to colonise the augmented surface area. Their structures can modify local fluid-flow patterns and provide surfaces for microbial colonisation, thereby increasing food resources for grazers. Additionally, the functionally distinct rare species that form 3D structures potentially act as 'cornerstone species' in small and limited niches, playing an important role in structuring the local space (as defined and observed in rocky intertidal communities in Bracken and Low (2012)). For example, the most distinct rare species (bivalves *Calyptogena starobogatovi* and *Idas washingtonius*) usually inhabit other chemosynthetic environments; but, in our tubeworm bush samples, their shells provide stable habitats for settlers of other species, even when the bivalves themselves are no longer alive.

Coexistence theory helps to explain the unique trait combination (UTC) contributions of these vent species. Kraft et al. (2008) tested coexistence theories (e.g., neutral and niche-based models) in Amazonian forest trees using functional traits. They compared measures of community trait structure to a null expectation of random assembly, with habitat filtering deemed to be taking place if the range of observed trait values was smaller than that of randomly assembled communities. In our study, the bristle worm *Paralvinella pandorae* offered a redundant trait combination more times than expected based on random assembly; the opposite was true for its congener, *Paralvinella palmiformis.* Indeed, these two alvinellid worms are competitors, with *Paralvinella pandorae* the inferior competitor because of its narrower trophic and space requirements (Tunnicliffe et al., 1997; Levesque et al., 2003; Marcus et al., 2009). Meanwhile, the worm, *Amphisamytha carldarei,* and snails, *Depressigyra globulus* and *Provanna variabilis,* make unique contributions to significantly fewer communities than we would expect by chance. The contributions of these species might, therefore, be affected by habitat filtering (in addition to, or instead of, competitive interactions). In contrast, the sea spider, *Sericosura verenae*, makes a unique contribution in more communities than in the null expectation, so its contributions might be affected by niche differentiation.

We used a novel approach to test whether the proportion of communities each species contributed a UTC to was significantly different from a random expectation. Trait-based studies of rarity and functional diversity have previously used a regional pool based approach, thereby incorporating species that, in reality, never co-occur. Our method may, in cases with representative sampling, provide a tool to identify species that are limited in functional distinctiveness by other co-occurring species. Thus, our approach could be used to test for community-assembly mechanisms - a common goal in trait-based ecology (Ackerly and Cornwell, 2007; de Bello, 2012; de Bello et al., 2012) - alongside analyses of other influential processes, such as larval dispersal, colonisation, and suitability of the abiotic environment (MacArthur and Levins, 1967; Kraft et al., 2015). Our approach could also prove a useful ecological tool for investigating more general relationships between rarity, species richness, functional distinctiveness, and co-occurrence patterns in communities.

In conclusion, our understanding of many ecological processes, biodiversity patterns, and resilience are based on systems that are significantly altered by human activities. Using sampled and artificial (randomly assembled) hydrothermal-vent communities, we show that rare and common species both offer functional distinctiveness, with contributions of species shaped by traits important for chemosynthesis, ecosystem engineering, and physico-chemical tolerance. Furthermore, functional uniqueness can be constrained by biotic interactions, such as competition, habitat filtering, and niche differentiation. Our findings offer new perspectives on rarity, commonness, distinctiveness, and redundancy; thus, we suggest that hydrothermal-vent habitats and other relatively untouched environments offer unique windows into ecology, conservation, and biodiversity theory. Ultimately, here we highlight a need to test ecological hypotheses in Earth's remaining untouched systems, to facilitate our ecological understanding of the systems that we, as humans, have already altered.

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<u>Chapter Three:</u> sFDvent: a global trait database for deep-sea hydrothermal-vent fauna

Chapter Three is submitted for publication in *Global Ecology and Biogeography*: Chapman, A. S. A., et al. (in review). sFDvent: a global trait database for deep-sea hydrothermal-vent fauna.

This database and chapter (as in review with *Global Ecology and Biogeography*) was proposed to the Synthesis Centre (sDiv) of the German Centre for Integrative Biodiversity Research (iDiv) by my lead supervisor, Dr Amanda Bates, and I, in response to a call for working group proposals in 2016. This proposal is provided on the USB storage device that accompanies this thesis. I led two working group meetings with Dr Amanda Bates to design and test the database as described in this chapter and **Appendix B**. I organised and led email, Google Drive, and newsletter communications with the international team that contributed data to sFDvent, maintaining a log of communications with each contributor, to ensure the project could be delivered within the timeframe of my PhD. I designed and presented a poster at the 6th International Symposium on Chemosynthesis-Based Ecosystems to request further contributions. I also managed volunteers, who contributed to the database using available literary and online sources, with Dr Amanda Bates and I. I also produced the video tutorial provided on the USB storage device that accompanies this thesis. I organised contributions from international collaborators, before: compiling, cleaning, and processing the data; conducting the analyses; and writing the first draft of the manuscript in review with *Global Ecology and Biogeography*. Dr Amanda Bates supervised and provided feedback on all stages. All authors on the manuscript in review with *Global Ecology and Biogeography* (listed below) contributed data to the database and checked and edited and/or approved the recommended dataset and manuscript.

Supporting Information for this chapter is presented in **Appendix B** and on the USB storage device that accompanies this thesis.

AUTHORS

Abbie S. A. Chapman[1*], Stace E. Beaulieu[2], Ana Colaço[3,4], Andrey V. Gebruk[5], Ana Hilario[6], Terue C. Kihara[7], Eva Ramirez-Llodra[8], Jozée Sarrazin[9], Verena Tunnicliffe[10], Diva J. Amon[11], Maria C. Baker[1], Rachel E. Boschen-Rose[10,12], Chong Chen[13], Isabelle J. Cooper[1], Jonathan T. Copley[1], Laure Corbari[14], Erik E. Cordes[15], Daphne Cuvelier[4], Sébastien Duperron[16], Cherisse Du Preez[17,18], Sabine Gollner[19], Tammy Horton[20], Stéphane Hourdez[21], Elena M. Krylova[5], Katrin Linse[22], P.A. LokaBharathi[23], Leigh Marsh[1], Marjolaine Matabos[9], Susan Wier Mills[2], Lauren S. Mullineaux[2], Hans Tore Rapp[24], William D. K. Reid[25], Elena Rybakova (Goroslavskaya)[5], Tresa Remya A. Thomas[23], Samuel James Southgate[26], Sabine Stöhr[27], Phillip J. Turner[28], Hiromi Kayama Watanabe[13], Moriaki Yasuhara[29], Amanda E. Bates[1,30].

Order of authorship is as follows: i) first author (ASAC); ii) alphabetical for core sFDvent working group members involved in database design; iii) alphabetical for all other contributors; and iv) senior author (AEB).

AFFILIATIONS

[1]University of Southampton, Ocean and Earth Science, University of Southampton Waterfront Campus, National Oceanography Centre, European Way, Southampton, SO14 3ZH, United Kingdom

[2]Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, MA 02543, USA

[3]IMAR Instituto do Mar, Departamento de Oceanografia e Pescas, University of the Azores, Horta, Portugal

[4]MARE - Marine Environmental Sciences Centre, Rua Prof. Dr. Frederico Machado 4, 9901-862 Horta, Portugal

[5]Shirshov Institute of Oceanology, Russian Academy of Sciences, Nakhimovsky Pr., 36, Moscow, 117997, Russia

[6]CESAM & Biology Department, University of Aveiro, Campus Universitario de Santiago, 3810-193 Aveiro, Portugal

[7]Senckenberg am Meer, German Center for Marine Biodiversity Research (DZMB), Südstrand 44, 26382 Wilhelmshaven, Germany

[8]Norwegian Institute for Water Research, Gaustadalléen 21, 0349 Oslo, Norway

[9]Ifremer, Centre de Bretagne, REM/EEP, Laboratoire Environnement Profond, 29280, Plouzané, France

[10]University of Victoria, Department of Biology and School of Earth & Ocean Sciences, University of Victoria, BC, Canada

[11]Natural History Museum, London, Life Sciences Department, Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom

[12]Seascape Consultants Ltd., Jermyns House, Jermyns Lane, Ampfield, Romsey, Hampshire, SO51 0QA, United Kingdom

[13]Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka-shi, Kanagawa 237-0061, Japan

[14]Muséum national d'Histoire naturelle, Institut Systématique Evolution Biodiversité (ISYEB), CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP 26, 75005 Paris, France

[15]Temple University, 1900 N 12th St, Philadelphia PA 19122, USA

[16]Muséum national d'Histoire naturelle, Mécanismes de Communication et Adaptation des Micro-organismes, UMR7245 MNHN CNRS, 12 rue Buffon, 75005 Paris, France

[17]Department of Biology, Pennsylvania State University, State College, PA, USA

[18]Fisheries and Oceans Canada, Institute of Ocean Sciences, 9860 West Saanich Rd, Sidney, British Columbia, V8L 5T5, Canada

[19]NIOZ Royal Netherlands Institute for Sea Research, Department of Ocean Systems, and Utrecht University, PO Box 59, 1790 AB Den Burg (Texel), The Netherlands

[20]National Oceanography Centre, Southampton, National Oceanography Centre, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, United Kingdom

[21]Station Biologique de Roscoff, UMR 7144, CNRS - Sorbonne Université, Place G. Teissier, 29680 Roscoff, France

[22]British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, United Kingdom

[23]Academy of Scientific and Innovative Research (AcSIR), Biological Oceanography Division, CSIR-National Institute of Oceanography, Dona Paula, Goa, 403 004, India

[24]University of Bergen, Department of Biology and KG Jebsen Centre for Deep-Sea Research, PO Box 7800, N-5020 Bergen, Norway

[25]Newcastle University, Marine Sciences - School of Natural and Environmental Sciences, Ridley Building, Newcastle University, Newcastle upon Tyne, NE1 7RU, United Kingdom

[26]Independent Researcher, Southampton, United Kingdom

[27]Swedish Museum of Natural History, Department of Zoology, Stockholm, Sweden

[28]Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA

[29]The University of Hong Kong, School of Biological Sciences and Swire Institute of Marine Science, The University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong SAR, China

[30]Memorial University of Newfoundland, St. John’s, Canada

ABSTRACT

Motivation

Traits are increasingly being used to quantify global biodiversity patterns, with trait databases growing in size and number, across diverse taxa. Despite growing interest in a trait-based approach to the biodiversity of the deep sea, where the impacts of human activities (including seabed mining) accelerate, there is no single repository for species traits for deep-sea chemosynthesis-based ecosystems, including hydrothermal vents. Using an international, collaborative approach, we have compiled the first global-scale trait database for deep-sea hydrothermal-vent fauna - sFDvent (**s**Div-funded trait database for the **F**unctional **D**iversity of **vent**s). We formed a funded working group to select traits appropriate to: i) capture the performance of vent species and their influence on ecosystem processes, and ii) compare trait-based diversity in different ecosystems. Forty contributors, representing expertise across most known hydrothermal-vent systems and taxa, scored species traits using online collaborative tools and shared workspaces. Here, we typify the sFDvent database, describe our approach, and evaluate its scope. Finally, we compare the sFDvent database to similar databases from shallow-marine and terrestrial ecosystems to highlight how the sFDvent database can inform cross-ecosystem comparisons. We also make the sFDvent database publicly available online by assigning a persistent, unique Digital Object Identifier (doi).

Main types of variable contained

646 vent species names, associated location information (33 regions), and scores for 13 traits (in categories: community structure, generalist/specialist, geographic distribution, habitat use, life history, mobility, species associations, symbiont, and trophic structure). Contributor IDs, certainty scores, and references are also provided.

Spatial location and grain

Global coverage (grain size: ocean basin), spanning eight ocean basins, including vents on 12 mid-ocean ridges and 6 back-arc spreading centres.

Time period and grain

sFDvent includes information on deep-sea vent species, and associated taxonomic updates, since they were first discovered in 1977. Time is not recorded. The database will be updated every five years.

Major taxa and level of measurement

Deep-sea hydrothermal-vent fauna with species-level identification present or in progress.

Software format

.csv and MS Excel (.xlsx)

Keywords: Biodiversity, collaboration, conservation, cross-ecosystem, database, deep sea, global-scale, hydrothermal vent, functional trait, sFDvent.

1. BACKGROUND

Traits provide a "common currency" that can be used across biogeographic regions to analyse global-scale biodiversity patterns and to evaluate links between species and ecosystem processes (Stuart-Smith et al., 2013; Violle et al., 2014). Taxonomic and phylogenetic information underpins traditional diversity metrics, such as species richness and phylogenetic diversity, whereas traits enable us to compare fish, mammal, bird, and other biodiversity, using a language common across phyla. Given increasing application of trait-based approaches in biodiversity research (Petchey and Gaston, 2006), trait databases are growing in number. For example, 25 databases have been published for terrestrial, freshwater, and marine environments since 2000; of these, around 25 per cent were published in 2017 (see **Appendix B**).

Some of the first and, now, largest trait databases focus on plants, where strong links exist between leaf traits (e.g., area, angle), plant growth, and primary production via photosynthesis (Kühn et al., 2004; Kattge et al., 2011). Similar relationships between organisms, traits and energy sources were relatively recently discovered in marine animals, when the first deep-sea hydrothermal vents were found forty years ago (Corliss et al., 1979; photosynthesis was first discovered 200 years before this (Ingen-Housz, 1779)). Instead of exploiting photosynthetic pathways, vent animals are strongly dependent on energy from reduced compounds in hydrothermal fluid through chemosynthetic microorganisms (Jannasch, 1985). Deep-sea hydrothermal vents therefore offer a compelling system for applying trait-based approaches (e.g., see Chapman et al., 2018 - Chapter 2). Moreover, the distribution of hydrothermal-vent communities has been shaped through geological and evolutionary time by the movement of tectonic plate boundaries (Tunnicliffe, 1988; Ramirez-Llodra et al., 2007). Vent fauna therefore group into distinct biogeographic provinces (Bachraty et al., 2009; Moalic et al., 2012; Rogers et al., 2012), which offer a pertinent framework upon which to compare taxon-based biodiversity patterns to those derived from biological trait data.

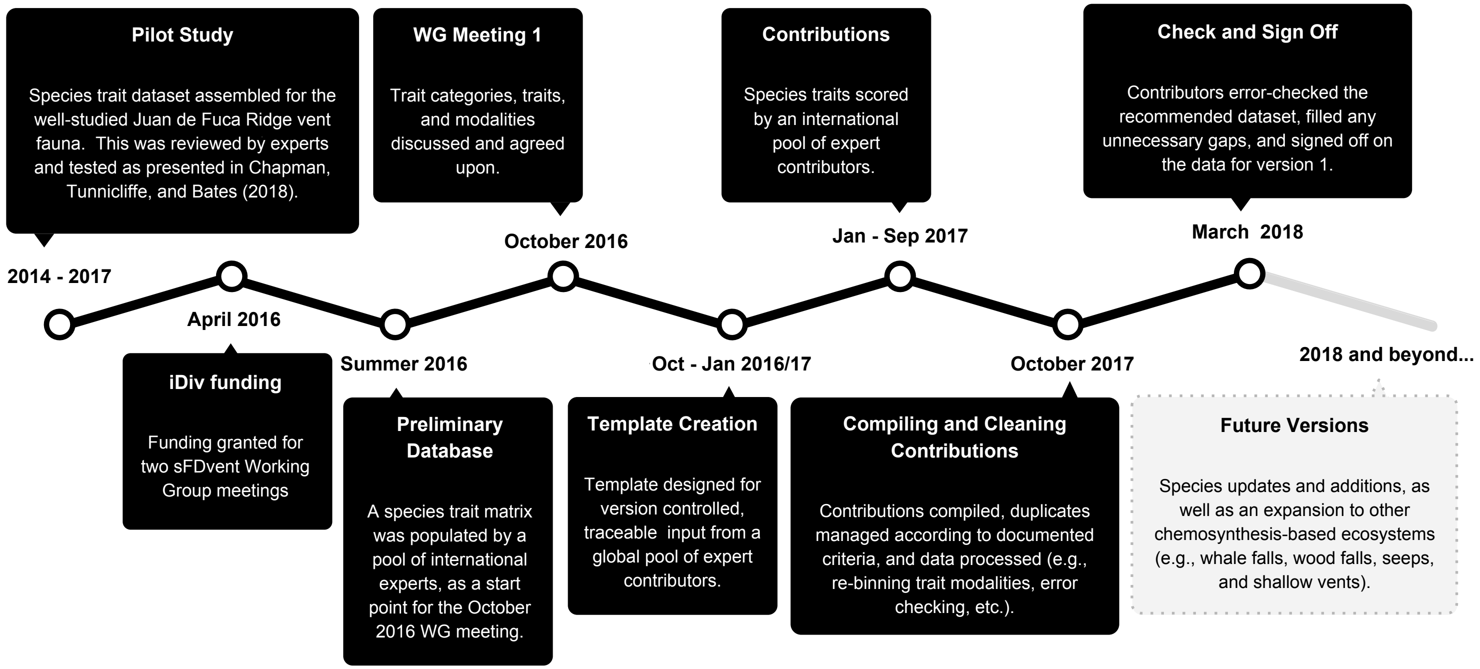
Trait-oriented analyses of global-scale biodiversity patterns can also inform conservation and management plans (Mouillot et al., 2013; Stuart-Smith et al., 2013, 2015). For vents, this is increasingly important, as commercial-scale mining - the first large-scale, direct human impact on these remote ecosystems - will begin before 2020 (Van Dover et al., 2017, 2018). Despite the potential for a trait-based approach to progress ecological understanding and to inform deep-sea mining policies and strategies for vent conservation, it was not possible to pursue this approach on large scales before now, due to a lack of suitable trait data for vent species.

Here, we describe, and make publicly available, a global-scale trait database for deep-sea hydrothermal-vent species - sFDvent (**s**Div-funded trait database for the **F**unctional **D**iversity of **vent**s). We: i) typify the database; ii) describe the international, collaborative compilation process, and highlight the importance of a working group and web-based document sharing tools in our workflow; and iii) provide summary statistics and usage guidelines for the recommended first version of the database. Through sFDvent, we aim: to promote the use of a trait-based approach in conjunction with taxonomic and phylogenetic methods when analysing deep-sea biodiversity patterns; to encourage international collaboration and knowledge sharing in the deep-sea chemosynthesis-based-ecosystem research community; and to facilitate macroecological analyses including vent fauna.

2. METHODS

2.1 An international, collaborative approach to trait data collection

A working-group meeting at the German Centre for Integrative Biodiversity Research (iDiv) facilitated the design of the sFDvent database, which was then populated by an international group of expert collaborators (detailed in **Figure 18** and **Appendix B**). We selected traits using a three-step process: i) creating a 'wishlist' of traits that could inform understanding of the performance of a species in its ecosystem, as well as its influence on ecosystem function (**Figure 19**); ii) reducing this trait list to those that could be scored for the majority of vent species across the globe; and iii) checking the traits selected in step ii) against similar traits in established trait databases (e.g., Stuart-Smith et al., 2013; Madin et al., 2016; Faulwetter et al., 2017), to ensure cross-ecosystem compatibility in terminology and definitions.



Pilot Study

Species trait dataset assembled for the well-studied Juan de Fuca Ridge vent fauna. This was reviewed by experts and tested as presented in Chapman, Tunnicliffe, and Bates (2018).

iDiv funding

Funding granted for two sFDvent Working Group meetings

Preliminary Database

A species trait matrix was populated by a pool of international experts, as a start point for the October 2016 WG meeting.

WG Meeting 1

Trait categories, traits, and modalities discussed and agreed upon.

Template Creation

Template designed for version controlled, traceable input from a global pool of expert contributors.

Contributions

Species traits scored by an international pool of expert contributors.

Compiling and Cleaning Contributions

Contributions compiled, duplicates managed according to documented criteria, and data processed (e.g., re-binning trait modalities, error checking, etc.).

Check and Sign Off

Contributors error-checked the recommended dataset, filled any unnecessary gaps, and signed off on the data for version 1.

Future Versions

Species updates and additions, as well as an expansion to other chemosynthesis-based ecosystems (e.g., whale falls, wood falls, seeps, and shallow vents).

Figure 18: Overview of the workflow undertaken to build the sFDvent database. The sFDvent working group (WG) was funded by the German Centre for Integrative Biodiversity Research (iDiv) under the Synthesis Centre for Biodiversity Studies (sDiv) (https://www.idiv.de/sdiv.html). The database - 'sFDvent' - is therefore named with an 's' to highlight that it is a product of sDiv. 'FDvent' is an abbreviation of '**f**unctional **d**iversity of **vent**s', which the sFDvent database can be used to study. This name may be updated for future versions, when other chemosynthesis-based ecosystems are added.

The working-group meeting was also a platform for data collection design. We used data compendia such as OBIS (OBIS, 2017), WoRMS (Horton et al., 2017), ChEssBase (Baker et al., 2010), and Desbruyères et al. (2006) to populate species trait scores as a starting point for further contributions from the wider deep-sea research community. Data collection was carried out using the Google Sheets platform, given its in-built capacity for version control and collaboration on shared documents stored online. Each contributor initially received a personal data-collection sheet, so entries could be tracked and credited appropriately. These sheets were designed to be as user-friendly as possible while also expediting processing. For example, fixed, drop-down scoring options were provided: i) for ease of entry for contributors, and ii) to ensure inconsistencies in spelling, grammar, and other symbols did not affect compilation or processing for database end-users. A unique contributor ID (email) column was provided, to ensure each contribution could be tracked and credited after compilation and processing. Example data sheets were tested before distribution to collaborators.

The sFDvent project aimed to engage as many members of the deep-sea research community as possible. Thus, several calls for contributors were made following the working-group meeting, including direct emails, mailing lists (INDEEP, 2018), the Deep-Sea Life newsletter (Baker et al., 2017), and a poster presentation at an international conference (Chapman et al., 2017). Forty contributors from 29 institutions in 13 countries contributed expert knowledge to the database.

2.2 Data compilation, processing, quality control, and analysis

Quality assurance measures were implemented to minimise errors in the database, including: an online video tutorial (**Video B.3.1, Appendix B.3**) demonstrating how to input data; a glossary (**Table B.3.1, Appendix B.3**), to ensure all contributors had a good understanding of each of the traits and scoring options (modalities); a certainty-score column, per trait, ranging from 0 (used when unknown, to show a cell was empty due to lack of knowledge) to 3 (high certainty); and a reference column per trait (permitting 'expert opinion' in place of a literary source where appropriate). Traits scored using available literature were peer-reviewed by experts as part of the database review process.

sFDvent contributions were compiled and processed according to strict, documented criteria, which are described in detail in **Appendix B.3** and files referenced therein. A summary of the traits, modalities (or scoring options), and associated rationale for raw and recommended data files is provided in **Table 3**. Finally, summary statistics were computed and a coverage map created (**Figure 20**) using the recommended dataset (**Table B.3.2**) to facilitate gap analysis and comparison with other well-known trait databases. sFDvent will be updated in future according to the processes outlined in **Appendix B.4** and **Figure 23**.

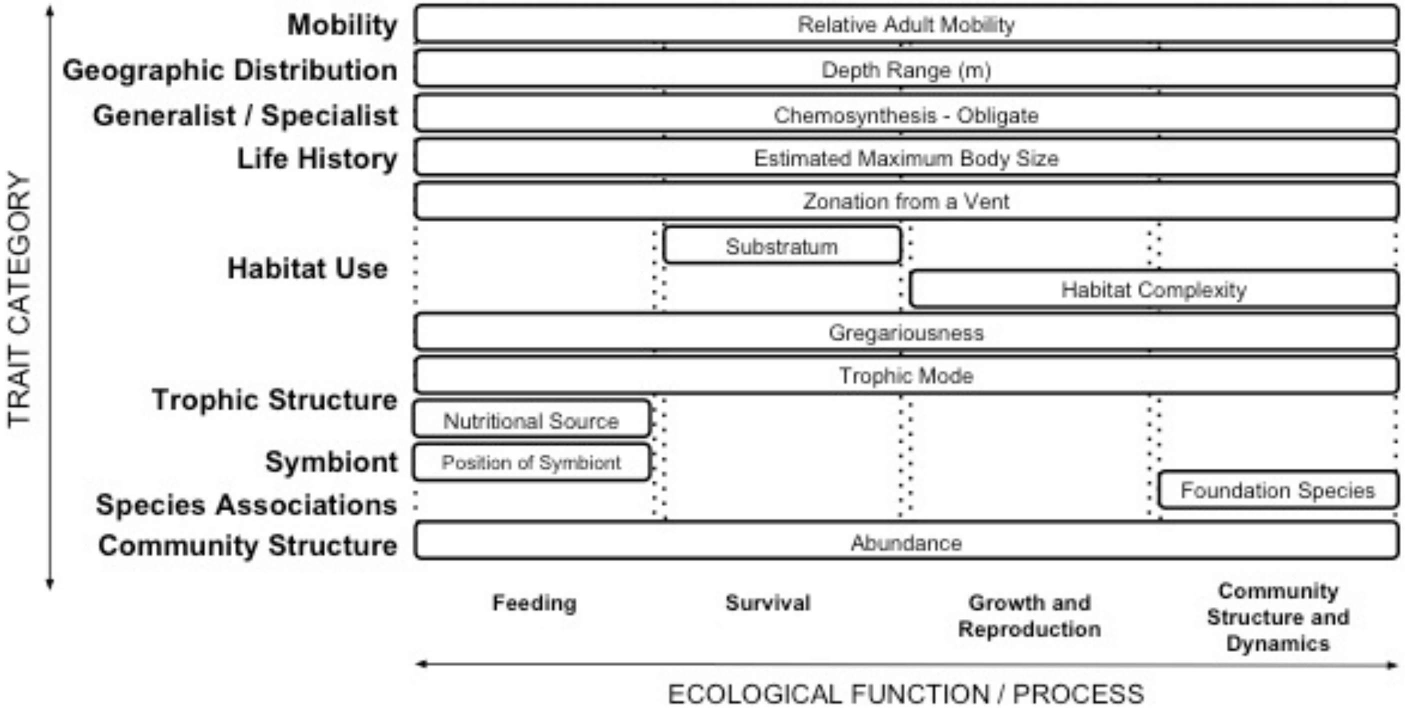


Figure 19: Deep-sea hydrothermal-vent species traits included in the sFDvent database, adapted from the Litchman et al. (2013) framework (see also Brun et al., 2017). Here, ecological functions and processes potentially influenced by a trait are shown on the x-axis, and trait categories are given on the y-axis (see **Table B.3.1** for a glossary of trait definitions).

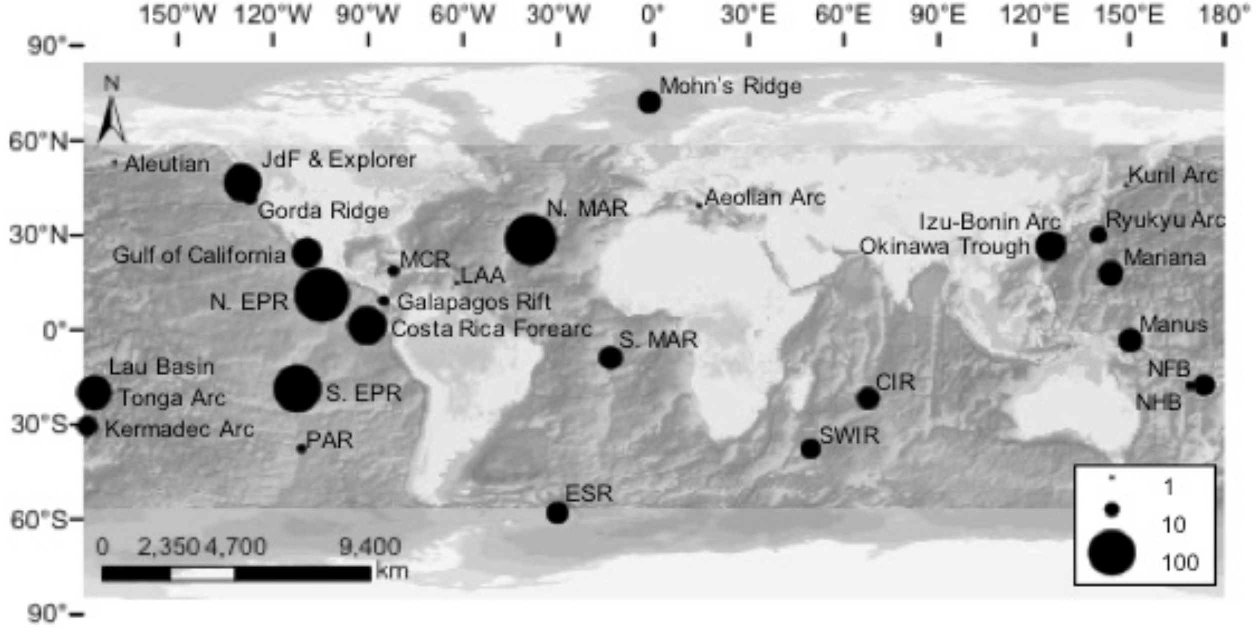


Figure 20: Data coverage map, showing the locations associated with taxa with trait information in the sFDvent database. Regions have been labelled according to the InterRidge Vents Database (Beaulieu, 2015). Labels shortened for display purposes are: Aleutian - Aleutian Arc; CIR - Central Indian Ridge; Costa Rica - Costa Rica Forearc; ESR - East Scotia Ridge; Galápagos - Galápagos Rift and Galápagos Spreading Centre; GoC - Gulf of California; JdF Ridge - Juan de Fuca Ridge; LAA - Lesser Antilles Arc; MCR - Mid Cayman Rise; N. EPR - North East Pacific Rise; N. Fiji Basin - North Fiji Basin; NH Arc - New Hebrides Arc; N. MAR - North Mid-Atlantic Ridge; PAR - Pacific-Antarctic Ridge; S. EPR - South East Pacific Rise; S. MAR - South Mid-Atlantic Ridge; SWIR - South West Indian Ridge; and T-F Arc - Tabar-Feni Arc. Point size is relative to the number of database records associated with each region (e.g., see legend). The bathymetric basemap ('World Ocean Basemap') is courtesy of ESRI et al. (2012). Geographic map projection with coordinate system WGS84.

Table 3: Species traits included in the sFDvent database, with further detail on category, type, and modalities. The 'Rationale' column is provided to outline the reasons for including each trait in the database (i.e. why it might be ecologically important for the performance of a vent species and/or its influence on ecosystem processes). The Glossary in **Table B.3.1** provides definitions for each of the trait modalities.

Trait Category	Trait	Modalities	Trait Type	Rationale
Mobility	Relative Adult Mobility	1, 2, 3, 4	Ordinal	The mobility of a species affects access to food, vent fluid (and the microbes within it), and also its ability to escape predation and/or relocate if, for example, vent fluid supplies shut down or competition becomes too strong.
Geographic Distribution	Depth Range (m)	Maximum and minimum depth ranges, from a choice of 11 (from 0 m to > 5000 m in 500 m increments)	Ordinal	Depth range captures information on relative geographic range size and also facilitates the assessment of trait-environment relationships in the vertical dimension of space. Thus, this trait can be included with the others, or used as an environmental variable, depending on the research question.
Generalist / Specialist	Chemosynthesis-Obligate	Vent, Other Chemosynthesis-Based Ecosystem(s) (CBE), No	Categorical, Ordinal	As highlighted in the category, this trait captures information on specialist/generalist adaptations that a species may have to thrive in given environments and is therefore also an important indicator of vulnerability to disturbance or environmental change. For instance, a species dependent on vent environments may be more prone to extinction given deep-sea mining impacts or the shutdown of vent fluid supply than a species that can also live in other chemosynthesis-based ecosystems.

Life History	Estimated Maximum Body Size (mm)	0.01, 0.1, 1, 10, 100, 1000	Ordinal	Body size is known to influence the contribution of a species to ecosystem functioning, as well as its own fitness within a system. This trait captures information on reproduction, life history, fitness, and resilience to change, as well as its energy demand.
Habitat Use	Zonation from a Vent	High, Medium, Low (Periphery)	Categorical, Ordinal	This trait is specific to vent species, but could be adapted for other environments (e.g., to capture the 'halo' zonation at seeps and wood falls). It captures the dependence of a species on vent fluid and the microbes it contains, as well as the thermal tolerance of a species (which can be a physiological indicator and thus related to fitness and energy demand).
	Substratum	Hard, Soft	Binary	This trait captures species-association information, assuming substratum preference can be indicative of shared niche space. The preferred substratum of a species may also be an indicator of resilience, as hard and soft substrata may be affected by different impact types and intensities during deep-sea mining, for example. This trait also facilitates prediction using trait information, as hard and soft substrata are often mapped during geological and geophysical surveys.
	Habitat Complexity	Does not add, Mat forming (< 10 cm), Bed forming (> 10 cm), Dense bush forming, Open bush forming, Burrow forming	Categorical	This trait is a shape indicator, providing insight into the structures and habitat complexity added by a species, and, thus, whether a species might be considered an ecosystem engineer or a foundation species. In adding habitat complexity, a vent species can alter fluid dynamics and access to nutritional resources and therefore influences ecosystem function, energy available to other species, and its own fitness.

	How often found in groups or clusters? (Gregariousness)	Never (Solitary), Sometimes, Always	Categorical, Ordinal	Gregariousness captures information on the potential of a species to influence other processes, as it might be assumed that gregarious species limit space available to other species and are likely to be more common than solitary species. Conversely, gregarious species may depend on others for nutritional and/or reproductive purposes and thus be more vulnerable than species that can thrive alone if population sizes are reduced by disturbance or environmental change.
Trophic Structure	Trophic Mode	Carnivore - scavenger, Carnivore - other, Detritivore, Bacterivore, Omnivore	Categorical	The trophic mode of a species affects its energy demand, as well as the amount of food it makes available to others during the feeding process. This trait is also an indicator of resilience, as more generalist feeders (such as detritivores and omnivores) are less likely to be affected by competition for food and/or changes to food supplies and quantities. Contrarily, carnivores depend on the presence of prey to survive and are potentially more vulnerable to environmental change affecting prey populations.
	Nutritional Source	Sediment or rock surface, Water column, Fauna, Symbiont	Categorical	This trait captures similar information to Trophic Mode, but also reflects the dependence of a species on a particular feature of the local environment. For example, a species dependent on nutritional sources in the water column might be more at risk if mining creates sediment plumes in the water column that clog the organism's feeding apparatus. On the other hand, if a species can supplement its chemosynthetic energy source with a water column supply when vent fluid dynamics change, it may survive better in an area where food supply is greater (e.g., in the water column of an area of high primary productivity). Thus, the importance of, and rationale behind use of, this trait, as with all traits in this table, will depend on the research question.

Symbiont	Position of Symbiont	Endosymbiont, Episymbiont, None	Categorical	Species with symbionts are maximising their access to chemosynthetic energy sources. On the other hand, those without symbionts might be more flexible, able to thrive in other ecosystems, and less vulnerable to vent fluid changes and/or shutdown. The type of symbiont is also important, as this captures the dependency of a species on a specific type of bacteria. For example, an endosymbiont host must be adapted to enable the bacteria to survive internally, while a species dependent on episymbiotic bacteria can harvest these from the surrounding environment.
Species Associations	Foundation Species	Yes, No	Binary	A foundation species facilitates other species and contributes to community structure, thereby playing a fundamental role in ecosystem function.
Community Structure	Abundance	High, Low	Binary	This trait captures a relative, most commonly observed state of abundance for a species. A species can be low in occupancy (i.e. not found at many vents) but high in abundance and abundance is therefore used as an indicator of rarity, resilience, and performance.

Table 4: Trait data coverage for the first clean, recommended version of the sFDvent database. The modal (most frequently recorded) trait value and mean certainty score associated with each trait are also provided.

Trait	Number of Records	Percentage of Records with Trait Scores	Modal Trait Value	Mean Certainty Score
Relative Adult Mobility	645	99.8	3	2.6
Depth Range (m)	Min: 588 Max: 587	Min: 91 Max: 90.9	Min: 2000 - 2500 Max: 2500 - 3000	2.7
Chemosynthesis-Obligate	646	100	Vent	2.6
Estimated Maximum Body Size (mm)	643	99.5	100	2.8
Zonation from a Vent	507	78.5	Medium	2.6
Substratum	527	81.6	Hard	2.6
Habitat Complexity	497	76.9	Does not add	2.6

How often found in groups or clusters? (Gregariousness)	450	69.7	Never (Solitary)	2.4
Trophic Mode	515	79.7	Bacterivore	2.4
Nutritional Source	582	90.1	Sediment or rock surface	2.4
Position of Symbiont	477	73.8	None	2.6
Foundation Species	523	81	No	2.8
Abundance	470	72.8	High	2.6

Table 5: A comparative review of animal trait databases. Superscript numbers are used to identify trait-database sources, as provided in **Table B.6.1**, and 'NA' is used to abbreviate 'not applicable'. Note that the summary information for each of these databases (e.g., number of records, species, and traits) is accurate as of 20th November 2017.

Database	**Geographic Scope**	**Environment**	**Number of Records**	**Number of Taxa**	**Number of Traits (or categories, as specified below)**	**Reference**
sFDvent	Global	Marine	646	646 species	13	*This chapter.*
Coral Trait Database[1]	Global	Marine	68,496	1,548 species	158	Madin et al., 2016
Marine Species Traits[2]	Global	Marine	NA - tags for species in other databases	NA as produced to link with other databases (e.g., WoRMS)	10 priority, 138 biological descriptors, 293 ecological descriptors	Marine Species Traits editorial board (2018)
Database for life history traits for European amphibians[3]	Europe	Terrestrial / Freshwater	86	86 species	14 morphological, 17 life history, 7 movement, 2 spatial distribution, and habitat preferences and threats	Trochet et al., 2014

Reptile Trait Database[4]	Europe	Terrestrial	122	122 species	18 (with some repeated for different life stages)	Grimm et al., 2014
carabids.org[5]	Global	Terrestrial	> 10,000	> 10,000 species	12	Homburg et al., 2013
Trait database of stream invertebrates[6]	SE Australia	Freshwater	172	172 (family level)	9	Schäfer, et al., 2011
European Chironomidae genera[7]	Europe	Freshwater	~164 genera and ~439 species	~439 species	37	Serra et al., 2016
The Global Ants Database[8]	Global	Terrestrial	3991 individuals, 8973 species/ morphospecies, 4482 assemblages	8,973 species / morphospecies	23	Parr et al., 2017
BIOTIC - Biological Traits Information Catalogue[9]	Global	Marine (benthic)	831	831 species / genera	42	MarLIN, 2006
Fish Traits Database[10]	U.S.	Freshwater	809	809 species	> 100	Frimpong and Angermeier, 2009

A trait database for marine copepods[11]	Global	Marine	9,306	9,306 taxa	14	Brun et al., 2017
Polytraits[12]	Mediterranean lagoons but expanding	Freshwater / Marine	27,198	952 species	47	Faulwetter et al., 2017
freshwaterecology.info database[13]	Europe	Freshwater	21,167	21,167 taxa	106 biological / ecological parameters	Schmidt-Kloiber and Hering, 2015
Freshwater Biological Traits Database[14]	North America	Freshwater	11,912	3,957 taxa	~160	U.S. EPA., 2012

Table 6: A proposed 'common terminology' for faunal trait databases to ensure their comparability across ecosystems, based on a comparative review presented in **Table B.6.1**. Italicised items are either: i) not ecological traits (e.g., location information), or ii) similar in what they capture but more context-dependent than other traits compared. Superscript numbers are used to identify trait-database sources, as provided in **Table B.6.1**. Traits with an asterisk were removed from the recommended sFDvent dataset (**Table B.3.2**) but are present in the raw dataset (**Table B.3.3**).

Ecological process / function	**Cross-system compatible trait example**	**Similar trait(s) in sFDvent database**	**Similar trait(s) in other databases**	**Potential scoring mechanism to enable scoring in less well-studied ecosystems**
Growth and reproduction	Estimated maximum body size (adult and offspring separately)	Estimated maximum body size (mm)	Body size[2, 10, 11, 12], Maximal body size (mm)[5, 14], Approximate size class[13]	Binned size classes to enable entry of rounded estimates.
	Body shape (adult and offspring separately)	*Foundation species* (as body shape affects the ability of a species to provide a foundation)	Body shape[14], Growth form(s)[9, 13], Shape factor[13]	Fixed options from a range of trait databases, to capture shape more broadly than per taxonomic group.
	Reproduction strategy	Reproductive type*	Reproduction / Reproductive type[6, 7, 9, 13], Mode of reproduction[12], Sexual system[1]	Options covering how many times an animal reproduces per lifetime, whether it requires a partner for reproduction, and whether reproduction can take place more than once per year.

	Development mechanism	Larval development*	Developmental mechanism[9, 12], Larval development[12]	Simple scoring options to capture extent to which offspring are dependent on parents or their resources for development.
Feeding	Primary diet (adult and offspring separately, and then also secondary diet)	Nutritional source	Diet[2, 8], Food source[6], Food[13], Feeding diet[13]	To enable cross-system comparisons, this would need to be broad. For example, ‘plant-based’, ‘animal-based’, ‘detritus-based’ or ‘other’, would capture major groups, including omnivory importance.
	Primary feeding mode (adult and offspring separately, and then also secondary feeding mode)	Trophic mode	Feeding mode[11], Feed mode [14], Characteristic feeding method[9], Feeding habits[7], Trophic level[5]	This could be used to capture the source of food and the energy required to find food. For example, broad options could be: ‘scavenging’, ‘hunting’, and ‘dependent on other fauna’.
	Food active or passive	*Nutritional source* (e.g., carnivorous species eating fauna would have ‘active’ food and and species depending on the water column would have ‘passive’)	Food active or passive[3], Hunting abilities[5]	This is a simplistic trait that could be used in place of ‘primary feeding mode’.

Survival	Relative mobility (adult and offspring separately)	Relative adult mobility	Mobility[2, 9], Mode of displacement[3], Locomotion[4], Swimming ability[14]	This could be an indicator of mobility on an ordinal scale (e.g., from sessile to free-moving and fast).
	Temperature preference indicator	Zonation from vent	Temperature preferences[7], Thermal indicator[14], Thermal preference[14]	Temperature ranges could be selected that are appropriate on a global scale. Alternatively, bands applicable to terrestrial, marine, and freshwater systems could be established (e.g., tropical, polar, temperate, extreme heat, extreme cold).
Community structure and dynamics	Habitat type	Tectonic setting*, Host rock*	Habitat type[1, 12], Habitat[3, 4, 13], Habitat preference[5, 10], General / gross habitat[7]	If this were to be cross-ecosystem comparable, this would likely need converting to scores such as: 'rock-based', 'plant-based', etc..
	Preferred substratum	Substratum	Substrate preferences[7], Substratum[2, 9], Substratum / substrate type[1, 12]	This, like habitat, would need to be categorised broadly, with scores such as: 'sediment', 'rock', 'water', 'air', and 'plant-origin'.
	Gregariousness	How often found in groups or clusters? (Gregariousness)	Sociability[9, 12], Coloniality[1], Occurrence in large quantities[13]	This could be simply broken down to: 'always found with others', 'sometimes found with others', and 'never found with others'.
	Dependency	Chemosynthesis-obligate, Position of symbiont	Dependency[9]	Symbiotic relationship types present across all ecosystems would need to be included as scoring options (e.g., mutualistic, parasitic).

Migration	*Dispersal mechanism**	Migration[13], Type of migration[7], Migration pattern[9]	This could be scaled as follows: ‘across ocean basins/continents’, ‘across ecoregions’, ‘across smaller areas’, ‘no migration’.
Ecosystem engineer	Habitat complexity	Ecosystem engineering[12]	This could be a ‘yes/no’ score, depending on whether a species modifies the habitat around them or creates habitat for other fauna by being present.
Average associated depth / altitude (m)	Depth range (m)	Water depth[1], Depth[2], Depth preferences[7], Altitudinal preference(s)[7, 13]	500 m - 1000 m intervals could be established from the deepest ocean basin to the highest mountain, to capture depths and altitudes in a comparable way (e.g., with ranges below sea level expressed with a minus sign).

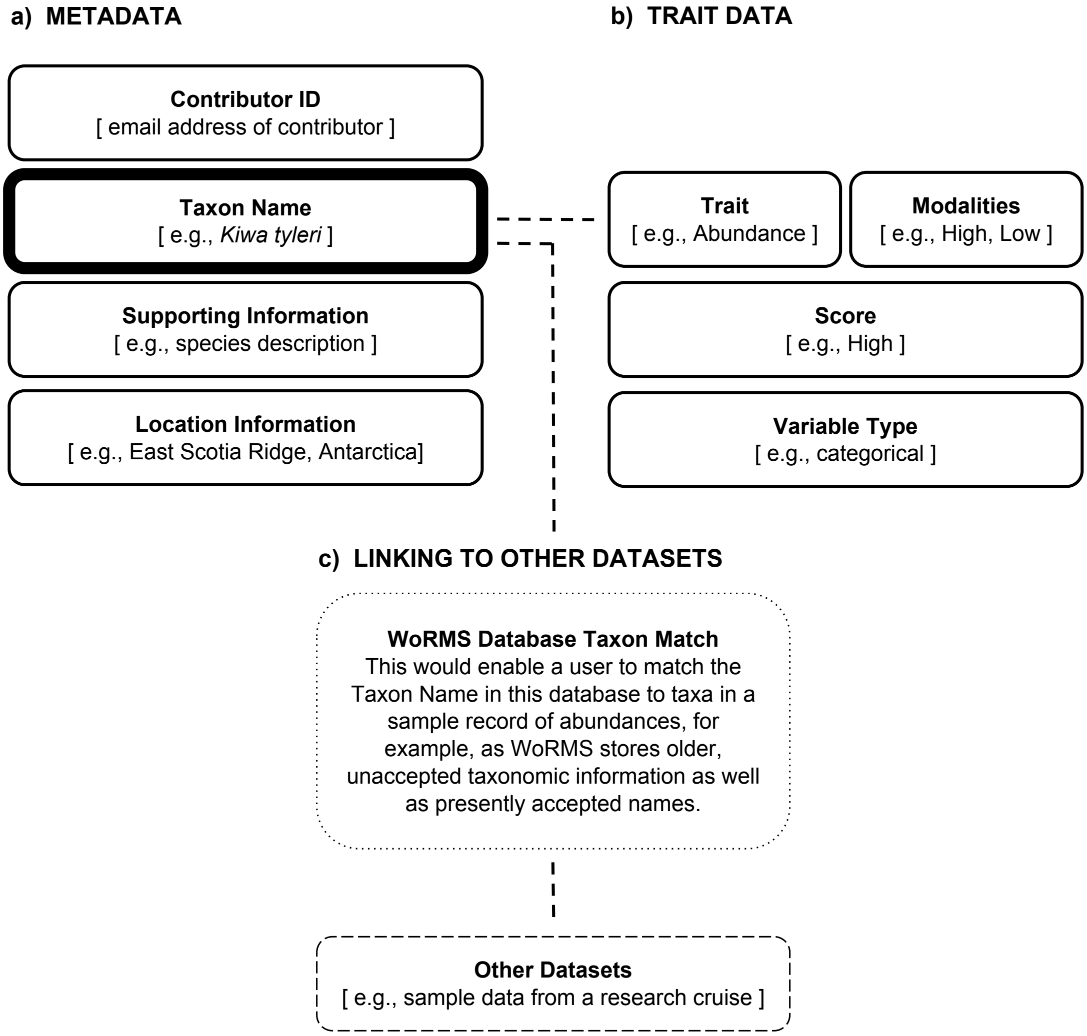


Figure 21: Overview of the sFDvent database design. Example information is given in square brackets beneath each database component. Taxon Name is shown with a darker outline because it is the component used to link datasets (as highlighted by the dashed line connectors). WoRMS Database Taxon Match has a dotted outline because it is a process a user could undertake to join the sFDvent database information with other datasets (for example, presence-absence data, abundances, and cruise report sample logs). Other Datasets has a dashed outline because these data are external to the sFDvent database

3. RESULTS

3.1 Data description

The clean sFDvent trait dataset (**Table B.3.2**) includes traits scored with the most coverage and certainty, comprising 646 records across 13 traits with 55 modalities (**Table 3**). Six of these traits are ordinal, three are binary, and four are qualitative, categorical traits (**Table 3**). The structure of the sFDvent database is outlined in **Figure 21**. The traits in sFDvent were scored at species-level for adult fauna, rather than individual-level or for different life stages, given the variability in effort associated with measurements, observations, and descriptions of vent species (Tunnicliffe, 1990).

In total, 646 taxa from 345 genera, 181 families, and 12 phyla have trait data with associated, expert-provided location information (**Table 4**, **Figure 22**). Arthropoda is the best-scored phylum, with 216 records, while Acanthocephala has the lowest number of records of the phyla in the dataset (one record; **Figure 22**) The best-populated ocean basin is the North Pacific (East and West), with 332 taxa with associated trait data (**Figure 20**), while the Mediterranean Sea has the fewest trait records - 2 (**Figure 20**).

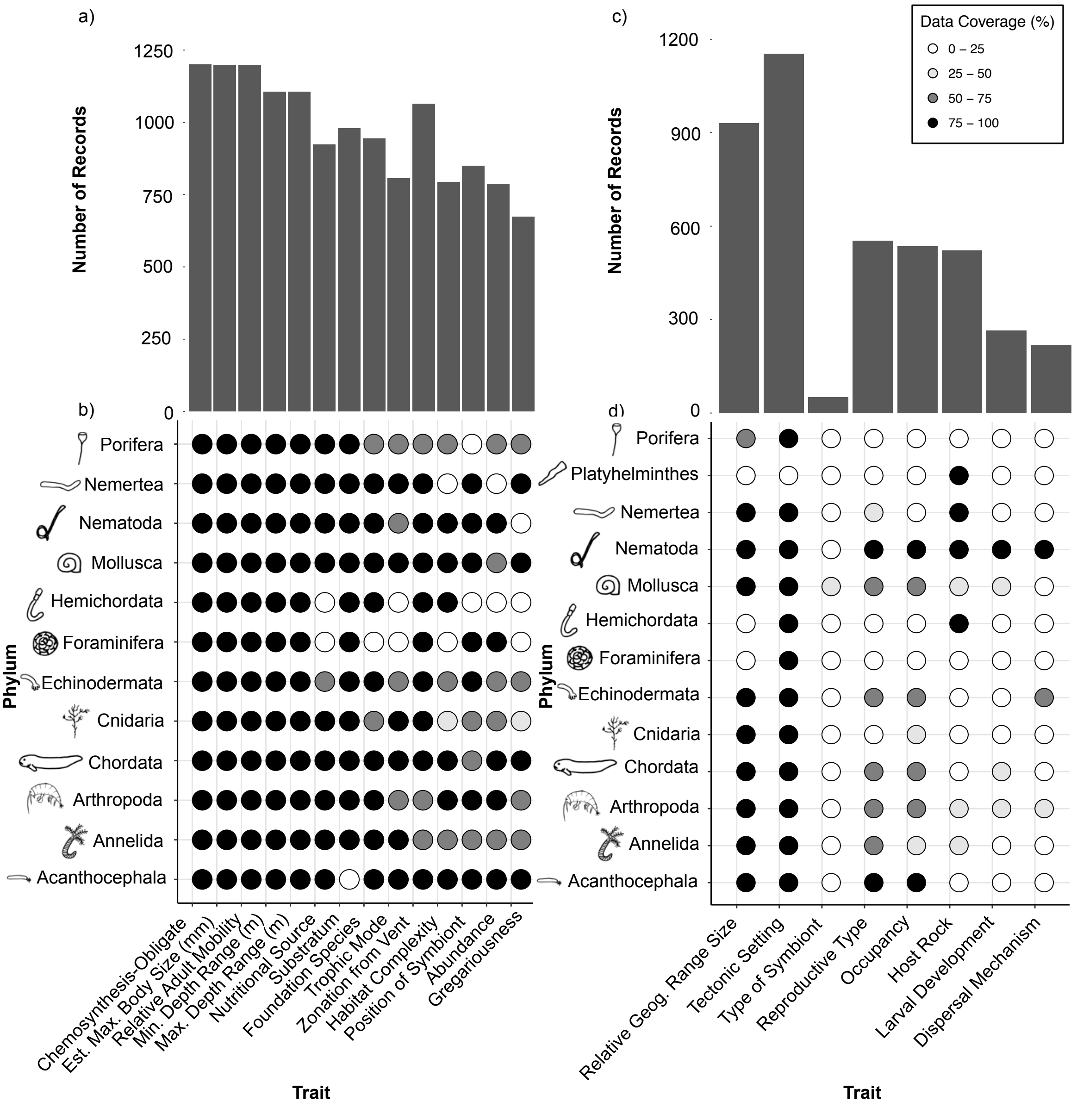


Figure 22 (caption continued overleaf): Data coverage with respect to trait (a, c) and phylum (b, d). The figure concept was developed from Brun et al. (2017) to depict the relative coverage per phylum for each trait using a dotplot (b) and to give an overview of the number of records per trait in a bar chart (a). Note that the 'Data Coverage' legend applies to panels (b) and (d). Panels (a) and

(b) represent the coverage for the recommended dataset. Panels (c) and (d) include data from the 'Clean Binned' file described in **Table B.3.5** and therefore include data that may need further cleaning, but demonstrate which traits removed from the recommended dataset have relatively high coverage for a given phylum. Some traits have been abbreviated for display purposes as follows: 'Est. Max. Body Size (mm)' - Estimated Maximum Body Size (millimetres); 'Min. Depth Range (m)' - Minimum Depth Range (metres); 'Max. Depth Range (m)' - Maximum Depth Range (metres); and 'Relative Geog. Range Size' - Relative Geographic Range Size.

Chemosynthesis-Obligate, Relative Adult Mobility, and Estimated Maximum Body Size traits are scored for more than 99% of taxa; Depth Range and Nutritional Source traits have greater than 90% coverage (**Figure 22**). The remaining traits are scored for at least 69% of taxa. Estimated Maximum Body Size is one of the best-scored traits and also has the highest average certainty (2.8 of a possible score of 3). Average certainty across all traits is greater than 2.5, apart from Gregariousness, Nutritional Source, and Trophic Mode (averaging 2.4; **Table 4**). For a trait-by-trait summary of results, see **Appendix B.5**.

3.2 Comparison with other datasets

The sFDvent dataset has fewer traits and records than many trait databases focusing on shallow-marine, freshwater, and terrestrial taxa (**Table 5**). Nonetheless, sFDvent has more traits than the carabids.org (Homburg et al., 2013) and stream invertebrates (Schäfer et al., 2011) databases, and more taxonomic entries than the amphibian (Trochet et al., 2014), reptile (Grimm et al., 2014), stream invertebrate (Schäfer et al., 2011), and chironomid (Serra et al., 2016) databases (**Table 5**). Traits limited in other databases (e.g., reproductive traits (Brun et al., 2017)) also have low coverage and/or certainty in the raw sFDvent data, and we have excluded these from the recommended dataset (**Table B.3.2**). However, body sizes are well scored, as in other databases (e.g., marine copepods (Brun et al., 2017)). Furthermore, the sFDvent database encompasses similar biological parameters to all of the trait databases described in **Table 5**, differing in terminology (trait names and modalities) rather than conceptual basis (e.g., see **Table 6**). For example, feeding, survival, growth, reproduction, and community-assembly processes can be assessed using the traits in this database (**Figure 19**) and in databases focusing on other ecosystems and/or fauna (**Table 5**).

4. DISCUSSION

sFDvent is a global-scale trait database for deep-sea hydrothermal-vent species, compiled using literary sources, existing taxonomic databases (ChEssBase (Baker et al., 2010), WoRMS (Horton et al., 2017), and Desbruyères et al. (2006)), and pooled expert knowledge based on research-cruise observations since 1977, with pioneer scientists in this field contributing. The first version (sFDvent v.1), released here (**Table B.3.2**), contains data for 646 taxa across 13 traits. In capturing species records (required to assign traits) up to the year 2017, we also update the last species compilation from 2009 (Bachraty et al., 2009) from 592 species to 740 (including species removed from the recommended dataset due to lacking trait scores, or 646 species with higher taxonomic certainty). The database has a global span and broad taxonomic coverage for use in macroecological trait-based studies of vent biodiversity and in research incorporating taxonomic-, phylogenetic-, and trait-based diversity indices.

Body size, for example, is a trait identified to play a fundamental role in ecosystem functioning, ecological processes, and shaping biodiversity (Mindel et al., 2015); this trait ('Estimated Maximum Body Size') has been scored for all but three taxa in sFDvent. Also scored with high coverage is mobility - identified in marine ecosystems as important for dispersal potential (Costello et al., 2015) and, thus, population dynamics, as well as ability to escape in the event of a disturbance. Scores for 'Relative Adult Mobility' are provided for more than 99% of taxa in sFDvent and can now be used in diversity-oriented studies as well as those investigating reproduction in vent fauna and its influence on vent biogeography (Mullineaux and France, 1995; Yahagi et al., 2017). Similarly, due to complete coverage, 'Chemosynthesis-Obligate' can be used to ascertain endemism levels in taxonomic, geographic, and other groups, which may be particularly important when considering the impacts of mining on vent ecosystems, given the close relationships between endemism and resilience (Vasconcelos et al., 2017).

The sFDvent database also has an important role in its capacity to highlight knowledge gaps and research biases. For instance, missing and/or low certainty scores in 'Gregariousness', 'Trophic Mode', and 'Nutritional Source' traits highlight a need for observational and behavioural studies. These traits would improve our understanding of community structure and dynamics, as well as macroecological-scale variability in vent food webs. In addition, despite literary focus on vent annelids and molluscs (**Appendix B.1**), arthropods are the best-scored fauna in the database. Meanwhile, as one might expect, given publication and sampling bias (**Appendix B.1**), the North Pacific has the highest number of scored taxa, emphasising a need to score traits in less well-sampled regions, such as the Pacific-Antarctic Ridge and the Kuril Arc. Furthermore, despite the fundamental importance of reproductive traits in ecology (Mullineaux et al., 2018), trait scoring for 'Reproductive Type', 'Larval Development', and 'Dispersal Mechanism' did not have sufficient coverage to be included sFDvent v.1. This is, however, now already being addressed by collaborators, further emphasising the importance of building databases like sFDvent for: highlighting gaps and biases that need to be filled and resolved; generating new directions for research agendas; and promoting collaborative approaches for gap filling across a research community.

In considering the compatibility of sFDvent traits with those in established databases for other environments and taxonomic groups, we have identified similarities and differences in data availability across ecosystems (**Table 5**, **Appendix B.6**). For example, reproductive and behavioural traits are poorly scored relative to other traits in many trait databases, while body size, and other more readily measurable traits are well scored (Brun et al., 2017; Madin et al., 2016; Parr et al., 2017). Highly-scored traits will facilitate cross-ecosystem analyses. Nevertheless, our traits were designed for highly-specialised fauna in remote, deep-sea environments. Therefore, to conduct a comparative analysis across different trait databases, we would need to 'translate' the trait terminology used (**Table 6**). Thus, we echo calls for common terminology across systems (Costello et al., 2015) to advance trait-based approaches for macroecological biodiversity studies. While important goals for ecological understanding can be met using species- and ecosystem-specific traits (e.g., mapping global biodiversity patterns), a common language linking databases and systems would enable us to investigate truly global-scale patterns, as well as human impacts upon these systems (CBD, 1992).

Comparing sFDvent to other databases also highlights our unique approach to data collection. Other databases have tended to focus on literary sources of information (including other databases; e.g., MarLIN (2006)), whereas sFDvent was predominantly filled using expert knowledge, and sFDvent entries scored using the literature were peer-reviewed by experts. Moreover, pooling expert opinion on species trait scores captured the current state of knowledge in a relatively quick timeframe (one year as opposed to ten or more for other databases; **Figure 18**), where knowledge from observations made during research cruises, and unpublished data, could be incorporated and credited using contributor ID metadata. Thus, we suggest that using a working-group approach and online collaboration tools to produce a shared data source, designed, tested, and agreed upon by experts who have contributed to, and will benefit from, the data, is a means to produce a quality product. We expect that sFDvent will form a baseline single repository for expert knowledge on deep-sea hydrothermal-vent species, with ongoing community input (**Figure 23**). In addition to promoting international collaboration in its design and population, the database showcases the benefits of a working-group approach and knowledge sharing among members of the chemosynthesis-based-ecosystem research community. Experts across the globe can use sFDvent to reduce uncertainty when developing conservation and management plans for deep-sea hydrothermal vents - previously untouched, but now under threat from human exploitation.

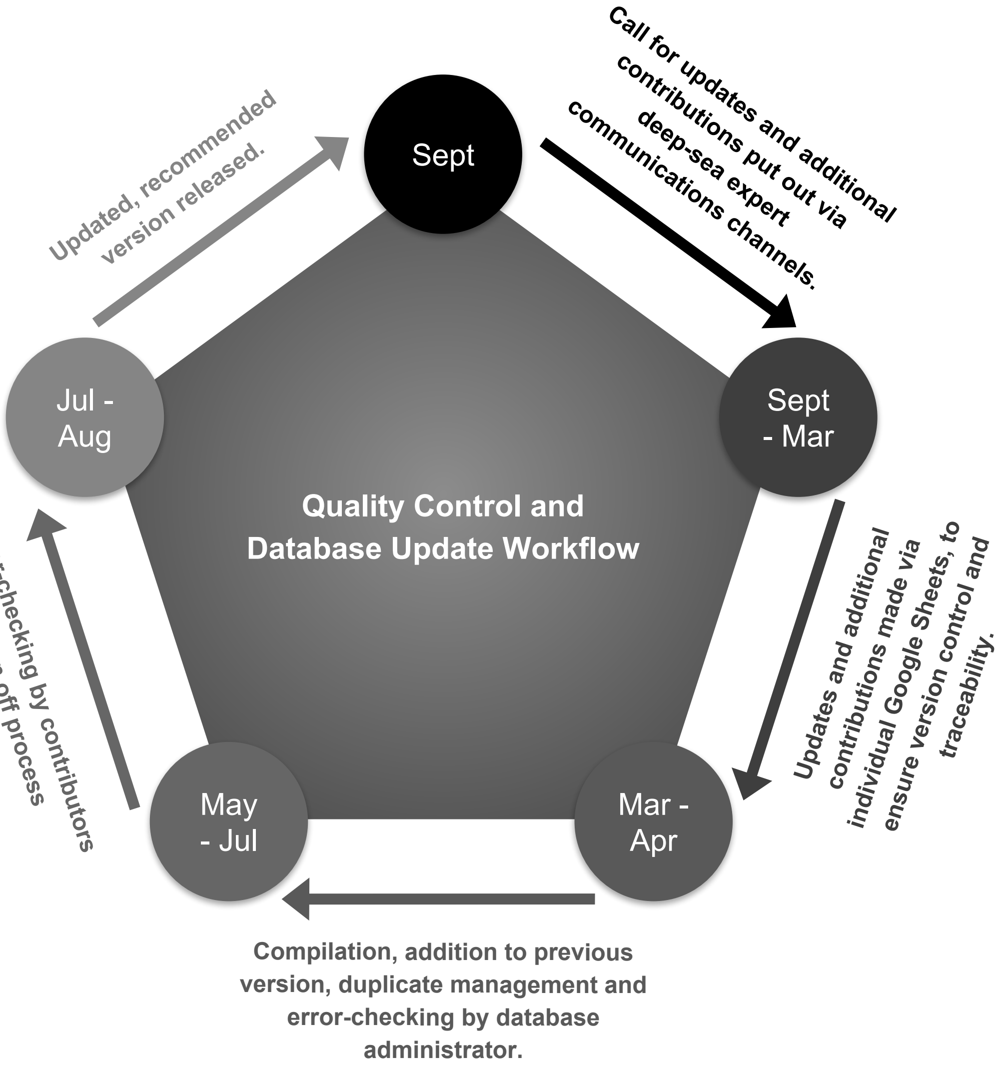


Figure 23: Proposed quality control and update release workflow for future versions of the sFDvent database. The cycle would begin every 4 years to enable a new version to be released every 5 years. This cycle illustrates the process that would take place over the course of the year. The process could begin to include species from other chemosynthesis-based ecosystems from version 2 onwards, though it is recommended that species would then be given an associated record to highlight the ecosystem(s) they are found in, to ensure that those wanting to focus on a specific ecosystem could filter the database. Further information on how to contribute to future versions of the sFDvent database is provided in **Appendix B**.

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Chapter Four: Global-scale, contemporary environmental variables defining the geography of deep-sea hydrothermal-vent communities

I designed this study, undertook the analyses, and drafted the chapter with comments and suggestions from lead supervisor Dr Amanda Bates. Ideas for environmental variables to consider include some pooled in a list made by experts participating in the first sFDvent Working Group meeting (see Chapter 3). Variables and possible ecological links to vent ecosystems were discussed, reviewed, and refined with Prof. Verena Tunnicliffe (University of Victoria, Canada).

Supporting Information for Chapter Four is provided in **Appendix C**.

ABSTRACT

Once deemed ephemeral systems, driven by small-scale physical and chemical processes, it is now known that large-scale oceanographic and environmental processes, such as tides and storms, shape the ecology of deep-sea hydrothermal vents. As technology has improved, these 'remote frontiers' have also become increasingly accessible to humans - to be mined commercially by 2020. Biodiversity loss often accompanies human activity and, across terrestrial, freshwater, and marine environments, we are becoming exceedingly aware of the need to conserve, manage, and monitor global biodiversity patterns to prevent this. A key step towards meeting conservation targets is the collection and dissemination of relevant environmental data, which enables us to: i) appraise the natural processes presently affecting the diversity of life in ecosystems, and ii) predict future influences and environmental change. Here, we extract, analyse, and map the geographic and oceanographic characteristics of vent fields using freely available, global-scale datasets. We describe a 'typical' vent field - young, sediment-poor, and nutrient-rich - and examine the correlations among environmental variables that may enable us to 'shortlist' the data we need to understand data-poor regions. Fundamental ecological processes are shaped by different variables, whose influences vary across space. For instance, chlorophyll, and carbon phytoplankton biomass at depth - important 'limits to life' - are only above minimal levels in the shallowest venting regions (Kolbeinsey Ridge and Reykjanes Ridge). While many environmentally similar fields are spatially clustered, some are not, with geographic and oceanographic characteristics joining fields across oceans and tectonic settings. For example, we find East Pacific Rise mid-ocean-ridge vents clustering with a North Fiji Basin back-arc spreading-centre hosted field. We also show that E9 vent field, in the Southern Ocean, and Steinaholl Vent Field, in the North Atlantic, are environmentally unique relative to other vent fields across the globe, forming distinct clusters. Overall, we demonstrate the utility of large-scale environmental data in improving our understanding of the geographic and oceanographic uniqueness of deep-sea hydrothermal-vent fields for the future conservation, management, and spatial representation of vent biodiversity. We

share our data for others to use in their future research.

Keywords: biodiversity, conservation, environmental variability, freely available data, global-scale, hydrothermal vent, oceanography.

1. BACKGROUND

In reviewing the planet's progress towards the Convention on Biological Diversity (CBD) Aichi Biodiversity Targets for 2011-2020 and the 2030 United Nations Agenda for Sustainable Development, it has become apparent that our capacity for progress tracking is limited by a lack of biodiversity indicators and freely available datasets (Skidmore et al., 2015). To attempt to solve this problem moving forward, scientists have proposed the identification of 'essential biodiversity variables', 'essential ocean variables', and 'global ocean observing systems', for which data should be gathered from readily accessible sources (Skidmore et al., 2015; Asaad et al., 2017; Miloslavich et al., 2018). Data already fit for this purpose include global-scale, satellite remote-sensing and *in situ* monitoring products (Anderson et al., 2017; Cord et al., 2017; Müller-Karger et al., 2018), as well as other open datasets (Scholes et al., 2012).

The urgent need for data assimilation and sharing is increasing in the deep sea, too, as a treaty is being negotiated for the conservation and sustainable use of biodiversity in seas beyond national boundaries (Gjerde et al., 2016). This involves the designation of Marine Protected Areas (MPAs) and the use of marine spatial planning tools - both dependent on large quantities of data collected on a range of spatial and temporal scales (Gjerde et al., 2016; Müller-Karger et al., 2018). For many conservation practices, such as the assignment of CBD MPA networks, 'important areas' should be geographically and oceanographically unique and networks must be 'representative' in diversity of species and habitats (Dunn et al., 2018; Rees et al., 2018). Indeed, to capture 'representativity', the CBD suggests that biodiversity drivers should be identified, particularly those that describe the seascape (Dunn et al., 2018). These conservation and management practices are becoming increasingly relevant for deep-sea hydrothermal-vent ecosystems, which are under threat from commercial-scale deep-sea mining for the polymetallic sulfides many active vents form (Van Dover et al., 2018).

It could be argued that the wider seascape is of minimal influence on relatively remote, deep-sea hydrothermal-vent ecosystems. Indeed, the dominance of research focusing on the local-scale geological, chemical, and physical anomalies associated with these unique environments (Luther III et al., 2001; Fisher et al., 2007; Tivey, 2007) promotes this idea. Nevertheless, deep-sea communities are generally also affected by primary productivity, deep-water chemistry, seabed geomorphology, and other large-scale environmental characteristics (Rengstorf et al., 2014). Data on variables such as these have been compiled using *in situ* measurements, remotely sensed imagery from satellites, and other global-scale datasets, to model the spatial distribution of non-vent deep-sea benthic species (Tittensor et al., 2010; Davies and Guinotte, 2011; Yesson et al., 2012). This suggests that similar data could be equally useful for advancing deep-sea hydrothermal-vent ecology and designing conservation and management strategies for these systems.

Research at vents has tended to focus on the local-scale environmental characteristics within vent fields, or regional-scale habitat characteristics (e.g., along a mid-ocean ridge). Vent ecologists have described species and characterised communities using traditional biodiversity metrics, like species richness and abundance, while geologists have focused on deposit types, ages, volcanism, and tectonics (Le Bris et al., 2017). As a result, to our knowledge, there are few, if any, large-scale studies linking vent fields and their geological, environmental, and oceanographic characteristics, outside a faunal or biogeographic context. Yet, vent fields are not random in space; they are fundamentally linked to, shaped by, and affecting the geography and oceanography around them (Le Bris et al., 2017).

In other ecosystems, global biodiversity patterns have been modelled successfully by combining biodiversity metrics with large-scale environmental data (Scholes et al., 2012). We are yet to combine such data for vent ecosystems on a global scale, despite calls for more interdisciplinary work and data compilations, and accumulating evidence on the influence of large-scale ocean processes on vent communities (Beaulieu et al., 2013; Cuvelier et al., 2017; Lelièvre et al., 2017). This limits our capacity to make conservation and management decisions regarding deep-sea hydrothermal-vent ecosystems. For vents, the 'Dinard Guidelines' have been developed, to shape the design of 'Chemosynthetic Ecosystem Reserves' (CERs) in line with CBD conservation objectives (Ardron et al., 2011). In these guidelines, the environmental characteristics of vent ecosystems are explicitly considered as a means for justifying a spatial approach to their management (Ardron et al., 2011). Building on CBD criteria for Ecologically and Biologically Significant Areas (EBSAs), Ardron et al. (2011) propose that biodiversity, connectivity, replication, viability, representativity, and sustainable use should guide conservation objectives and, as such, CERs should incorporate natural variability and habitat heterogeneity. Specifically, Ardron et al. (2011) suggest that plans should be made on the bioregion scale, with a bioregion comprising a cluster of ecosystems that share species compositions and environmental conditions.

The increasing recognition of the importance of environmental variables for the conservation and monitoring of the Earth's ecosystems and biodiversity presents the opportunity for a global-scale analysis of variables of potential influence on deep-sea hydrothermal-vent communities. Here, we will begin the work of mapping vent bioregions by clustering vent fields according to their prevailing environmental conditions. We aim to assess where environmental variability is greatest, to identify environmental characteristics shaping the uniqueness of vent fields.

Of the environmental variables included in this study, we hypothesise that spreading rate will be the primary driver of similarity among vent fields (Juniper and Tunnicliffe, 1997; Baker et al., 2016; Baker, 2017). We know from previous work that spreading rate is linked to the number of vent habitats (Juniper and Tunnicliffe, 1997; Baker et al., 2016; Baker, 2017). We therefore expect spreading rate to shape the environmental similarity of vent fields because more vent fields in a faster-spreading region might mean that the vent fields themselves influence ambient temperature, seafloor topography, available dissolved oxygen, and other environmental characteristics. In addition, larger vents tend to be found on slower-spreading ridges, so we might expect proximity to nearest vent field to decrease with spreading rate, as larger individual vents would logically mean fewer vent fields per region (Hannington et al., 1995; Tivey 2007).

Overall, our goal is to compile geographic and oceanographic data for active, confirmed vent fields in the InterRidge Vents Database (Beaulieu, 2015), before releasing these data publicly. We expect the data to be useful to deep-sea researchers studying connectivity among vent fields, and vent biodiversity and biogeography, as well as those designing CERs for the management and protection of vent ecosystems.

2. METHODS

2.1 Selecting and processing environmental variables

We relate environmental parameters measuring large-scale ocean processes to deep-sea vent fields (with "deep sea" referring to fields below 200 m water depth) as outlined in the conceptual framework in **Figure 24**. This framework centres on five key areas influencing the ecology of deep-sea hydrothermal-vent fields: i) limits to life in vent communities; ii) access to nutritional resources beyond the vent field; iii) disturbance; iv) stability; and v) access to 'stepping stone' environments, influencing larval survival and metapopulation dynamics (**Figure 24**). We sourced environmental variables fitting into these areas, from well-established data collections, to map the global-scale geography of vent fields (**Table 7**, **Table 8**). We extracted variables for active, confirmed vent-field locations as described in **Appendix C** and included in analyses those for which all environmental variables were populated (i.e. a vent-field could not have NA values for any variable).

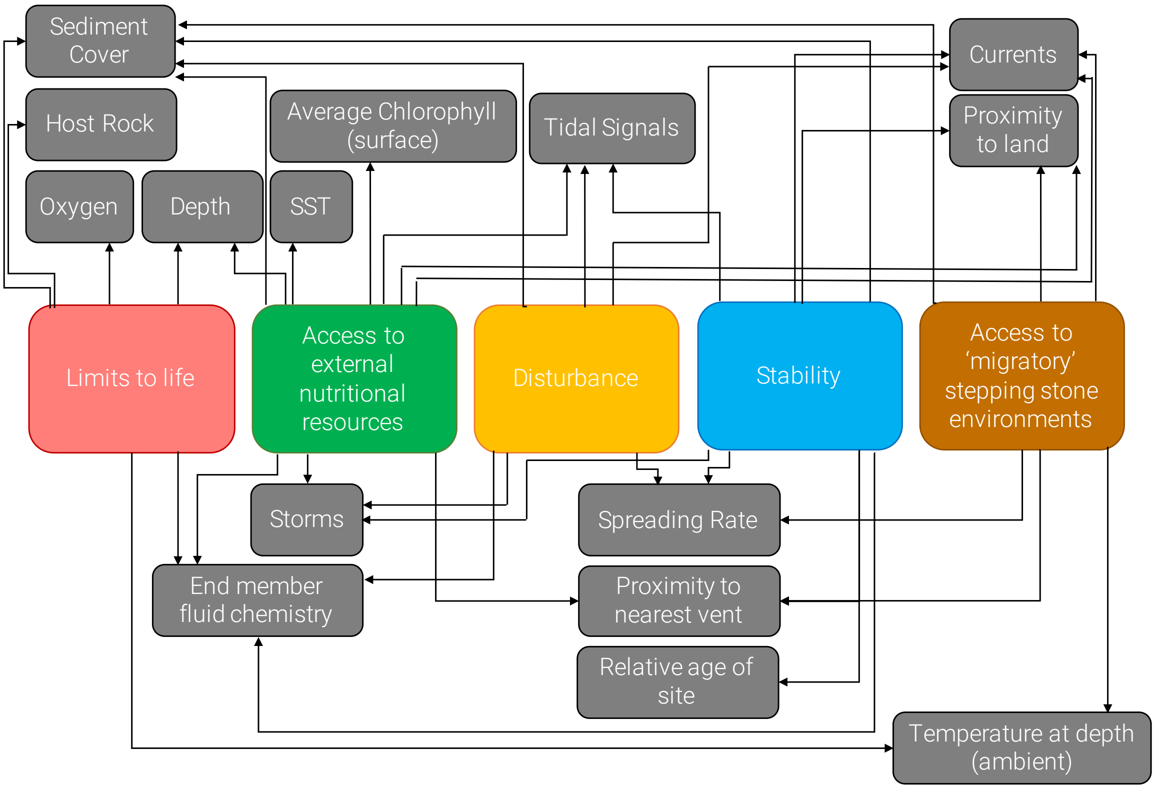
2.2 Analysing variability in environmental parameters among vent fields

First, we computed summary statistics (e.g., mean, standard deviation, range) across all vent fields for each of the environmental variables, to compare overall variability. Next, to visualise the spatial variability of each of the environmental variables, we mapped each at a global scale using ArcMap software (ESRI, 2014). Given the spatial constraint on storm intensity (predominantly tropical), we removed this variable before conducting subsequent analyses. We then performed a cluster analysis to group vent fields based on environmental similarity (and to identify outliers and remove 'noise'; Greenacre and Primicerio, 2013). While k-means clustering has been commonly selected for similar purposes (likely due to its relatively low computational intensity; Spector, 2011; Sayre et al., 2017), we did not use this method, as the results were unstable (i.e. different numbers of clusters were identified, using the pseudo-F statistic, each time the k-means clustering algorithm was run). We therefore selected the more robust (Spector, 2011; Greenacre and Primicerio, 2013) 'partitioning around medoids' (PAM) clustering method, implemented in R (R Core Team, 2017) using the 'cluster' package (Maechler et al., 2017). We used the 'manhattan' distance dissimilarity structure, as this is more robust to outliers, which were present in some variables. We selected eleven clusters following an analysis of optimal clusters using multiple indices computed via the 'clValid' and 'NbClust' R packages (centroid method; Brock et al., 2008; Charrad et al., 2014). Eleven was the number of clusters consistently optimal, after three, which we deemed uninformative for the identification of manageable bioregions, given different maximum possible cluster selections. As the PAM approach is still limited by its requirement for pre-selection of the number of clusters, we compared the clusters identified using this approach to those from a hierarchical agglomerative cluster analysis, using the 'hclust' function of the 'stats' package built into R (R Core Team, 2017). We used the 'Ward D2' agglomeration method on the 'manhattan' distance to seek compact, spherical clusters.

Finally, we ran a correlation test (Pearson's rank correlation, using the 'rcorr' function of the 'Hmisc' R package; Harrell Jr., 2018) to determine the strength of correlations among variables included in this analysis (including storm intensity). As many variables were correlated, we used a principal component analysis (PCA, on all variables except storm intensity) to identify: i) which variables are most associated with one another, and ii) which variables explain the most dissimilarity among global deep-sea hydrothermal-vent fields. We conducted and presented this analysis using the 'stats' and 'ggbiplot' R packages (Vu, 2011; R Core Team, 2017). We scaled the data for cluster and PCA analyses, to standardise to a mean of zero and standard deviation of one, as the environmental variables have different units.

Figure 24 (overleaf, and caption continues overleaf): The overall conceptual framework, highlighting how environmental characteristics influence vent systems: limits to life (i.e. environmental factors affecting which species can survive, given their physiology); access to external nutritional resources; disturbance events; factors influencing stability; and access to 'stepping stone' environments (e.g. possible migratory pathways for mobile fauna or long-distance dispersers, and through evolutionary time for others). Panel a) is an overview of the framework, wherein SST is sea-surface temperature. Panel b) highlights the overlap in both the variables and the five key areas, with some variables abbreviated for display purposes as follows: FLUID CHEM - end-member fluid chemistry, SPR - spreading rate, TEMP - ambient temperature at depth, SST - sea-surface temperature, CHL-A - average surface chlorophyll, VENT - proximity to nearest vent, LAND - proximity to land, ST - storms, TIDE - tidal signals, CURR - currents.

a)


Sediment Cover
Host Rock
Oxygen
Depth
SST
Average Chlorophyll (surface)
Tidal Signals
Currents
Proximity to land
Limits to life
Access to external nutritional resources
Disturbance
Stability
Access to 'migratory' stepping stone environments
Storms
Spreading Rate
End member fluid chemistry
Proximity to nearest vent
Relative age of site
Temperature at depth (ambient)

b)

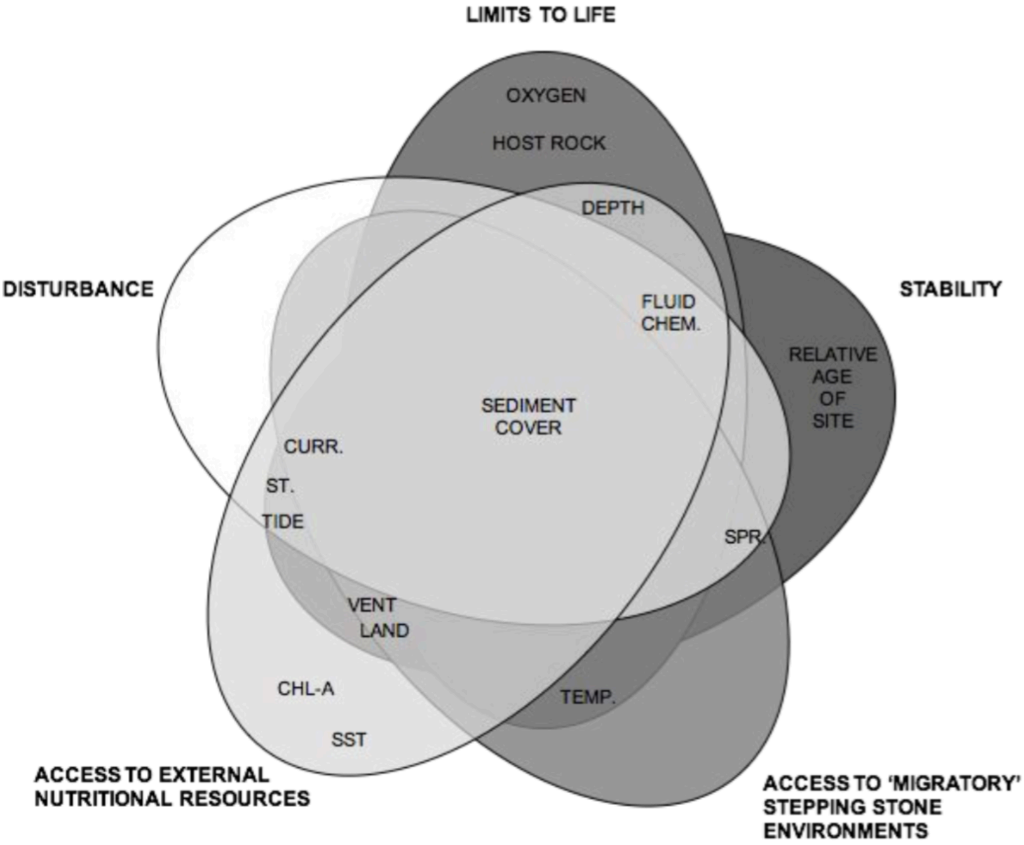

LIMITS TO LIFE
OXYGEN
HOST ROCK
DEPTH
DISTURBANCE
STABILITY
FLUID CHEM.
RELATIVE AGE OF SITE
SEDIMENT COVER
CURR.
ST.
TIDE
SPR.
VENT
LAND
CHL-A
TEMP.
SST
ACCESS TO EXTERNAL NUTRITIONAL RESOURCES
ACCESS TO 'MIGRATORY' STEPPING STONE ENVIRONMENTS

Table 7: Rationale for the selection of environmental variables in this study, with literary support. Codes link the variables to overarching ecological processes, defined as follows: OCEANGEO - oceanography and geology working together to influence nutrient and habitat availability, as well as the stability of the environment; PROD - nutrient availability and productivity; and COMP - community assembly and composition. The 'Variable in Conceptual Framework' column links the variables to the influences on vent ecosystems (either as given in **Figure 24**, or similar to a given variable in the figure). Note that the references provided as literary support are examples and do not comprise an exhaustive list.

VARIABLE and CODE	AFFECTING…	VARIABLE IN CONCEPTUAL FRAMEWORK	LITERARY SUPPORT FOR RELEVANCE TO VENT ECOSYSTEMS
Depth OCEANGEO PROD COMP	Diversity and physiology of fauna Interactions between systems (e.g. chemical exchanges, productivity, dispersal; thus taxonomic/functional/phylogenetic similarity between systems) Relative contribution of chemosynthetic vs. photosynthetic productivity (and thus community composition, recruitment, and diversity)	Depth	Sarrazin et al., 2015 Levin et al., 2016
Sediment thickness **Total organic carbon in sediments**	Fluid chemistry composition (and thus habitat availability) Sediment cover (and thus habitat availability, type, and setting)	Sediment cover, host rock, end-member fluid chemistry	Baumberger et al., 2010 Levin et al., 2016

OCEANGEO PROD COMP	Delivery of organic material (and thus productivity and food supply)		Dunn et al., 2018
Tidal range **Tidal form factor** OCEANGEO PROD	Species density Recruitment Species distribution Mixing, which affects habitat availability via: • Ambient temperature • Chemistry • Bioavailability of potentially toxic compounds • Exposure to radionuclides	Tidal signals	Cuvelier et al., 2017 Lelievre et al., 2017
Storm intensity OCEANGEO PROD	Species distribution Bottom pressure and mixing (re-suspension), which affects habitat availability via: • Ambient temperature	Storms	Lelievre et al., 2017

	• Chemistry • Bioavailability of potentially toxic compounds • Exposure to radionuclides		
Current velocity OCEANGEO PROD	Turbidity / particle flux (and thus food availability, sedimentation, and dispersal) Larval transport and exchange Interactions between systems (e.g. chemical exchanges, productivity, dispersal; thus taxonomic/functional/phylogenetic similarity between systems)	Currents	Cuvelier et al., 2017 Tyler, 2003 Gonnella et al., 2016 Levin et al., 2016 Mitarai et al., 2016 Zhang et al., 2014
Turbidity OCEANGEO PROD	Mixing, which affects habitat availability via: • Ambient temperature • Chemistry • Bioavailability of potentially toxic compounds • Exposure to radionuclides	Currents	Cuvelier et al., 2017

Primary production (Chl-a at surface and at depth, dissolved iron, phosphate, nitrate, carbon in phytoplankton, and silicate) PROD	Productivity and nitrogen fixation Diversity Abundance and survival of larvae (through predation) Flux of materials/food to deep sea (2000 m) and to larvae	Average chlorophyll (surface)	Sarrazin et al., 2015 Tyler, 2003 Luther III et al., 2001
Temperature at depth **Salinity at depth** **Sea-ice cover** **Dissolved oxygen at depth** PROD	Water masses and ocean circulation, affecting chemical exchanges, productivity, dispersal, and other interactions between systems	SST, temperature at depth (ambient), proximity to land	Luther III et al., 2001 Johnson et al., 1988
Seafloor roughness OCEANGEO COMP	Diversity Larval transport Ocean circulation / currents, vertical mixing, and energy dissipation (and the processes affected by this – see previous row)	Currents, sediment cover, end member fluid chemistry, host rock	Cuvelier et al., 2017 Sarrazin et al., 2015 Mitarai et al., 2016 Ramirez-Llodra et al., 2007

	Fluid chemistry (rock composition/porosity; and thus habitat availability)		Von Damm, 1995
Spreading rate (full rate, in mm per year) COMP	Stability (relative disruption of subsurface flow paths) Species richness and diversity	Spreading rate	Cuvelier et al., 2017 Sarrazin et al., 2015 Baker et al., 2016 Juniper and Tunnicliffe, 1997
Proximity to nearest vent field COMP	Species richness and diversity Larval dispersal (duration of survival approximately related to spacing/distance between vent fields, affecting recruitment success/failure) Metapopulation dynamics	Proximity to nearest vent	Cuvelier et al., 2017 Sarrazin et al., 2015 Ramirez-Llodra et al., 2007 Baker et al., 2016
Longevity of vents (Seafloor age) COMP	Species richness and diversity Larval dispersal Physical, chemical and biological conditions at vents (and thus	Relative age of site	Cuvelier et al., 2017 Sarrazin et al., 2015 Lelievre et al., 2017

	taxonomic/functional/phylogenetic similarity between systems) Stability and habitat age		Ramirez-Llodra et al., 2007
Proximity to nearest seep COMP	Larval transport and metapopulation dynamics	Access to ‘migratory’ stepping stone environments	Larval transport among systems suggested in Levin et al., 2016

Table 8: Environmental variables included in this analysis, with associated source information. For information on data processing, see **Appendix C.1**. 'ABBREV.' is short for 'ABBREVIATION' and, in this case, refers to the short code given to each variable in some figures and tables in this chapter (and variables in **Appendix C.5**).

VARIABLE	DESCRIPTION / PARAMETER(S)	SOURCE	FILE TYPE	ABBREV.
Longitude	Longitudinal location of active, confirmed vent fields.	Beaulieu, 2015	.csv	-
Latitude	Latitudinal location of active, confirmed vent fields.	Beaulieu, 2015	.csv	-
Seafloor depth (maximum and average)	Average seafloor depth (bathymetry) in metres, and maximum seafloor depth (in metres). Note that average depth was used in analyses in this chapter as deeper depths were recorded in this variable than in maximum in some cases.	BioORACLE: Tyberghein et al. (2012) and Assis et al. (2017)	Direct import in R using 'sdmpredictors' package.	DEPTHmean
Seafloor age	Crustal age in millions of years (multiplied by 100 for storage in short integer form) for each vent field, based on data modelled and presented on a geographic grid with 2-minute resolution. More information about the origin data for this variable is provided here: https://www.ngdc.noaa.gov/mgg/ocean_age/.	Müller et al., 2008	NetCDF	AGE
Proximity to nearest vent field	Minimum distance (km) between all active, confirmed vent fields (including those shallower than 200 m), as computed using geodesic distances between vent fields (which account for the curvature of the Earth and handle fields near the poles and International Date Line appropriately).	Calculated using location data available in: Beaulieu, 2015	.csv	PROXVENT
Sediment thickness	Sediment thickness estimates (average thickness over each 5-minute grid cell) in metres for the locations of each active, confirmed vent field location.	Whittaker et al., 2013; Amante and Eakins, 2009	NetCDF	THICKNESS

Seafloor roughness	Seafloor roughness for active, confirmed vent field locations in mGals (multiplied by 100 for storage purposes) and in 2-minute resolution (computed using a 100 km filter width). More information is provided in the accompanying paper stored here: http://earthbyte.org/Resources/Pdf/Whittaker_etal_seafloor_roughness_Nature2008.pdf.	Whittaker et al., 2008	NetCDF	ROUGHNESS
Proximity to nearest seep	Minimum distance (km) between each active, confirmed vent field (including those shallower than 200 m) and its nearest seep, according to publically available seep location data, compiled in 2010. Distances were computed using geodesic distances between vent fields and seeps (which account for the curvature of the Earth and handle fields near the poles and International Date Line appropriately).	Baker and Cuvelier, 2010, as published in German et al., 2011	.csv	PROXSEEP
Storm intensity	Maximum storm intensity recorded at the location of each active, confirmed vent field, on a scale from 0 to 4 (Saffir-Simpson categories), extracted from data on tropical cyclone wind-speed buffer footprint estimates from 1970-2009.	Raw data: IBTrACS; compilation and GIS processing: UNEP/DEWA/GRID-Europe.	Geotiff	STORM
Full spreading rate (mm/yr)	Full spreading rate (in millimetres per year) for the ridge upon which each active, confirmed vent field is located.	Beaulieu, 2015	.csv	SPREADING
Tidal range	Tidal range for each location of each active, confirmed vent field.	Extracted for vent fields by I. Haigh from data as per Figure 9 of Haigh, 2017	.csv	TIDALRANGE
TOC in sediment	Organic carbon content of sediments (calcite).	Seiter et al., 2004a; Seiter et al., 2004b	.asc	TOC

Tidal form factor	Tidal form factor for the location of each active, confirmed vent field, on a scale between 0 and 4, wherein: a score of < 0.25 indicates a semidiurnal tide; 0.25-3 suggests that it can vary between diurnal and semidiurnal; and > 3 implies a diurnal tide.	Extracted for vent fields by I. Haigh from data as per Figure 9 of Haigh, 2017	.csv	TIDALFORM
Turbidity (Kd)	Turbidity measured for the location of each active, confirmed vent field location using the downwelling diffuse attenuation coefficient based on satellite observations of downwelling spectral irradiance at 490 nm wavelength (K-d(490)) using the Visible Infrared Imaging Radiometer Suite (VIIRS).	NASA Goddard Space Flight Center, Ocean Biology Processing Group, 2014	NetCDF	TURBIDITY
Sea-surface Chl-a concentration	Chlorophyll-a concentration at the sea surface.	BioORACLE: Tyberghein et al. (2012) and Assis et al. (2017), accessible via: http://www.bio-oracle.org/index.php	Direct import in R using 'sdmpredictors' package (Bosch, 2017).	CHLss
Chlorophyll concentration at depth	Long-term maximum mass concentration of chlorophyll in seawater at maximum depth.	As above	As above	CHLdepth
Seawater velocity at depth	Long-term maximum seawater velocity at maximum depth.	As above	As above	CURRENT
Dissolved oxygen at depth	Long-term maximum mole concentration of dissolved oxygen (molecular) in seawater at maximum depth.	As above	As above	DISSOXY
Dissolved iron at depth	Long-term maximum mole concentration of dissolved iron in seawater at maximum depth.	As above	As above	IRON

Phosphate at depth	Long-term maximum mole concentration of phosphate in seawater at maximum depth.	As above	As above	PHOSPHATE
Nitrate at depth	Long-term maximum mole concentration of nitrate in seawater at maximum depth.	As above	As above	NITRATE
Seawater temperature at depth	Long-term maximum seawater temperature at maximum bottom depth.	As above	As above	TEMP
Seawater salinity at depth	Long-term maximum seawater salinity at the bottom at maximum bottom depth.	As above	As above	SALINITY
Phytoplankton (as carbon) at depth	Long-term maximum mole concentration of phytoplankton (as carbon) in seawater at maximum depth.	As above	As above	CARBONPHYTO
Silicate at depth	Long-term maximum mole concentration of silicate in seawater at maximum bottom depth.	As above	As above	SILICATE
Sea ice	Long-term maximum sea ice concentration.	As above	As above	ICE

3. RESULTS

3.1 A 'typical' vent field

On the global scale, the average deep-sea vent field experiences the environmental conditions highlighted in **Table 9**. For instance, vent fields are typically located on relatively young areas of seafloor with thin sediments and low total organic carbon content. Other vent fields are usually close by (~20 km), while seeps are generally further afield (~1,500 km). Turbidity and current speeds tend to be minimal. While chlorophyll tends to be low at the sea surface and at depth, phosphate, nitrate, and silicate levels are generally relatively high. The average depth of a vent field is around 2,600 metres, where dissolved oxygen is available and ambient temperatures are low. The average full-spreading rate for vent fields across the globe is around 56 millimetres per year. The maximum rate is 194 millimetres per year and the minimum is 4 millimetres per year.

3.2 Correlation among environmental variables

Some of the environmental variables summarised in **Table 9** are correlated, as shown in **Figure 26**. Seafloor roughness is significantly ($p < 0.05$) and strongly (correlation coefficient greater than 0.5 or less than -0.5) correlated with spreading rate, total organic carbon in sediments, dissolved oxygen, phosphate, nitrate, and silicate, as well as proximity to nearby vent fields. The amount of total organic carbon in seafloor sediments is significantly negatively correlated with long-term maximum dissolved oxygen concentration and salinity at depth, as well as proximity to nearest seeps; total organic carbon is significantly and strongly, positively correlated with long-term maximum bottom phosphate, nitrate, and silicate records. Turbidity is strongly positively correlated with average Chl-a at the sea surface. Long-term maximum dissolved oxygen concentration at depth has some of the strongest significant correlations of all environmental variables (e.g., with long-term maximum salinity (positive), and phosphate, nitrate, and silicate (negative) at depth). Phosphate, nitrate, silicate, and salinity records are also significantly and strongly correlated with one another.

3.3 Spatial variability in the environmental characteristics of vent fields

Given the correlations between environmental variables identified in **Figure 26**, **Figure 25** and **Figure 27** can be used to identify key spatial differences in the environmental characteristics of vent fields for parameters that: i) have relatively high variability across space (and might help to group similar vent fields), and ii) are correlated with other variables, for which additional maps are then available in **Appendix C**. Note that all discussions refer to characteristics of ambient seawater at depth, rather than vent-fluid chemistry.

Within the framework of **Figure 24**, the parameters falling under 'limits to life' include: depth, sediment thickness, dissolved oxygen concentration, primary productivity and nutrients available at depth, and temperature and salinity. Depth is one of the most variable of these parameters across vent fields (**Figure 25a**). The shallowest fields are in the North Atlantic and Arctic oceans and the deepest are in the Mariana Trough (**Figure 25a**; **Figure 27c**). The northern part of the Mid-Atlantic Ridge (MAR) has the highest within-region depth variability (**Figure 25a; Figure 27c**). Sediment thickness is greatest in Gulf of California and Juan de Fuca Ridge vent fields, while thick sediments are also found in Mohns Ridge, Mariana Trough, East Scotia Ridge, and Reykjanes Ridge vent fields (**Figure 25s; Figure 27h**). The thinnest sediments are associated with Indian Ocean (Central Indian Ridge (CIR) and South West Indian Ridge (SWIR)), East Pacific Ocean (Galapagos, Gulf of California, North East Pacific Rise (NEPR) and South East Pacific Rise (SEPR)), North Fiji Basin, Pacific-Antarctic Ridge, and South MAR vent fields (**Figure 25s; Figure 27h**). Dissolved oxygen is distinctive among oceans (**Figure 25g; Figure 27d**), with Arctic Ocean fields associated with the highest concentrations of dissolved oxygen at depth, and eastern North Pacific vent fields with the lowest.

Regarding nutrient availability and primary productivity, the records for long-term maximum chlorophyll at the seafloor are consistent across many venting regions, but Reykjanes Ridge in the North Atlantic Ocean has notably higher productivity at depth than other regions (**Figure 25c**). Kolbeinsey Ridge in the Arctic Ocean also has relatively high chlorophyll levels at depth (**Figure 25c**). These patterns are consistent with those for average surface Chl-a, though the East Scotia Ridge and Gulf of California also have relatively high surface chlorophyll values that do not translate to long-term deep-water productivity (**Figure 25b; Figure 27a**). Iron (long-term maximum concentration at depth) is highest at Kolbeinsey Ridge in the Arctic Ocean, while Southern Ocean and Pacific-Antarctic Ridge vent fields are low in iron (**Figure 25e**). Phosphate shows a different pattern to the other nutrient-related variables (apart from nitrate, with which it is highly correlated); Northeast Pacific fields are associated with the highest long-term maximum phosphate and nitrate records and Arctic and North Atlantic vent fields the lowest (**Figure 25f**). The northern MAR vent fields have the highest within-region variability in phosphate (**Figure 25f**). Silicate values are highest in Northeast Pacific vent fields and lowest in the Arctic and North Atlantic (**Figure 25h**). Reykjanes Ridge vent fields have the highest long-term maximum temperature at depth, with Terceira Rift and North MAR fields also coincident with relatively high values (**Figure 25i**). Total organic carbon (TOC) in seafloor sediments is greatest and highly variable in Northeast Pacific vent fields (**Figure 25t; Figure 27l**). SEPR fields also have variable and relatively high TOC in their sediments (**Figure 25t; Figure 27l**). Fields with the lowest TOC in sediments are in the CIR, East Scotia Ridge, Kolbeinsey Ridge, MAR, and Terceira Rift regions

(**Figure 25t; Figure 27l**).

Oceanographic variables affecting 'limits to life' include salinity and temperature. Salinity is highest in North Atlantic vent fields (e.g., Reykjanes Ridge and Terceira Rift), and the lowest long-term maximum salinity record across all vent fields is associated with a field on the Juan de Fuca Ridge (**Figure 25j**). Relatively high salinity values are associated with Arctic and MAR vent fields (**Figure 25j**). The lowest long-term maximum temperature values are associated with Arctic and Southern Ocean vent fields (**Figure 25i**). Contrastingly, the MAR has relatively high long-term maximum temperature values, given the global pattern for this variable (**Figure 25i**).

Access to 'migratory' stepping stone environments is likely to be influenced by proximity to nearby vent fields and seeps, seafloor roughness, and currents. SWIR vent fields are furthest from other known vent fields (**Figure 25k; Figure 27f**). As most vent fields are proximal to other vent fields, the distances noted for the East Scotia Ridge, some MAR, and Woodlark Basin vent fields are relatively large (**Figure 25k; Figure 27f**). Vent fields furthest from known seeps are in the Woodlark Basin, with vents on the SWIR, SEPR, Pacific-Antarctic Ridge, North Fiji Basin, and CIR further from seeps more generally (**Figure 25l; Figure 27e**). Northeast Pacific fields are typically relatively close to seeps, as are South MAR fields and fields on the East Scotia Ridge (**Figure 25l; Figure 27e**). Seafloor roughness is greatest in northern MAR and SWIR vent fields (**Figure 25p**). CIR, Gorda Ridge, and Mohns Ridge fields are also associated with relatively high seafloor roughness, while Reykjanes Ridge and SEPR fields have relatively low roughness values (**Figure 25p**). Long-term maximum current velocity at depth is highest in some EPR vent fields, as well as fields in the Galapagos Rift, Reykjanes Ridge, and CIR (**Figure 25m; Figure 27b**). The lowest current speeds are associated with Juan de Fuca Ridge, Mohns Ridge, and Terceira Rift vent fields (**Figure 25m; Figure 27b**).

In addition to some previously described variables, parameters influencing access to external nutritional resources include: ice cover, storm intensity, turbidity, and tidal signals. Based on long-term records, sea-ice cover only affects vent fields in the Southern Ocean (**Figure 25o**). Tropical cyclones have historically been associated with CIR, Gulf of California, Lau Basin, Mariana Trough, NEPR, North MAR, North Fiji Basin, Reykjanes Ridge, and Terceira Rift vent fields, with the highest intensity cyclones having affected the Mariana Trough, as well as CIR, Lau Basin, and North Fiji Basin fields (**Figure 25n; Figure 27j**). Turbidity is greatest in Kolbeinsey Ridge, Reykjanes Ridge, and Mohns Ridge vent fields and lowest in CIR, Mariana Trough, and SEPR fields (**Figure 25w**). Tides vary between semidiurnal and diurnal in many Pacific Ocean and East Scotia Ridge vent fields, whereas tides are semidiurnal in CIR, Galapagos Rift, Lau Basin, Mohns Ridge, MAR, Reykjanes Ridge, and Terceira Rift fields. Woodlark Basin is the region most likely to be associated with diurnal tides (**Figure 25q**). Tidal range is greatest in Northeast Pacific vent fields and those on Reykjanes Ridge. Ranges are also relatively high in CIR, North Fiji Basin and Terceira Rift fields (**Figure 25r; Figure 27k**). The lowest tidal ranges are associated with Pacific-Antarctic Ridge, SEPR, and SWIR vent fields (**Figure 25r; Figure 27k**).

Spreading rate and seafloor age influence disturbance and stability in vent ecosystems, in addition to some of the variables mentioned previously. East Scotia Ridge, Terceira Rift, and Woodlark Basin vent fields are associated with some of the oldest seafloor (**Figure 25v; Figure 27g**). The Galapagos Rift, Kolbeinsey Ridge, Mariana Trough, North Fiji Basin, and Reykjanes Ridge are also relatively old, but seafloor age is more variable among vent fields in these regions (**Figure 25v; Figure 27g**). Full-spreading rate is fastest in the South Pacific (SEPR) and slowest in Terceira Rift, SWIR, Reykjanes Ridge, and Arctic regions (**Figure 25u; Figure 27i**). Lau Basin vent fields have the highest within-region variability in spreading (**Figure 25u; Figure 27i**).

3.4 Clustering vent fields according to environmental similarity

The PAM and hierarchical clustering outputs are generally similar in that they both tend to demonstrate environmental similarities within ocean basins (**Figures 28** and **29**). In the PAM output (**Figure 28**), however, vent fields in the Galapagos Rift, SEPR, Gulf of California, N.MAR, East Scotia Ridge, and North Fiji Basin regions are found in multiple clusters, spanning beyond single provinces. In the hierarchical clustering output (**Figure 29**), the Galapagos Rift is firmly placed with the NEPR in terms of environmental characteristics and Terceira Rift is placed with N. MAR - separate in the PAM results (**Figure 28**). A major difference in the outcomes of the two clustering approaches lies in the Indian Ocean vent fields, which group with Pacific-Antarctic Ridge, East Scotia Ridge, and western Pacific Ocean vent fields under hierarchical classification but remain separated according to PAM results (**Figures 28** and **29**).

While many vent fields differ in their environmental characteristics, as discussed above, there is also environmental similarity among vent fields (hence the clusters in **Figure 28** and **Figure 29; Appendices C.3** and **C.4**). Some environmentally similar fields are, however, geographically and tectonically distinct. For instance, PAM cluster 4 (**Figure 28; Appendix C.3**) is dominated by southern Pacific Ocean mid-ocean-ridge vent fields (n = 25), but also contains Mussel Valley vent field, found on a back-arc spreading centre in the North Fiji Basin. Cluster 6 (**Figure 28**; **Appendix C.3**) contains vent fields from the Explorer, Gorda, and Juan de Fuca ridges, as well as the Guaymas Basin - mid-ocean-ridge hosted vent fields in the Northeast Pacific separated from one another by fracture zones. Indeed, clusters also span oceans and tectonic settings in the hierarchical cluster analysis. For example, cluster 1 contains vent fields on the CIR, SWIR, Mariana Trough, East Scotia Ridge, Lau Basin, Pacific-Antarctic Ridge, and SEPR mid-ocean ridges and back-arc spreading centres (**Figure 29**; **Appendix C.4**).

We can also use the clusters from both approaches (**Figure 28** and **Figure 29**; **Appendices C.3** and **C.4**) to identify relatively unique vent fields, in terms of their environmental characteristics. For instance, PAM cluster 11 separates out Steinaholl Vent Field - a mid-ocean-ridge hosted field on the Reykjanes Ridge in the North Atlantic Ocean. This field, as well as E9 vent field - a back-arc spreading-centre hosted field on the East Scotia Ridge in the Southern Ocean - is also separated when analysed using hierarchical clustering and the 'Ward D2' agglomeration method (clusters 7 and 5, respectively; **Figure 29**; **Appendix C.4**). The results of the Ward D2 and PAM clustering methods are similar, with the main difference being the further separation of vent fields from hierarchical agglomerative cluster analysis cluster 1 to multiple clusters in the PAM outputs (**Appendix C.3** and **Appendix C.4**).

3.5 Drivers of dissimilarity among vent fields

Although many vent fields can be clustered according to environmental similarity on a global scale (**Figure 28** and **Figure 29**), the presence of separate clusters also highlights environmental dissimilarity among vent fields. Potential environmental 'drivers' of this dissimilarity are shown using a principal component analysis (PCA) in **Figure 30**. Here, the Arctic vent fields (shown in salmon-coloured text) are primarily separated from other vent fields due to sediment thickness, primary productivity, depth, and iron concentration at depth, as well as long-term maximum temperature records at depth. Meanwhile, North Pacific vent fields (labelled in turquoise) cluster due to their tidal ranges and the total organic carbon present in their sediments. Some Northwest Pacific vent fields are dissimilar to Northeast Pacific vent fields because of differences in long-term maximum deep-water silicate, phosphate, nitrate, and current velocity values, and spreading rate. A vent field in the Mariana Trough is isolated from other vent fields in the Pacific due to its proximity to nearby seeps. The South Pacific cluster (highlighted in purple) is shaped by long-term maximum deep-water current velocity, spreading rate, and proximity to seeps, and Indian Ocean vent fields (shown in gold) are also clustered because of seep distances. The East Scotia Ridge E2 field (labelled in blue) separates from E9 (in pink font) because E9 is associated with different nutrients, depths, and seafloor sediment thickness, and is the only vent field to be affected by ice cover. In the Atlantic, southern fields (highlighted in light blue) are similar due to proximity to nearby vents, seafloor roughness, and dissolved oxygen concentration at depth, while northern fields (in light green), though more similar to South Atlantic fields than other fields, have distinct long-term maximum deep-water salinity and/or dissolved oxygen values, seafloor roughness, and proximity to nearby vents.

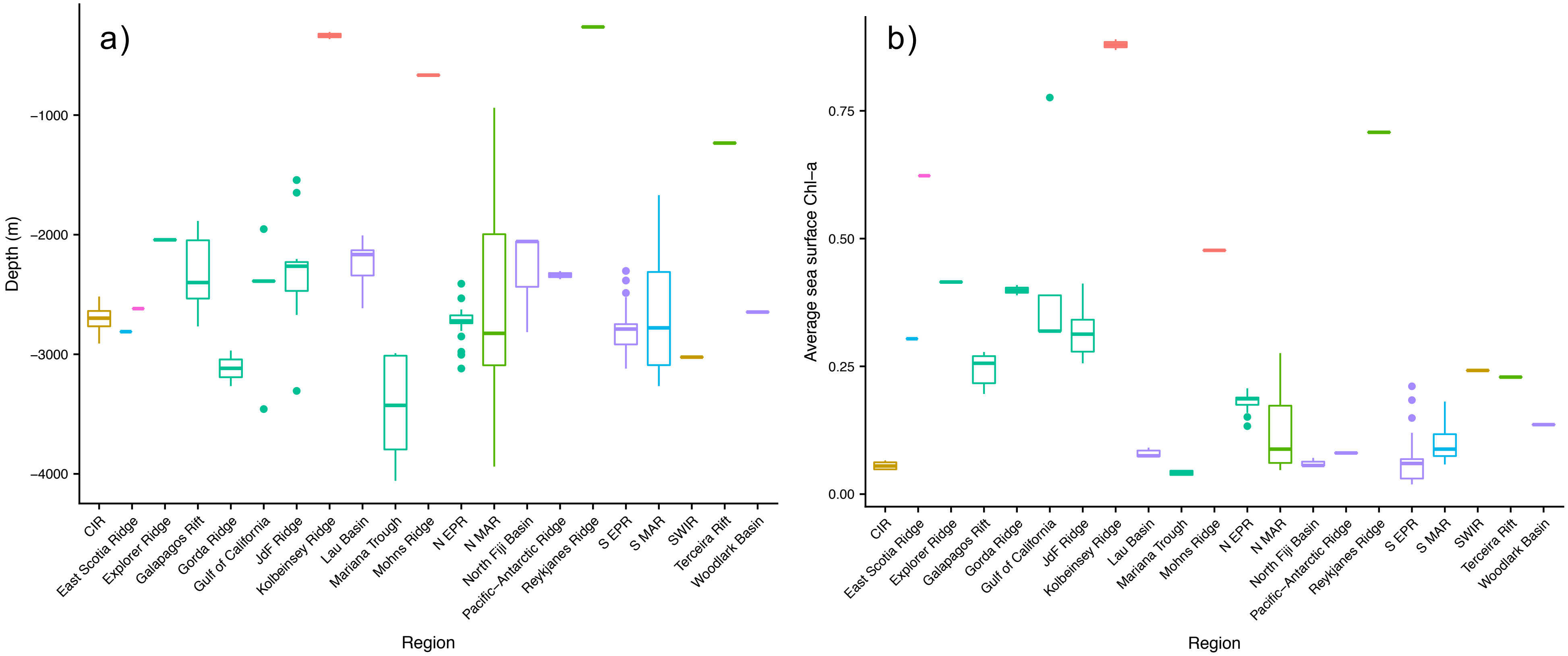
Table 9: Summary statistics for each environmental variable included in this study (excluding storm intensity, as this is mostly constrained to tropical fields), with the median shown in grey shading to highlight 'typical' vent-field conditions. 'Temp.' is an abbreviation of 'temperature' and 'TOC' of 'total organic carbon'; 'LTmax' is short for 'long-term maximum'. 'Chl-a' refers to chlorophyll-a – important for photosynthesis. Furthermore, 'S.E.' is the abbreviated form of Standard Error, 'C.I.' of Confidence Interval, 'Std. dev.' refers to standard deviation and 'Coef. var.' is the coefficient of variance.

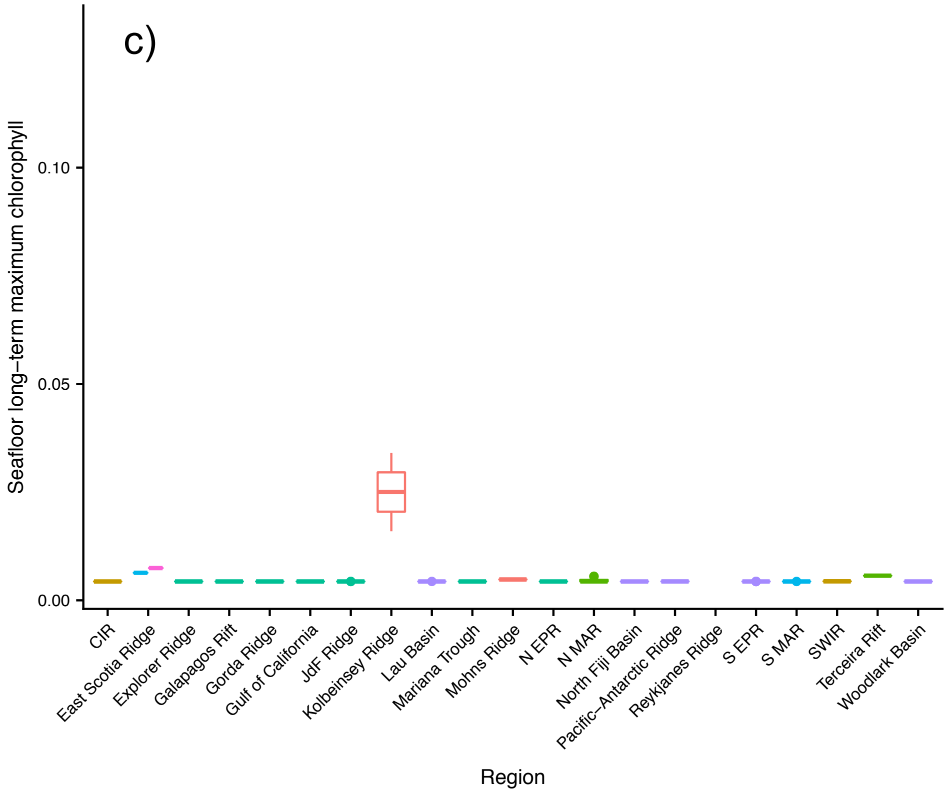
	Seafloor age (Ma)	**Proximity to nearest vent field (km)**	**Seafloor roughness**	**Sediment thickness**	**Proximity to nearest seep (km)**	**Tidal range**	**Tidal form factor**	**TOC in sediment**	**Full-spreading rate (mm per year)**
Records	146	146	146	146	146	146	146	146	146
Null	8	0	0	0	0	0	0	0	0
Min.	0	1.5	315	9	2.6	0.3	0.1	0.1	4.2
Max.	3941	2369.8	5607	671	4179.8	3.3	3	2.8	194.2
Range	3941	2368.3	5292	662	4177.3	3	2.9	2.7	190
Median	26	20.2	1043	25	1524.4	1	0.3	0.8	56.2
Mean	142.8	94.5	1469.3	63.9	1673.2	1.3	0.4	1.2	70.5
S.E. mean	37.2	19	93.6	6.5	99.3	0.1	0.03	0.1	3.4
C.I. mean (0.95)	73.5	37.5	185	12.9	196.3	0.1	0.06	0.1	6.8
Variance	201985.5	52687.3	1278800.2	6190.3	1440893.7	0.7	0.1	0.7	1733.3
Std. dev.	449.4	229.5	1130.8	78.7	1200.4	0.8	0.4	0.8	41.6
Coef. var.	3.1	2.4	0.8	1.2	0.7	0.7	0.9	0.7	0.6

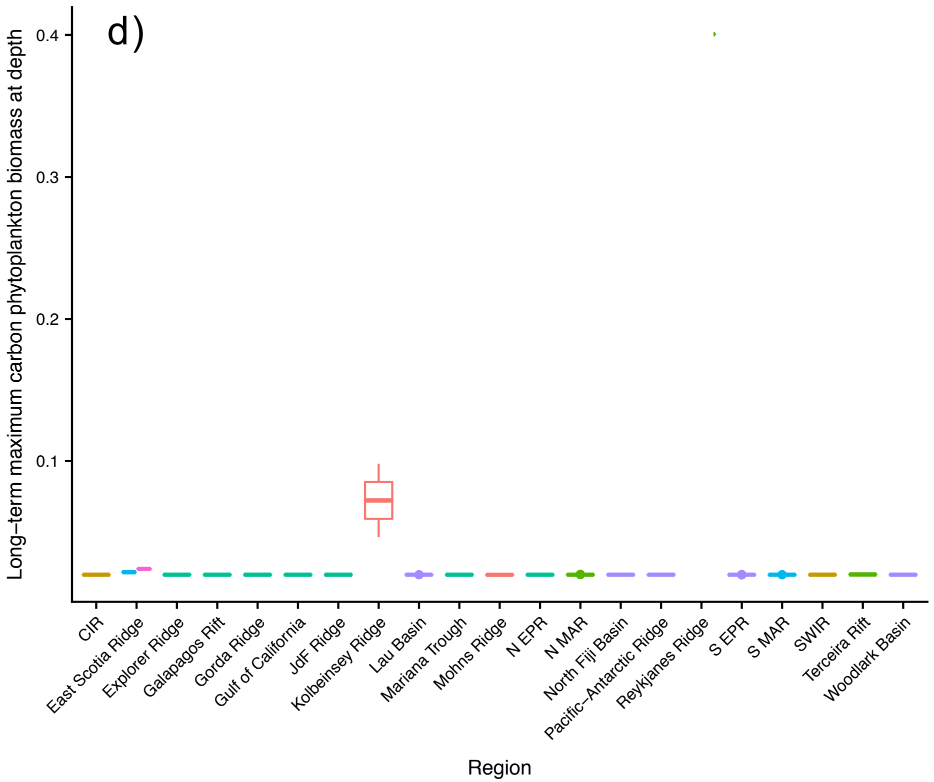
	Turbidity (Kd)	Average surface Chl-a	Mean depth (m)	LTmax chlorophyll at depth	LTmax current velocity at depth	LTmax dissolved oxygen at depth	LTmax iron concentration at depth	LTmax phosphate at depth	LTmax nitrate at depth
Records	146	146	146	146	146	146	146	146	146
Null	0	0	0	0	0	0	0	0	0
Min.	0.02	0.02	-263	0.004	0.001	55.9	0	0.8	11.3
Max	0.13	0.9	-4058	0.131	0.117	301.3	0.001	3.1	43.3
Range	0.11	0.9	3795	0.127	0.116	245.4	0.001	2.3	32.0
Median	0.03	0.2	-2625	0.004	0.021	148.8	0.001	2.6	37
Mean	0.04	0.2	-2514.8	0.006	0.026	155.7	0.001	2.4	34.8
S.E. mean	0.001	0.01	52.9	0.001	0.002	5	0	0.05	0.7
C.I. mean (0.95)	0.003	0.03	104.5	0.002	0.003	9.8	0	0.1	1.3
Variance	0	0.03	408037.6	0	0	3625.3	0	0.4	62.8
Std. dev.	0.02	0.2	638.8	0.011	0.019	60.2	0	0.6	7.9
Coef. var.	0.5	0.9	-0.25	1.93	0.712	0.4	0.128	0.2	0.2

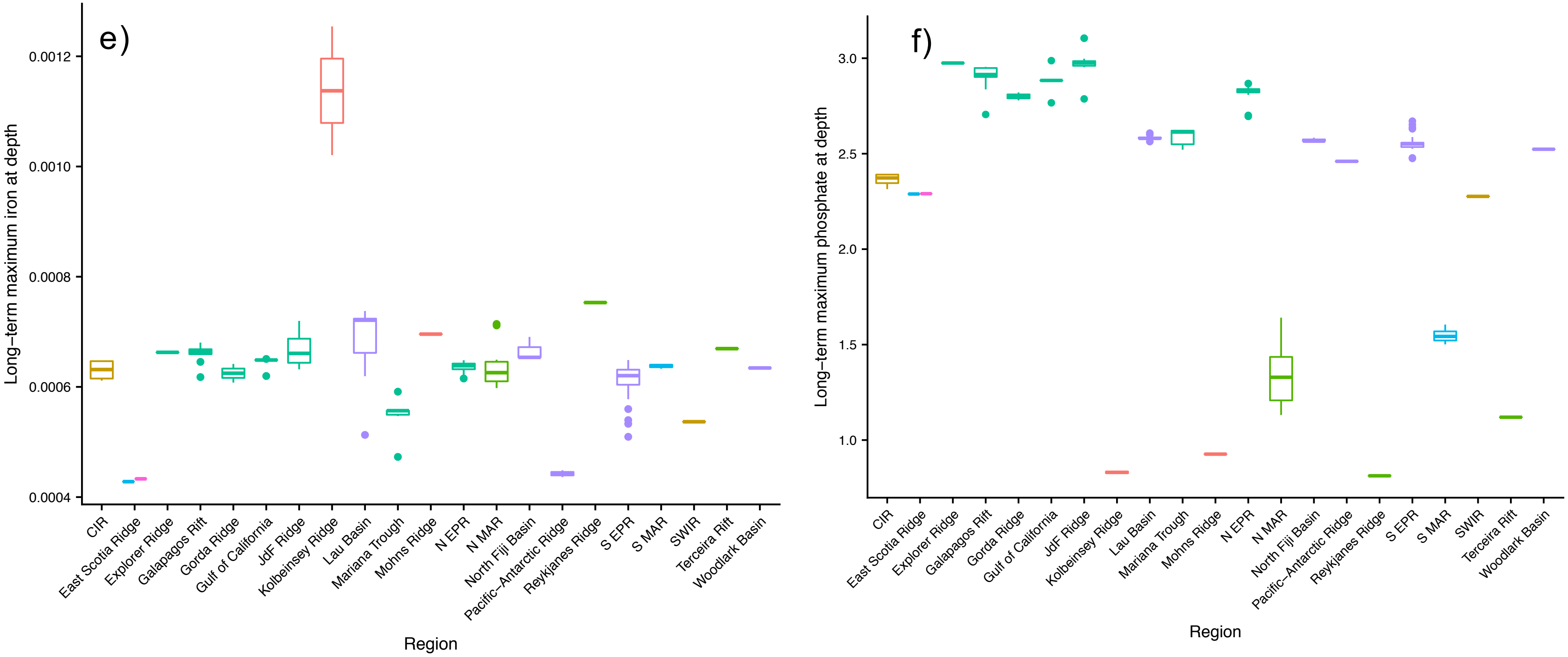
	LTmax temp. at depth	Long-term carbon in phytoplankton at depth	LTmax salinity at depth	LTmax silicate at depth	LTmax ice cover at the sea surface
Records	146	146	146	146	146
Null	0	0	0	0	140
Min.	-0.1	0.02	34.6	6.9	0
Max.	8.1	0.4	35.2	189.1	0.9
Range	8.2	0.4	0.7	182.3	0.9
Median	1.6	0.02	34.7	138.1	0
Mean	1.8	0.02	34.7	129	0.01
S.E. mean	0.07	0.003	0.01	4.4	0.01
C.I. mean (0.95)	0.1	0.005	0.02	8.6	0.01
Variance	0.8	0.001	0.02	2794.3	0.01
Std. dev	0.9	0.03	0.1	52.9	0.07
Coef. var.	0.5	1.4	0.004	0.4	11.1

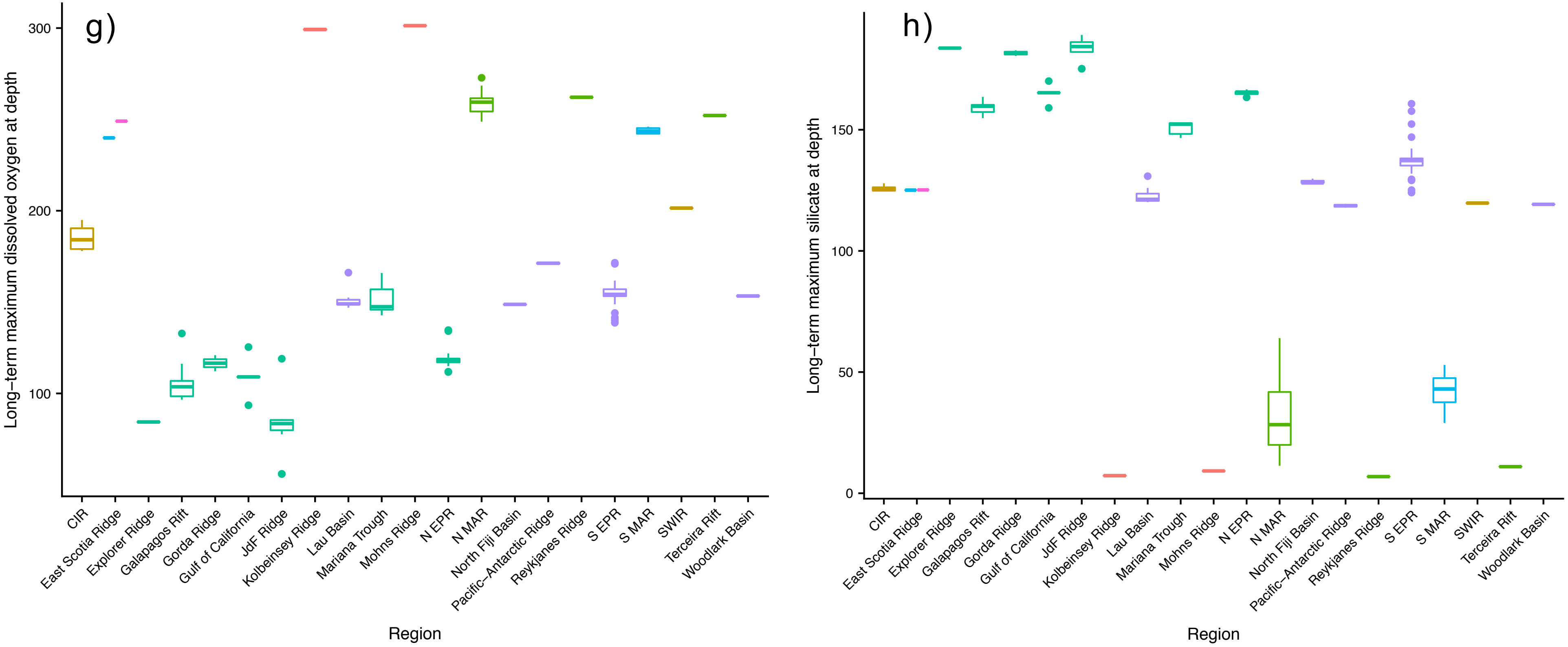
Figure 25 (overleaf): Boxplots summarising within-parameter, and spatial, variability in each of the environmental parameters. Note that long-term maximum nitrate concentration at depth has been excluded, as it shows the same pattern as long-term maximum phosphate concentration at depth. Variables included are as follows: a) average seafloor depth (metres); b) average sea-surface Chl-a (milligrams per cubic metre); c) long-term maximum chlorophyll at depth (milligrams per cubic metre); d) long-term maximum carbon phytoplankton biomass at depth (micromoles per cubic metre); e) long-term maximum iron concentration at depth (micromoles per cubic metre); f) long-term maximum phosphate concentration at depth (showing the same pattern as nitrate; micromoles per cubic metre); g) long-term maximum dissolved oxygen concentration at depth (micromoles per cubic metre); h) long-term maximum silicate at depth (micromoles per cubic metre); i) long-term maximum temperature at depth (degrees Celsius); j) long-term maximum salinity at depth (PSS - practical salinity scale); k) proximity to nearest vent field (kilometres); l) proximity to nearest seep (km); m) long-term maximum current velocity at depth (metres per second); n) tropical cyclone intensity (based on wind-speed buffer footprint and shown on a Saffir-Simpson scale, where higher values mean higher intensity storms have passed over the location); o) long-term maximum sea-surface ice cover; p) seafloor roughness (mGals, multiplied by 100 for display and processing purposes); q) tidal form factor; r) tidal range (metres); s) sediment thickness (millimetres); t) total organic carbon (TOC) in sediment (%); u) full spreading rate (millimetres per year); v) seafloor age (Ma, multiplied by 100 for display and processing purposes); and w) turbidity (Kd). Boxplots are colour-coded by ocean, as shown in panel w), consistent with the colour coding of **Figure 30**.

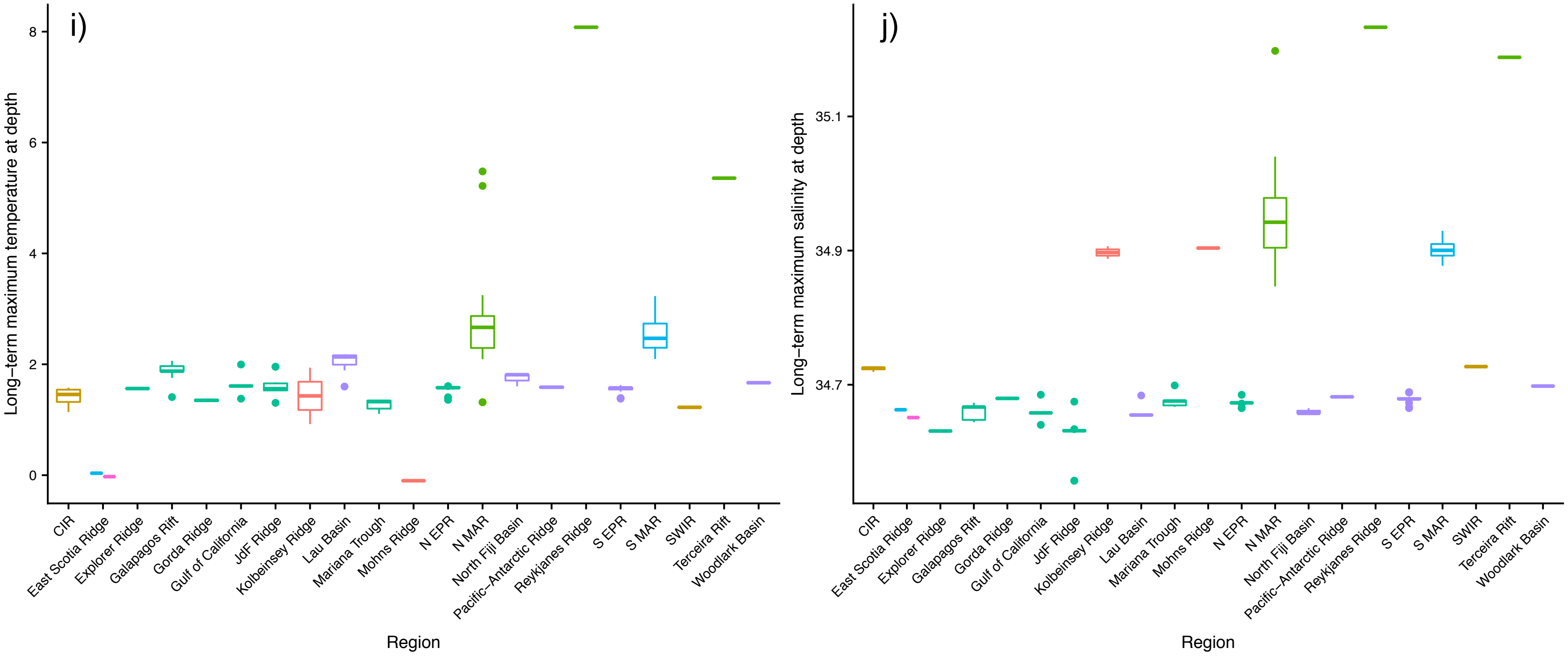

a)
Depth (m)
−1000
−2000
−3000
−4000
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
b)
Average sea surface Chl−a
0.75
0.50
0.25
0.00
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin

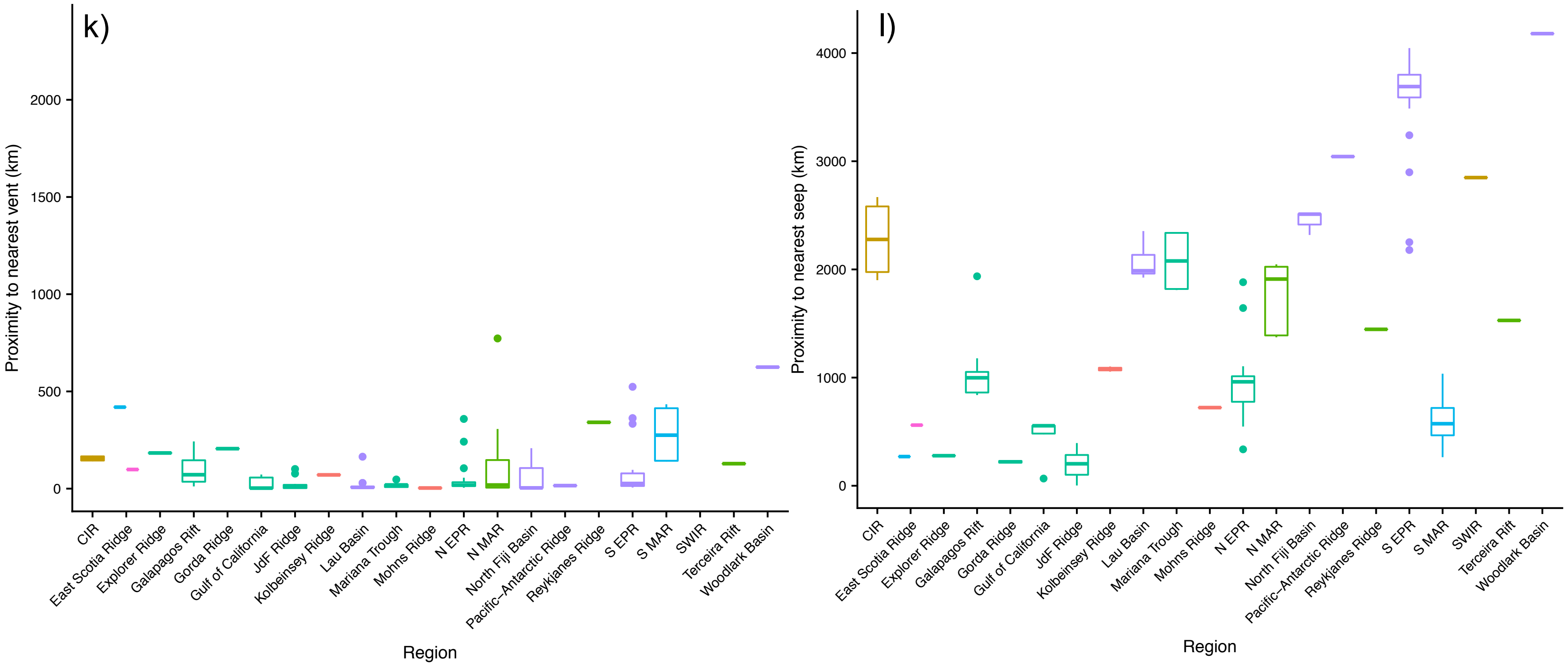

c)
Seafloor long−term maximum chlorophyll
0.10
0.05
0.00
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region

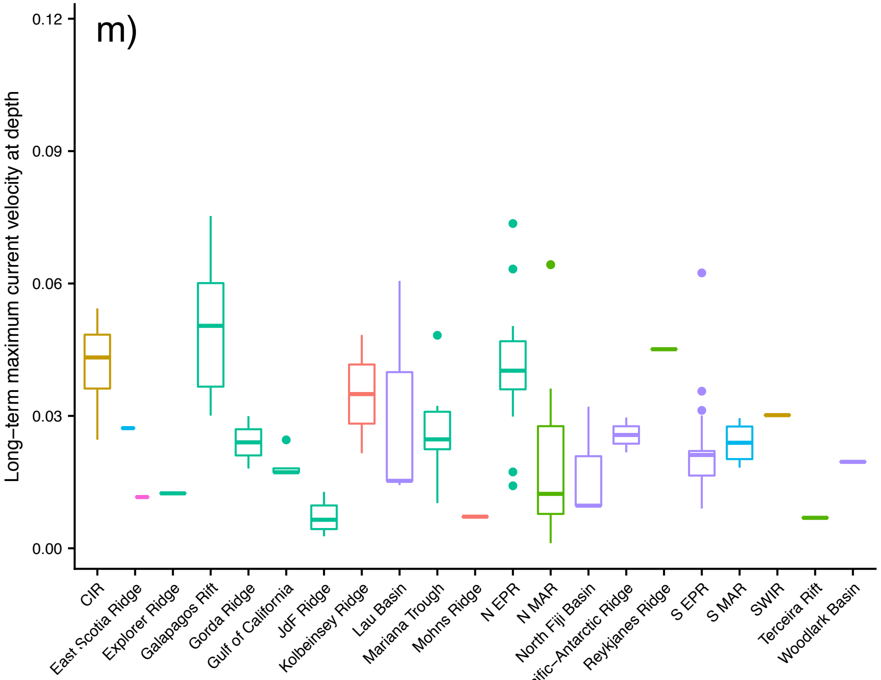

d)
Long−term maximum carbon phytoplankton biomass at depth
0.4
0.3
0.2
0.1
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region

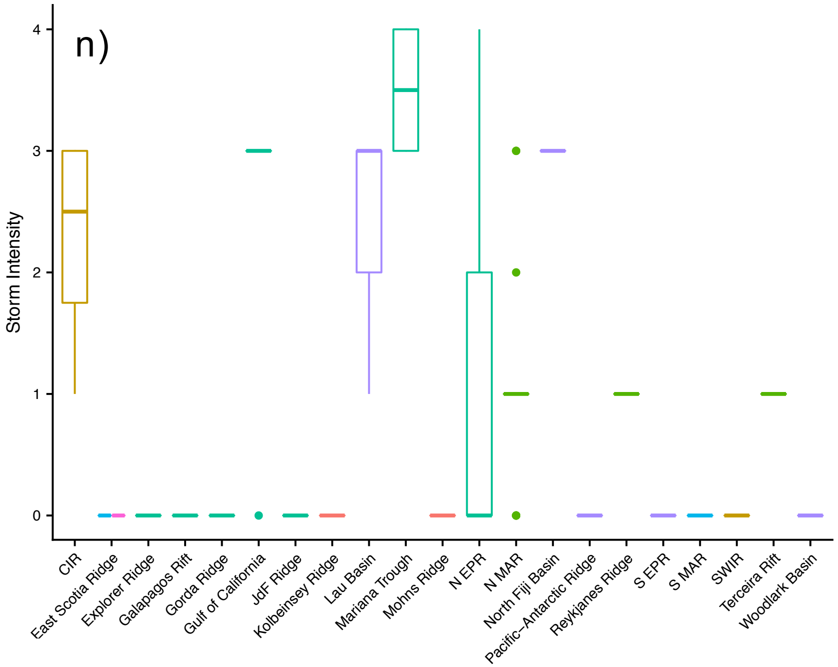

e)
Long−term maximum iron at depth
0.0012
0.0010
0.0008
0.0006
0.0004
Region
f)
Long−term maximum phosphate at depth
3.0
2.5
2.0
1.5
1.0
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin

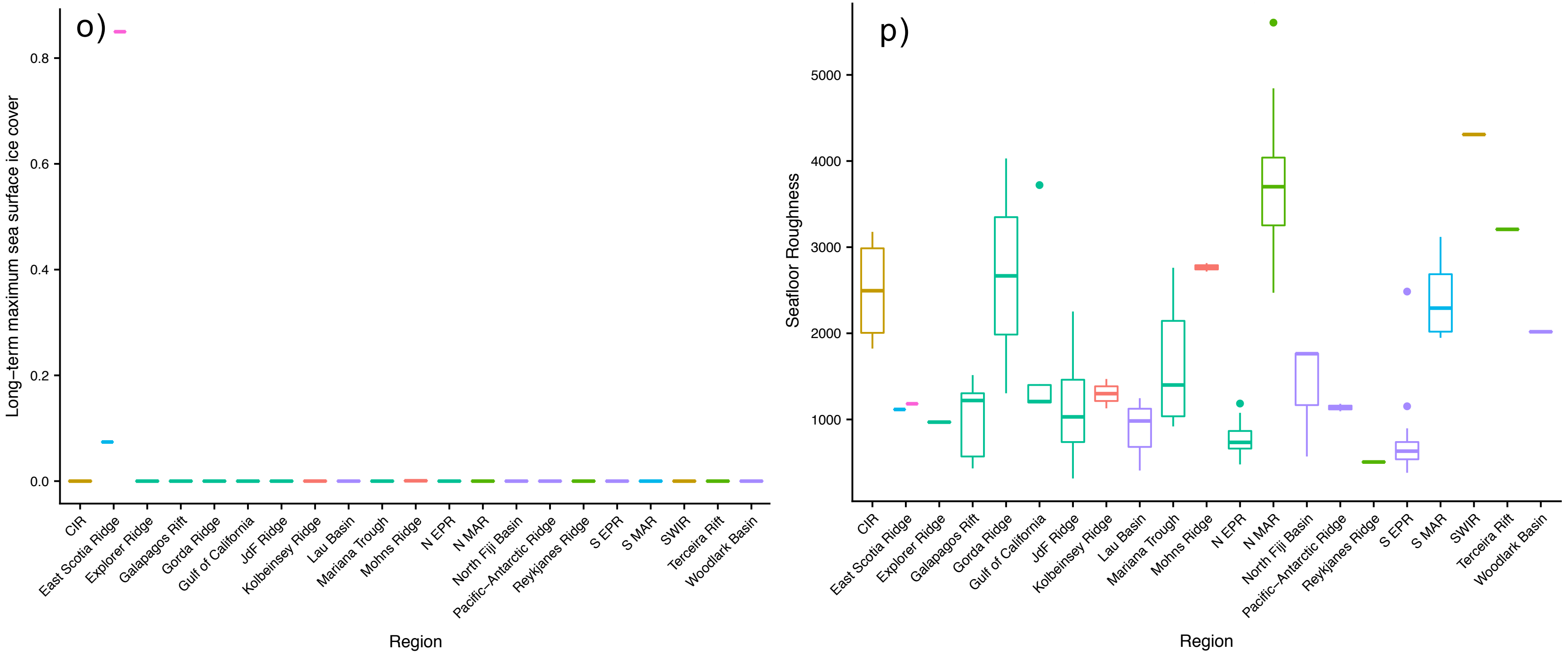

g)
Long−term maximum dissolved oxygen at depth
300
200
100
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region
h)
Long−term maximum silicate at depth
150
100
50
0
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region

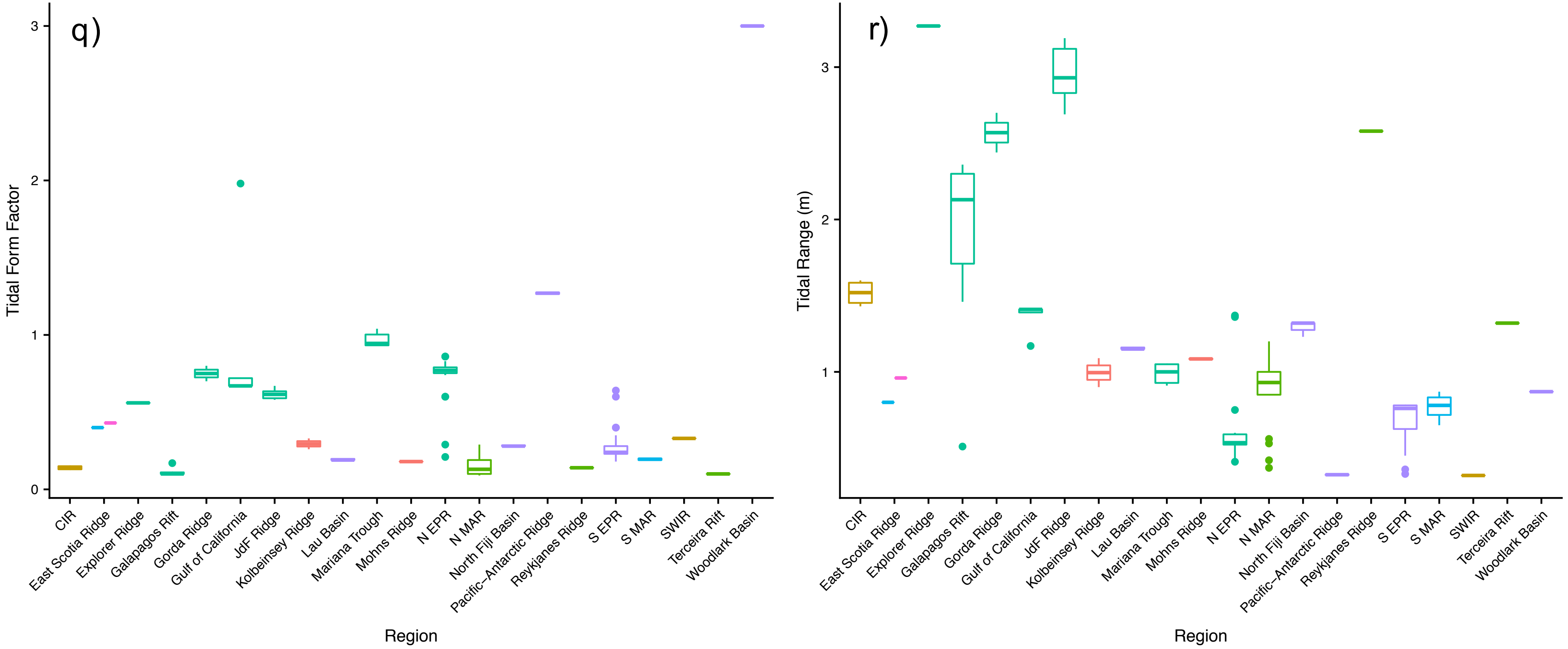

i)
Long−term maximum temperature at depth
0
2
4
6
8
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
j)
Long−term maximum salinity at depth
34.7
34.9
35.1
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin

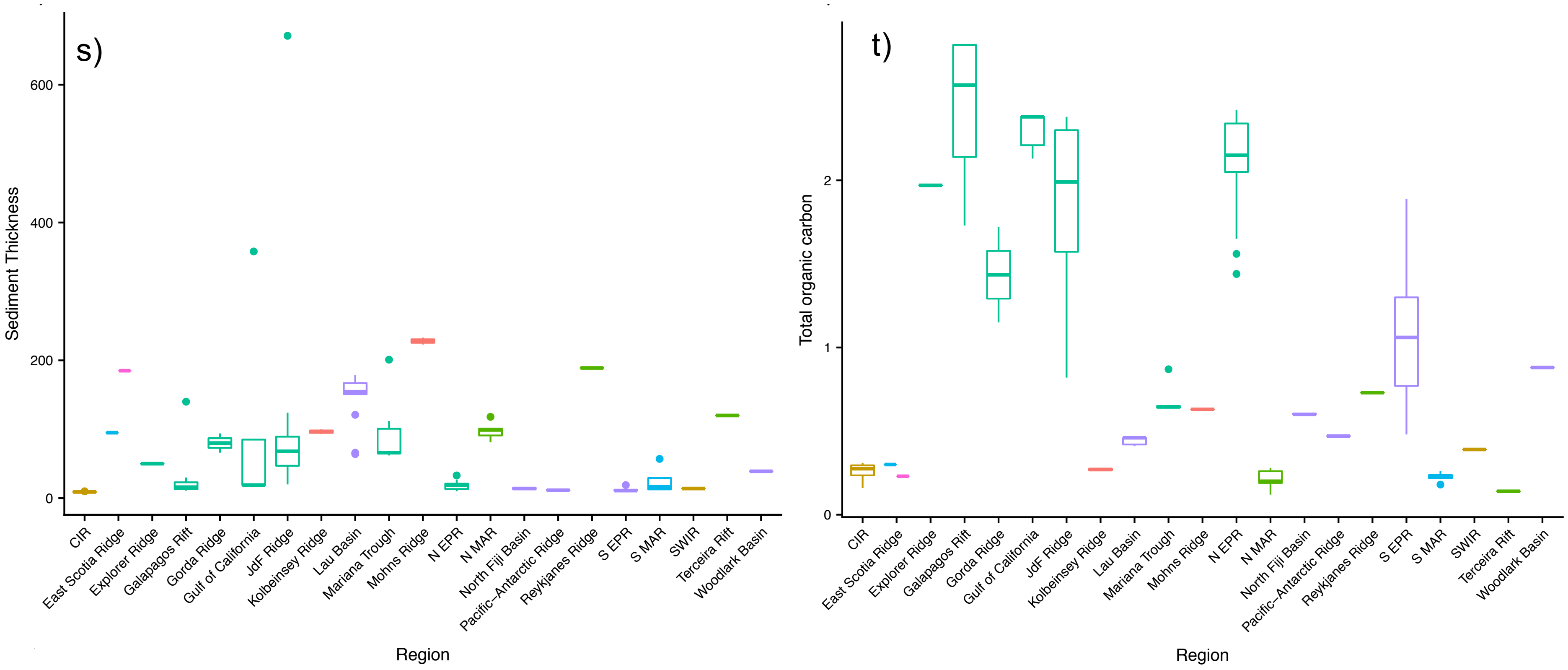

k)
Proximity to nearest vent (km)
0
500
1000
1500
2000
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region
l)
Proximity to nearest seep (km)
0
1000
2000
3000
4000
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region

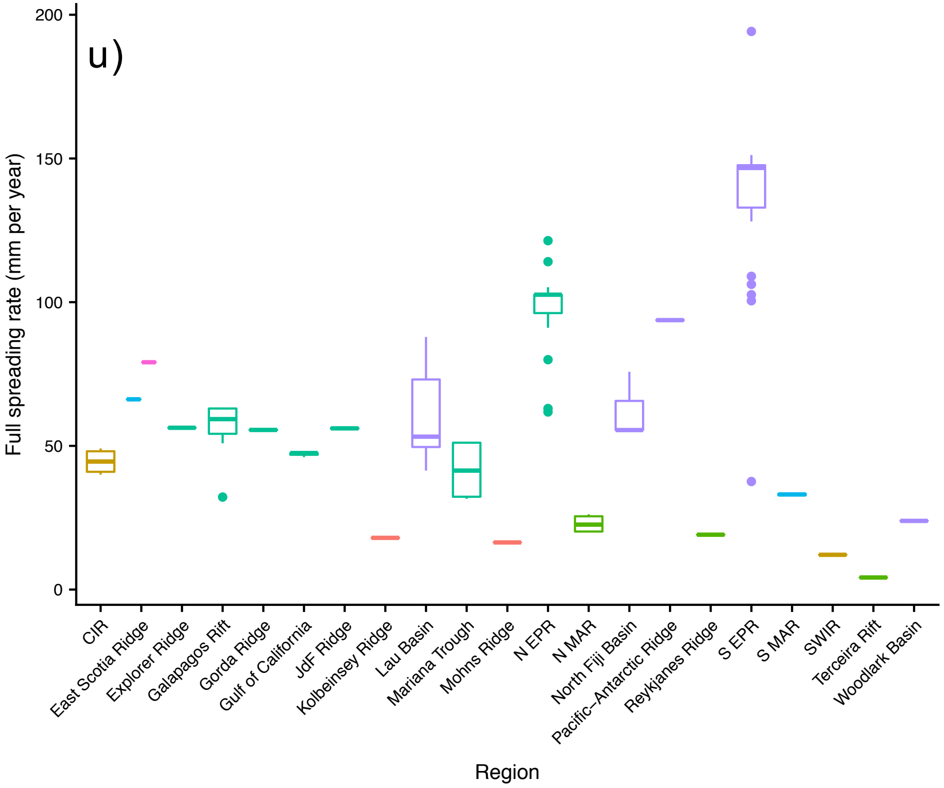

m)
Long−term maximum current velocity at depth
0.12
0.09
0.06
0.03
0.00
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin

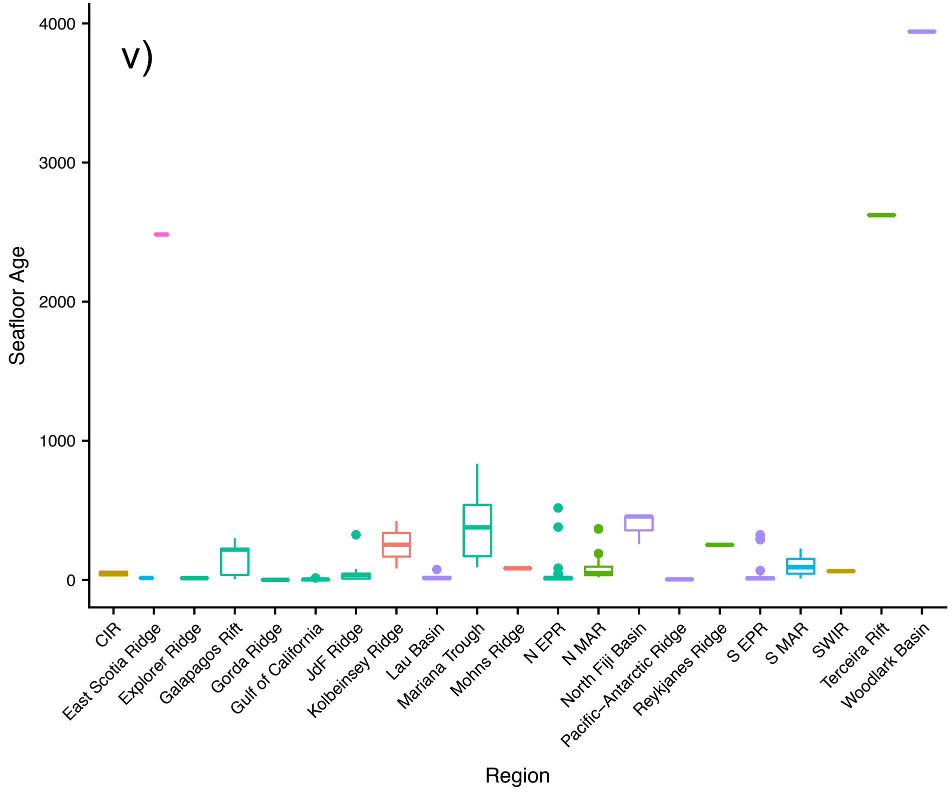

n)
Storm Intensity
4
3
2
1
0
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin

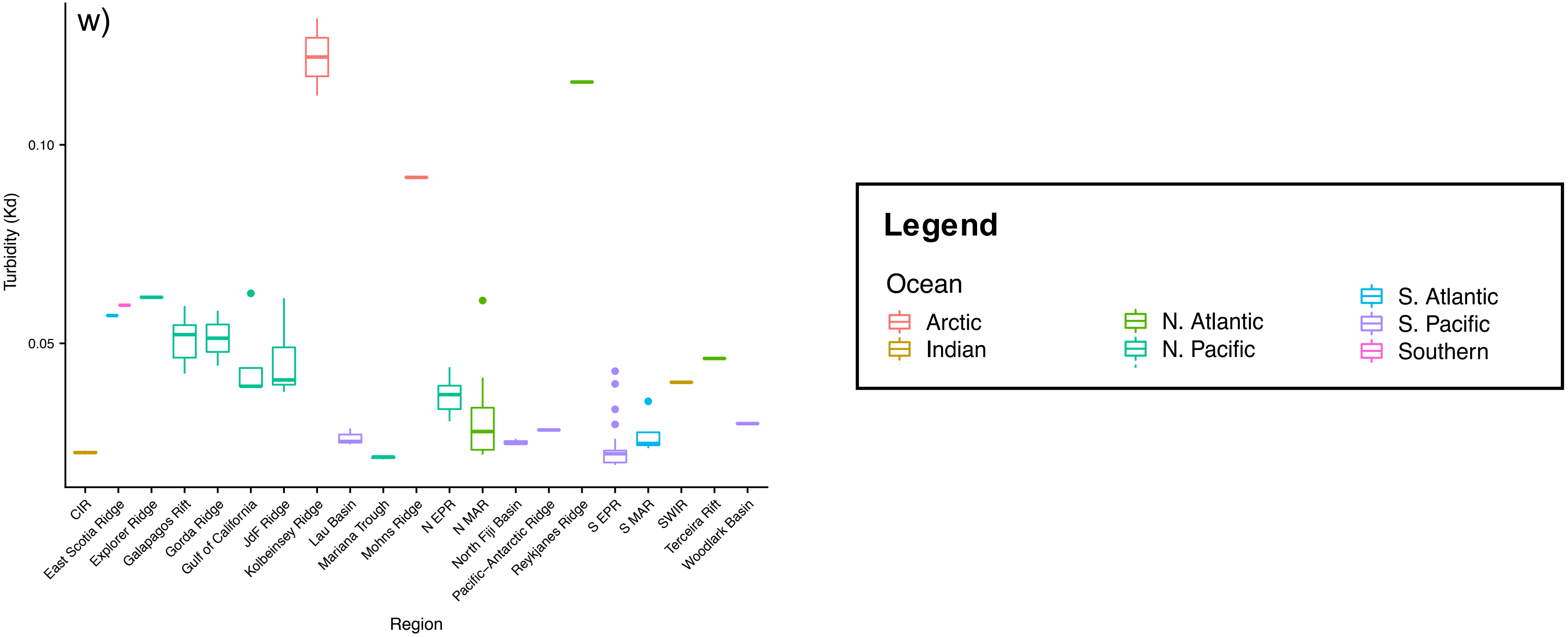

o)
Long−term maximum sea surface ice cover
0.0
0.2
0.4
0.6
0.8
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region
p)
Seafloor Roughness
1000
2000
3000
4000
5000
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific−Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region


q)
Tidal Form Factor
0
1
2
3
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region
r)
Tidal Range (m)
1
2
3
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region


s)
Sediment Thickness
0
200
400
600
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region
t)
Total organic carbon
0
1
2
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Region


u)
Full spreading rate (mm per year)
0
50
100
150
200
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin


v)
Seafloor Age
0
1000
2000
3000
4000
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin


w)
Turbidity (Kd)
0.10
0.05
Region
CIR
East Scotia Ridge
Explorer Ridge
Galapagos Rift
Gorda Ridge
Gulf of California
JdF Ridge
Kolbeinsey Ridge
Lau Basin
Mariana Trough
Mohns Ridge
N EPR
N MAR
North Fiji Basin
Pacific–Antarctic Ridge
Reykjanes Ridge
S EPR
S MAR
SWIR
Terceira Rift
Woodlark Basin
Legend
Ocean
Arctic
Indian
N. Atlantic
N. Pacific
S. Atlantic
S. Pacific
Southern

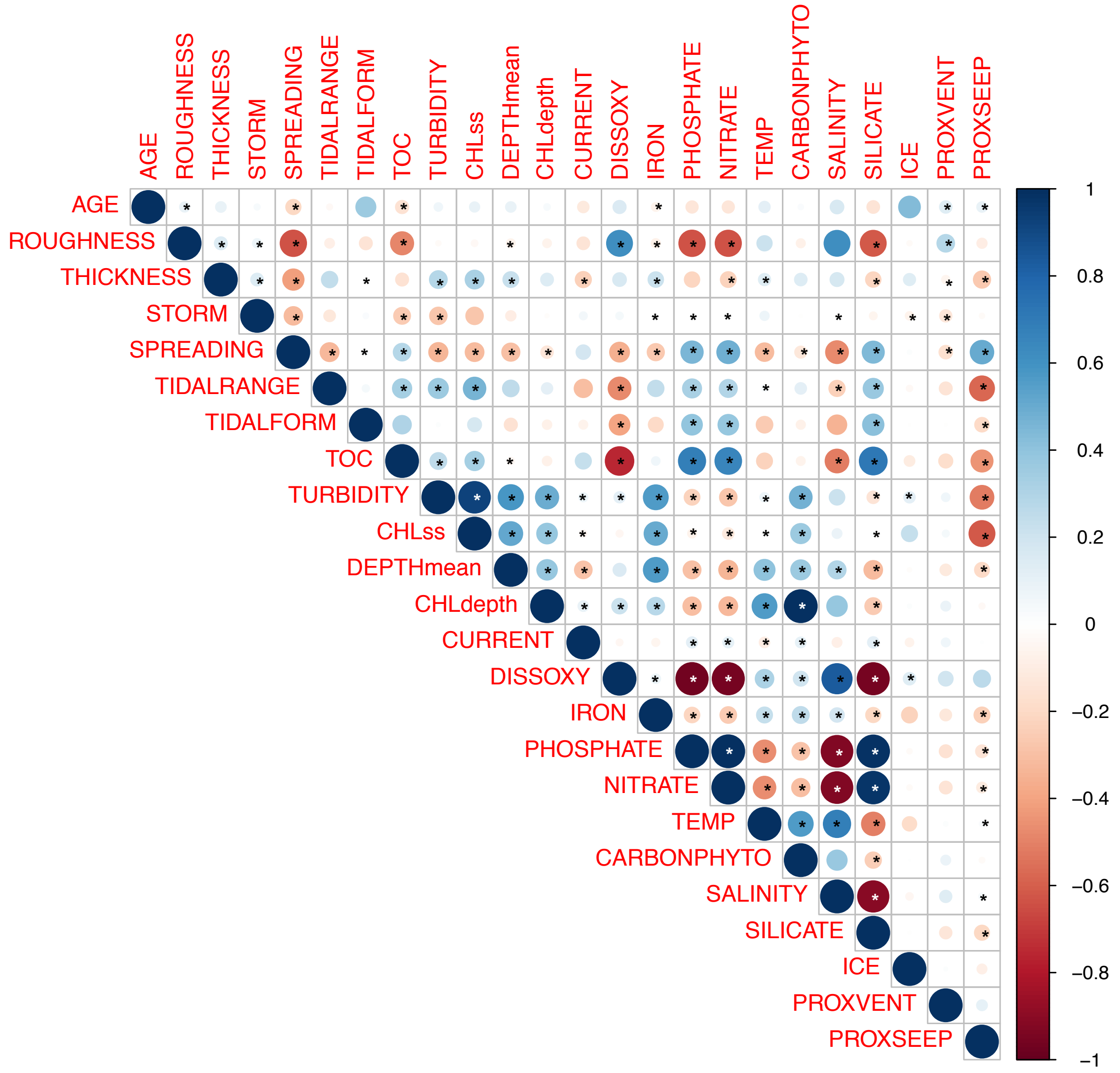
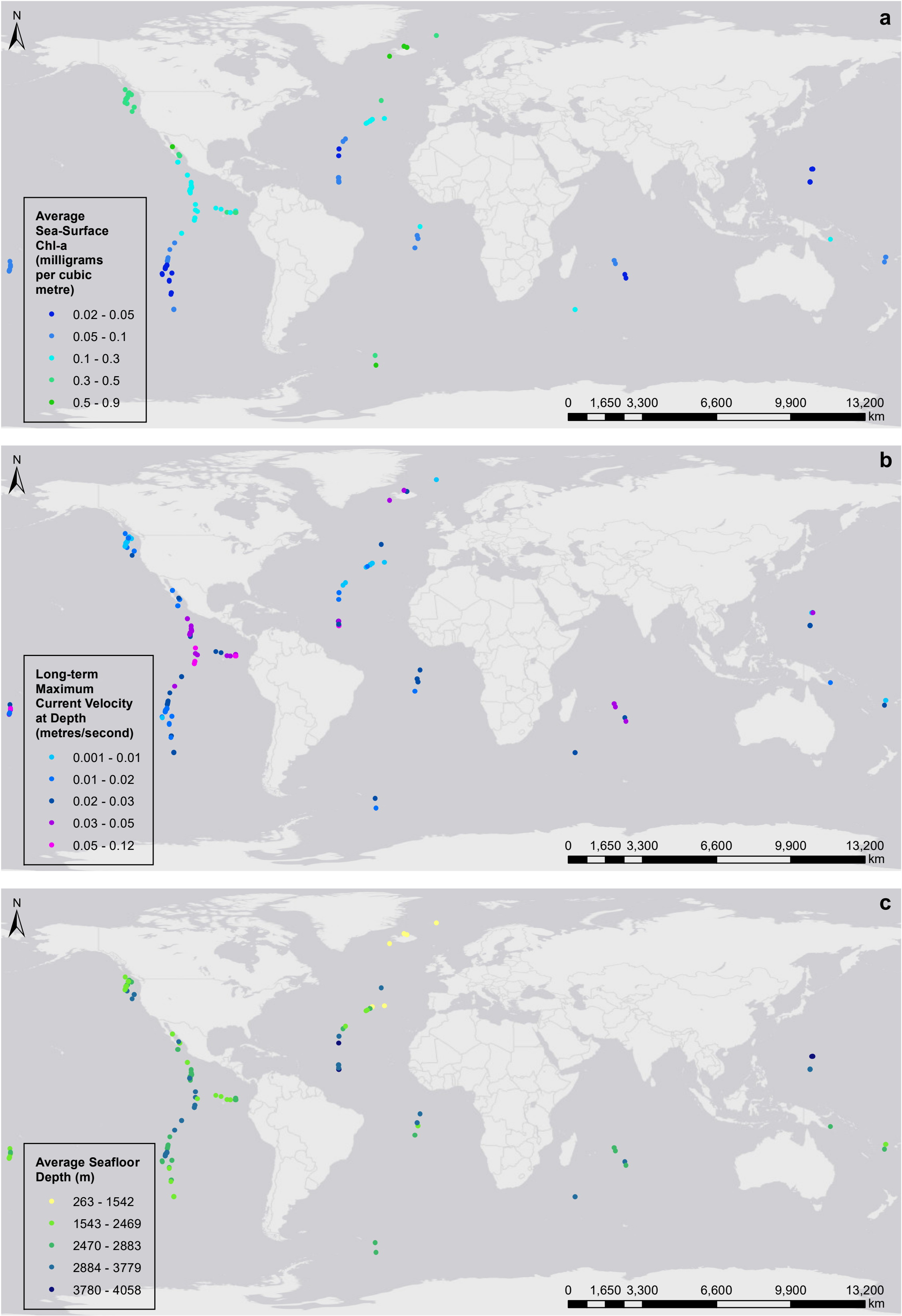
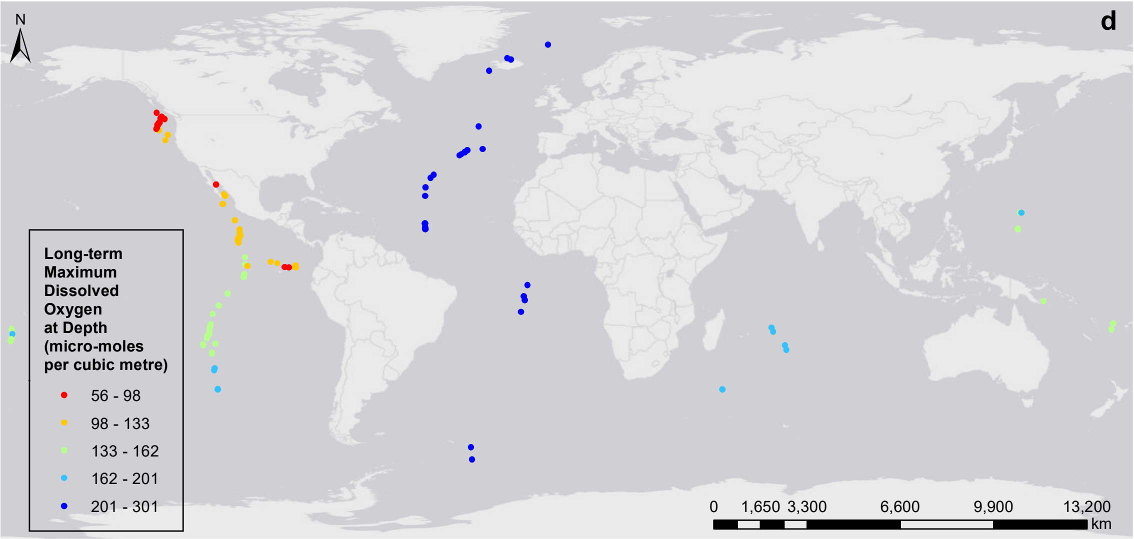


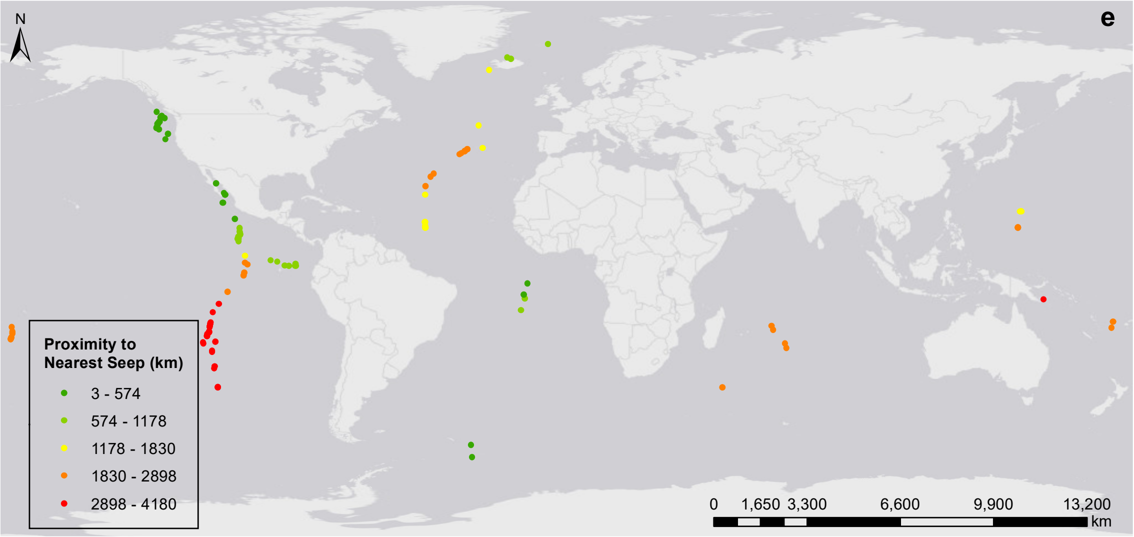
Figure 26: Pairwise correlations for each of the environmental variables included in this study, with significant correlations marked with a * for each member of the pair. Variable names have been shortened for presentation purposes, in accordance with **Table 8**. Only complete cases (vent fields with scores across all variables) were included in this analysis.

Figure 27 (overleaf)**:** Maps selected to document spatial variability in the environmental characteristics of vent fields on a global scale. The variables presented are as follows: a) average sea-surface Chl-a (milligrams per cubic metre); b) long-term maximum current velocity at depth (Kd); c) mean depth (metres); d) long-term maximum dissolved oxygen concentration at depth (micromoles per cubic metre); e) proximity to nearest seep (kilometres); f) proximity to nearest vent field (kilometres); g) seafloor age (Ma, multiplied by 100 for display and processing purposes); h) seafloor sediment thickness (millimetres); i) full spreading rate (millimetres per year); j) storm intensity (based on tropical cyclone footprint data - Saffir-Simpson scale); k) tidal range (metres); and l) total organic carbon (TOC) in seafloor sediments (%). Variables excluded from this selection, due to high correlation with those included, are mapped in **Appendix C.2**.

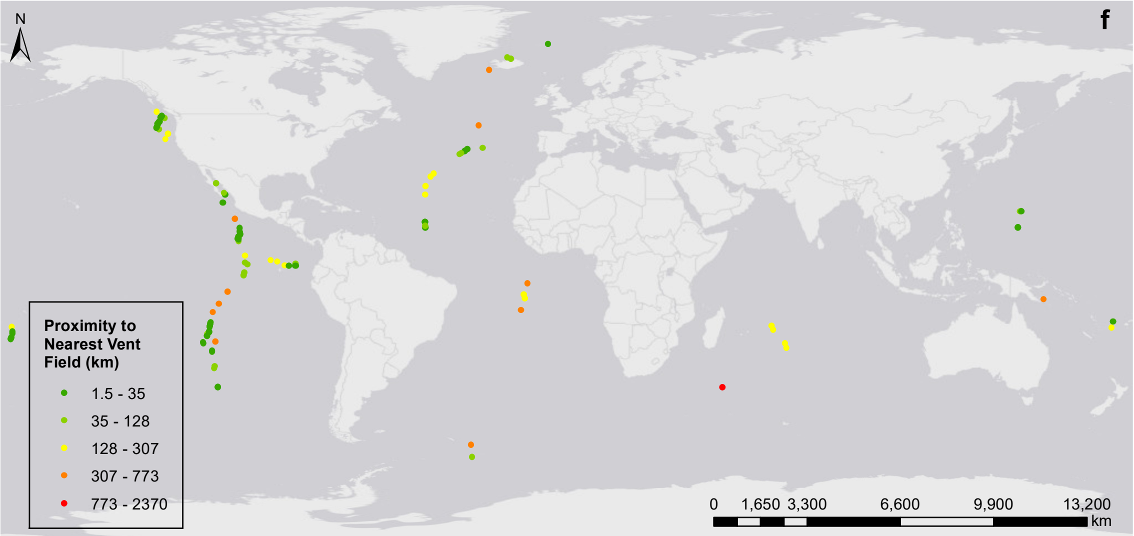

N
a
Average Sea-Surface Chl-a (milligrams per cubic metre)
● 0.02 - 0.05
● 0.05 - 0.1
● 0.1 - 0.3
● 0.3 - 0.5
● 0.5 - 0.9
0 1,650 3,300 6,600 9,900 13,200
km
N
b
Long-term Maximum Current Velocity at Depth (metres/second)
● 0.001 - 0.01
● 0.01 - 0.02
● 0.02 - 0.03
● 0.03 - 0.05
● 0.05 - 0.12
0 1,650 3,300 6,600 9,900 13,200
km
N
c
Average Seafloor Depth (m)
● 263 - 1542
● 1543 - 2469
● 2470 - 2883
● 2884 - 3779
● 3780 - 4058
0 1,650 3,300 6,600 9,900 13,200
km



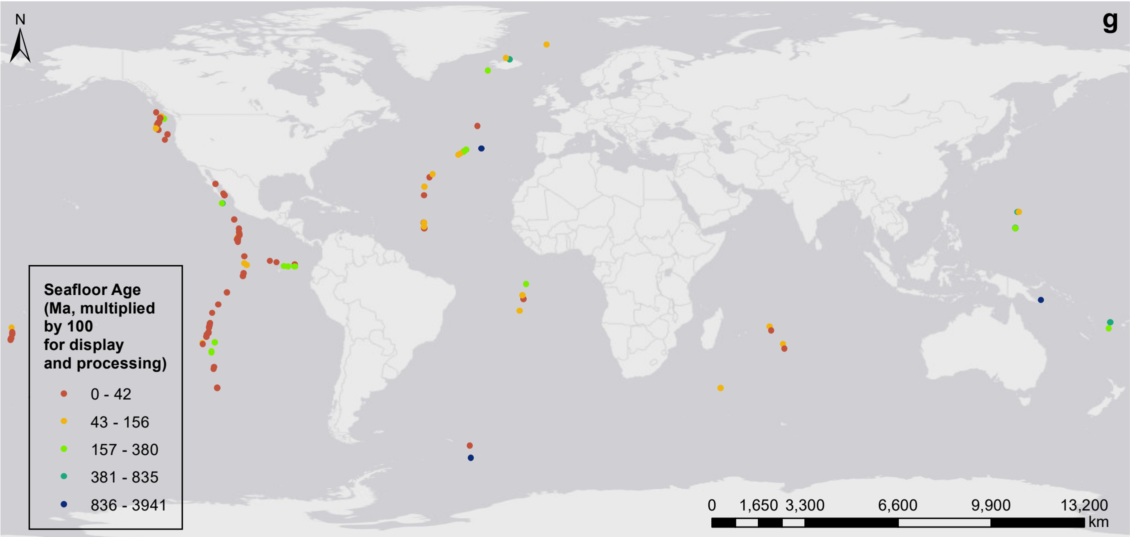
d
N
Long-term Maximum Dissolved Oxygen at Depth (micro-moles per cubic metre)
● 56 - 98
● 98 - 133
● 133 - 162
● 162 - 201
● 201 - 301
0 1,650 3,300 6,600 9,900 13,200 km

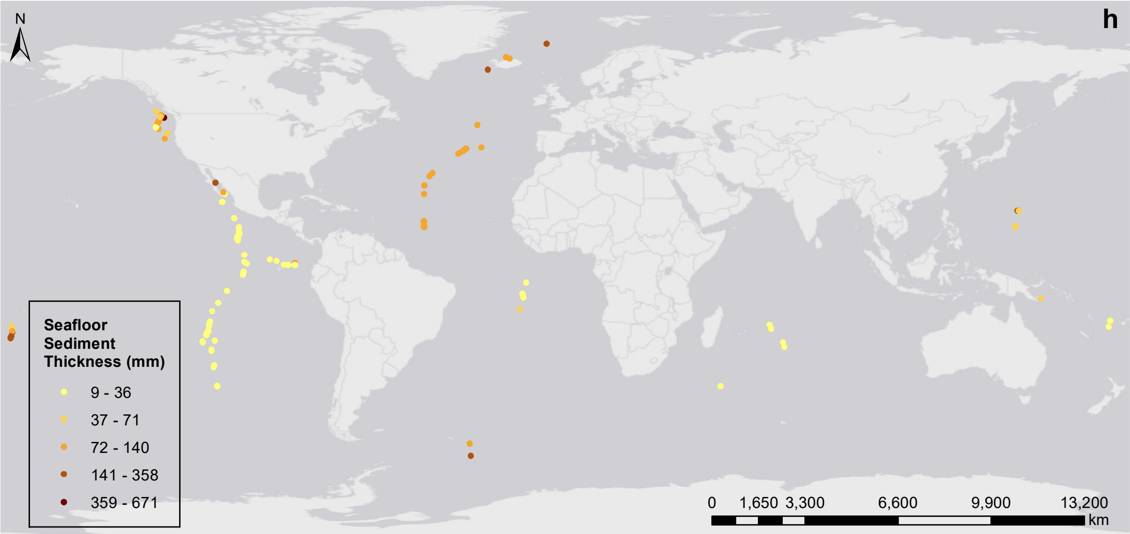


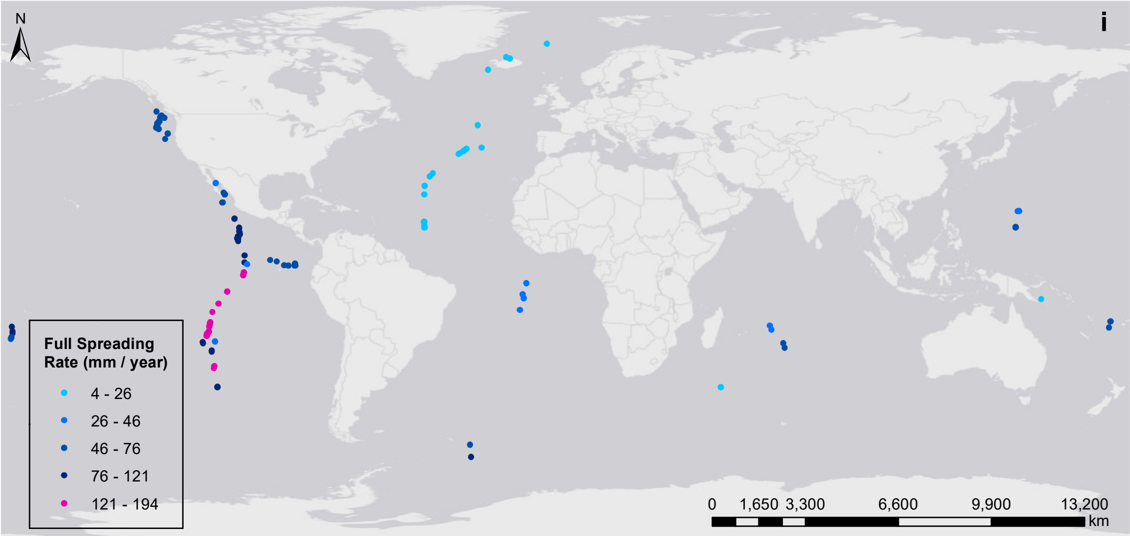
e
N
Proximity to Nearest Seep (km)
● 3 - 574
● 574 - 1178
● 1178 - 1830
● 1830 - 2898
● 2898 - 4180
0 1,650 3,300 6,600 9,900 13,200 km



f
N
Proximity to Nearest Vent Field (km)
● 1.5 - 35
● 35 - 128
● 128 - 307
● 307 - 773
● 773 - 2370
0 1,650 3,300 6,600 9,900 13,200 km


N
g
Seafloor Age (Ma, multiplied by 100 for display and processing)
0 - 42
43 - 156
157 - 380
381 - 835
836 - 3941
0 1,650 3,300 6,600 9,900 13,200
km


N
h
Seafloor Sediment Thickness (mm)
9 - 36
37 - 71
72 - 140
141 - 358
359 - 671
0 1,650 3,300 6,600 9,900 13,200
km


N
i
Full Spreading Rate (mm / year)
4 - 26
26 - 46
46 - 76
76 - 121
121 - 194
0 1,650 3,300 6,600 9,900 13,200
km

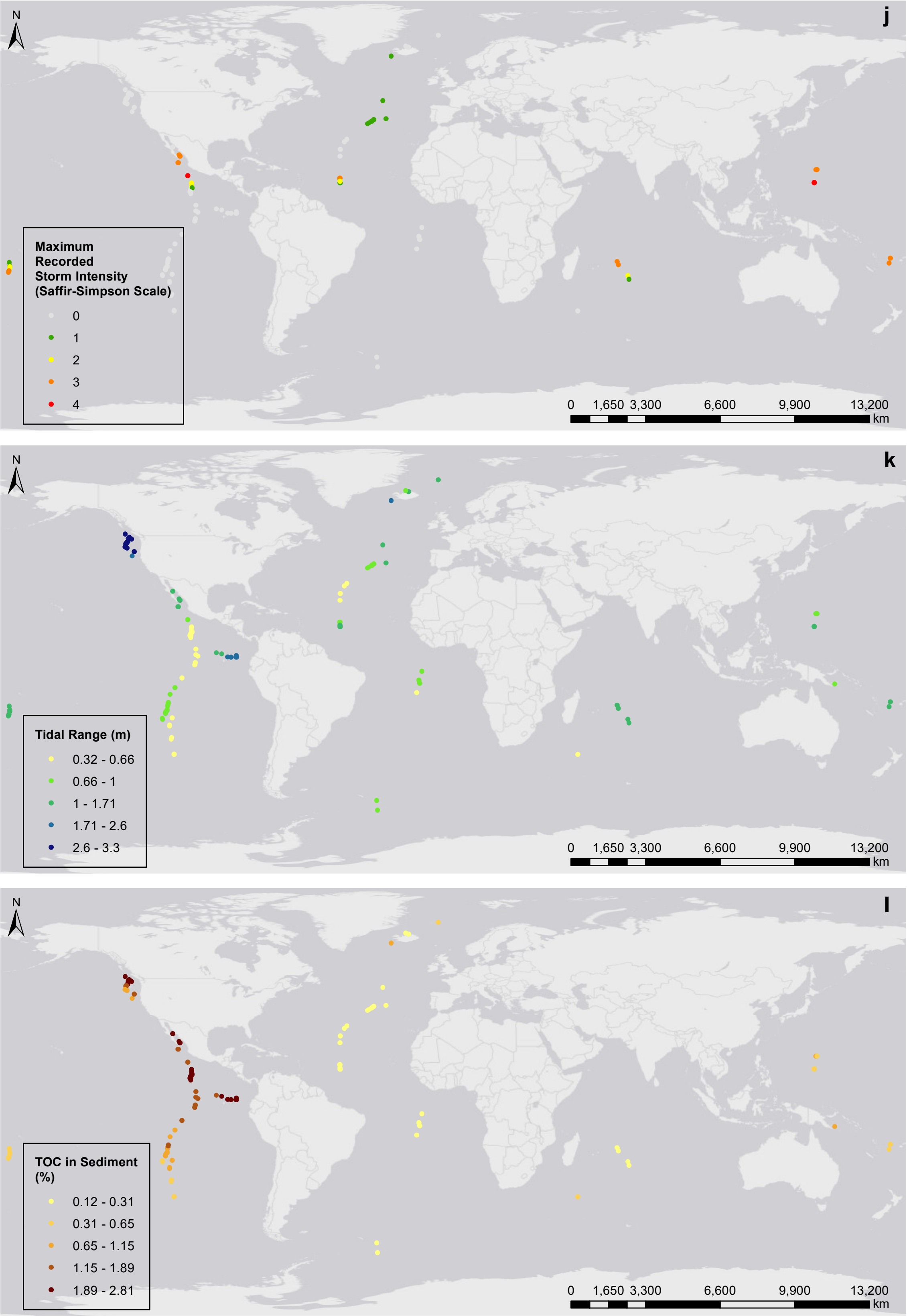

j
N
Maximum Recorded Storm Intensity (Saffir-Simpson Scale)
0
1
2
3
4
0 1,650 3,300 6,600 9,900 13,200 km
k
N
Tidal Range (m)
0.32 - 0.66
0.66 - 1
1 - 1.71
1.71 - 2.6
2.6 - 3.3
0 1,650 3,300 6,600 9,900 13,200 km
l
N
TOC in Sediment (%)
0.12 - 0.31
0.31 - 0.65
0.65 - 1.15
1.15 - 1.89
1.89 - 2.81
0 1,650 3,300 6,600 9,900 13,200 km

Figure 28 (overleaf)**:** Panel a) illustrates the outcome of a cluster analysis (Partitioning Around Medoids method) for all environmental parameters (excluding storm intensity). The two dimensions shown in this panel together explain 49.7% of the variation in environmental variables. The vent fields (points) contained within each cluster can be identified using panel b). **Appendix C.3** pairs variables with information on tectonic settings and larger-scale geographic boundaries (i.e. oceans and regions), with colour coding in panels a) and b) consistent with the colour coding in this table (except in b) where regions found in multiple clusters are shown with white points). Shaded areas in a) are used to outline the points of each cluster as a convex hull. Some PAM clusters are relatively weak (average silhouette width of the total dataset ~0.4), while two are strong (average silhouette width > 0.5). Low-confidence cluster assignments (fields with negative silhouette widths) are shown in the silhouette plot in **Appendix C.3**.

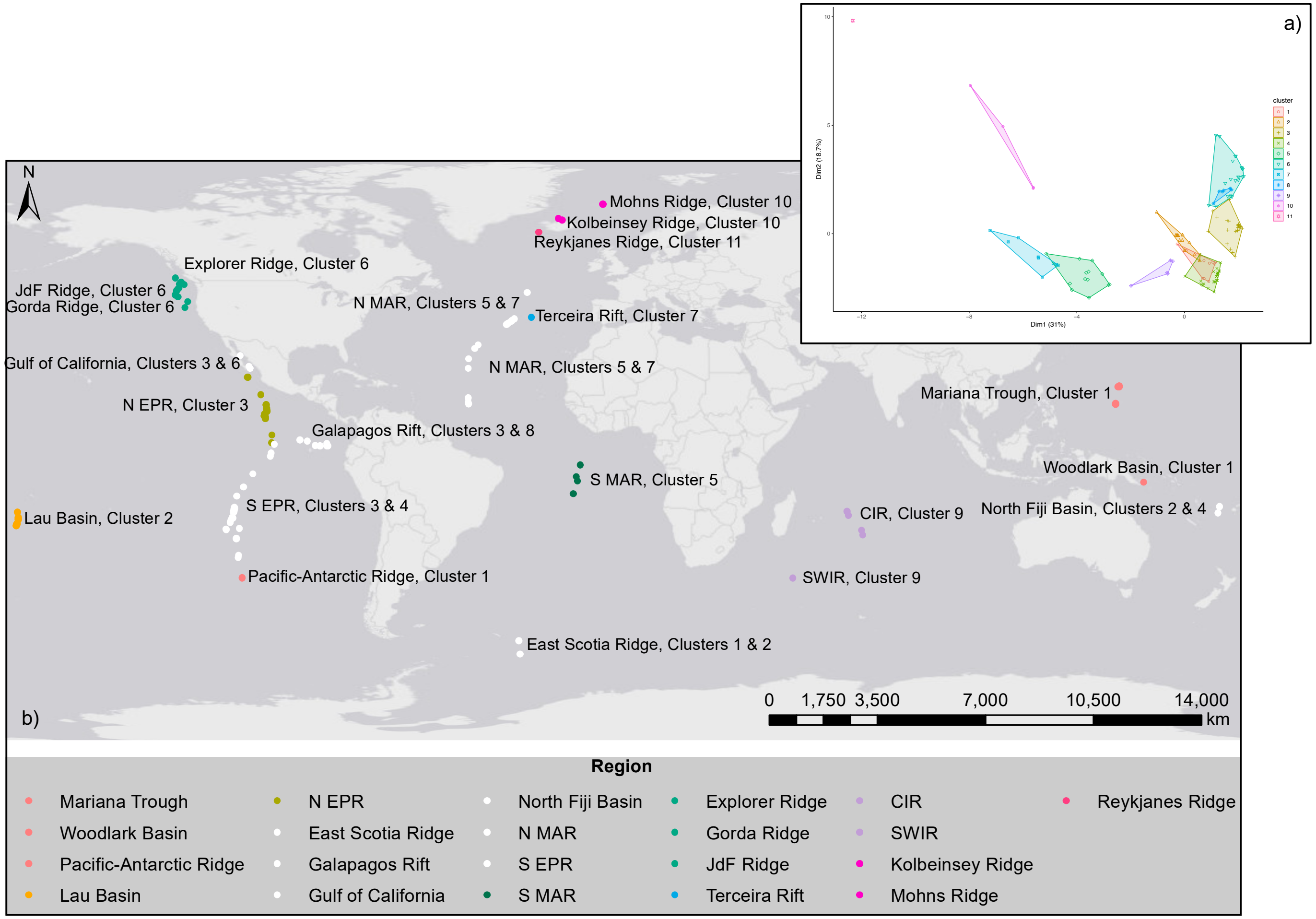
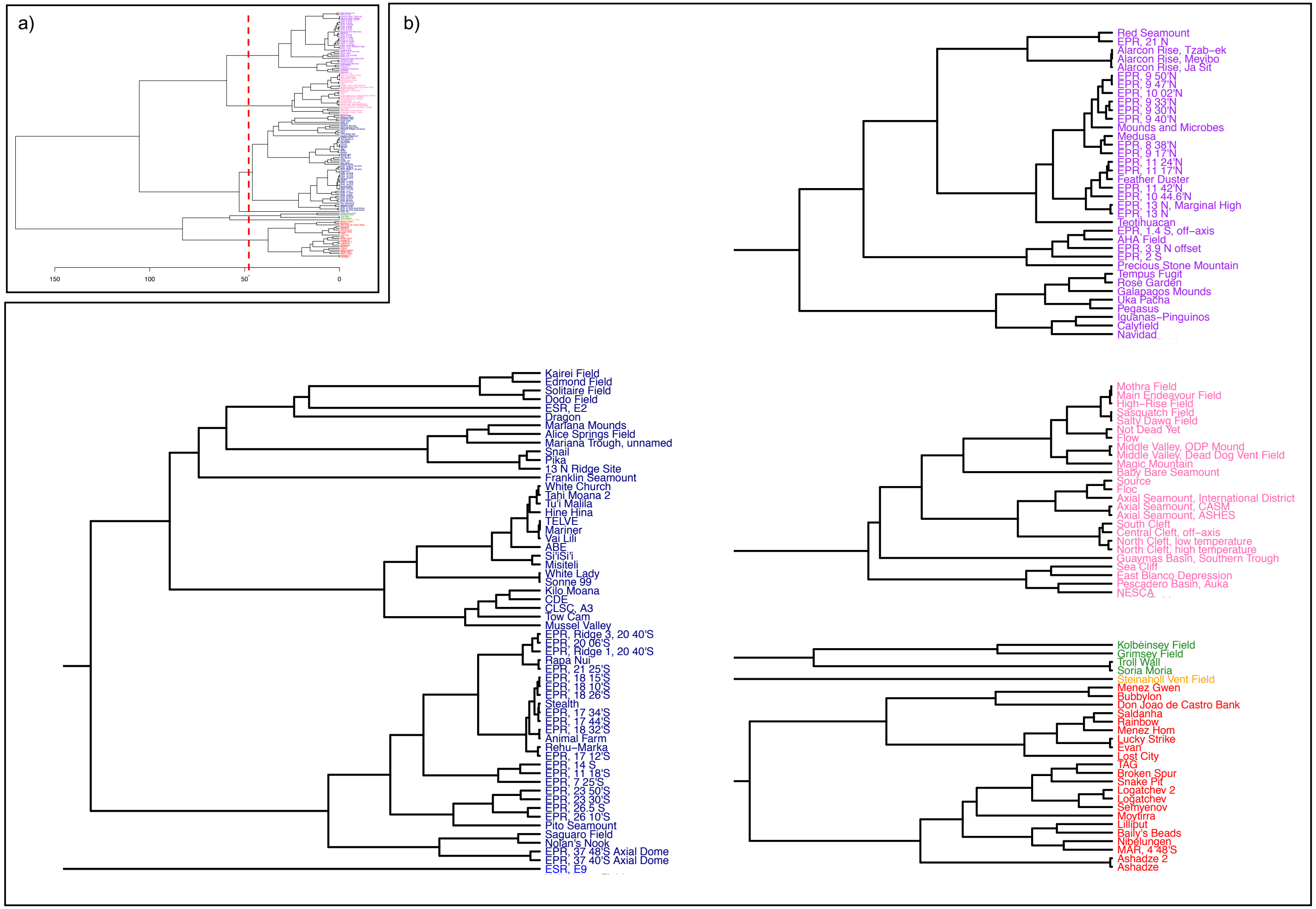
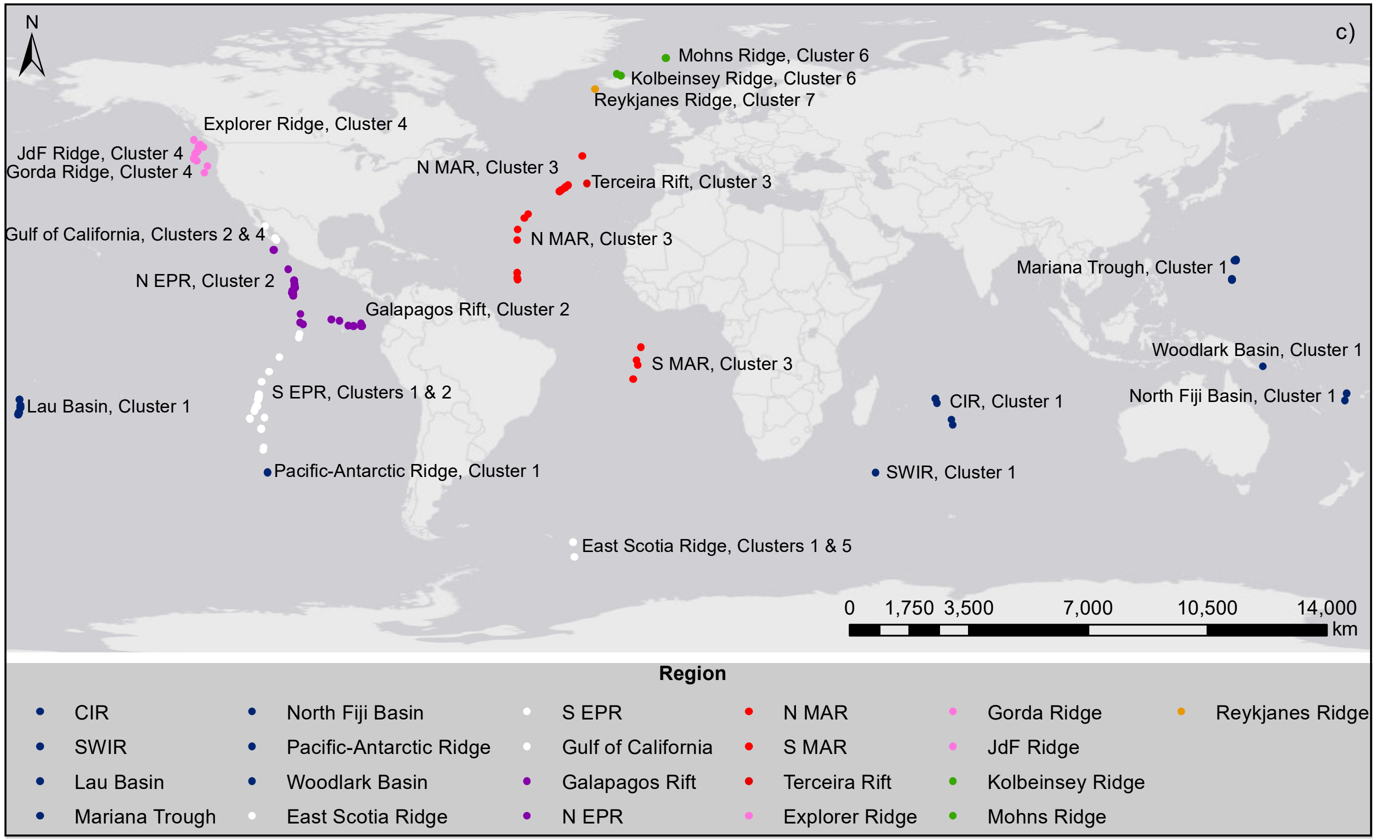

a)
Dim1 (31%)
Dim2 (18.7%)
-12
-8
-4
0
0
5
10
cluster
1
2
3
4
5
6
7
8
9
10
11
b)
N
Mohns Ridge, Cluster 10
Kolbeinsey Ridge, Cluster 10
Reykjanes Ridge, Cluster 11
Explorer Ridge, Cluster 6
JdF Ridge, Cluster 6
Gorda Ridge, Cluster 6
N MAR, Clusters 5 & 7
Terceira Rift, Cluster 7
Gulf of California, Clusters 3 & 6
N MAR, Clusters 5 & 7
Mariana Trough, Cluster 1
N EPR, Cluster 3
Galapagos Rift, Clusters 3 & 8
Woodlark Basin, Cluster 1
S MAR, Cluster 5
S EPR, Clusters 3 & 4
CIR, Cluster 9
North Fiji Basin, Clusters 2 & 4
Lau Basin, Cluster 2
Pacific-Antarctic Ridge, Cluster 1
SWIR, Cluster 9
East Scotia Ridge, Clusters 1 & 2
0
1,750
3,500
7,000
10,500
14,000
km
Region
Mariana Trough
Woodlark Basin
Pacific-Antarctic Ridge
Lau Basin
N EPR
East Scotia Ridge
Galapagos Rift
Gulf of California
North Fiji Basin
N MAR
S EPR
S MAR
Explorer Ridge
Gorda Ridge
JdF Ridge
Terceira Rift
CIR
SWIR
Kolbeinsey Ridge
Mohns Ridge
Reykjanes Ridge

Figure 29(overleaf)**:** Dendrogram of hierarchical cluster analysis conducted on a scaled dissimilarity matrix of the environmental variables using the 'Ward D2' method, to produce compact, spherical clusters (with 7 the most appropriate for the cutting of the tree - see red dashed line in a) for cut points). The dendrogram has been split into pieces in b) for display purposes, but the overall dendrogram is shown in a). The sites within the clusters produced are highlighted in the map in panel c), while information on geographic and tectonic settings is listed in **Appendix C.4**. The colour coding of panels a-c is consistent with that of the table in **Appendix C.4**, apart from in c) where regions found in multiple clusters are shown with white points. A copy of this figure is available on the USB storage device that accompanies this thesis, to the facilitate zoom functionality necessary to read dendrograms of this size.


a)
150
100
50
0
b)
Red Seamount
EPR, 21 N
Alarcon Rise, Tzab–ek
Alarcon Rise, Meyibo
Alarcon Rise, Ja Sit
EPR, 9 50'N
EPR, 9 47'N
EPR, 10 02'N
EPR, 9 33'N
EPR, 9 30'N
EPR, 9 40'N
Mounds and Microbes
Medusa
EPR, 8 38'N
EPR, 9 17'N
EPR, 11 24'N
EPR, 11 17'N
Feather Duster
EPR, 11 42'N
EPR, 10 44.6'N
EPR, 13 N, Marginal High
EPR, 13 N
Teotihuacan
EPR, 1.4 S, off–axis
AHA Field
EPR, 3.9 N offset
EPR, 2 S
Precious Stone Mountain
Tempus Fugit
Rose Garden
Galapagos Mounds
Uka Pacha
Pegasus
Iguanas–Pinguinos
Calyfield
Navidad
Mothra Field
Main Endeavour Field
High–Rise Field
Sasquatch Field
Salty Dawg Field
Not Dead Yet
Flow
Middle Valley, ODP Mound
Middle Valley, Dead Dog Vent Field
Magic Mountain
Baby Bare Seamount
Source
Floc
Axial Seamount, International District
Axial Seamount, CASM
Axial Seamount, ASHES
South Cleft
Central Cleft, off–axis
North Cleft, low temperature
North Cleft, high temperature
Guaymas Basin, Southern Trough
Sea Cliff
East Blanco Depression
Pescadero Basin, Auka
NESCA
Kairei Field
Edmond Field
Solitaire Field
Dodo Field
ESR, E2
Dragon
Mariana Mounds
Alice Springs Field
Mariana Trough, unnamed
Snail
Pika
13 N Ridge Site
Franklin Seamount
White Church
Tahi Moana 2
Tu'i Malila
Hine Hina
TELVE
Mariner
Vai Lili
ABE
Si'iSi'i
Misiteli
White Lady
Sonne 99
Kilo Moana
CDE
CLSC, A3
Tow Cam
Mussel Valley
EPR, Ridge 3, 20 40'S
EPR, 20 06'S
EPR, Ridge 1, 20 40'S
Rapa Nui
EPR, 21 25'S
EPR, 18 15'S
EPR, 18 10'S
EPR, 18 26'S
Stealth
EPR, 17 34'S
EPR, 17 44'S
EPR, 18 32'S
Animal Farm
Rehu–Marka
EPR, 17 12'S
EPR, 14 S
EPR, 11 18'S
EPR, 7 25'S
EPR, 23 50'S
EPR, 23 30'S
EPR, 26.5 S
EPR, 26 10'S
Pito Seamount
Saguaro Field
Nolan's Nook
EPR, 37 48'S Axial Dome
EPR, 37 40'S Axial Dome
ESR, E9
Kolbeinsey Field
Grimsey Field
Troll Wall
Soria Moria
Steinaholl Vent Field
Menez Gwen
Bubbylon
Don Joao de Castro Bank
Saldanha
Rainbow
Menez Hom
Lucky Strike
Evan
Lost City
TAG
Broken Spur
Snake Pit
Logatchev 2
Logatchev
Semyenov
Moytirra
Lilliput
Baily's Beads
Nibelungen
MAR, 4 48'S
Ashadze 2
Ashadze


N
c)
Mohns Ridge, Cluster 6
Kolbeinsey Ridge, Cluster 6
Reykjanes Ridge, Cluster 7
Explorer Ridge, Cluster 4
JdF Ridge, Cluster 4
Gorda Ridge, Cluster 4
N MAR, Cluster 3
Terceira Rift, Cluster 3
Gulf of California, Clusters 2 & 4
N MAR, Cluster 3
Mariana Trough, Cluster 1
N EPR, Cluster 2
Galapagos Rift, Cluster 2
Woodlark Basin, Cluster 1
S MAR, Cluster 3
S EPR, Clusters 1 & 2
CIR, Cluster 1
North Fiji Basin, Cluster 1
Lau Basin, Cluster 1
Pacific-Antarctic Ridge, Cluster 1
SWIR, Cluster 1
East Scotia Ridge, Clusters 1 & 5
0
1,750
3,500
7,000
10,500
14,000
km
Region
CIR
SWIR
Lau Basin
Mariana Trough
North Fiji Basin
Pacific-Antarctic Ridge
Woodlark Basin
East Scotia Ridge
S EPR
Gulf of California
Galapagos Rift
N EPR
N MAR
S MAR
Terceira Rift
Explorer Ridge
Gorda Ridge
JdF Ridge
Kolbeinsey Ridge
Mohns Ridge
Reykjanes Ridge

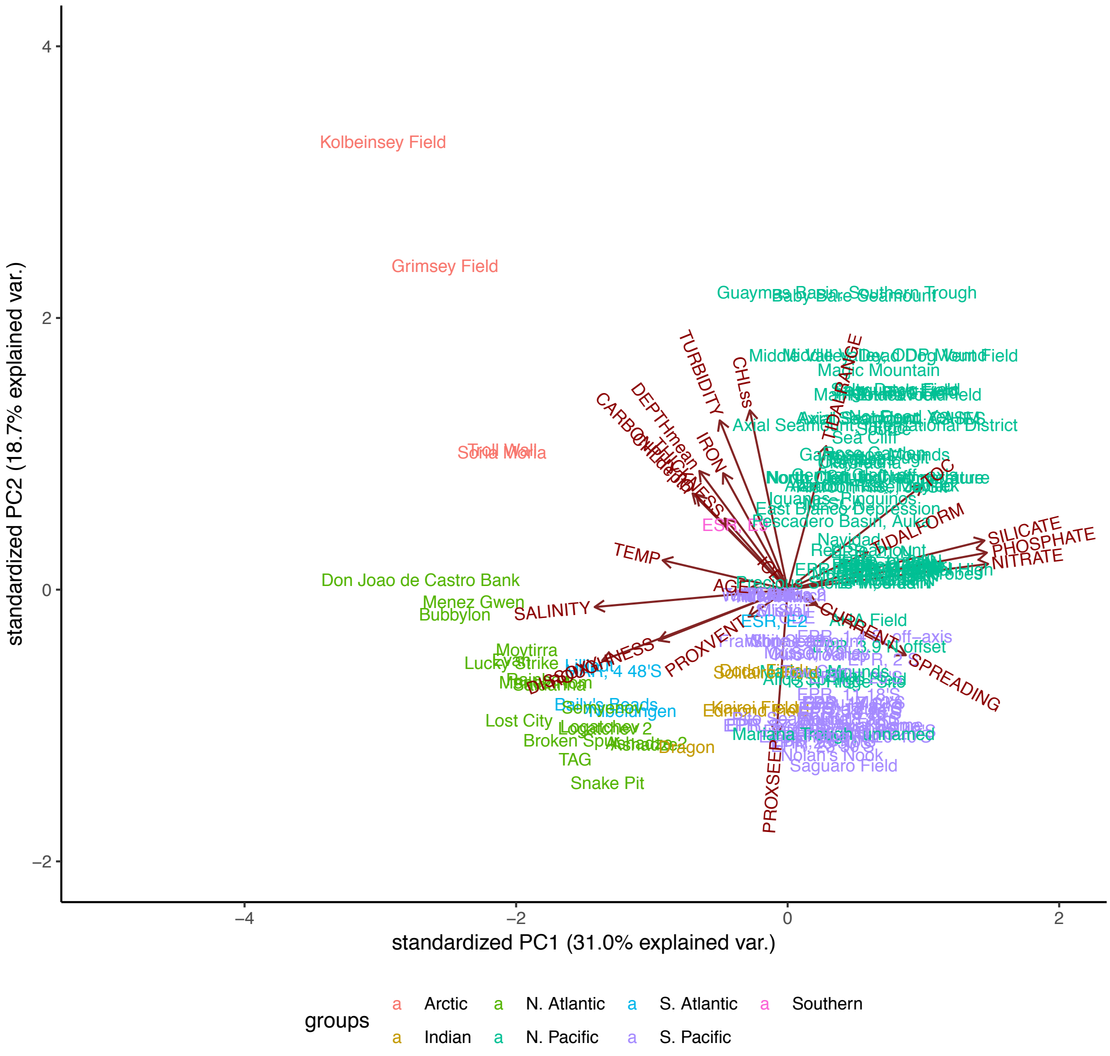


Figure 30: Principal component analysis (PCA) used to identify potential drivers of environmental similarity among vent fields from 23 environmental variables. This scatterplot shows the first two axes of this PCA, together explaining 49.7% of the total variance. Each point is labelled according to the vent field it represents and coloured according to the ocean basin the vent field is found within (for consistency with **Figure 25** and to aid interpretation given overlapping vent-field labels). Brown arrows represent the environmental variables influencing the clustering of fields, with the length of each arrow corresponding to the strength of influence (e.g., proximity to nearby vents is similar in influence to roughness and dissolved oxygen, but dissolved oxygen is the strongest 'driver' variable for the fields in the North Atlantic). The arrows are labelled according to the abbreviations given in **Table 8**.

4. DISCUSSION

4.1 Characterising the environmental uniqueness of vent fields

Deep-sea hydrothermal vents are some of the 'wilderness' areas of our oceans - increasingly rare in our human-impacted world (Ramirez-Llodra et al., 2011; Jones et al., 2018). To protect representative areas, as recommended in the CBD (1992), we need to identify environmental data available across vent fields that capture habitat diversity and map the seascape (Ardron et al., 2011; Dunn et al., 2018). Here, we begin this work for active, confirmed deep-sea hydrothermal-vent fields. We make 24 environmental variables, mapped to vent-field locations, freely available for ecological research and conservation and management planning.

In assessing which of these variables best explain(s) environmental similarity among vent fields, we refute our hypothesis that spreading rate is the primary driver of spatial clustering. Much of the research conducted to date discusses the spatial distribution of vents in relation to spreading rate (Von Damm, 1995; Juniper and Tunnicliffe, 1997; Tivey, 2007; Baker et al., 2016, 2017). Thus, we expected similarity among vent fields to be predominantly influenced by this variable. While spreading rate is an important 'driver' variable, shaping dissimilarity among vent fields across the globe, deep-water dissolved oxygen concentration, seafloor roughness, proximity to nearby seeps, nutrients (e.g., phosphate, nitrate, and silicate), tidal range, turbidity, and depth are also key drivers (**Figure 30**). Here, we therefore highlight how other large-scale geographic and oceanographic characteristics vary spatially across vent fields - an important starting point for the future mapping of habitats and bioregions for conservation and management purposes.

Furthermore, we classify two vent fields as environmentally unique, in terms of the characteristics included in our analyses. E9 vent field, on the East Scotia Ridge, and Steinaholl Vent Field, on Reykjanes Ridge, are both isolated from all other vent fields according to different clustering methods (**Figure 29** and **Figure 29; Appendices C.3** and **C.4**). The uniqueness of these vent fields is supported when we compare the raw environmental data for their locations (**Appendix C.5**) to the summary statistics for all vent fields in **Table 9**. For instance, E9 vent field: is the only field that has been covered by sea-ice; has thicker than average sediments; is on relatively old seafloor; has above-average dissolved oxygen concentration at depth and relatively low carbon in phytoplankton biomass at depth; has below-average long-term maximum temperatures at depth (-0.026 degrees); and is further from nearby vent fields than other fields and closer to nearby seeps. Meanwhile, Steinaholl Vent Field is very shallow (263 m), which increases the surface Chl-a likely to reach this location, as well as the temperature (which is above average). It also has other relatively unique characteristics, such as: low carbon in phytoplankton biomass at depth, despite high surface Chl-a; a relatively high tidal range (2.58 m); a tidal form factor of 0.14 (semidiurnal); below-average seafloor roughness and above-average sediment thickness, dissolved oxygen concentration, and turbidity; and a relatively slow spreading rate (19.1 mm per year), leaving it further than average from nearby vents and seeps. In identifying these relatively unique vent fields, we demonstrate the potential of large-scale environmental datasets for identifying candidate regions for CERs, based on seascape variability.

Overall, however, the uniqueness of the E9 field and Steinaholl Vent Field is unsurprising, given E9 is particularly cold and oceanographically isolated, and Steinaholl Vent Field is exceptionally shallow. Nevertheless, if we assess the spatial variability of the environmental characteristics themselves, we can identify venting regions that, while not separated using cluster analyses, are relatively more environmentally unique (e.g., based on the maps in **Figure 27** and **Appendix C.2**). North Atlantic vent fields, for example, are characterised by slow spreading rates, relatively old seafloor, high tidal ranges, higher temperatures and salinities, and low nutrient concentrations. Arctic Ocean vent fields (forming a separate cluster using both PAM and hierarchical approaches - **Figure 28** and **Appendix C.3**) are also slow spreading, with low nutrient concentrations, and high salinities. Yet, the Arctic also has low temperatures, low current speeds, high dissolved-oxygen concentrations, high turbidity, and high iron concentrations, based on available data. The Southern Ocean, on the other hand, has similarly old seafloor and low temperatures, but vent fields here are also characterised by ice cover, low iron, and proximity to nearby seeps. In Gulf of California and Juan de Fuca Ridge vent fields, sediment thickness is higher than elsewhere. The Northeast Pacific also contrasts more generally with the North Atlantic and Arctic Ocean, with low dissolved oxygen, high nutrient concentrations, high total organic carbon in sediments, high tidal ranges, and close proximity to nearby seeps. Dragon vent field on the SWIR is relatively environmentally unique given its distance from other vent fields, high seafloor roughness, low tidal range, and very slow spreading rate. In the Lau Basin, spreading rates are unusually variable and seeps are far from vent fields.

The geographic uniqueness of these regions is supported in biogeographic studies. For instance, if we look to the most recent global biogeography of vent fauna in Rogers et al. (2012), we can see that most of these regions form their own, unique biogeographic provinces. For example, the MAR province in Rogers et al. (2012) is the North Atlantic region described herein, and the Northeast Pacific region in our analyses matches the Rogers et al. (2012) northern EPR province. The East Scotia Ridge - our Southern Ocean region - is its own biogeographic province in Rogers et al. (2012), as is a province south of the Easter Microplate (our 'Pacific-Antarctic Ridge' region). Nonetheless, the Lau Basin, SWIR, Mariana Trough, Gulf of California, and Juan de Fuca Ridge seem to be more environmentally unique than we might expect, given their taxonomy-based biogeography (Rogers et al., 2012). While we cannot explore detailed reasons for this with confidence using environmental data alone, these results suggest that these regions could provide interesting future avenues for research into ecological, environmental, and evolutionary relationships shaping the uniqueness of deep-sea hydrothermal-vent ecosystems.

4.2 A 'typical' vent field

In contrast to unique vent fields, we have also been able to update the description of a 'typical' vent field presented in work by Von Damm (1995). Despite more fields having been discovered, and thus included in our analyses, the average water depths of vent fields are similar to those recorded by Von Damm in 1995 (~2,600 m in our **Table 9** and 2,200 - 2,600 in Von Damm, 1995); although, the deepest depth recorded is now ~5,700 metres (in raw data), compared to the 3,670-metre maximum depth recorded for TAG in 1995 (Von Damm, 1995). Average spreading rate is also similar to that of 1995, at around 56 millimetres per year, compared with the 60 millimetres per year recorded in the 1995 summary (Von Damm, 1995). Again, however, we can update the maximum spreading rate, from 162 millimetres per year to 194 millimetres per year, and also the minimum spreading rate to 4 millimetres per year (from 25 millimetres per year recorded in 1995 for MAR systems; Von Damm, 1995).

We are also able to characterise 'typical' vent fields in terms of environmental variables compiled from remote sensing and *in situ* monitoring (**Table 9**). For instance, here, we are able to assess: whether vent fields have been affected by severe tropical cyclones; how chlorophyll and associated phytoplankton biomass vary across space at depth; and how nutrients and dissolved oxygen, among other biological oceanographic variables, vary spatially in proximity to vent-field locations. While we appreciate that large-scale data sources such as those used here are limited in resolution and can have coverage issues resulting from cloud cover, for instance, our findings demonstrate the power of using global datasets when higher-resolution data are unavailable on scales, or in units, that can be compared across the globe. These data will likely be a valuable resource for large-scale studies of relatively inaccessible deep-sea hydrothermal-vent ecosystems.

4.3 Drivers of vent-field dissimilarity

Another aim of our research was to map the variability of environmental characteristics across space, with respect to vent-field locations, before assessing their environmental similarity. It is important to note that, here, we analyse vent fields in their environmental context without any biodiversity information (e.g., richness, abundances, or distributions of species). As such, while we identify variables that influence vent ecology, as described **Figure 24** and **Table 7**, the variables that are key in shaping the spatial clustering of venting locations will likely differ from those we would expect to shape small-scale ecological processes (e.g., colonisation, larval dispersal, physiology, etc.). Thus, we might expect vent fields to cluster geographically, as their surrounding environmental characteristics will be mostly unrelated to their distribution, predominantly shaped by: spreading rate, as faster spreading tends to mean more vent fields (Juniper and Tunnicliffe, 1997); total organic carbon in sediments, and chlorophyll or carbon in phytoplankton biomass, as these depend on surface primary productivity and are geographically constrained (Tyler, 2003; Levin et al., 2016); and sediment cover, tides, and currents, as these affect the flow rates of hydrothermal fluids (Juniper and Tunnicliffe, 1997; Cuvelier et al., 2017) and therefore might affect likelihood of vent-field discovery, and, thus, relate to vent-field locations confirmed as active to date. Indeed, we find support for this expectation in the outcome of our PCA (**Figure 30**), where environmental variables separate vent fields according to geographic location. In general, the cluster analyses we conducted (**Figure 28** and **Figure 29**; **Appendices C.3** and **C.4**) also support this expectation.

On the other hand, we identify some cluster groupings suggesting that there are environmental similarities among vent fields across large spatial scales (**Figures 28** and **29**). The North Fiji Basin in the western Pacific Ocean, for instance, clusters with relatively nearby Lau Basin vent fields, as well as vent fields on the distant SEPR (**Figures 28** and **29**). In addition, an East Scotia Ridge vent field shares environmental characteristics with the Pacific-Antarctic Ridge, according to both PAM and hierarchical clustering approaches (**Figures 28** and **29**). These environmental similarities shared across large spatial scales likely result from ocean transport processes. The North Fiji Basin, Lau Basin, and SEPR are connected via large currents operating in the South Pacific, which will shape the temperature, salinity, and chemistry of their waters, among other environmental characteristics. The East Scotia Ridge and Pacific-Antarctic Ridge are similarly connected by currents, which may increase the similarity of their environmental settings, as discussed in Rogers et al. (2012).

Nevertheless, we expect mid-ocean ridges and back-arc basins to differ in sediment thickness, spreading rates, water depths, and connectivity (as might be determined in this study using proximity to nearest vent field, among other variables) (Hannington et al., 1995; Tunnicliffe et al., 1998; Beaulieu et al., 2013); thus, we expect clusters to be tectonically constrained. This is the case for most of the clusters identified using PAM and hierarchical-agglomerative clustering approaches (**Appendices C.3 and C.4**). However, Mussel Valley vent field (North Fiji Basin) is located on a back-arc spreading centre that clusters with SEPR mid-ocean-ridge fields in the results of both cluster analyses (**Appendices C.3 and C.4**). In identifying it in **Figure 30** using its PC1 and PC2 coordinates (0.571 and -0.958, respectively), we can see that it is separated from other South Pacific vent fields due to different spreading rate, maximum long-term current velocity, and its proximity to nearby seeps. It also has different average chlorophyll values (surface and deep), iron concentrations, turbidity, and sediment thickness - characteristics we can see it has in common with SEPR fields in the maps presented in **Figure 27** and **Appendix C.2**. The grouping of Mussel Valley with SEPR fields therefore provides an example of how non-geological features of the vent-field environment might influence ecology. For instance, Mussel Valley vent field might be more ecologically similar to SEPR vent fields than one might expect, given their different tectonic settings and geographic locations. Clusters like these highlight a benefit of incorporating global-scale environmental data into an analysis of vent-field dissimilarity - geological, oceanographic, or biological - as such data enable us to identify habitat characteristics common across ocean basins and tectonic settings.

4.4 Limitations

As with all studies dependent on large-scale data sources, interpolated from satellite and *in situ* observations, our study is limited by data quality, resolution, and coverage (e.g., Assis et al., 2017). We justify our approach because other data are not readily available and/or comparable on the global scale for vent fields. In addition, given the sensitivity of clustering methods to the number of pre-selected clusters, variables, and metrics specified, we are careful to discuss only results that are consistent among clustering methods and represent general, broad-scale trends. For instance, the Terceira Rift appears to be relatively environmentally distinct according to PAM clustering, but is grouped with the N.MAR fields under a hierarchical clustering classification (**Figures 28** and **29**). Furthermore, we propose the conceptual framework linking the variables analysed here to ecological processes at vents (**Figure 24** and **Table 7**) to highlight the relevance of these variables in vent ecosystems. We do not then discuss possible links between environmental characteristics of vent fields and their ecological communities because of potential resolution, or scaling, issues. The intensity and frequency of ecological sampling of vent fields also varies across the globe, potentially biasing the understanding we have of links between the physical environment and vent-field ecology at this time.

The variables with the greatest number of gaps for the vent fields included in our study are: seafloor age, sediment thickness, storm intensity, long-term maximum ice cover, and full spreading-rate (**Table 9**). We expect to see missing values in tropical-storm intensity and ice cover, as we these environmental parameters are confined to tropical (for the most part) and polar areas of the globe, respectively (**Figure 27**, **Appendix C.2**). The other variables, however, limit our analyses, as we cannot include fields with missing values in cluster analyses. As such, we use complete data for clustering and PCA, omitting fields in arc volcanoes and other locations for which spreading rate, seafloor age, and sediment thickness have not been characterised. We therefore recommend the relatively under-populated variables as priorities for future gap filling, given their importance in the conceptual framework in **Figure 24** and **Table 7** and their relative importance in shaping spatial clustering of vent fields (**Figure 30**).

Nonetheless, we tested for correlation among variables (**Figure 26**) and note that some variables might, in the meantime, be used as 'proxy' variables for others for some research purposes. We identify significant, strong correlations that could potentially assist researchers in selecting a subset of best-populated variables to focus on for their study region and/or project purpose (**Figure 26**). For instance, if total organic carbon records are missing for a particular location, we can assume, given the significant and strong positive correlation between total organic carbon in sediments and long-term maximum bottom phosphate, silicate, and nitrate (**Figure 26**), that we might be able to use one of these other environmental variables as a proxy for total organic carbon in the sediments at said location. However, we recommend statistically testing the relationships between variables for the subset of data being analysed (e.g., for a given region), as some variables that are significantly correlated when ranked on the global scale might not be significantly or strongly correlated on smaller scales. Moreover, as environmental uniqueness will depend on the variables included in a study, we recommend that future work completed using the environmental variables provided in **Appendix C.5**, or similar datasets, uses only variables appropriate for the research purpose and/or scale, to avoid artificially inflating or reducing uniqueness among vent fields.

4.5 Future directions and applications

Through our investigations, we can see which variables vary most across space (**Figure 25**). For instance, we can see that depth, average sea-surface Chl-a, long-term maximum dissolved oxygen concentration at depth, long-term maximum current velocity at depth, seafloor roughness, tidal range, proximity to nearby seeps, and total organic carbon in sediments vary most across vent fields. Given the importance of these variables for limits to life, access to nutritional resources, disturbance, stability, and access to 'migratory' stepping stone environments (**Figure 24**, **Table 7**), we expect these variables to be informative for biogeographic research and assigning bioregions to aid management decisions, when paired with ecological data, in the future.

Dunn et al. (2018) express a need for data on habitat distributions, oceanographic currents, and other parameters, for species distribution modelling and other conservation network design tools - previously hindered in deep-sea environments by the expensive and time-consuming nature of surveys (Rengstorf et al., 2014). Until more small-scale, high-resolution studies are completed at vent fields across the globe, we demonstrate with this work that large-scale, satellite-derived and *in situ* monitoring data can be used to map the geography and oceanography of vent fields and to identify unique habitats. While this study focuses on active, confirmed vents, we believe that similar work should be conducted for inactive vents, unconfirmed fields, hydrothermal sediments, and other ecosystems (e.g., habitats highlighted in the first World Ocean Assessment - Le Bris et al., 2017). Furthermore, we expect that including more geological variables, such as fault locations and sulfide deposit sizes, might provide insights relevant for understanding the geographic uniqueness, and general ecology, of vent fields, and their associated communities, across the globe (e.g., as transform faults are considered to be potential barriers to larval dispersal along a ridge - Desbruyères et al., 2000).

Finally, in searching for appropriate data for this study, we came across examples of 'hidden' data that are freely available, but not ready to use in a large-scale analysis. For instance, there are useful chemistry data presented in Von Damm (1995). These data, and data like these, are likely under-used at present, as they are stored in a PDF table and are thus not 'analysis-ready'. We believe that future work involving the mapping of deep-sea hydrothermal-vent bioregions and habitats could benefit from data tables stored within publication manuscripts, and we call for raw data to be made available in a standardised (e.g., Microsoft Excel) format, for old and new publications, where possible. This would prove invaluable for future work and for the conservation and management of the ecosystems many have worked hard sampling, counting, and studying to understand since their discovery around 40 years ago.

4.6 Conclusion

In compiling a suite of environmental variables for active, confirmed vent fields across the globe, we have: i) created a shared resource for deep-sea researchers and those conserving and managing vent environments; ii) identified environmentally unique vent fields and regions, relative to other vent fields across the globe; and iii) discussed environmental characteristics, in addition to spreading rate, that affect, and are possibly shaped by, the distribution of vent fields, crossing ocean basins and tectonic settings. Vent fields offer scientists a unique opportunity. We are working to conserve environments not yet affected by human activities, and yet the findings of the Aichi Biodiversity Targets and Agenda for Sustainable Development progress reviews are particularly relevant. In deciding how best to protect vent ecosystems, we need information on environmental characteristics that enable us to identify vent fields representative of their natural seascapes that are connected to one another and to other chemosynthesis-based environments (e.g., seeps). Here, we support terrestrial and shallow-marine ecologists calling for the use of large-scale environmental data when other, higher-resolution data are unavailable, or inappropriate given the scale of study, as we show that large-scale environmental variables can be used to compare vent fields. Overall, the environmental characteristics of vent fields are similar within ocean basins, but we should not limit analyses within provinces, as vents can also be environmentally similar across tectonic settings and seas.

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Chapter Five: Identifying biodiversity hotspots in some of the hottest environments on Earth

I designed this study, undertook the analyses, and drafted the chapter with comments and suggestions from lead supervisor Dr Amanda Bates. The work presented here forms the basis for a publication to be contributed to by sFDvent Working Group members.

Supporting Information for Chapter Five is provided in **Appendix D**.

ABSTRACT

There is an urgent need to design conservation strategies for deep-sea hydrothermal vents. By 2020, it is expected that commercial-scale mining will begin, to extract the polymetallic sulfides many active vents form. Deep-sea mining is expected to have deleterious environmental effects on the vent-field scale, with local removal of species likely also impacting regional species pools. The conservation and management of ecosystems already affected by human activities typically centres on priority areas. These areas are generally selected for protection based on the likely extinction risk for species present. This risk is evaluated using traditional diversity measures, like species richness and presence of endemic species. While these approaches have been used successfully on land and in the seas, the complex evolutionary histories of hydrothermal-vent fauna, and the distinct taxonomic biogeographic provinces historic processes have created, make it difficult to compare vent regions on the global scale. In coral-reef ecosystems, trait-based approaches have proved useful for identifying diversity hotspots to inform the protection of reefs under pressure from fishing. This approach is yet to be tested for hydrothermal vents. Here, we combine trait, taxonomic, and environmental data, aiming to classify active-vent hotspots. We find low spatial congruence between trait, taxonomic, and environmental measures of uniqueness. This suggests that a unified approach, incorporating multiple dimensions of faunal diversity, and environmental characteristics, is required for appropriate, comprehensive management of active, deep-sea hydrothermal-vent ecosystems.

Keywords: conservation, deep-sea mining, diversity, environmental impact, hotspots, priority areas, traits, uniqueness.

1. INTRODUCTION

Deep-sea hydrothermal vents are relatively pristine systems, untouched by commercial human activities since their discovery in 1977 (Ramirez-Llodra et al., 2011; Van Dover et al., 2018). By 2020, it is expected that these remote wildernesses will be under threat from commercial-scale mining of the polymetallic sulfides formed by the precipitation of vent fluids (Jones et al., 2018;

Van Dover et al., 2018). The impacts of deep-sea mining are unprecedented and, thus, relatively unknown (Boschen et al., 2013). It is expected, however, that the impacts will be severe on the local scale, including: removal of vent fauna when cutting away habitat; crushing of peripheral organisms and compacting sediment during mining-vehicle transit; and the generation of sediment plumes that could smother filter feeders (Ramirez-Llodra et al., 2011; Van Dover, 2014, 2018; Jones et al., 2018). The effects of removing local communities could be far-reaching, given the importance of large-scale larval transport pathways and source-sink dynamics for vent populations, and the role of large-scale oceanography and topography in shaping such processes (Thomson et al., 2003; Metaxas, 2004; Mullineaux et al., 2010; Van Dover et al., 2018; Vic et al., 2018).

Given the imminent threat posed by deep-sea mining, management and conservation guidelines are currently being written to manage the exploration and exploitation of deep-sea ecosystems, including vents (International Seabed Authority, 2010, 2016, 2017; Van Dover et al., 2018). Marine spatial planning (Caldow et al., 2015), and systematic conservation planning more generally (Margules and Pressey, 2000), requires an understanding of the diversity of life and environmental conditions in an ecosystem across the globe (Ardron et al., 2011; Wedding et al., 2013; Caldow et al., 2015). It is unlikely that all active deep-sea hydrothermal vents will be protected globally, given the growing demand for minerals present in high concentrations in deep-sea ecosystems like vents (Hein et al., 2013; though see Van Dover et al., 2018, who argue for the protection of all active vents). The identification of priority areas for the conservation and protection of vents is therefore urgently required. This pressing need is compounded in vent ecosystems, as restoration is unlikely to be successful or possible in these extreme, unusual, and remote environments (Van Dover et al., 2014, 2018).

In terrestrial and shallow-marine ecosystems, such as tropical rainforests and coral reefs, conservation plans typically focus on extinction risk, using species richness and endemism to indicate priority areas for conservation (Brooks et al., 2006; Butchart et al., 2010; Selig et al., 2014; Maréchaux et al., 2017). This approach would likely not work for vent ecosystems, which have low numbers of species, of which the majority are endemic (Tunnicliffe and Fowler, 1996; Chapman, Bates et al., in review - Chapter 3). The global biogeography of deep-sea hydrothermal-vent ecosystems has been shaped by vicariance events, wherein geological, chemical, and oceanographic processes shape larval dispersal pathways, creating geographically constrained species pools (Tunnicliffe et al., 1998; Tyler and Young, 2003; Vrijenhoek, 2010a, 2010b; Zhou et al., 2018). These constraints have enabled biogeographers to separate vents into distinct provinces, given their unique taxonomic compositions (for example, most recently: Bachraty et al., 2009; Moalic et al., 2012; Rogers et al., 2012; Copley et al., 2016). Nevertheless, these biogeographic models cannot be used to prioritise regions for conservation and management purposes. Firstly, the models typically change with every newly explored vent region, as many new species are found, creating distinct taxonomic provinces (e.g., **Figure 7**). Secondly, the spatial clustering of biogeographic provinces makes it difficult to compare regions using taxonomic information alone. Furthermore, the species richness of vent regions is shaped by differences in sampling intensity, methodology, and frequency, driven by the history of vent-field discovery. For example, vents were first discovered in the East Pacific (Tunnicliffe et al., 1986; Fustec et al., 1987; Tunnicliffe and Fontaine, 1987), and have been repeatedly sampled there since, while Arctic Mid-Ocean Ridge and South West Indian Ridge vent communities were only explored relatively recently (Pedersen et al., 2010; Copley et al., 2016).

Trait-based approaches enable us to compare fauna on a global scale and have been used to identify conservation 'hotspots' in terrestrial and shallow-marine ecosystems (Stuart-Smith et al., 2013, 2015; Ribeiro et al., 2016; Pollock et al., 2017). However, traits have not yet been used to compare vents across large scales. It is therefore unknown whether a trait-based approach will simply emphasize differences in the functional roles of vent species, yielding similar distinctiveness to that shown using taxonomy and biogeography. Using traits could, alternatively, reveal functional convergence across provinces that cannot be identified using taxonomy due to the different evolutionary origins that have shaped vent species pools. We might expect deep-sea hydrothermal-vent ecosystems to have relatively high functional convergence, as they share characteristics with the forests described to be high convergence by Hubbell (2005). For instance, vents host relatively slow-moving or sessile foundation species (Grassle, 1985; Lutz and Kennish, 1993), like trees. They are colonised via restricted larval dispersal pathways (Mullineaux and France, 1995; Tyler and Young, 2003), conceptually similar to pollen transport. Furthermore, vent species pools are limited by suitable habitat for recruitment (Mullineaux and France, 1995), as in dense forests.

Functional diversity hotspots, and areas of functional convergence, can be identified using measures of functional dispersion, and redundancy. These measures can influence the resilience of a regional species pool (Oliver et al., 2015). Functional dispersion captures the spread of species in trait space, measuring the mean distance of each species to the centroid of a multidimensional trait space, which is created using the traits of all species in a given pool (Laliberté and Legendre, 2010; Laliberté et al., 2014; **Table 2**). Independent of species richness, functional dispersion can thus be used to identify regions comprising species that are relatively distinct from one another, in terms of their traits - 'hotspots' of uniqueness. Contrastingly, functional redundancy is a measure of overlap among species traits, grouping species that perform similar functional roles (Rosenfeld, 2002). Redundancy is high when species share combinations of traits. It is thus considered a measure of 'insurance', wherein high redundancy means more species can perform the same functional role as other species, should any be lost from the pool (Walker, 1992; Yachi and Loreau, 1999; Fonseca and Ganade, 2001).

In addition to defining hotspots and convergence using taxonomic and trait-based approaches, the conservation of terrestrial, freshwater, and shallow-marine ecosystems also depends on the distribution of diversity within and across ecoregions (Olson et al., 2001; Spalding et al., 2007; Abell et al., 2008). While ecoregions are defined using biogeographic information, they tend to represent areas with distinct environmental conditions (e.g., tropical vs. temperate, flooded, tundra, and montane; Olson et al., 2001; Spalding et al., 2007). Ecoregions can be used for priority setting in conservation and management strategies. For instance, hotspots in different ecoregions may require contrasting conservation strategies to account for the influence of environmental conditions on species pools and responses to disturbances. In the same way, the environmental characteristics of vent fields could be used to identify vent ecoregions, or bioregions (Ward et al., 2012; Woolley et al., 2013). These regions could, in turn, be used to prioritise vents for conservation (Dunn et al., 2018).

Combining trait, taxonomic, and environmental information for vent regions should therefore enable us to identify priority areas for the conservation of vents before the first impacts of deep-sea mining affect these deep-sea ecosystems. Thus, here, we first update the taxonomic biogeography of vents and build a new functional biogeography of vent species using data from the sFDvent trait database (Chapman, Bates et al., in review - Chapter 3). This allows us to test for congruence in functional and taxonomic biogeographic patterns. Next, to quantify the degree of functional redundancy and uniqueness in regional species pools across the globe, we identify functional groups unique to, or redundant across, different vent regions. We then use functional redundancy and dispersion metrics to identify hotspots of diversity and vulnerability. Finally, we quantify the relative uniqueness of vent regions across the globe according to species traits, taxonomy, and environmental characteristics. In combining these measures, we capture different facets of diversity, and the environmental characteristics defining bioregions, to establish priority regions, or 'hotspots', for vents. We expect our approach, and findings, to inform conservation and management strategies.

2. METHODS

2.1 Data selection and processing

We assembled trait, taxonomic, and regional occupancy data from the sFDvent database (Chapman, Bates et al., in review - Chapter 3) for the analyses in this study, as well as environmental data extracted for deep-sea hydrothermal-vent-field locations across the globe (Chapman et al., in prep. - Chapter 4). Species in the sFDvent database were assigned location information by expert contributors, but this information could not be used in the format provided, as locations varied in spatial resolution and scale. Thus, we re-assigned each location to a region, as defined in the InterRidge vent database (v.3.4; Beaulieu, 2015), and computed an average (mean) location for each region, using the field locations associated with each region in this database, before pairing with species occupancy information from sFDvent. For Kermadec Arc vent fields, which cross the International Date Line, we selected a single field location to represent the region, to avoid positive and negative coordinates interacting to produce a mean location far from the actual location of this arc volcano. Hereafter, we refer to these data on recorded presences of species as ‘taxonomic’ data, though we also have separate information on the taxonomic groups of each species and use this in some analyses.

The aforementioned data are biased in terms of sampling intensity, as some regions have been studied for many more years than others, as is the case for most ecological data. To minimise the effects of this, we only included regions with 20 or more species (the median number of species across all regions) in our analyses. This enabled us to capture 17 regions, whereas a harsher threshold - of 30 species or more - only allowed us to study 10 regions, which are spatially clustered and would bias our results and limit our interpretations. In addition, we removed meiofauna (taxa greater than 63 microns but smaller than 1 mm in size; Gollner et al., 2015), as these are mostly limited to the East Pacific Rise and Juan de Fuca Ridge, where meiofauna experts have identified species in this size class. We removed the only Foraminifera in the database as it might stand out as being exceptionally unique when, in fact, there has simply been undersampling or under-identification in this taxonomic group. Thereafter, 547 taxa could be included in this study. Here, we will refer to these taxa as ‘species’, as we only included species yet to be formally named if they: i) could be linked to a taxonomist soon to identify them, and/or ii) were known to be distinct from other species in the sFDvent database, given expert advice.

In line with previous studies and metric-naming conventions, we refer to trait-based patterns and metrics computed using sFDvent trait data as ‘functional’, though many of our traits are not linked directly to, or measuring, ecosystem functioning. The traits we included were ecological traits, relevant for the fitness and survival of a species within and across venting regions. We included the following traits in our analyses: Relative Adult Mobility (1-4, with 4 being the most mobile - likely an active swimmer); Estimated Maximum Body Size (mm, though scored by rounding the estimated maximum body size up to the nearest size class); Chemosynthesis-Obligate (with scores of: ‘Vent’, for species only found at vents; ‘Other CBE’, for species also found in other chemosynthesis-based ecosystems; and ‘No’ for species also found in other environments); Position of Symbiont (‘None’, ‘Episymbiont’, or ‘Endosymbiont’); Zonation from Vent (‘High’, ‘Medium’ or ‘Low’, referring to level of vent-fluid flow and/or temperature); and Nutritional Source (scored as:

'Symbiont', 'Fauna', 'Water Column' or 'Sediment and/or Rock Surface'). We ordered the scores according to specialism or adaptation required, or 'selectiveness', (so the number increases for each trait with increasing specialism or selectiveness). For example, 'Position of Symbiont' was scored from 1-3, with 1 being 'none' (as no adaptation is required for this) and 3 being 'endosymbiont' (as this requires more adaptation than being an episymbiont host; Dubilier et al., 2008). We plotted the traits against one another to check for covariance. This was difficult to assess, as most traits were categorical and simply converted to numeric form for analyses. Nevertheless, there was no clear evidence for covariance in any of the traits included in our analyses. We removed several traits from the trait dataset used for our analyses, due to coverage and certainty limitations, as described in **Table 10**.

Table 10: Traits removed from the sFDvent database (Chapman, Bates, et al., in review - Chapter 3), with rationale for their exclusion.

Trait	**Reason for exclusion**
Gregariousness	<60% of taxa have trait scores for this trait.
Foundation species	Misunderstanding of the definition of this trait was evident when reviewing the scores and comments provided by contributors in the sFDvent database.
Habitat complexity	Contributor bias was evident in this trait (e.g., in number of species scored, as well as the scores assigned) during preliminary analyses (e.g., in comparing trait scores across regions).
Abundance	<60% of taxa have trait scores for this trait.
Minimum / Maximum Depth Range	This is not an ecological trait, particularly when scored in the way contributors to sFDvent did. For instance, on review, it seems that most contributors gave the range for the vent field a species is found in, rather than the known range of a species. This can therefore be used as an environmental variable, but not a trait.
Substratum	This is not a true ecological trait, as this relates to the available substratum in a vent habitat. For example, whether a substratum is comprised of sulfide, basalt, or other sediments will largely depend on the location of a habitat and its underlying geology. This trait may, therefore, geographically constrain clusters during trait-based analysis if included.
Trophic Mode	This trait has lower certainty than nutritional source, which captures similar ecological information. The option to score 'omnivore', and to include multiple scores, for this trait also over-complicated its interpretation. Thus, instead of scoring the dominant trophic mode, many sFDvent contributors provided all trophic modes, which does not enable us to distinguish resource-dependence in the way that the nutritional source trait facilitates.

For analyses involving functional-diversity metrics computed using the 'FD' R package (Laliberté and Legendre, 2010; Laliberté et al., 2014; R Core Team, 2017), or the prior computation of a Gower distance matrix, we weighted traits. We did not assign more or less weight to any trait; instead, we used the weighting to standardise across traits with different numbers of modalities (**Table 11**).

Table 11: Trait weights assigned to standardise traits. These were used to prevent some traits having more influence on results simply because they had more scoring options, or modalities.

Trait	Number of scoring options / modalities	Weighting
Relative Adult Mobility	4	¼
Estimated Maximum Body Size (mm)	4	¼
Chemosynthesis-Obligate	3	⅓
Position of Symbiont	3	⅓
Zonation from Vent	3	⅓
Nutritional Source	4	¼

To compile environmental data for our analyses, we used the data extracted and described for vent fields in Chapman et al. (in prep. - Chapter 4) and computed the per-region average for each 'driver variable', seen to influence the geographic clustering of vent fields in Chapman et al. (in prep. - Chapter 4). We reduced these to variables that were not significantly correlated and for which data were available for all regions (**Appendix D.1**). We assigned a full-spreading rate of zero millimetres per year for regions in arc volcano settings - the Mariana and Kermadec arcs.

2.2 Measuring trait, taxonomic, and environmental dissimilarities among vent regions

First, we computed taxonomic dissimilarities among regions using information on the presence of species in each region. We used Sørensen's dissimilarity over the Jaccard dissimilarity measure, as Jaccard would bias our results given the relatively poor sampling of vent sites and the emphasis of this metric on absence-absence (double zero) entries. In our case, these entries may represent lack of information rather than a certain absence. We computed Sørensen's distances using the 'vegdist' function of the 'vegan' R package (wherein Sørensen distance is called 'bray'; Oksanen et al., 2018). We calculated distances and cluster analyses on both a species-by-region matrix and a region-by-species matrix, to present both species groupings and regional biogeographic provinces, respectively. Next, we computed functional (trait-based) dissimilarity using a Gower distance matrix, given a mix of numeric and categorical variables, calculated using the 'vegdist' function of the 'vegan' R package (Oksanen et al., 2018). Finally, for environmental data, we computed a

Euclidean distance matrix, as these data are numeric, using the ‘dist’ function of the ‘stats’ R package (R Core Team, 2017). We further used the environmental data to conduct a principal component analysis (PCA), to identify potential environmental influences on the regions included in this study, and the regional clusters identified using taxonomic and environmental dissimilarities. We computed the PCA using the ‘prcomp’ function of the ‘stats’ package (R Core Team, 2017). We plotted the first two principal components of this analysis, explaining the highest proportion of variance, using the ‘ggbiplot’ R package (Vu, 2011). This enabled us to label the results for oceanographic context.

To identify an appropriate clustering method for all distance matrices, we compared single, complete, average, centroid and ward (D2) approaches using a measure of cophenetic correlation (computed using the ‘cophenetic’ function of the ‘stats’ R package; R Core Team, 2017). For the trait data we tested this on, we identified the average-linkage method to be best, based on cophenetic correlation. However, the average-linkage approach maximises cophenetic correlation by its nature (Oksanen, 2014). We therefore considered other high-scoring options in the context of our analyses, to ensure it was most appropriate for our data, before selecting this approach. We did not use the ‘clustsig’ R package (Whitaker and Christman, 2014) to conduct SIMPROF tests to identify significant clusters as: i) this approach cannot be applied where NAs are present in the data (as for some trait scores), so would further reduce our species pools and limit statistical power; and ii) this method was not robust given different numbers of iterations or minor parameter changes. We did not use fusion diagrams or silhouette widths to identify suitable numbers of clusters in our analyses, as these measures were not robust under repeat testing. Instead, we produced dendrograms using hierarchical clustering with the average-linkage approach using the ‘hclust’ function in the ‘stats’ R package (R Core Team, 2017). We then visually identified the number of coherent clusters that: i) separated at a relatively high height, where confidence is higher; and ii) did not over-separate clusters, inflating dissimilarity.

We compared the trait and taxonomic dendrograms to one another using statistical tests that were robust to testing (e.g., Fowlkes-Mallows Index and an Entanglement Measure were not used, as they differ given permutations and the standard distance selected to measure distance between two trees, respectively). We computed Baker’s Gamma and cophenetic-correlation coefficients using the ‘dendextend’ package (Galili, 2015) to determine whether the trait and taxonomic dendrograms were significantly different based on relative branch positions (Galili, 2015). We also calculated the Robinson Foulds distance, or number of distinct edges, for the dendrograms, as another test for significant differences between the two approaches (Galili, 2015). We further computed the Mantel statistic to determine whether the trait and taxonomic distance matrices were significantly different, to ensure our results were not an outcome of clustering methodology (‘vegan’ R package;

Oksanen et al., 2018).

2.3 Identifying functional groups in the vent taxa of regional species pools

We identified functional groups (FGs) by average-linkage clustering data for the global pool of vent species, in the context of regional occupancy. We used the ‘dbFD’ function of the ‘FD’ package, as it enabled us to incorporate both trait and taxonomic data (Laliberté and Legendre, 2010; Laliberté et al., 2014). We weighted the trait matrix, as described in **Table 11**, and used the ‘cailliez’ correction to ensure that the multidimensional space created was Euclidean. We identified 19 FGs using the dendrogram produced by this analysis, and checked for differences in trait composition using raw trait data. We did not compute unique trait combinations (Keyel and Wiegand, 2016) to classify FGs, as this approach would be less conservative in measuring the uniqueness of species and regions. We matched FGs to taxonomic and location information to identify taxonomic or geographic constraints on FGs and to analyse trends in the distribution of FGs across regions.

2.4 Combining redundancy, dispersion, and dissimilarity to measure the relative uniqueness of vent regions

We used the ‘FD’ package (Laliberté and Legendre, 2010; Laliberté et al., 2014) to calculate both functional dispersion and functional redundancy. We chose to use functional dispersion (‘FDis’), as it: is appropriate for categorical and ordinal traits; is not as affected by extremes as functional divergence (‘FDiv’); and we do not have abundance data, so this measure represents the average distance of a species from the centroid - capturing how species are spread in trait space. As functional redundancy is not built in to the ‘FD’ package, we computed it as follows, where N_{unique} is the number of unique, or singular species (computed with the ‘dbFD’ function of the ‘FD’ package; Laliberté and Legendre, 2010; Laliberté et al., 2014), and S is the overall number of species:

$$1 - \frac{N_{unique}}{S}$$

We subtracted from one to ensure our measure was one of redundancy, rather than relative uniqueness.

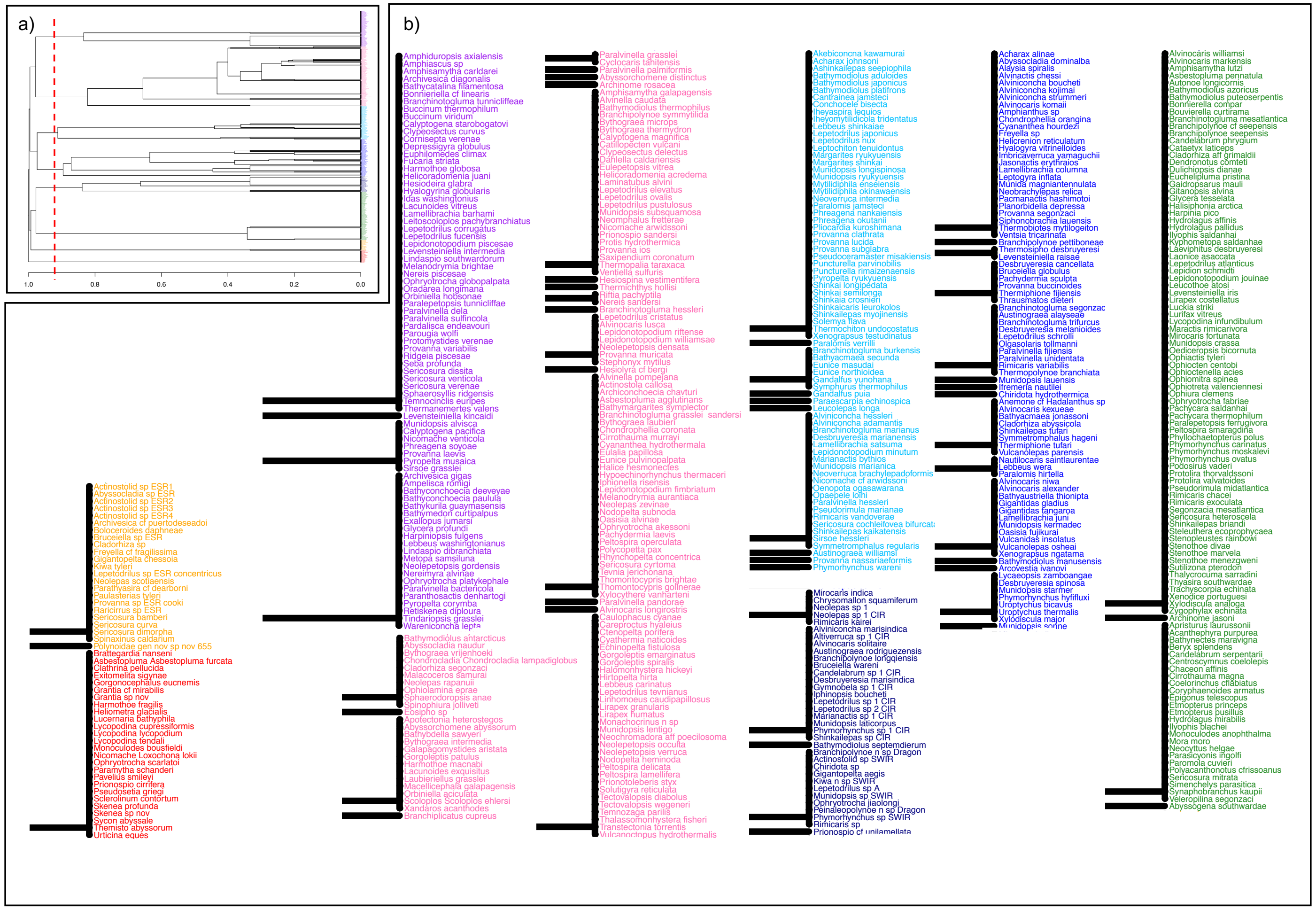
We modelled and plotted the residuals of functional dispersion and redundancy relative to the total number of species in a regional pool, to determine the relative functional dispersion and redundancy of each region without a sampling effect. For instance, for redundancy, we used a linear model to determine the relationship between the redundancy of a region and the number of species in its pool (using the ‘lm’ function of the R ‘stats’ package; R Core Team, 2017). We modelled this relationship with a second-order polynomial term to account for the shape of the relationship between these variables, before computing model residuals. We also modelled the relationship between functional dispersion and the number of species in a region, using a linear model with a second-order polynomial term, before recording the residuals. Finally, we plotted the relationship between residual values for functional redundancy and dispersion. We added a 0-0 line to compare the functional redundancy and dispersion of regions, using quadrants.

Following this analysis, we computed measures of functional, taxonomic, and environmental uniqueness for venting regions. To measure functional uniqueness, we used the 'distinctiveness' measure of the 'funrar' package (Grenié et al., 2017a, 2017b), incorporating information from the taxonomic region-by-species matrix and a Gower distance matrix computed using species trait data. We calculated the mean functional uniqueness per region for mapping and analyses. We used the 'taxondive' function of the 'vegan' R package (Oksanen et al., 2018) to calculate the 'taxonomic distinctness' (which we refer to as uniqueness, for consistency) for each vent region, using the taxonomic data and Sørensen's distance matrix as inputs. Next, we calculated environmental uniqueness using an approach similar to that of Doherty et al. (2017), wherein we computed a Euclidean distance matrix and divided all values by the maximum distance value identified in the whole matrix. We computed the distance matrix using the environmental data compiled for vent fields in Chapman et al. (in prep. - Chapter 4), to ensure that all available information was captured in this uniqueness measure. As such, to compare environmental uniqueness among the vent regions included in this study, we computed the average distance for each vent region, given distances output for fields within each region. We plotted the functional, taxonomic, and environmental uniqueness measures against one other, and calculated the Spearman's rank correlation coefficient for each pair, to determine whether there was a significant relationship between functional and/or taxonomic and/or environmental uniqueness. Finally, we summed each uniqueness value for each region, to quantify and map the overall uniqueness of each of the vent regions included in this analysis, across the globe. We summed these values, rather than multiplying them, as they originated from distance measures and are thus already comparable, or standardised.

3. RESULTS

3.1 Updating the global biogeography of deep-sea hydrothermal vents

Figure 31 (overleaf)**:** Dendrogram of hierarchical cluster analysis conducted on a Sørensen's distance matrix of the taxonomic (presence-absence) data using the average-linkage method. The tree was cut into eight coherent clusters (see red dashed line in a) for cut points and colour coding of labels). The resulting dendrogram has been split into pieces in b) for display purposes, but the overall dendrogram is shown in a). A copy of this figure is available on the USB storage device that accompanies this thesis, to the facilitate zoom functionality necessary to read dendrograms of this size. This provides an update to previous models of taxonomic biogeography, as discussed in **Appendix D.3**.


a)
1.0
0.8
0.6
0.4
0.2
0.0
b)
Actinostolid sp ESR1
Abyssocladia sp ESR
Actinostolid sp ESR2
Actinostolid sp ESR3
Actinostolid sp ESR4
Archivesica cf puertodeseadoi
Boloceroides daphneae
Bruceiella sp ESR
Cladorhiza sp
Freyella cf fragilissima
Gigantopelta chessoia
Kiwa tyleri
Lepetodrilus sp ESR concentricus
Neolepas scotiaensis
Parathyasira cf dearborni
Paulasterias tyleri
Provanna sp ESR cooki
Raricirrus sp ESR
Sericosura bamberi
Sericosura curva
Sericosura dimorpha
Spinaxinus caldarium
Polynoidae gen nov sp nov 655
Brattegardia nanseni
Asbestopluma Asbestopluma furcata
Clathrina pellucida
Exitomelita sigynae
Gorgonocephalus eucnemis
Grantia cf mirabilis
Grantia sp nov
Harmothoe fragilis
Heliometra glacialis
Lucernaria bathyphila
Lycopodina cupressiformis
Lycopodina lycopodium
Lycopodina tendali
Monoculodes bousfieldi
Nicomache Loxochona lokii
Ophryotrocha scarlatoi
Paramytha schanderi
Pavelius smileyi
Prionospio cirrifera
Pseudosetia griegi
Sclerolinum contortum
Skenea profunda
Skenea sp nov
Sycon abyssale
Themisto abyssorum
Urticina eques
Amphiduropsis axialensis
Amphiascus sp
Amphisamytha carldarei
Archivesica diagonalis
Bathycatalina filamentosa
Bonnieriella cf linearis
Branchinotogluma tunnicliffeae
Buccinum thermophilum
Buccinum viridum
Calyptogena starobogatovi
Clypeosectus curvus
Cornisepta verenae
Depressigyra globulus
Euphilomedes climax
Fucaria striata
Harmothoe globosa
Helicoradomenia juani
Hesiodeira glabra
Hyalogyrina globularis
Idas washingtonius
Lacunoides vitreus
Lamellibrachia barhami
Leitoscoloplos pachybranchiatus
Lepetodrilus corrugatus
Lepetodrilus fucensis
Lepidonotopodium piscesae
Levensteiniella intermedia
Lindaspio southwardorum
Melanodrymia brightae
Nereis piscesae
Ophryotrocha globopalpata
Oradarea longimana
Orbiniella hobsonae
Paralepetopsis tunnicliffae
Paralvinella dela
Paralvinella sulfincola
Pardalisca endeavouri
Parougia wolfi
Protomystides verenae
Provanna variabilis
Ridgeia piscesae
Seba profunda
Sericosura dissita
Sericosura venticola
Sericosura verenae
Sphaerosyllis ridgensis
Temnocinclis euripes
Thermanemertes valens
Levensteiniella kincaidi
Munidopsis alvisca
Calyptogena pacifica
Nicomache venticola
Phreagena soyoae
Provanna laevis
Pyropelta musaica
Sirsoe grasslei
Archivesica gigas
Ampelisca romigi
Bathyconchoecia deeveyae
Bathyconchoecia paulula
Bathykurila guaymasensis
Bathymedon curtipalpus
Exallopus jumarsi
Glycera profundi
Harpiniopsis fulgens
Lebbeus washingtonianus
Lindaspio dibranchiata
Metopa samsiluna
Neolepetopsis gordensis
Nereimyra alvinae
Ophryotrocha platykephale
Paralvinella bactericola
Paranthosactis denhartogi
Pyropelta corymba
Retiskenea diploura
Tindariopsis grasslei
Wareniconcha lepta
Bathymodiolus antarcticus
Abyssocladia naudur
Bythograea vrijenhoeki
Chondrocladia Chondrocladia lampadiglobus
Cladorhiza segonzaci
Malacoceros samurai
Neolepas rapanuii
Ophiolamina eprae
Sphaerodoropsis anae
Spinophiura jolliveti
Eosipho sp
Apotectonia heterostegos
Abyssorchomene abyssorum
Bathybdella sawyeri
Bythograea intermedia
Galapagomystides aristata
Gorgoleptis patulus
Harmothoe macnabi
Lacunoides exquisitus
Laubieriellus grasslei
Macellicephala galapagensis
Orbiniella aciculata
Scoloplos Scoloplos ehlersi
Xandaros acanthodes
Branchiplicatus cupreus
Paralvinella grasslei
Cyclocaris tahitensis
Paralvinella palmiformis
Abyssorchomene distinctus
Archinome rosacea
Amphisamytha galapagensis
Alvinella caudata
Bathymodiolus thermophilus
Branchipolynoe symmytilida
Bythograea microps
Bythograea thermydron
Calyptogena magnifica
Catillopecten vulcani
Clypeosectus delectus
Dahlella caldariensis
Eulepetopsis vitrea
Helicoradomenia acredema
Laminatubus alvini
Lepetodrilus elevatus
Lepetodrilus ovalis
Lepetodrilus pustulosus
Munidopsis subsquamosa
Neomphalus fretterae
Nicomache arwidssoni
Prionospio sandersi
Protis hydrothermica
Provanna ios
Saxipendium coronatum
Thermopalia taraxaca
Ventiella sulfuris
Hesiospina vestimentifera
Thermichthys hollisi
Riftia pachyptila
Nereis sandersi
Branchinotogluma hessleri
Lepetodrilus cristatus
Alvinocaris lusca
Lepidonotopodium riftense
Lepidonotopodium williamsae
Neolepetopsis densata
Provanna muricata
Stephonyx mytilus
Hesiolyra cf bergi
Alvinella pompejana
Actinostola callosa
Archiconchoecia chavturi
Asbestopluma agglutinans
Bathymargarites symplector
Branchinotogluma grasslei sandersi
Bythograea laubieri
Chondrophellia coronata
Cirrothauma murrayi
Cyananthea hydrothermala
Eulalia papillosa
Eunice pulvinopalpata
Halice hesmonectes
Hypoechinorhynchus thermaceri
Iphionella risensis
Lepidonotopodium fimbriatum
Melanodrymia aurantiaca
Neolepas zevinae
Nodopelta subnoda
Oasisia alvinae
Ophryotrocha akessoni
Pachydermia laevis
Peltospira operculata
Polycopetta pax
Rhynchopelta concentrica
Sericosura cyrtoma
Tevnia jerichonana
Thomontocypris brightae
Thomontocypris gollnerae
Xylocythere vanharteni
Paralvinella pandorae
Alvinocaris longirostris
Caulophacus cyanae
Careproctus hyaleius
Ctenopelta porifera
Cyathermia naticoides
Echinopelta fistulosa
Gorgoleptis emarginatus
Gorgoleptis spiralis
Halomonhystera hickeyi
Hirtopelta hirta
Lebbeus carinatus
Lepetodrilus tevnianus
Linhomoeus caudipapillosus
Lirapex granularis
Lirapex humatus
Monachocrinus n sp
Munidopsis lentigo
Neochromadora aff poecilosoma
Neolepetopsis occulta
Neolepetopsis verruca
Nodopelta heminoda
Peltospira delicata
Peltospira lamellifera
Prionotoleberis styx
Solutigyra reticulata
Tectovalopsis diabolus
Tectovalopsis wegeneri
Temnozaga parilis
Thalassomonhystera fisheri
Transtectonia torrentis
Vulcanoctopus hydrothermalis
Akebiconcha kawamurai
Acharax johnsoni
Ashinkailepas seepiophila
Bathymodiolus aduloides
Bathymodiolus japonicus
Bathymodiolus platifrons
Cantrainea jamsteci
Conchocele bisecta
Iheyaspira lequios
Iheyomytilidicola tridentatus
Lebbeus shinkaiae
Lepetodrilus japonicus
Lepetodrilus nux
Leptochiton tenuidontus
Margarites ryukyuensis
Margarites shinkai
Munidopsis longispinosa
Munidopsis ryukyuensis
Mytilidiphila enseiensis
Mytilidiphila okinawaensis
Neoverruca intermedia
Paralomis jamsteci
Phreagena nankaiensis
Phreagena okutanii
Pliocardia kuroshimana
Provanna clathrata
Provanna lucida
Provanna subglabra
Pseudoceramaster misakiensis
Puncturella parvinobilis
Puncturella rimaizenaensis
Pyropelta ryukyuensis
Shinkai longipedata
Shinkai semilonga
Shinkaia crosnieri
Shinkaicaris leurokolos
Shinkailepas myojinensis
Solemya flava
Thermochiton undocostatus
Xenograpsus testudinatus
Paralomis verrilli
Branchinotogluma burkensis
Bathyacmaea secunda
Eunice masudai
Eunice northioidea
Gandalfus yunohana
Symphurus thermophilus
Gandalfus puia
Paraescarpia echinospica
Leucolepas longa
Alviniconcha hessleri
Alviniconcha adamantis
Branchinotogluma marianus
Desbruyeresia marianensis
Lamellibrachia satsuma
Lepidonotopodium minutum
Marianactis bythios
Munidopsis marianica
Neoverruca brachylepadoformis
Nicomache cf arwidssoni
Oenopota ogasawarana
Opaepele loihi
Paralvinella hessleri
Pseudorimula marianae
Rimicaris vandoverae
Sericosura cochleifovea bifurcat
Shinkailepas kaikatensis
Sirsoe hessleri
Symmetromphalus regularis
Austinograea williamsi
Provanna nassariaeformis
Phymorhynchus wareni
Mirocaris indica
Chrysomallon squamiferum
Neolepas sp 1
Neolepas sp 1 CIR
Rimicaris kairei
Alviniconcha marisindica
Altiverruca sp 1 CIR
Alvinocaris solitaire
Austinograea rodriguezensis
Branchipolynoe longqiensis
Bruceiella wareni
Candelabrum sp 1 CIR
Desbruyeresia marisindica
Gymnobela sp 1 CIR
Iphinopsis boucheti
Lepetodrilus sp 1 CIR
Lepetodrilus sp 2 CIR
Marianactis sp 1 CIR
Munidopsis laticorpus
Phymorhynchus sp 1 CIR
Shinkailepas sp CIR
Bathymodiolus septemdierum
Branchipolynoe n sp Dragon
Actinostolid sp SWIR
Chiridota sp
Gigantopelta aegis
Kiwa n sp SWIR
Lepetodrilus sp A
Munidopsis sp SWIR
Ophryotrocha jiaolongi
Peinaleopolynoe n sp Dragon
Phymorhynchus sp SWIR
Rimicaris sp
Prionospio cf unilamellata
Acharax alinae
Abyssocladia dominalba
Alaysia spiralis
Alvinactis chessi
Alviniconcha boucheti
Alviniconcha kojimai
Alviniconcha strummeri
Alvinocaris komaii
Amphianthus sp
Chondrophellia orangina
Cyananthea hourdezi
Freyella sp
Helicrenion reticulatum
Hyalogyra vitrinelloides
Imbricaverruca yamaguchii
Jasonactis erythraios
Lamellibrachia columna
Leptogyra inflata
Munida magniantennulata
Neobrachylepas relica
Pacmanactis hashimotoi
Planorbidella depressa
Provanna segonzaci
Siphonobrachia lauensis
Thermobiotes mytilogeiton
Ventsia tricarinata
Branchipolynoe pettiboneae
Thermosipho desbruyeresi
Levensteiniella raisae
Desbruyeresia cancellata
Bruceiella globulus
Pachydermia sculpta
Provanna buccinoides
Thermiphione fijiensis
Thrausmatos dieteri
Branchinotogluma segonzac
Austinograea alayseae
Branchinotogluma trifurcus
Desbruyeresia melanioides
Lepetodrilus schrolli
Olgasolaris tollmanni
Paralvinella fijiensis
Paralvinella unidentata
Rimicaris variabilis
Thermopolynoe branchiata
Munidopsis lauensis
Ifremeria nautilei
Chiridota hydrothermica
Anemone cf Hadalanthus sp
Alvinocaris kexueae
Bathyacmaea jonassoni
Cladorhiza abyssicola
Shinkailepas tufari
Symmetromphalus hageni
Thermiphione tufari
Vulcanolepas parensis
Nautilocaris saintlaurentae
Lebbeus wera
Paralomis hirtella
Alvinocaris niwa
Alvinocaris alexander
Bathyaustriella thionipta
Gigantidas gladius
Gigantidas tangaroa
Lamellibrachia juni
Munidopsis kermadec
Oasisia fujikurai
Vulcanidas insolatus
Vulcanolepas osheai
Xenograpsus ngatama
Bathymodiolus manusensis
Arcovestia ivanovi
Lycaeopsis zamboangae
Desbruyeresia spinosa
Munidopsis starmer
Phymorhynchus hyfifluxi
Uroptychus bicavus
Uroptychus thermalis
Xylodiscula major
Munidopsis sonne
Alvinocaris williamsi
Alvinocaris markensis
Amphisamytha lutzi
Asbestopluma pennatula
Autonoe longicornis
Bathymodiolus azoricus
Bathymodiolus puteoserpentis
Bonnierella compar
Bouvierella curtirama
Branchinotogluma mesatlantica
Branchipolynoe cf seepensis
Branchipolynoe seepensis
Candelabrum phrygium
Cataetyx laticeps
Cladorhiza aff grimaldii
Dendronotus comteti
Dulichiopsis dianae
Euchelipluma pristina
Gaidropsarus mauli
Gitanopsis alvina
Glycera tesselata
Halisiphonia arctica
Harpinia pico
Hydrolagus affinis
Hydrolagus pallidus
Ilyophis saldanhai
Kyphometopa saldanhae
Laeviphitus desbruyeresi
Laonice asaccata
Lepetodrilus atlanticus
Lepidion schmidti
Lepidonotopodium jouinae
Leucothoe atosi
Levensteiniella iris
Lirapex costellatus
Luckia striki
Lurifax vitreus
Lycopodina infundibulum
Maractis rimicarivora
Mirocaris fortunata
Munidopsis crassa
Oediceropsis bicornuta
Ophiactis tyleri
Ophiocten centobi
Ophioctenella acies
Ophiomitra spinea
Ophiotreta valenciennesi
Ophiura clemens
Ophryotrocha fabriae
Pachycara saldanhai
Pachycara thermophilum
Paralepetopsis ferrugivora
Peltospira smaragdina
Phyllochaetopterus polus
Phymorhynchus carinatus
Phymorhynchus moskalevi
Phymorhynchus ovatus
Podosirus vaderi
Protolira thorvaldssoni
Protolira valvatoides
Pseudorimula midatlantica
Rimicaris chacei
Rimicaris exoculata
Segonzacia mesatlantica
Sericosura heteroscela
Shinkailepas briandi
Steleuthera ecoprophycaea
Stenopleustes rainbowi
Stenothoe divae
Stenothoe marvela
Stenothoe menezgweni
Sutilizona pterodon
Thalycrocuma sarradini
Thyasira southwardae
Trachyscorpia echinata
Xenodice portuguesi
Xylodiscula analoga
Zygophylax echinata
Archinome jasoni
Apristurus laurussonii
Acanthephyra purpurea
Bathynectes maravigna
Beryx splendens
Candelabrum serpentarii
Centroscymnus coelolepis
Chaceon affinis
Cirrothauma magna
Coelorinchus cflabiatus
Coryphaenoides armatus
Epigonus telescopus
Etmopterus princeps
Etmopterus pusillus
Hydrolagus mirabilis
Ilyophis blachei
Monoculodes anophthalma
Mora moro
Neocyttus helgae
Parasicyonis ingolfi
Paromola cuvieri
Polyacanthonotus cfrissoanus
Sericosura mitrata
Simenchelys parasitica
Synaphobranchus kaupii
Veleropilina segonzaci
Abyssogena southwardae

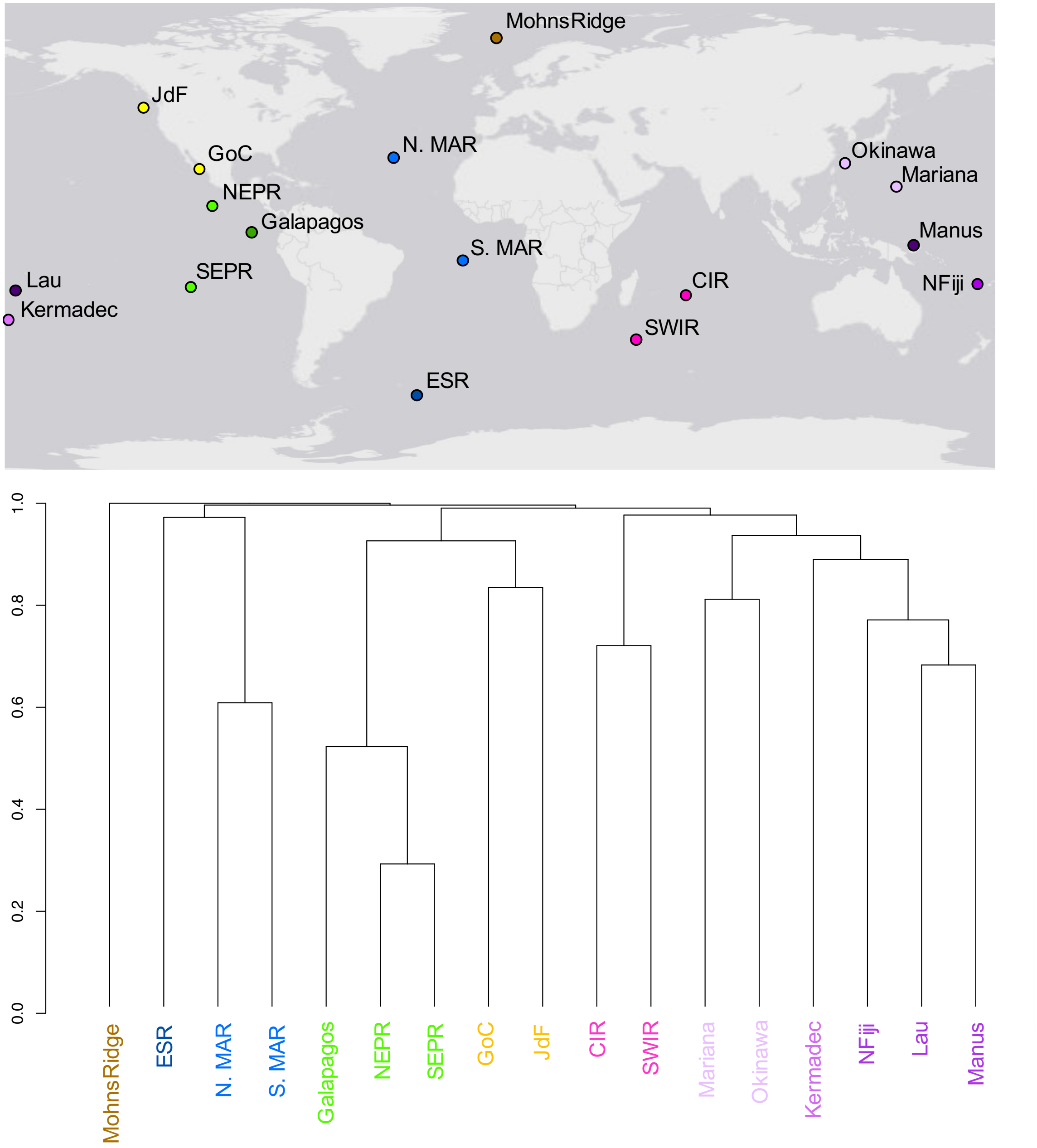


Figure 32: Dendrogram of hierarchical cluster analysis conducted on a Sørensen's distance matrix of the transposed taxonomic (presence-absence) data using the average-linkage method, with regions mapped to aid interpretation. The tree was cut into nine coherent clusters as per the coloured region labels, updating previous models of taxonomic biogeography, as discussed in **Appendix D.3**.

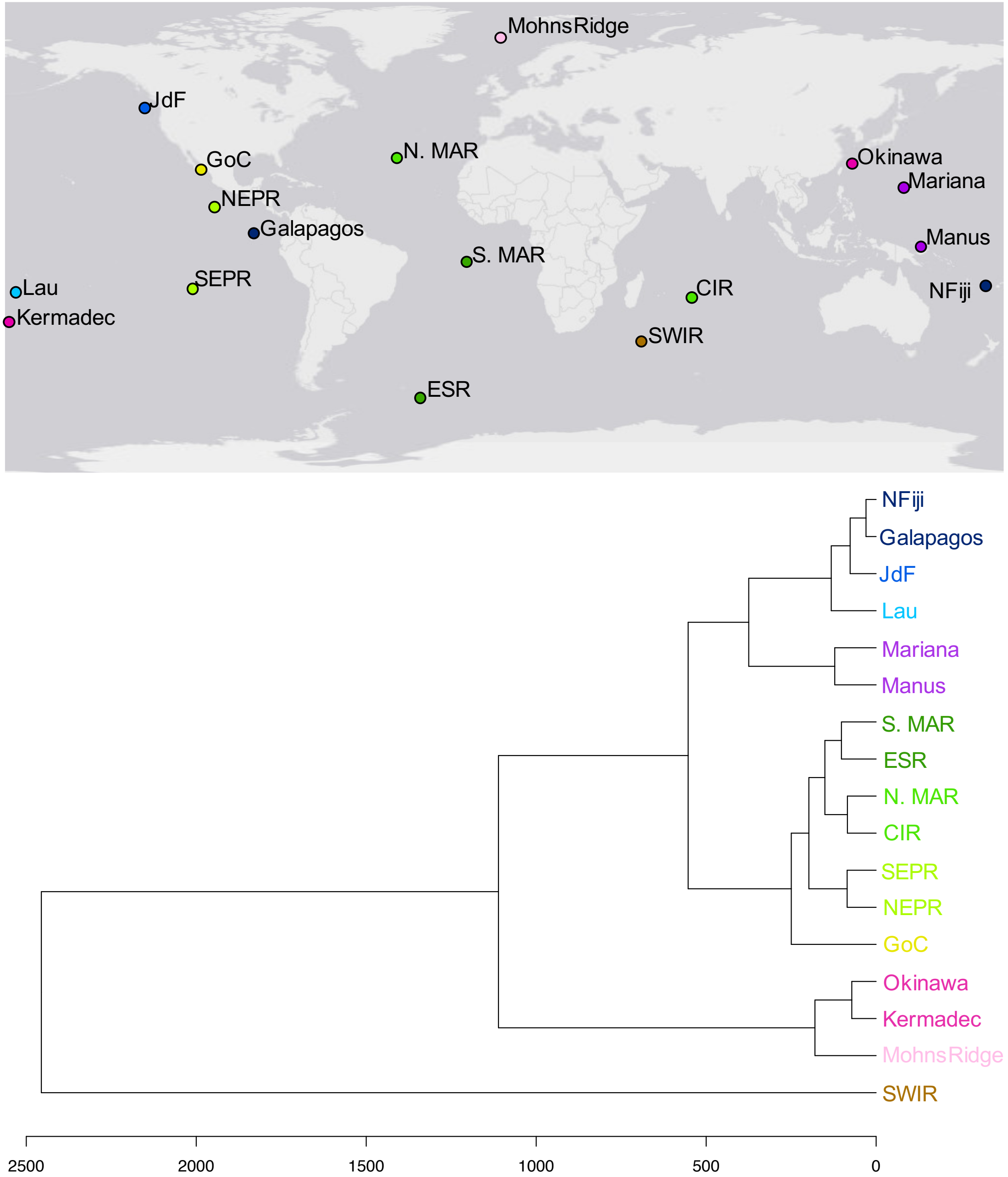


Figure 33: Dendrogram of hierarchical cluster analysis conducted on a Euclidean distance matrix of environmental variables using the average-linkage method, to produce nine clusters (colour-coded, with regions mapped to aid interpretation). Region names have been shortened for display purposes as described in **Appendix D.2**.

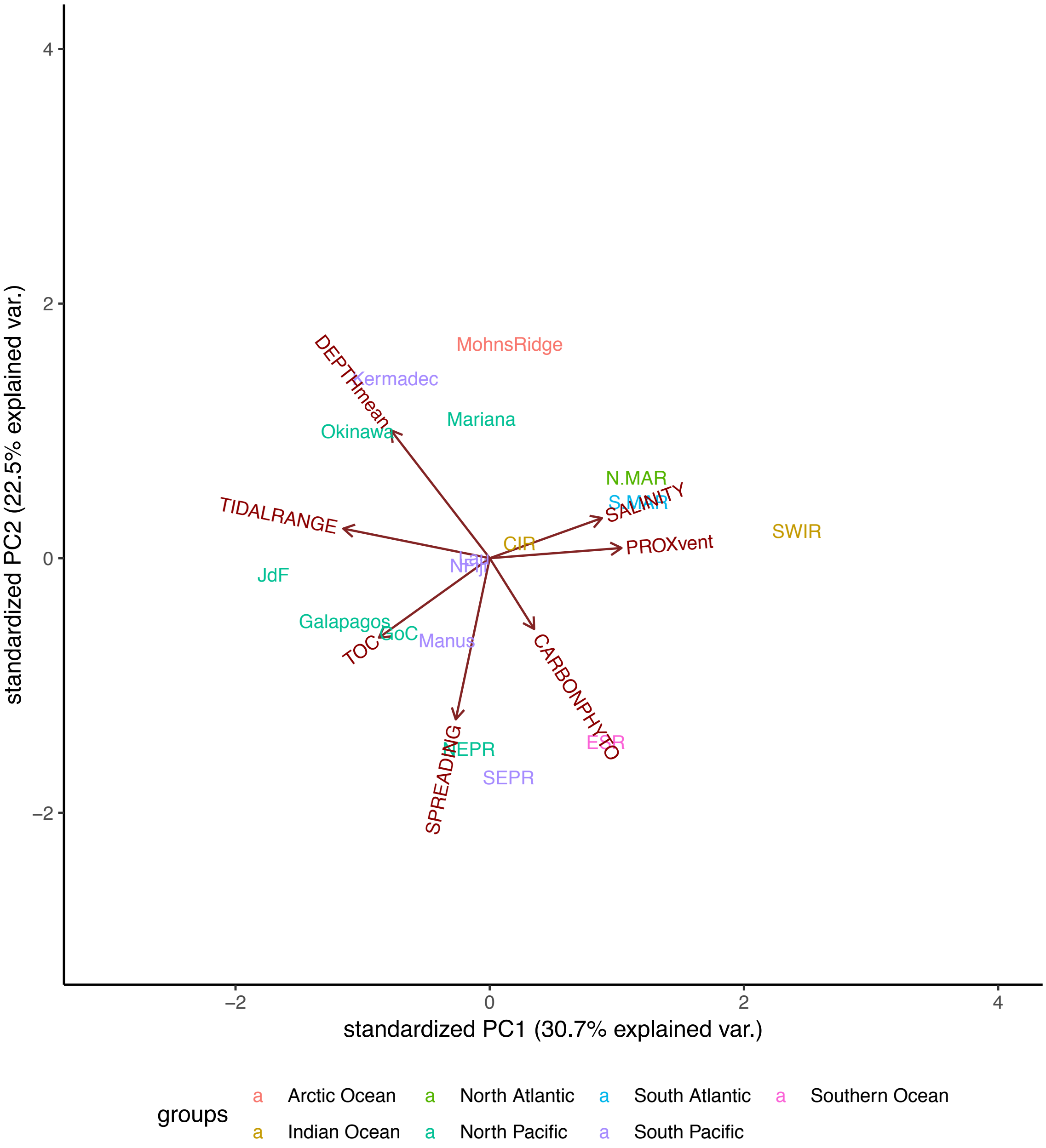
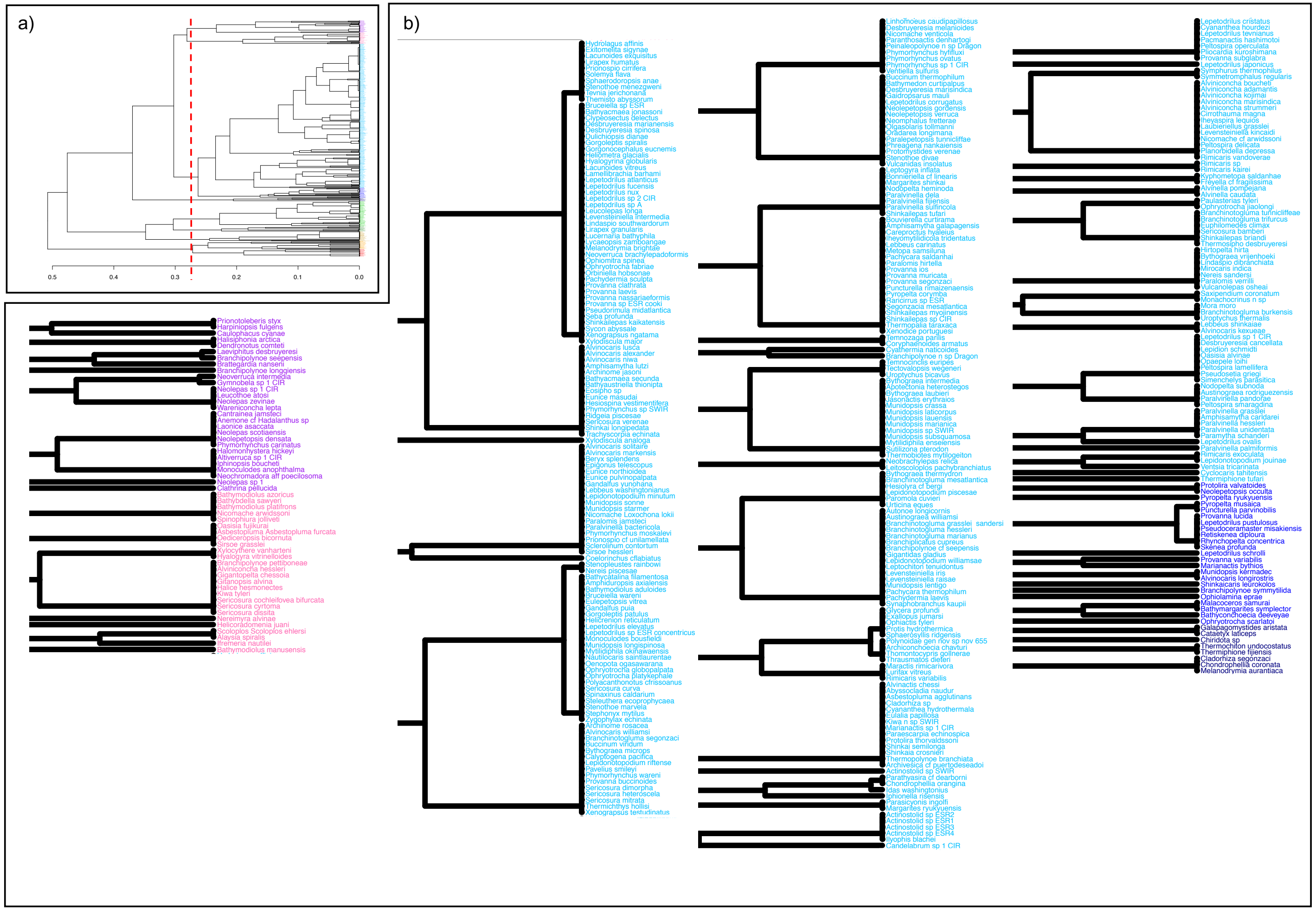


Figure 34: Principal component analysis (PCA) used to identify potential drivers of environmental similarity among regions based on seven environmental variables. This scatterplot shows the first two axes of this PCA, together explaining 53.2% of the total variance. Each point is labelled according to the region it represents and coloured according to the ocean basin the region is found within. Brown arrows represent the environmental variables influencing the clustering of regions, with the length of each arrow corresponding to the strength of influence (e.g., TOC - or total organic carbon in sediment - has less strong of an influence on points near it than tidal range has on regions in its vicinity). The arrows are labelled according to the abbreviations given in **Appendix D.2**.

Using the taxonomic and location, or occupancy, information accompanying the sFDvent global database of trait data for deep-sea hydrothermal-vent fauna, we identify eight coherent clusters of vent species (**Figure 31**), grouping into nine geographic clusters (**Figure 32**). We also distinguish nine clusters based on the environmental characteristics of these geographic regions, though these differ from the taxonomic groupings in many cases (**Figure 33**). For instance, in the taxonomic clustering, the Arctic Ocean Mohns Ridge region is isolated from all others, and the East Scotia Ridge in the Southern Ocean is also relatively separate from other venting regions (**Figure 32**). Contrastingly, these regions are located with Kermadec Arc and Okinawa Trough vents (due to similar average depths and deep-water productivity; **Figure 33**), and southern Mid-Atlantic Ridge (MAR) vents, respectively, when clustered according to environmental characteristics (**Figure 33**). The Galapagos and northern and southern East Pacific Rise (EPR) regions group with Gulf of California and Juan de Fuca Ridge vents taxonomically (**Figure 32**). Environmentally, Galapagos vents cluster with those of the North Fiji Basin, Juan de Fuca Ridge, and Lau Basin (**Figure 33**), predominantly due to similarities in the total organic carbon in their sediments, though tidal range also influences the position of the Juan de Fuca Ridge in this cluster (**Figure 34**). The northern MAR clusters with southern MAR vents taxonomically and Central Indian Ridge vents environmentally, given similar salinities (**Figure 32**, **Figure 33**, **Figure 34**). The South West Indian Ridge is isolated environmentally, far from other vent fields (**Figure 33**) but similar to the Central Indian Ridge (CIR) in terms of taxonomy (**Figure 32**). Contrary to the overall trend towards non-congruence, northern and southern East Pacific Rise (EPR) vents group both taxonomically and environmentally (**Figure 32** and **Figure 33**). These regions are, however, more closely associated with Gulf of California vents in terms of environmental characteristics (e.g., spreading rate and total organic carbon in sediments; **Figure 34**) than taxonomic composition (**Figure 32**).

Figure 35(a-c) (overleaf)**:** Dendrogram of hierarchical cluster analysis conducted on a Gower distance matrix of the trait data (species-by-trait matrix) using the average-linkage method. The tree was cut into ten coherent clusters (see red dashed line in a) for cut points and colour coding of labels). The resulting dendrogram has been split into pieces in b) for display purposes, but the overall dendrogram is shown in a). A copy of this figure is available on the USB storage device that accompanies this thesis, to the facilitate zoom functionality necessary to read dendrograms of this size.


a)
0.5
0.4
0.3
0.2
0.1
0.0
b)
Prionotoleberis styx
Harpiniopsis fulgens
Caulophacus cyanae
Halisiphonia arctica
Dendronotus comteti
Laeviphitus desbruyeresi
Branchipolynoe seepensis
Brattegardia nanseni
Branchipolynoe longqiensis
Neoverruca intermedia
Gymnobela sp 1 CIR
Neolepas sp 1 CIR
Leucothoe atosi
Neolepas zevinae
Wareniconcha lepta
Cantrainea jamsteci
Anemone cf Hadalanthus sp
Laonice asaccata
Neolepas scotiaensis
Neolepetopsis densata
Phymorhynchus carinatus
Halomonhystera hickeyi
Altiverruca sp 1 CIR
Iphinopsis boucheti
Monoculodes anophthalma
Neochromadora aff poecilosoma
Neolepas sp 1
Clathrina pellucida
Bathymodiolus azoricus
Bathybdella sawyeri
Bathymodiolus platifrons
Nicomache arwidssoni
Spinophiura jolliveti
Oasisia fujikurai
Asbestopluma Asbestopluma furcata
Oediceropsis bicornuta
Sirsoe grasslei
Xylocythere vanharteni
Hyalogyra vitrinelloides
Branchipolynoe pettiboneae
Alviniconcha hessleri
Gigantopelta chessoia
Gitanopsis alvina
Halice hesmonectes
Kiwa tyleri
Sericosura cochleifovea bifurcata
Sericosura cyrtoma
Sericosura dissita
Nereimyra alvinae
Helicoradomenia juani
Scoloplos Scoloplos ehlersi
Alaysia spiralis
Ifremeria nautilei
Bathymodiolus manusensis
Hydrolagus affinis
Exitomelita sigynae
Lacunoides exquisitus
Lirapex humatus
Prionospio cirrifera
Solemya flava
Sphaerodoropsis anae
Stenothoe menezgweni
Tevnia jerichonana
Themisto abyssorum
Bruceiella sp ESR
Bathyacmaea jonassoni
Clypeosectus delectus
Desbruyeresia marianensis
Desbruyeresia spinosa
Dulichiopsis dianae
Gorgoleptis spiralis
Gorgonocephalus eucnemis
Heliometra glacialis
Hyalogyrina globularis
Lacunoides vitreus
Lamellibrachia barhami
Lepetodrilus atlanticus
Lepetodrilus fucensis
Lepetodrilus nux
Lepetodrilus sp 2 CIR
Lepetodrilus sp A
Leucolepas longa
Levensteiniella intermedia
Lindaspio southwardorum
Lirapex granularis
Lucernaria bathyphila
Lycaeopsis zamboangae
Melanodrymia brightae
Neoverruca brachylepadoformis
Ophiomitra spinea
Ophryotrocha fabriae
Orbiniella hobsonae
Pachydermia sculpta
Provanna clathrata
Provanna laevis
Provanna nassariaeformis
Provanna sp ESR cooki
Pseudorimula midatlantica
Seba profunda
Shinkailepas kaikatensis
Sycon abyssale
Xenograpsus ngatama
Xylodiscula major
Alvinocaris lusca
Alvinocaris alexander
Alvinocaris niwa
Amphisamytha lutzi
Archinome jasoni
Bathyacmaea secunda
Bathyaustriella thionipta
Eosipho sp
Eunice masudai
Hesiospina vestimentifera
Phymorhynchus sp SWIR
Ridgeia piscesae
Sericosura verenae
Shinkai longipedata
Trachyscorpia echinata
Xylodiscula analoga
Alvinocaris solitaire
Alvinocaris markensis
Beryx splendens
Epigonus telescopus
Eunice northioidea
Eunice pulvinopalpata
Gandalfus yunohana
Lebbeus washingtonianus
Lepidonotopodium minutum
Munidopsis sonne
Munidopsis starmer
Nicomache Loxochona lokii
Paralomis jamsteci
Paralvinella bactericola
Phymorhynchus moskalevi
Prionospio cf unilamellata
Sclerolinum contortum
Sirsoe hessleri
Coelorinchus cflabiatus
Stenopleustes rainbowi
Nereis piscesae
Bathycatalina filamentosa
Amphiduropsis axialensis
Bathymodiolus aduloides
Bruceiella wareni
Eulepetopsis vitrea
Gandalfus puia
Gorgoleptis patulus
Helicrenion reticulatum
Lepetodrilus elevatus
Lepetodrilus sp ESR concentricus
Monoculodes bousfieldi
Munidopsis longispinosa
Mytilidiphila okinawaensis
Nautilocaris saintlaurentae
Oenopota ogasawarana
Ophryotrocha globopalpata
Ophryotrocha platykephale
Polyacanthonotus cfrissoanus
Sericosura curva
Spinaxinus caldarium
Steleuthera ecoprophycaea
Stenothoe marvela
Stephonyx mytilus
Zygophylax echinata
Archinome rosacea
Alvinocaris williamsi
Branchinotogluma segonzaci
Buccinum viridum
Bythograea microps
Calyptogena pacifica
Lepidonotopodium riftense
Pavelius smileyi
Phymorhynchus wareni
Provanna buccinoides
Sericosura dimorpha
Sericosura heteroscela
Sericosura mitrata
Thermichthys hollisi
Xenograpsus testudinatus
Linhomoeus caudipapillosus
Desbruyeresia melanioides
Nicomache venticola
Paranthosactis denhartogi
Peinaleopolynoe n sp Dragon
Phymorhynchus hyfifluxi
Phymorhynchus ovatus
Phymorhynchus sp 1 CIR
Ventiella sulfuris
Buccinum thermophilum
Bathymedon curtipalpus
Desbruyeresia marisindica
Gaidropsarus mauli
Lepetodrilus corrugatus
Neolepetopsis gordensis
Neolepetopsis verruca
Neomphalus fretterae
Olgasolaris tollmanni
Oradarea longimana
Paralepetopsis tunnicliffae
Phreagena nankaiensis
Protomystides verenae
Stenothoe divae
Vulcanidas insolatus
Leptogyra inflata
Bonnieriella cf linearis
Margarites shinkai
Nodopelta heminoda
Paralvinella dela
Paralvinella fijiensis
Paralvinella sulfincola
Shinkailepas tufari
Bouvierella curtirama
Amphisamytha galapagensis
Careproctus hyaleius
Iheyomytilidicola tridentatus
Lebbeus carinatus
Metopa samsiluna
Pachycara saldanhai
Paralomis hirtella
Provanna ios
Provanna muricata
Provanna segonzaci
Puncturella rimaizenaensis
Pyropelta corymba
Raricirrus sp ESR
Segonzacia mesatlantica
Shinkailepas myojinensis
Shinkailepas sp CIR
Thermopalia taraxaca
Xenodice portuguesi
Temnozaga parilis
Coryphaenoides armatus
Cyathermia naticoides
Branchipolynoe n sp Dragon
Temnocinclis euripes
Tectovalopsis wegeneri
Uroptychus bicavus
Bythograea intermedia
Apotectonia heterostegos
Bythograea laubieri
Jasonactis erythraios
Munidopsis crassa
Munidopsis laticorpus
Munidopsis lauensis
Munidopsis marianica
Munidopsis sp SWIR
Munidopsis subsquamosa
Mytilidiphila enseiensis
Sutilizona pterodon
Thermobiotes mytilogeiton
Neobrachylepas relica
Leitoscoloplos pachybranchiatus
Bythograea thermydron
Branchinotogluma mesatlantica
Hesiolyra cf bergi
Lepidonotopodium piscesae
Paromola cuvieri
Urticina eques
Autonoe longicornis
Austinograea williamsi
Branchinotogluma grasslei sandersi
Branchinotogluma hessleri
Branchinotogluma marianus
Branchiplicatus cupreus
Branchipolynoe cf seepensis
Gigantidas gladius
Lepidonotopodium williamsae
Leptochiton tenuidontus
Levensteiniella iris
Levensteiniella raisae
Munidopsis lentigo
Pachycara thermophilum
Pachydermia laevis
Synaphobranchus kaupii
Glycera profundi
Exallopus jumarsi
Ophiactis tyleri
Protis hydrothermica
Sphaerosyllis ridgensis
Polynoidae gen nov sp nov 655
Archiconchoecia chavturi
Thomontocypris gollnerae
Thrausmatos dieteri
Maractis rimicarivora
Lurifax vitreus
Rimicaris variabilis
Alvinactis chessi
Abyssocladia naudur
Asbestopluma agglutinans
Cladorhiza sp
Cyananthea hydrothermala
Eulalia papillosa
Kiwa n sp SWIR
Marianactis sp 1 CIR
Paraescarpia echinospica
Protolira thorvaldssoni
Shinkai semilonga
Shinkaia crosnieri
Thermopolynoe branchiata
Archivesica cf puertodeseadoi
Actinostolid sp SWIR
Parathyasira cf dearborni
Chondrophellia orangina
Idas washingtonius
Iphionella risensis
Parasicyonis ingolfi
Margarites ryukyuensis
Actinostolid sp ESR2
Actinostolid sp ESR1
Actinostolid sp ESR3
Actinostolid sp ESR4
Ilyophis blachei
Candelabrum sp 1 CIR
Lepetodrilus cristatus
Cyananthea hourdezi
Lepetodrilus tevnianus
Pacmanactis hashimotoi
Peltospira operculata
Pliocardia kuroshimana
Provanna subglabra
Lepetodrilus japonicus
Symphurus thermophilus
Symmetromphalus regularis
Alviniconcha boucheti
Alviniconcha adamantis
Alviniconcha kojimai
Alviniconcha marisindica
Alviniconcha strummeri
Cirrothauma magna
Iheyaspira lequios
Laubieriellus grasslei
Levensteiniella kincaidi
Nicomache cf arwidssoni
Peltospira delicata
Planorbidella depressa
Rimicaris vandoverae
Rimicaris sp
Rimicaris kairei
Kyphometopa saldanhae
Freyella cf fragilissima
Alvinella pompejana
Alvinella caudata
Paulasterias tyleri
Ophryotrocha jiaolongi
Branchinotogluma tunnicliffeae
Branchinotogluma trifurcus
Euphilomedes climax
Sericosura bamberi
Shinkailepas briandi
Thermosipho desbruyeresi
Hirtopelta hirta
Bythograea vrijenhoeki
Lindaspio dibranchiata
Mirocaris indica
Nereis sandersi
Paralomis verrilli
Vulcanolepas osheai
Saxipendium coronatum
Monachocrinus n sp
Mora moro
Branchinotogluma burkensis
Uroptychus thermalis
Lebbeus shinkaiae
Alvinocaris kexueae
Lepetodrilus sp 1 CIR
Desbruyeresia cancellata
Lepidion schmidti
Oasisia alvinae
Opaepele loihi
Peltospira lamellifera
Pseudosetia griegi
Simenchelys parasitica
Nodopelta subnoda
Austinograea rodriguezensis
Paralvinella pandorae
Peltospira smaragdina
Paralvinella grasslei
Amphisamytha carldarei
Paralvinella hessleri
Paralvinella unidentata
Paramytha schanderi
Lepetodrilus ovalis
Paralvinella palmiformis
Rimicaris exoculata
Lepidonotopodium jouinae
Ventsia tricarinata
Cyclocaris tahitensis
Thermiphione tufari
Protolira valvatoides
Neolepetopsis occulta
Pyropelta ryukyuensis
Pyropelta musaica
Puncturella parvinobilis
Provanna lucida
Lepetodrilus pustulosus
Pseudoceramaster misakiensis
Retiskenea diploura
Rhynchopelta concentrica
Skenea profunda
Lepetodrilus schrolli
Provanna variabilis
Marianactis bythios
Munidopsis kermadec
Alvinocaris longirostris
Shinkaicaris leurokolos
Branchipolynoe symmytilida
Ophiolamina eprae
Malacoceros samurai
Bathymargarites symplector
Bathyconchoecia deeveyae
Ophryotrocha scarlatoi
Galapagomystides aristata
Cataetyx laticeps
Chiridota sp
Thermochiton undocostatus
Thermiphione fijiensis
Cladorhiza segonzaci
Chondrophellia coronata
Melanodrymia aurantiaca

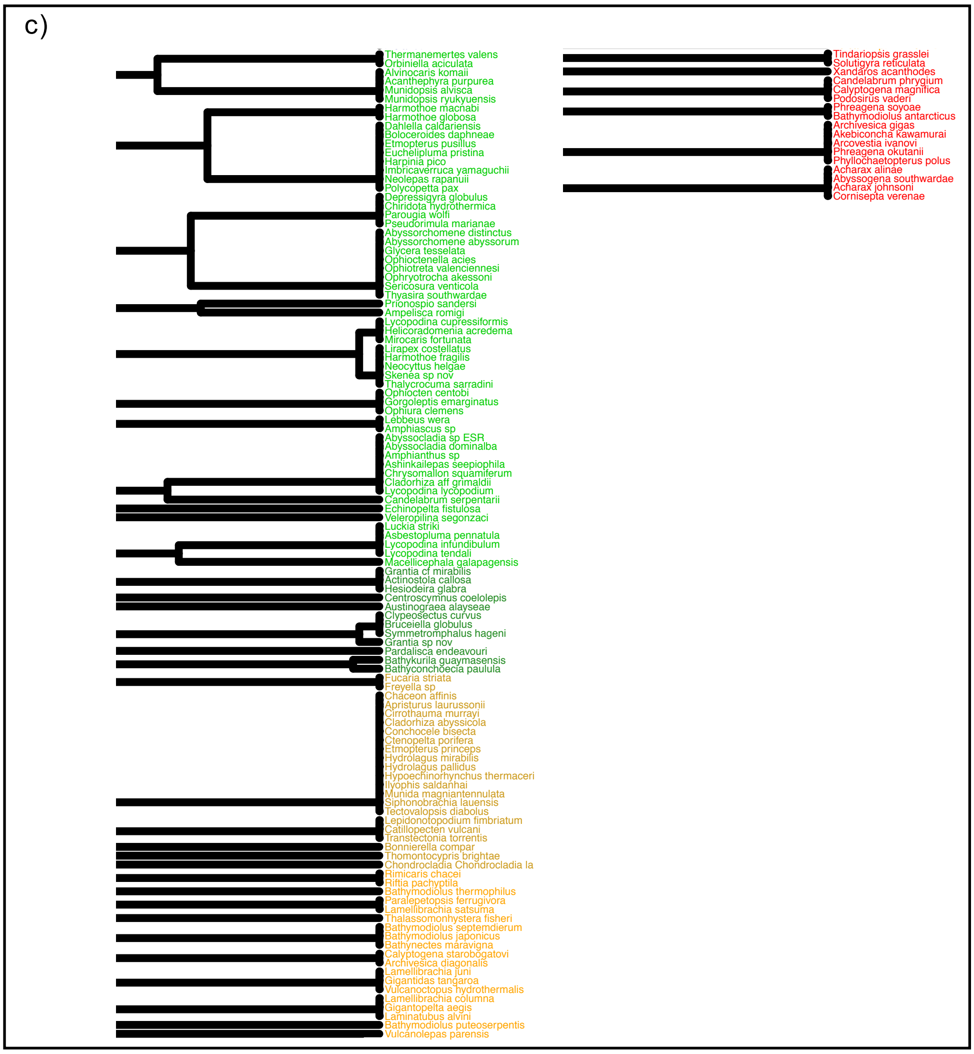


Table 12: Comparing trait-based and taxonomic dendrograms using statistical tests conducted using the 'dendextend' (Galili, 2015) and 'vegan' (Oksanen et al., 2018) R packages (R Core Team, 2017). The Mantel statistic was computed using Spearman's Rank correlation method and 999 permutations.

Metric	Output	Interpretation
Baker's Gamma Correlation Coefficient	-0.004	Trees are dissimilar
Cophenetic Correlation Coefficient	0.038	Trees are dissimilar
Robinson Foulds Distance	1090	1090 is the length of distinct edges in the trees (high, suggesting the trees are dissimilar)
Mantel Statistic	0.047	The trait-based and taxonomic distance matrices have very low similarity (significance 0.001)

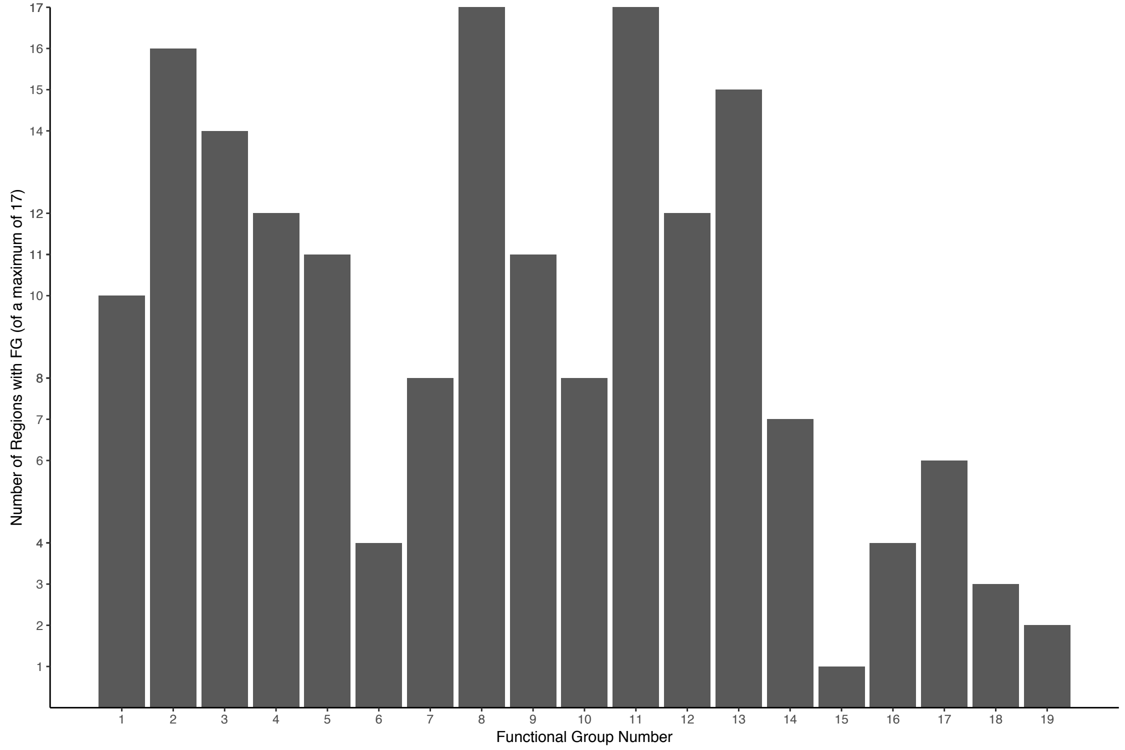
The sFDvent trait database for vent fauna also enables us to describe a trait-based global vent biogeography, or functional biogeography (**Figure 35**), in which we classify ten coherent clusters. These clusters are significantly different from those identified using occupancy data, according to the dendrograms produced for both datasets (**Table 12**), though two species (gastropod *Ifremeria nautilei* and paralvinellid worm *Paralvinella palmiformis*) are relatively isolated from others in their clusters in both trait and taxonomic dendrograms (**Figure 35** and **Figure 31**, respectively).

3.2 Compiling the evidence for functional equivalence across the globe

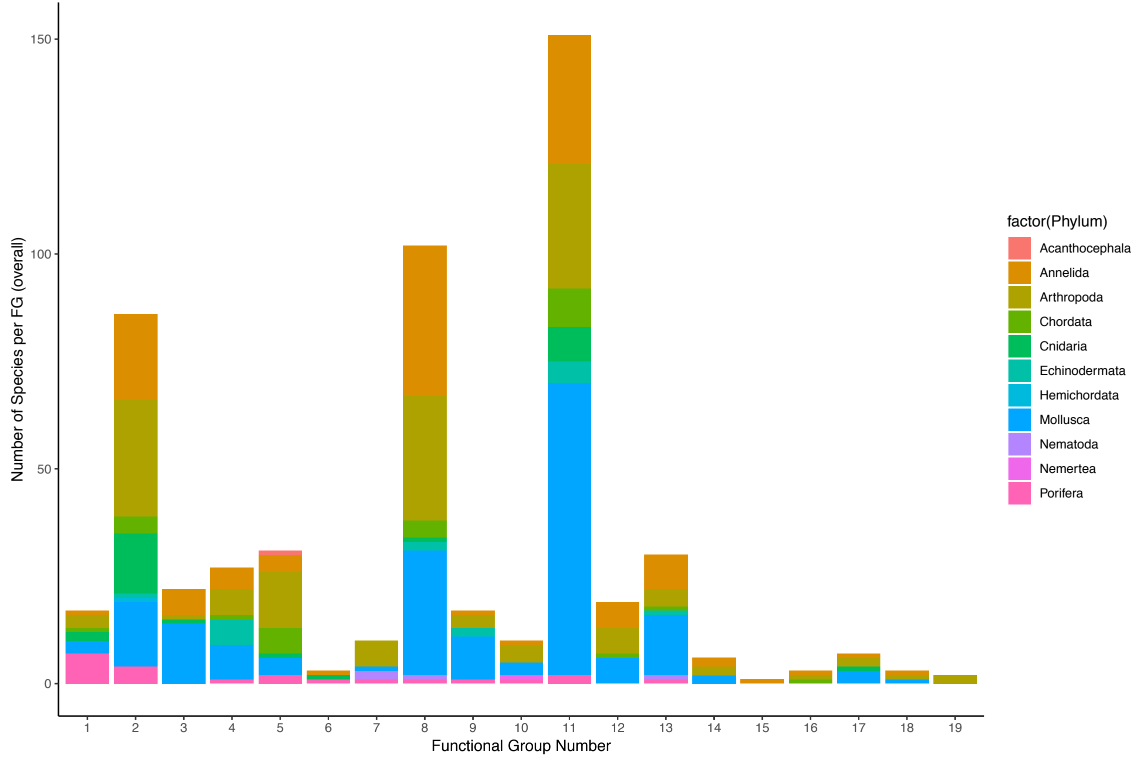
In identifying trait-based species clusters for vent fauna across the globe, we classify vent species into 19 functional groups (FGs; **Figure 36** and **Figure 37**). FGs 8 and 11 are found in all venting regions included in this study. These groups comprise taxa from all well-populated classes and phyla (e.g., excluding Acanthocephela, Nemertea, and Nematoda, which are relatively poorly populated in the sFDvent database; **Figure 36** and **Appendix D.2**). Taxa in FG 8 are, most commonly, relatively mobile, medium-sized, vent-endemic fauna that have endosymbionts and are found in the high-flow zones of vent fields, depending on the water column for nutrition (**Table 14**). FG 11 taxa are similar to the FG 8 taxa, but smaller in size (**Table 14**). FG 8 is predominantly comprised of polychaetes and FG 11 gastropods (**Figure 36c**). FGs 2, 3, and 13 are present in more than 12 of the 17 regions analysed (**Figure 36a**). While FG 2 also has relatively good representation of phyla (**Figure 36b**), the majority of taxa are from classes Malacostraca and Polychaeta (**Figure 36c**). Taxa in this group are commonly very mobile, medium-sized, vent-endemic fauna with endosymbionts, found in high-flow zones depending on the sediment and/or rock surface for nutrition (**Table 14**). Meanwhile, FGs 13 and 3 host a relatively high proportion of bivalves (**Figure 36c**). FG 3 taxa are generally large, low mobility fauna also found in other chemosynthesis-based ecosystems and without symbionts, found in the medium-flow zone, and feeding on fauna (**Table 14**). FG 13 taxa are also large, without symbionts, and feed on fauna, but are immobile and found in the high-flow zone (**Table 14**).

Figure 36 (overleaf)**:** Bar charts summarising the overall composition of the functional groups (FGs) across all regions. In plot a), we can see which FGs are best populated, as this chart shows how many of the 17 regions (y-axis) has taxa in each of the FGs (x-axis). The taxonomic composition of each FG is shown in plot b) in terms of Phyla and in plot c) by Class, with the y-axis used to show the number of species in each FG summed across all regional pools.

a) How many regions have a given FG?



b) How many species are there in each FG overall?



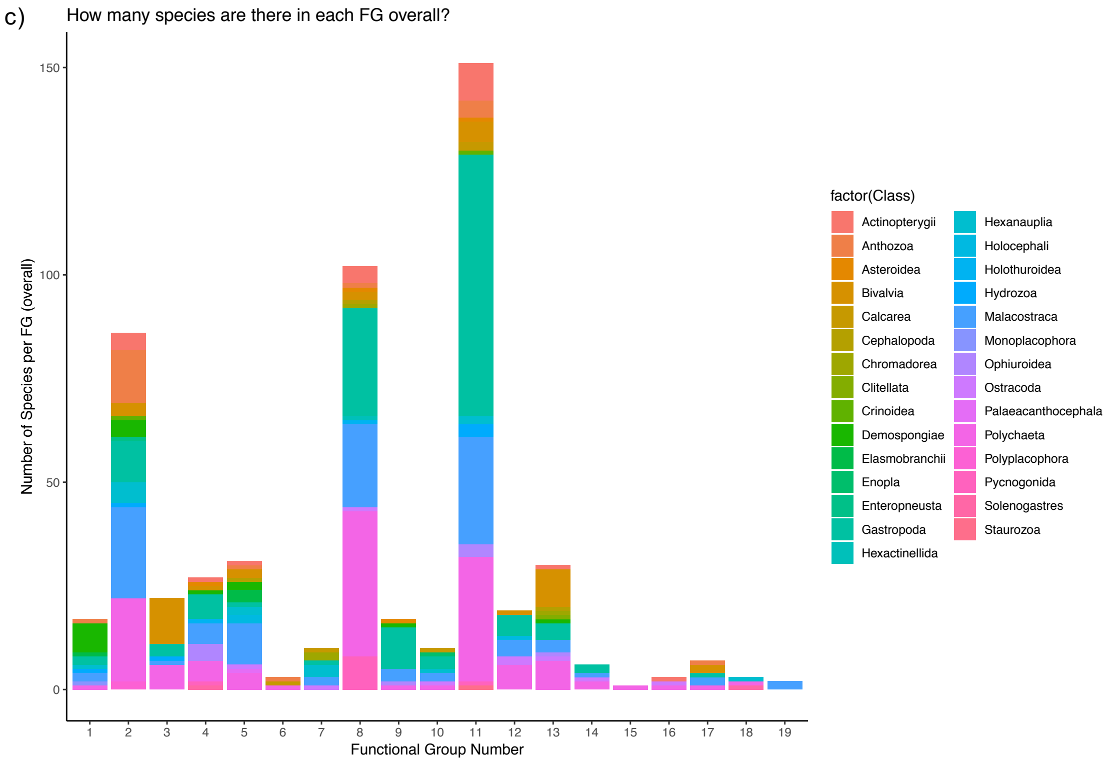
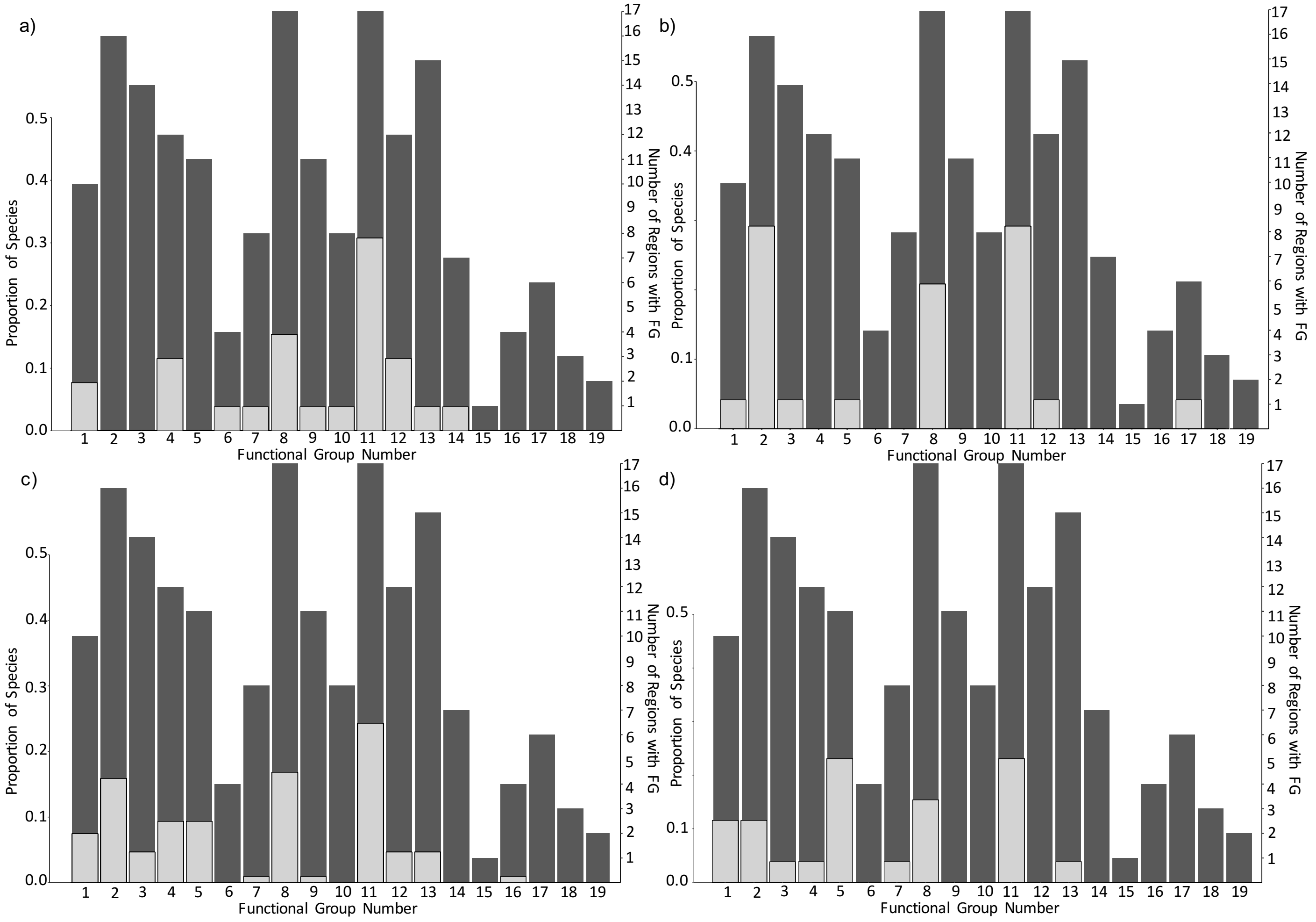
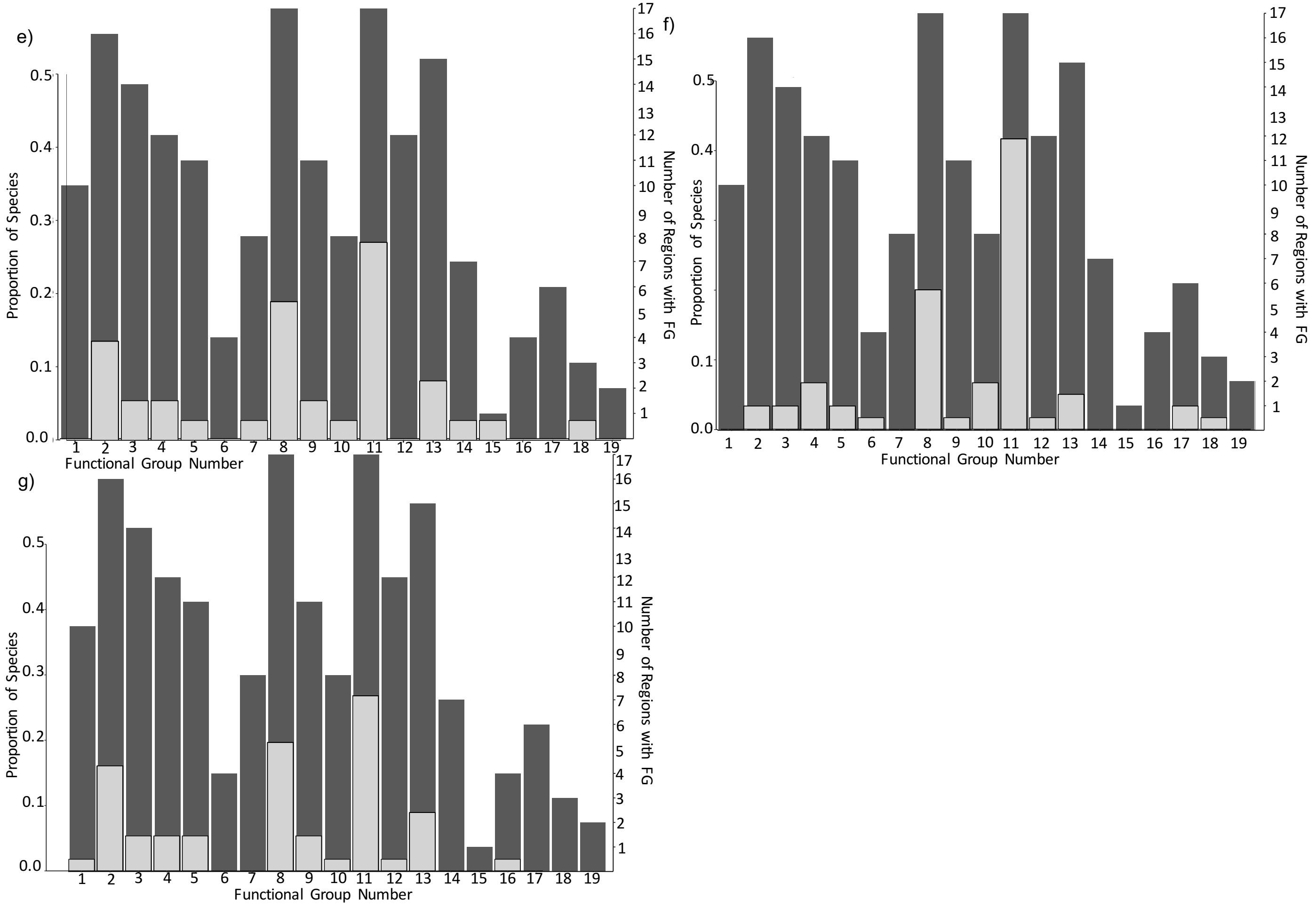
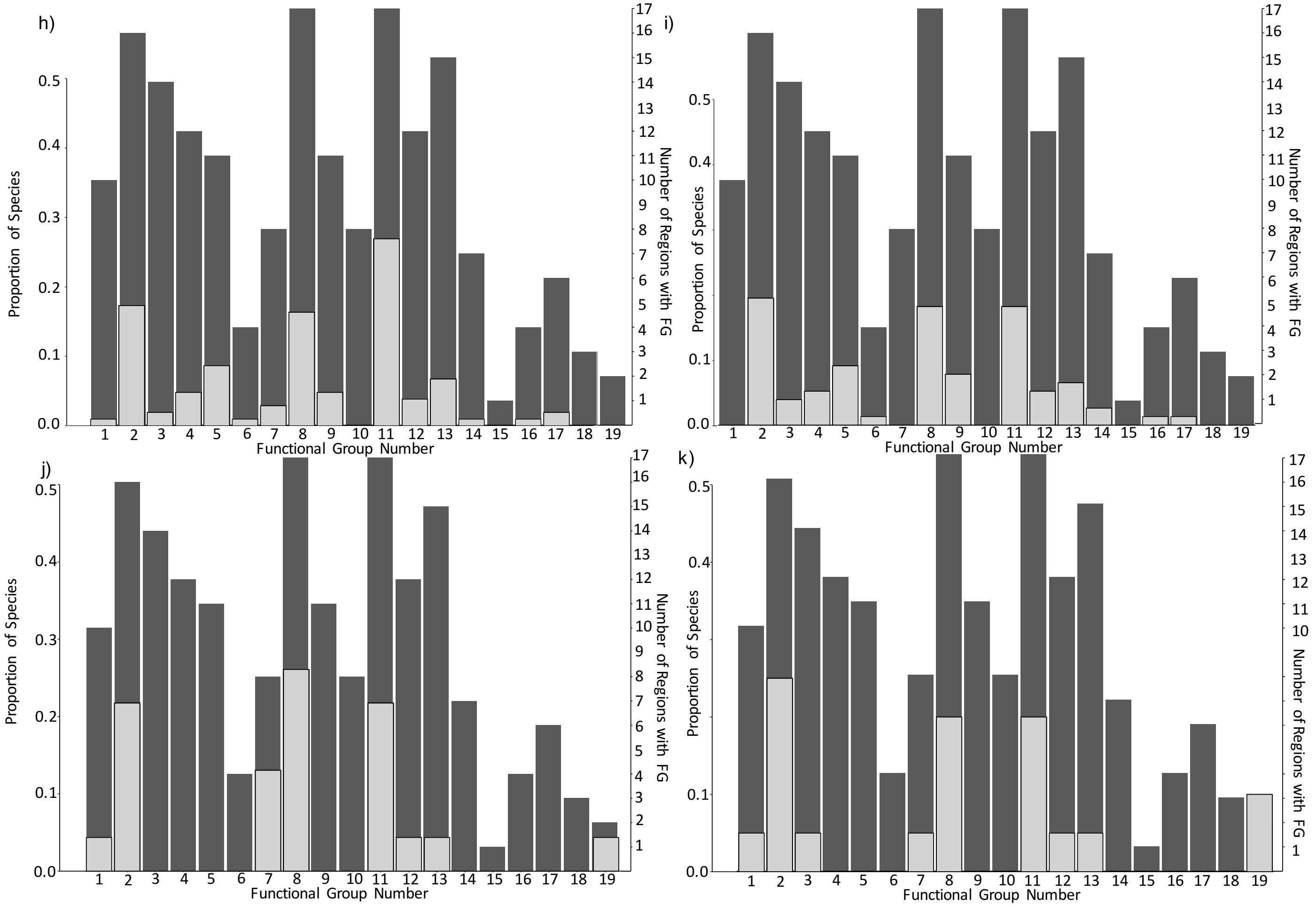
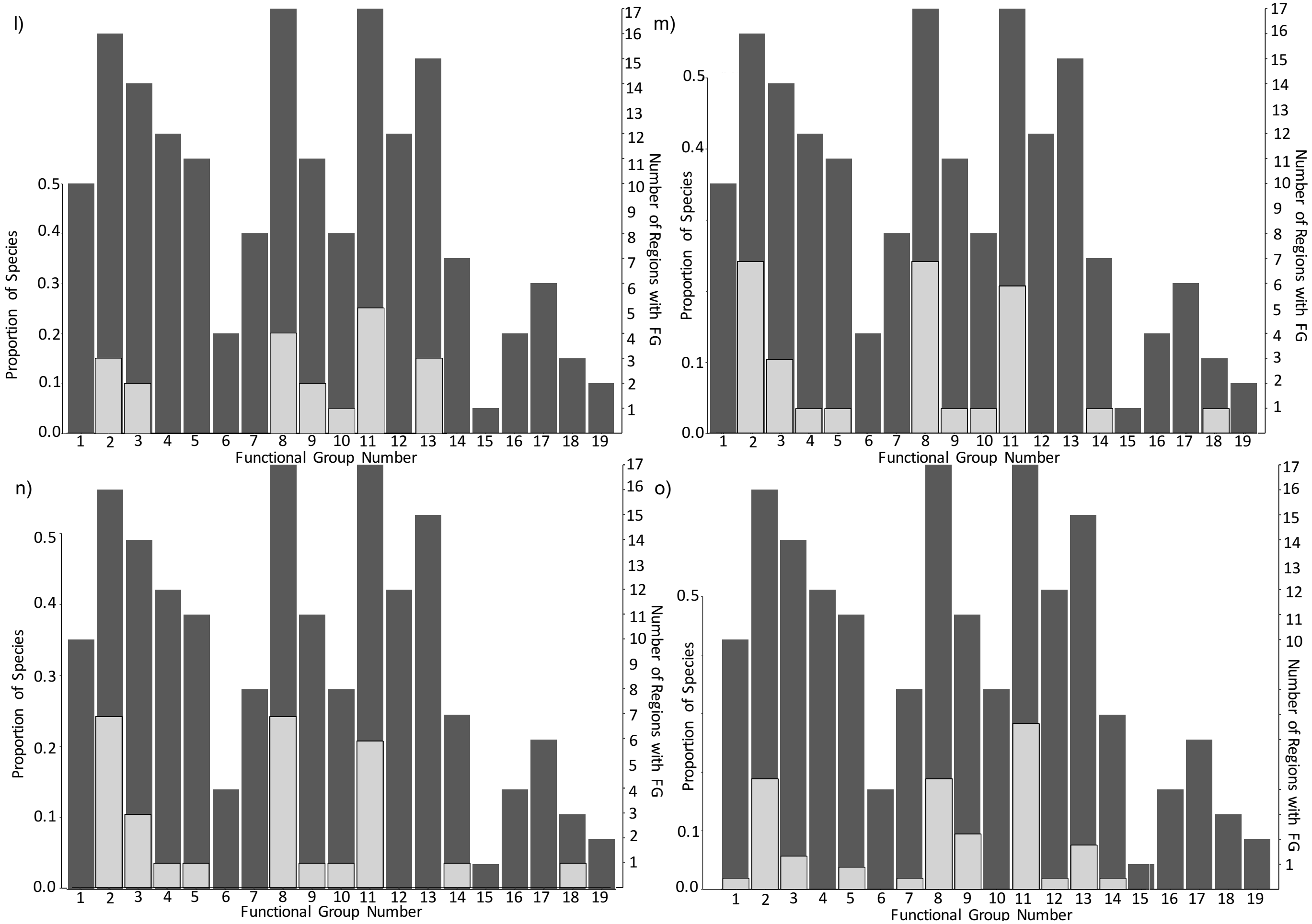


Figure 37 (overleaf)**:** Bar charts showing the proportion of species comprising each functional group (FG) for each region included in this study, grouped on each page according to taxonomic similarity (**Figure 32**): a) Mohns Ridge, b) East Scotia Ridge (ESR), c) North Mid-Atlantic Ridge (N. MAR), d) South Mid-Atlantic Ridge (S. MAR), e) Gulf of California, f) Juan de Fuca Ridge, g) Galapagos, h) North East Pacific Rise (NEPR), i) South East Pacific Rise (SEPR), j) Central Indian Ridge (CIR), k) South West Indian Ridge (SWIR), l) Kermadec Arc, m) Manus Basin, n) Mariana Arc, o) Okinawa Trough, p) North Fiji Basin, and q) Lau Basin. The proportion is relative to the species pool for the region the chart represents but the 0 to 1 scale facilitates comparison of the FG composition of different regions. Behind each plot is a silhouette of **Figure 36a**, to facilitate comparisons between: i) the general distribution of FGs in each region, and ii) the overall population of FGs across all regions. For example, while the plots are on different scales, we can see which FGs are missing in a given region, and determine whether these are FGs also poorly populated across all regions or not, and we can also determine which FGs are well-populated for a given region, and establish how this compares to the general trend.


a)
b)
c)
d)
Proportion of Species
0.0
0.1
0.2
0.3
0.4
0.5
Number of Regions with FG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Functional Group Number
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19


e)
f)
g)
Proportion of Species
0.0
0.1
0.2
0.3
0.4
0.5
Number of Regions with FG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Functional Group Number
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19


h)
Proportion of Species
0.0
0.1
0.2
0.3
0.4
0.5
Number of Regions with FG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Functional Group Number
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
i)
Proportion of Species
0.0
0.1
0.4
0.5
Number of Regions with FG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Functional Group Number
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
j)
Proportion of Species
0.0
0.1
0.2
0.3
0.4
0.5
Number of Regions with FG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Functional Group Number
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
k)
Proportion of Species
0.0
0.1
0.4
0.5
Number of Regions with FG
1
10
11
12
13
14
15
16
17
Functional Group Number
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19


l)
m)
n)
o)
Proportion of Species
Number of Regions with FG
Functional Group Number
0.0
0.1
0.2
0.3
0.4
0.5
1
2
3
4
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6
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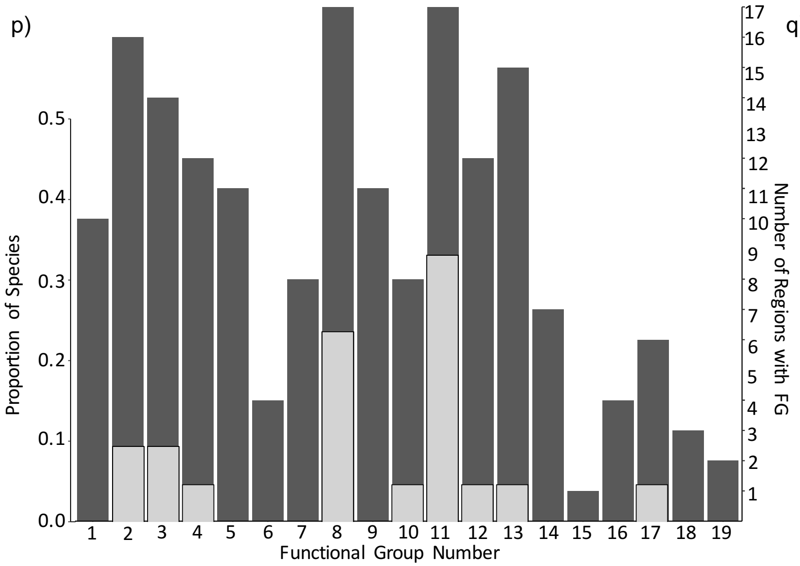
18
19


p)
Proportion of Species
0.0
0.1
0.2
0.3
0.4
0.5
Number of Regions with FG
1
2
3
4
5
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7
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15
16
17
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
Functional Group Number

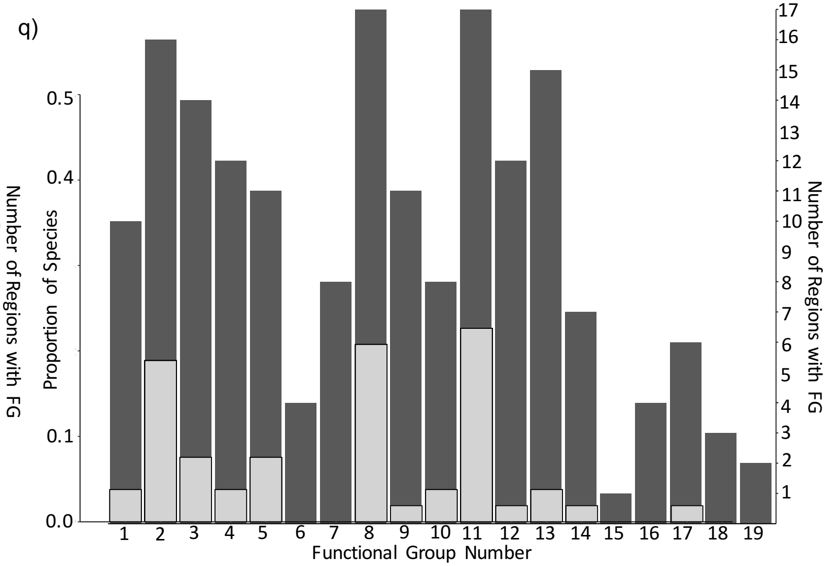

q)
Proportion of Species
0.0
0.1
0.4
0.5
Number of Regions with FG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
Functional Group Number

Table 13: The number of functional groups (FGs) populated by taxa in each of the regions analysed in this study ('Sum' column), with by-group occupancy information (columns 1 to 19, representing each of the FGs) to compare across regions (rows). The mean number of FGs per region (the mean of the Sum column) is 10. In this table, in addition to the abbreviations already used in this chapter, Mohns Ridge is abbreviated to 'M. Ridge'.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**Sum**
M. Ridge	x			x		x	x	x	x	x	x	x	x	x						11
ESR	x	x	x		x			x			x	x					x			8
N. MAR	x	x	x	x	x		x	x	x		x	x	x			x				12
S. MAR	x	x	x	x	x		x	x			x		x							9
JdF		x	x	x	x	x		x	x	x	x	x	x				x	x		13
GoC		x	x	x	x		x	x	x	x	x		x	x	x			x		13
Galapagos	x	x	x	x	x			x	x	x	x	x	x			x				12
NEPR	x	x	x	x	x	x	x	x	x		x	x	x	x		x	x			15
SEPR		x	x	x	x	x		x	x		x	x	x	x		x	x			13
CIR	x	x					x	x			x	x	x						x	8
SWIR	x	x	x				x	x			x	x	x						x	9
Mariana		x		x				x			x		x							5
Okinawa	x	x	x		x		x	x	x		x	x	x	x						11
Kermadec		x	x					x	x	x	x		x							7
N. Fiji		x	x	x				x		x	x	x	x				x			9

Lau	x	x	x	x	x			x	x	x	x	x	x	x			x		13
Manus		x	x	x	x			x	x	x	x			x				x	10

Table 14: Modal trait values, representing the typical fauna comprising each functional group (FG). A dash (-) is used to show insufficient data for computing the mode, which applies to FG 15 as it comprises one species with data gaps. 'Chemosynthesis-based' ecosystems is abbreviated to 'CBEs' under Chemosynthesis-Obligate.

FG	Relative Adult Mobility	Estimated Maximum Body Size (mm)	Chemosynthesis-Obligate	Position of Symbiont	Zonation from Vent	Nutritional Source
1	1 (immobile)	100	Also found in other ecosystems	Endosymbiont	Medium	Sediment and/or rock surface
2	4 (very mobile)	100	Vent-endemic	Endosymbiont	High	Sediment and/or rock surface
3	2	1000	Also found in other CBEs	None	Medium	Fauna
4	3	10	Also found in other ecosystems	Endosymbiont	Medium	Sediment and/or rock surface
5	4	1000	Also found in other ecosystems	Endosymbiont	Medium	Sediment and/or rock surface
6	2	100	Also found in other ecosystems	Endosymbiont	Medium	Symbiont
7	1 (immobile)	10	Vent-endemic	Endosymbiont	Medium	Symbiont
8	3	100	Vent-endemic	Endosymbiont	High	Water column
9	3	10	Also found in other CBEs	Endosymbiont	High	Water column
10	4 (very mobile)	10	Also found in other ecosystems	Endosymbiont	High	Symbiont
11	3	10	Vent-endemic	Endosymbiont	High	Water column
12	3	1	Vent-endemic	Endosymbiont	High	Water column
13	1 (immobile)	1000	Vent-endemic	None	High	Fauna
14	4 (very mobile)	10	Also found in other CBEs	Endosymbiont	Medium	Sediment and/or rock surface
15	4 (very mobile)	1	Also found in other ecosystems	-	-	Symbiont
16	3	1000	Vent-endemic	Endosymbiont	High	Sediment and/or rock surface

17	2	10	Vent-endemic	Endosymbiont	Medium	Sediment and/or rock surface
18	1 (immobile)	10	Vent-endemic	Episymbiont	High	Fauna
19	4 (very mobile)	100	Vent-endemic	Episymbiont	Low	Fauna

Investigating the FG composition of each of the regions included in our analyses enables us to establish which venting regions have relatively high, and low, numbers of FGs (**Table 13**). For instance, the NEPR, SEPR, Juan de Fuca Ridge, Gulf of California, Lau Basin, Okinawa Trough, Galapagos, N. MAR, and Mohns Ridge regions have above-average (> 11) numbers of FGs (**Table 13**). Most of the FGs in these regions are proportionally highest in polychaetes, though: the NEPR has relatively high proportions of both polychaetes and gastropods; the Lau Basin is dominated by gastropods; and a large proportion of the N. MAR fauna are Malacostraca (**Appendix D.2**). The FGs of Okinawa Trough and Mohns Ridge have a more even distribution of taxonomic classes, though bivalves are found in relatively high proportions in these regions (**Appendix D.2**). The Gulf of California has relatively few taxonomic classes (6) in general, despite an above-average number of FGs (13; **Figure 37e**; **Table 13**). This region also has less within-FG taxonomic variability than other regions.

The Mariana and Kermadec Arc regions have the lowest numbers of FGs, with 5 and 7, respectively (**Table 13**). While Kermadec Arc has relatively few taxonomic classes overall (4), Mariana Arc has 8 classes, similar to many of the regions with high numbers of FGs (**Appendix D.2**). The taxonomic compositions of Mariana and Kermadec arc FGs are not dominated by polychaetes in the same way that many of the regions with high numbers of FGs are. Instead, Mariana Arc has: FG 8 with Gastropoda, Malacostraca, Polychaeta, and Pycnogonida classes; FG 11 with the classes in FG 8 in addition to Anthozoa; FG 13 with a mix of Actinopterygii, Bivalvia, Gastropoda, and Polychaeta; FG 2 comprising Malacostraca and Polychaeta; and FG 4, hosting a small number of gastropod taxa (**Figure 37n**). Kermadec Arc FGs are predominantly comprised of Malacostraca and/or Bivalvia taxa (e.g., FGs 8-11), though FG 3 and 13 contain taxa from the Polychaeta and Bivalvia classes and FG 2 has bivalves, arthropods, and members of the Hexanauplia class (**Figure 37l**).

Overall, in comparing the FGs with the highest proportion of taxa in each region, FGs 2, 8, and 11 tend to be dominant (**Figure 37**). FG 8 is the most speciose group for the CIR and Mariana Arc regions (**Figure 37j** and **Figure 37n**). More species occupy FG 2 than any other FG in the SEPR and SWIR, and FG 11 is the most species-rich group for the Galapagos, NEPR, Gulf of California, Juan de Fuca Ridge, Kermadec Arc, Mohns Ridge, N. MAR, Lau Basin, Okinawa Trough, and North Fiji Basin regions. East Scotia Ridge and S. MAR vent taxa predominantly occupying FGs 2 and 11, and 5 and 11, respectively (**Figure 37b** and **Figure 37d**), and the Manus Basin taxa are mostly found in FGs 2 and 8 (**Figure 37m**). Across all regions, the most speciose FG is FG 11 (**Figure 36**) - the group with small-bodied, mobile, vent-endemic fauna hosting endosymbionts in the high-flow zone and feeding from the water column (**Table 14**).

3.3 A comparison of the functional, taxonomic, and environmental uniqueness of venting regions

In comparing functional redundancy with functional dispersion, we highlight: i) 'functional diversity hotspots', where redundancy is low and dispersion is high; ii) 'well-insured' regions, where redundancy and dispersion are both high; iii) 'unique but constrained' regions, with low redundancy and dispersion; and iv) regions where we could say that communities have 'all their eggs in one basket' - that is, they have high redundancy and low dispersion (**Figure 38**). Of the 'functional diversity hotspots', the regions with lowest redundancy and highest dispersion are S. MAR and the Lau Basin (**Figure 38**). While Kermadec Arc and Okinawa Trough vents are in the 'well-insured' group, they have lower redundancy than the Juan de Fuca Ridge, which has the highest (**Figure 38**). Mariana Arc is firmly in the 'all eggs in one basket' group, with high redundancy and low dispersion, and the Central Indian Ridge is the most 'unique but constrained' region (**Figure 38**). The Juan de Fuca Ridge has the highest functional redundancy of all the regions, based on the traits included in our analyses, and the Lau Basin the lowest (**Figure 38**). The regions with the highest functional dispersion are S. MAR and the Gulf of California, while the Mariana Arc has the lowest functional dispersion of all regions (**Figure 38**).

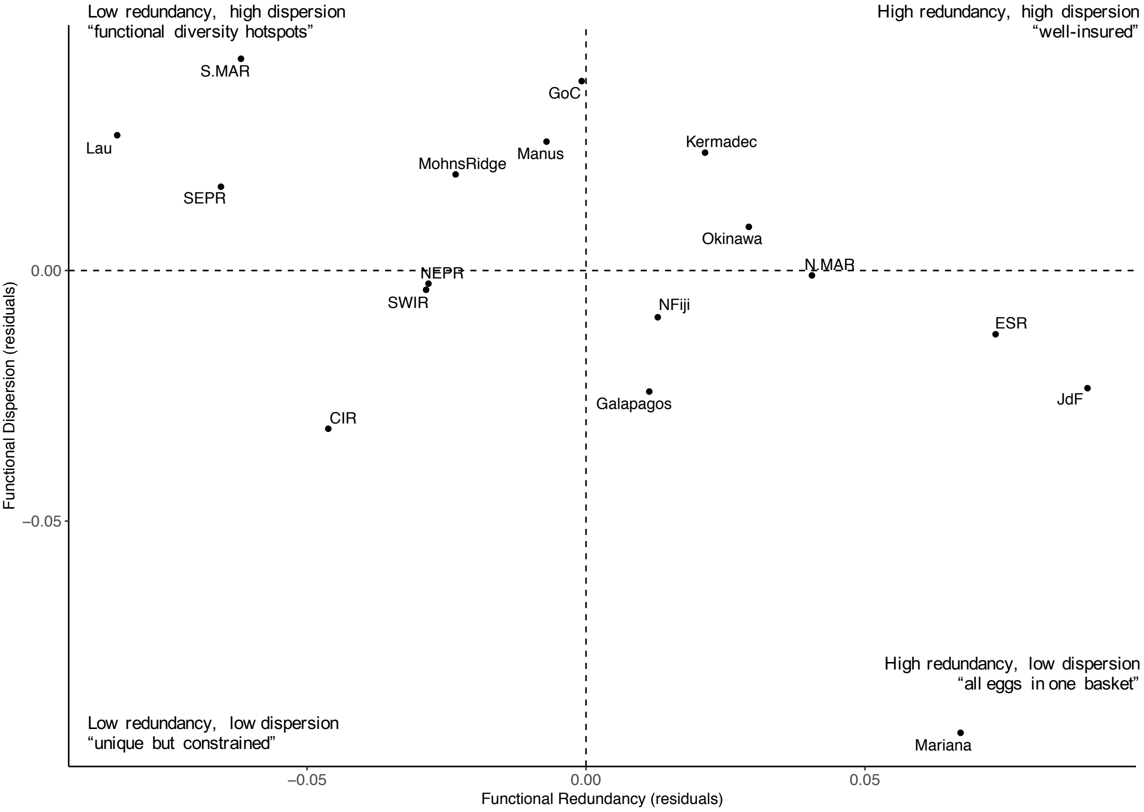
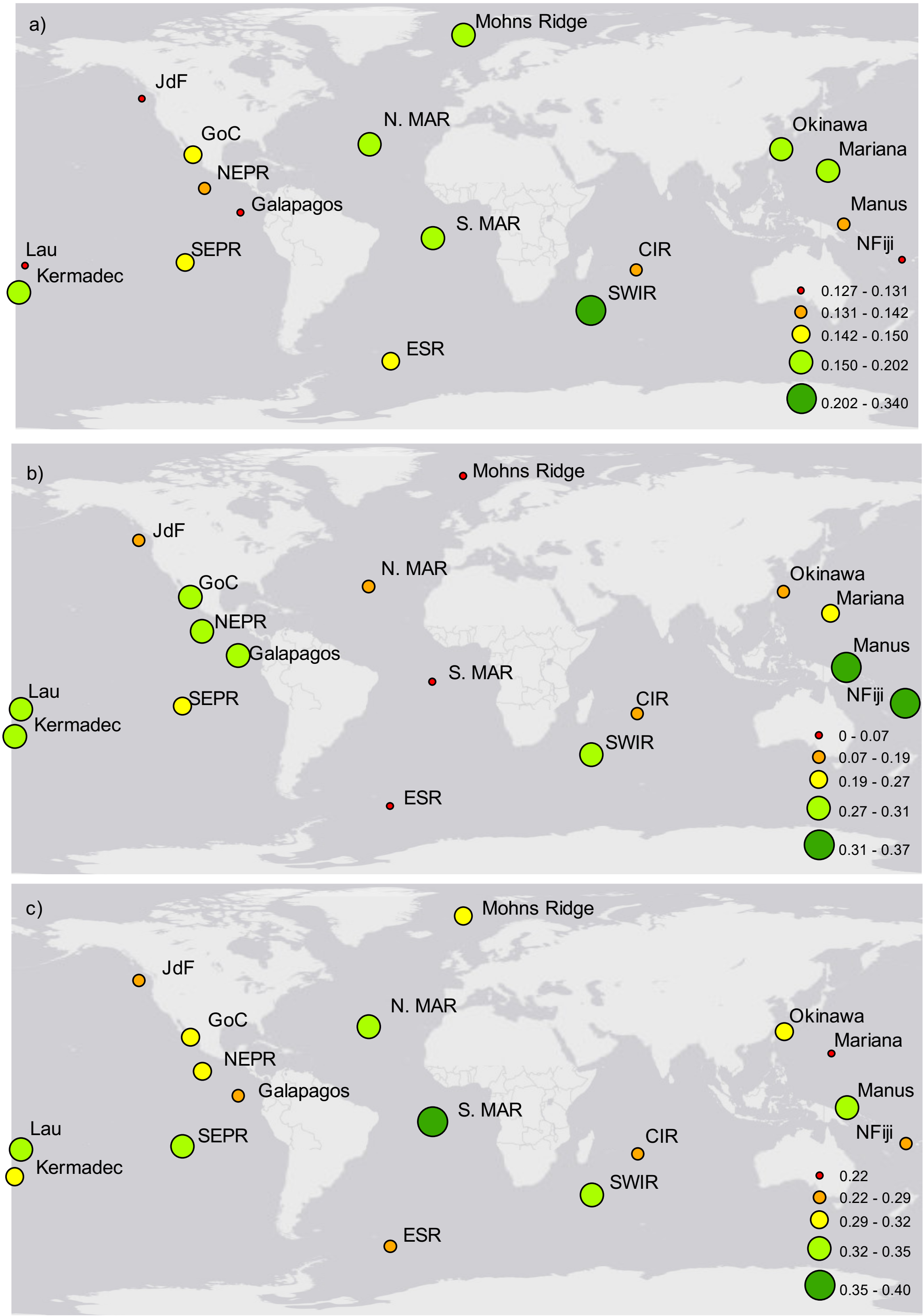


Figure 38 (caption continues overleaf): A quadrant plot illustrating the relative functional redundancy and functional dispersion (computed using a species-by-trait matrix and the 'FD' R package (Laliberté and Legendre, 2010; Laliberté et al., 2014)) of each of the regions included in

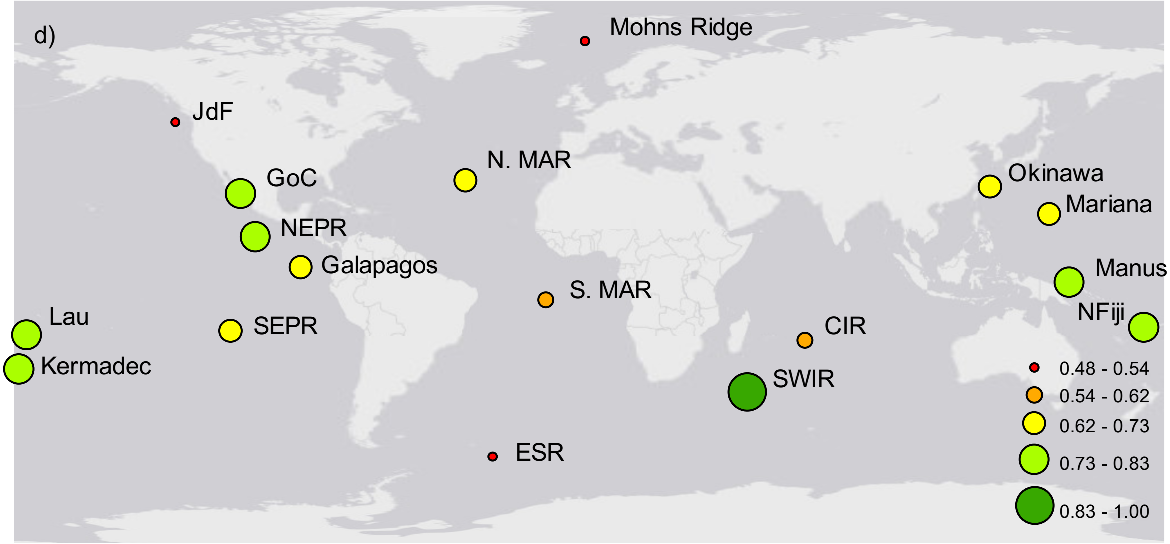
this study. There is a weak significant linear relationship between these variables (slope -0.341, p = 0.028, intercept $1.683^{\wedge}10^{-18}$). Region names have been abbreviated for display purposes as per the description in **Appendix D.2**. Each quadrant has been assigned a 'scenario' title, to describe its general pattern: 'functional diversity hotspots', where regions are well-spread in trait space and relatively unique, given low functional redundancy; 'well-insured', incorporating regions that have redundancy and also a good spread across trait space; 'unique but constrained', where regions are relatively unique, or low redundancy, but taxa occupy only a small area of trait space; and 'all eggs in one basket', where there is high redundancy but all in one small area of trait space.

The uniqueness of vent regions can be compared across the globe using **Figure 39**. Based on trait data, the S. MAR is the most functionally unique, with Lau Basin, SEPR, N. MAR, SWIR, and Manus Basin regions also quite unique (**Figure 39c**). The least functionally unique region is the Mariana Arc, based on the traits included in our analyses (**Figure 39c**). The North Fiji Basin, and the Manus Basin, are the most taxonomically unique regions included in this analysis, with Lau Basin, Kermadec, Gulf of California, NEPR, Galapagos, and SWIR regions also relatively unique in terms of their regional species pools (**Figure 39b**). The least taxonomically unique regions, based on the data used for these analyses, are Mohns Ridge, S. MAR, and the East Scotia Ridge (**Figure 39b**). The most environmentally unique region is SWIR, with Mohns Ridge, MAR, Okinawa, and Kermadec regions also relatively unique in terms of their environmental characteristics (**Figure 39a**). The least environmentally unique regions are the Juan de Fuca Ridge, Galapagos, and Lau and North Fiji basins (**Figure 39a**). Combining all three metrics to assess overall uniqueness highlights SWIR as a particularly unique region, with Lau Basin, Kermadec Arc, Gulf of California, NEPR, Manus Basin, and North Fiji Basin regions also relatively unique (**Figure 39d**). Mohns Ridge, the Juan de Fuca Ridge, and the East Scotia Ridge regions are the least unique overall, based on the data used for these analyses (**Figure 39d**).

Figure 39 (overleaf)**:** Geographic (a), taxonomic (b), functional (c), and overall (d) uniqueness of venting regions across the globe. On each map, the scale from red to green (with increasing circle size) represents a gradient from lower (red, small) to higher (green, large) uniqueness. Uniqueness was computed for each dataset using a distance measure. Geographic uniqueness (mapped in (a)) represents the average geographic dissimilarity value for a region based on the Euclidean distance among regions given the environmental variables included in this study (described in **Appendix D.2**), scaled to the overall maximum Euclidean distance across all regions. Taxonomic uniqueness (mapped in (b)) was calculated using raw presence-absence data, as well as a Sørensen's distance matrix, using the 'taxondive' function of the 'vegan' R package (Oksanen et al., 2018). Functional uniqueness (mapped in (c)) was computed using the 'distinctiveness' function of the 'funrar' R package (Grenié et al., 2017a, 2017b), using presence-absence information for each species and a species-by-trait Gower distance matrix. Overall uniqueness (mapped in (d)) is the sum of geographic (a), taxonomic (b), and functional (c) uniqueness.

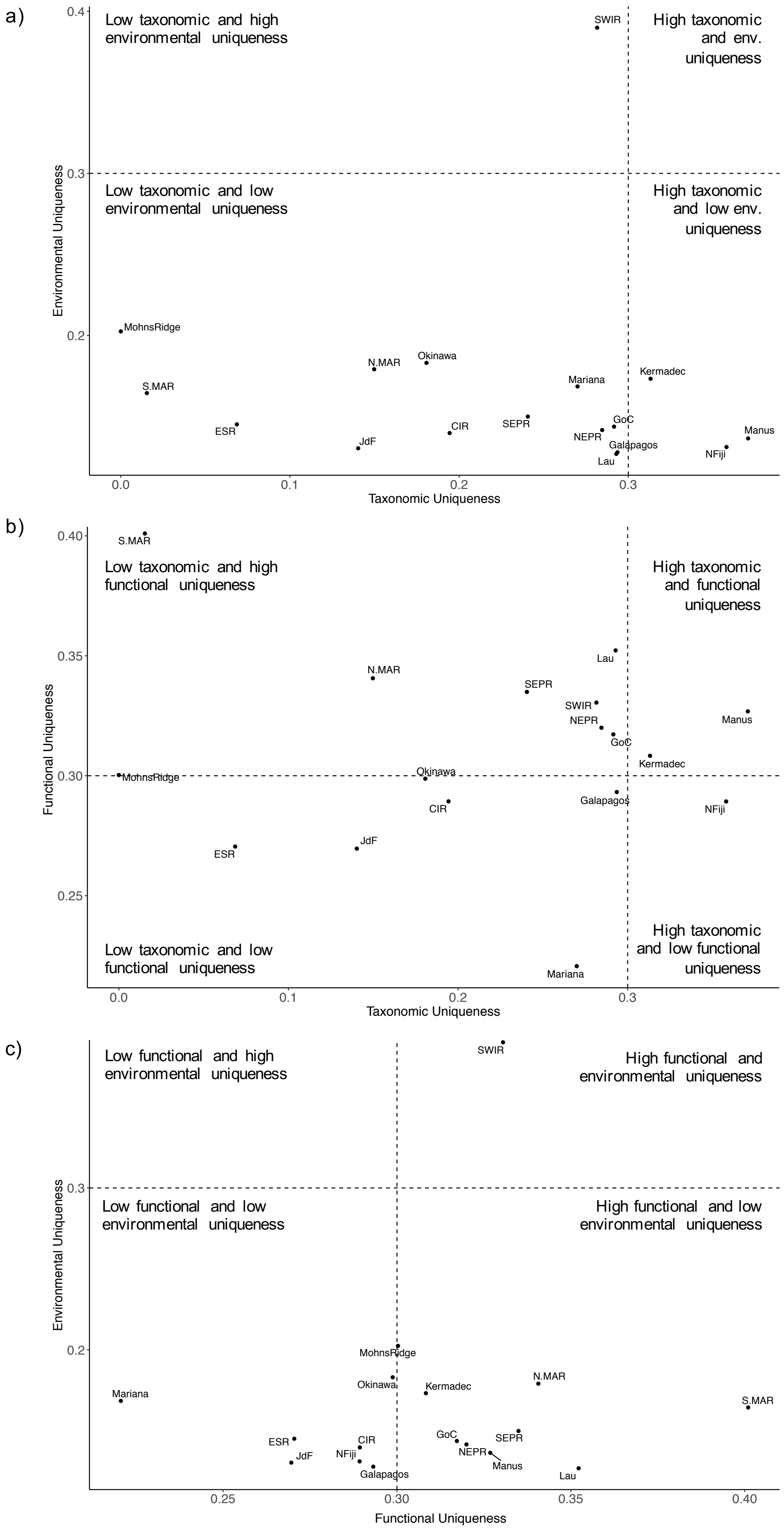


a)
Mohns Ridge
JdF
N. MAR
GoC
NEPR
Galapagos
Okinawa
Mariana
Manus
NFiji
S. MAR
Lau
SEPR
Kermadec
CIR
SWIR
ESR
0.127 - 0.131
0.131 - 0.142
0.142 - 0.150
0.150 - 0.202
0.202 - 0.340
b)
Mohns Ridge
JdF
N. MAR
GoC
NEPR
Galapagos
Okinawa
Mariana
Manus
NFiji
S. MAR
Lau
SEPR
Kermadec
CIR
SWIR
ESR
0 - 0.07
0.07 - 0.19
0.19 - 0.27
0.27 - 0.31
0.31 - 0.37
c)
Mohns Ridge
JdF
N. MAR
GoC
NEPR
Galapagos
Okinawa
Mariana
Manus
NFiji
S. MAR
Lau
SEPR
Kermadec
CIR
SWIR
ESR
0.22
0.22 - 0.29
0.29 - 0.32
0.32 - 0.35
0.35 - 0.40



We find there are neither hotspots of taxonomic and environmental uniqueness, nor regions that are low in functional uniqueness but high in environmental uniqueness (**Figure 40a** and **Figure 40c**). However, the SWIR falls in the low taxonomic uniqueness, high environmental uniqueness quadrant, and the high functional uniqueness and high environmental uniqueness quadrant (**Figure 40a** and **Figure 40c**). The Manus Basin is in the high taxonomic uniqueness, low environmental uniqueness, and the high taxonomic uniqueness, high functional uniqueness quadrants (**Figure 40a** and **Figure 40b**). The North Fiji Basin and Kermadec Arc are also in the high taxonomic uniqueness, low environmental uniqueness quadrant (**Figure 40a**), while Mohns Ridge, S. MAR, and East Scotia Ridge regions are located in the low taxonomic uniqueness and low environmental uniqueness section (**Figure 40a**). S. MAR is also in the low taxonomic uniqueness, high functional uniqueness quadrant (**Figure 40b**) and the North Fiji Basin is high in taxonomic uniqueness but low in functional uniqueness (**Figure 40b**). The East Scotia Ridge and Juan de Fuca Ridge regions are low in both taxonomic and functional uniqueness (**Figure 40b**). The Mariana Arc is low in both functional and environmental uniqueness (**Figure 40c**).

Figure 40 (overleaf)**:** Quadrant plots illustrating the relationships for each region (abbreviated as described in **Appendix D.2**) between: a) taxonomic and environmental uniqueness - a non-significant linear relationship (p = 0.8, slope -0.1, intercept 0.2); b) taxonomic and functional uniqueness - a non-significant linear relationship (p = 0.6, slope -0.3, intercept 0.3); and c) functional and environmental uniqueness - also non-significantly linearly related (p = 0.6, slope 0.1, intercept 0.3). The quadrants are defined using a 0.3-0.3 line to best represent higher and lower uniqueness levels, proportional to the overall uniqueness values. ‘Env.’ is an abbreviation of ‘environmental’, used for display purposes.


a)
Low taxonomic and high environmental uniqueness
High taxonomic and env. uniqueness
Low taxonomic and low environmental uniqueness
High taxonomic and low env. uniqueness
Environmental Uniqueness
Taxonomic Uniqueness
0.4
0.3
0.2
0.0
0.1
0.2
0.3
SWIR
MohnsRidge
N.MAR
Okinawa
S.MAR
Mariana
Kermadec
ESR
JdF
CIR
SEPR
GoC
NEPR
Galapagos
Lau
NFiji
Manus
b)
Low taxonomic and high functional uniqueness
High taxonomic and functional uniqueness
Low taxonomic and low functional uniqueness
High taxonomic and low functional uniqueness
Functional Uniqueness
Taxonomic Uniqueness
0.40
0.35
0.30
0.25
0.0
0.1
0.2
0.3
S.MAR
Lau
N.MAR
SEPR
SWIR
NEPR
GoC
Manus
Kermadec
MohnsRidge
Okinawa
CIR
Galapagos
NFiji
ESR
JdF
Mariana
c)
Low functional and high environmental uniqueness
High functional and environmental uniqueness
Low functional and low environmental uniqueness
High functional and low environmental uniqueness
Environmental Uniqueness
Functional Uniqueness
0.3
0.2
0.25
0.30
0.35
0.40
SWIR
MohnsRidge
Okinawa
Kermadec
N.MAR
Mariana
S.MAR
ESR
CIR
GoC
SEPR
JdF
NFiji
NEPR
Manus
Galapagos
Lau

4. DISCUSSION

Functional, taxonomic, and environmental measures reveal different hotspots of uniqueness in vent regions across the globe (**Figure 40**). The low spatial conformity among these three measures contrasts with previous work, including studies of ants and birds, which found that functional and taxonomic diversity patterns were at least partly spatially congruent on a global scale (Devictor et al., 2010; Arnan et al., 2017). Here, we show that different dimensions of biodiversity - species traits and taxonomic composition - as well as environmental characteristics, offer contrasting perspectives on the uniqueness of vent ecosystems (**Figure 39** and **Figure 40**). As many conservation measures have been designed on the assumption that protecting taxonomically unique areas will automatically protect functionally and environmentally unique areas (Brooks et al., 2006; Devictor et al., 2010; Parravicini et al., 2014), our results have important conservation and management implications. Here, we show, even without phylogenetic information (which will be a key ecological dimension to include in future research when available), that conservation approaches need to integrate functional, or trait-based, taxonomic, and environmental information to truly ensure an area being considered for protection is 'representative' (**Figure 39** and **Figure 40**; Dunn et al., 2018). If policymakers do not consider all dimensions, our work suggests that priority areas for conservation could be missed.

An alternative mechanism for identifying priority areas could involve a hotspot approach (e.g., Stuart-Smith et al., 2013), though, here, we find that vent hotspots depend on the diversity metrics used to characterise them and the environmental attributes of vents themselves. We find no general rules that could be applied to identify vent hotspots in unexplored regions. For instance, we distinguish hotspots with different spreading rates, depths, and tectonic settings. Thus, we cannot use historic, geological, or oceanographic characteristics to simultaneously prioritise relatively unique vent ecosystems.

Nevertheless, we find hotspots using functional dispersion and redundancy, suggesting that these metrics could be used to highlight priority areas for conservation. These measures, in turn, relate to taxonomic and environmental uniqueness through: the ecological processes shaping dispersion and redundancy; the environmental, evolutionary, and dispersal constraints on these functional-diversity facets; and taxonomy, which can constrain traits. We define functional diversity hotspots according to high dispersion, low redundancy, and the distribution of species across FGs. Accordingly, we classify the Lau Basin and the South Mid-Atlantic Ridge as hotspot regions (**Figure 38**). We expect high dispersion and good coverage across FGs in regions where competition is prevalent, niches remain unfilled, or species pools are low in richness (Weiher and Keddy, 1995). Low redundancy would be expected in regions with higher speciation, or plentiful niche space. The Lau Basin has been highly stable over decadal timescales (Du Preez and Fisher, 2018). As such, it has many small, separated vents with plentiful niche space and high habitat heterogeneity (Juniper and Tunnicliffe, 1997), facilitating colonisation by many, unique species. Indeed, the Lau Basin is one of the most unique regions included in this study, according to all three dimensions of uniqueness (**Figure 39**). The less well-sampled southern Mid-Atlantic Ridge has low redundancy (**Figure 38**) despite low taxonomic uniqueness (**Figure 39**). It also has high environmental uniqueness (**Figure 39**), suggesting that this region, too, could be home to a variety of habitats within which unique species can spread in trait space.

Hotspots alone do not give us the full picture needed to achieve conservation goals, however. They capture high-diversity regions, but likely miss vulnerable areas that should also be prioritised in conservation and management strategies. Here, we show that functional dispersion and redundancy can be used to pinpoint regions that might be more vulnerable to future anthropogenic impacts. We classify vent regions into four categories, according to functional dispersion and redundancy, as follows: i) unique but constrained, ii) all eggs in one basket, iii) well-insured, or iv) functional diversity hotspots (**Figure 38**). The most vulnerable of these groups might be the 'all eggs in one basket' group, as the high redundancy here might encourage decision-makers to prioritise other regions over these ones under the insurance hypothesis (Yachi and Loreau, 1999). However, this decision does not account for the low functional dispersion in this group. Here, species are clumped in a small area of trait space and particularly vulnerable to environmental or anthropogenic change. We expect the 'all eggs in one basket' scenario (**Figure 38**) to unfold where abiotic filtering has limited the traits of species but the environment is not unique, so species are relatively redundant with others when compared on a global scale. This is the case in the Mariana Arc region, supported by its low environmental uniqueness (**Figure 39**). The Galapagos and Juan de Fuca Ridge regions are also relatively high in redundancy and low in dispersion, and also have low environmental uniqueness. Our findings for the Juan de Fuca Ridge, the most functionally redundant of all regions included in this study, are in line with expectations, as this region has low-diversity fauna, low speciation rates, and is relatively isolated (Tunnicliffe, 1988). The evidence supporting the redundancy and dispersion of Juan de Fuca Ridge species suggests that the uniqueness, dispersion, and redundancy metrics we employed capture ecologically meaningful dissimilarities among vent regions.

According to the insurance hypothesis (Yachi and Loreau, 1999), areas least vulnerable to future disturbances should be found in the 'well-insured' group (**Figure 38**), where redundancy and dispersion are both relatively high. 'Well-insured' regions should also have numerous species within each present FG. Despite these characteristics, to maintain high redundancy, a regional species pool must comprise species occupying similar areas of trait space. This suggests that there is plentiful niche space; otherwise, we would expect biotic interactions to limit this trait-space sharing. This idea is supported by the Okinawa Trough, which is relatively well insured (**Figure 38**) and comprises many, small areas of venting (Juniper and Tunnicliffe, 1997). We therefore propose that the plentiful niche space here enables species with similar traits to occupy different geographic spaces; the species appear redundant with one another simply because we include them in a regional-scale species pool in our analyses. Contrarily, Kermadec Arc is also relatively well insured (**Figure 38**), and generally unique, but does not have good coverage across FGs (**Figure 37** and **Table 13**). Perhaps, if non-vent fauna were included our analyses, more FGs would be occupied in this region, as Kermadec Arc is relatively shallow (**Figure 34**). Like Mohns Ridge, a relatively shallow Arctic system, Kermadec Arc fauna might be relatively more similar to peripheral taxa than vent taxa alone (Schander et al., 2010), sharing trait space. This suggests a future research direction could be to incorporate the non-vent fauna, found in the periphery of vents, into large databases like sFDvent.

The presence of well-insured regions suggests that some vents will be relatively more resilient to future change than others. This is useful for conservation decision-making, but also appears to contradict the idea that vent fauna are particularly unique and highly endemic. Here, we find functional overlap in vent species with different phylogenetic histories from regions across the globe, suggesting that some level of functional equivalence (Hubbell, 2005), or convergence, exists in vent ecosystems. We find support for a degree of functional equivalence among species from different vent regions through significant differences in the outcomes of hierarchical cluster analyses on occupancy, or taxonomic, data, and trait data, respectively (**Table 12**). We also identify functional groups in common among regions with otherwise dissimilar species-pool compositions and functional-group distributions (**Figure 36, Figure 37** and **Table 13**). This suggests, based on work conducted in other ecosystems (Schluter, 1986; Lamouroux et al., 2004; Heino et al., 2013), that some trait combinations are selected for in vent ecosystems. At vents, convergent functional groups differ in taxonomic composition, suggesting different evolutionary pathways can converge if an environment is sufficiently extreme in its filtering. As we see disproportionate packing of species into two functional groups across all vent regions (**Figure 36** and **Figure 37**), we propose that future work investigating the abundance distributions of species in functional groups could, as suggested for reef fish (Mouillot et al., 2014), prove useful for the assessment of whether functional redundancy truly reflects the 'insurance' of a species pool against environmental, or anthropogenically induced, change.

While the presence of hotspots and 'vulnerable spots' ('all eggs in one basket' regions) appears to challenge the finding of functional convergence across vent regions, it may be their distinct histories that render them relatively more unique and/or vulnerable than regions with higher functional convergence. This conflict might also arise as a result of the different metrics used to identify overall convergence versus uniqueness. For instance, functional dispersion captures the spread of species relative to one another in trait space. Species distant in trait space could still share traits, and occupy the same FGs, as species from other areas of trait space. The apparent conflict may thus be an artefact of the different dimensions of functional diversity being compared. FGs are formed on similarities, but there can still be functional dispersion within these. Moreover, these seemingly contrasting states of convergence and divergence have also been recorded in ecosystems like coral reefs, wherein hotspots have been identified as well as repetition of FGs across the globe (Hoeinghaus et al., 2007; Stuart-Smith et al., 2013; Mouillot et al., 2014; Hemingson and Bellwood, 2016).

As with all macroecological investigations, our study is limited by data availability. In this case, we have known spatial biases in sampling, and ecological understanding, of different vent regions. For instance, the Galapagos Rift vents were the first vents to be discovered, so vents here and in nearby East Pacific Rise and Northeast Pacific regions are likely better sampled and understood than relatively recently discovered Southern, Arctic, and Indian Ocean vents. Here, we managed this bias by only including regions that have been relatively comprehensively sampled and comprise more than 20 species. In addition to these criteria, the spatial resolutions of sFDvent occupancy data limited us to 17 study regions. In future, we hope that the spatial resolution of the occupancy data accompanying sFDvent trait data will improve. If so, we recommend the following approaches for exploring drivers of uniqueness: a fourth-corner approach (Dray et al., 2014), for investigating trait-environment interactions; a random-forest analysis (Breiman, 2001), to explore the relative influence of different environmental variables on the taxonomic and trait compositions of vent species pools; and a distance-based Moran's Eigenvector Map approach, to analyse environmental influences on the spatial structures of vent communities (Dray et al., 2006; Legendre and Gauthier, 2014). Lastly, as with all trait-based ecological research, our findings are dependent on the traits and environmental variables we chose to include. We managed this limitation by selecting traits and variables that: i) did not correlate with one another, and ii) were relevant to the ecology of vent fauna, and the resilience of regional species pools. Nevertheless, our results should be used in the context of the traits, species pools, and environmental characteristics included in our study.

Despite these limitations, we quantified and mapped the relative trait, taxonomic, and environmental uniqueness of 17 regional vent species pools across the globe to identify hotspot regions and areas with potential for future vulnerability to anthropogenic change. The results, however, are not spatially congruent across uniqueness metrics, emphasizing the importance of measuring different characteristics of diversity and environmental conditions when designing conservation strategies for vents. Here, we find that the priority-setting methods employed in terrestrial, freshwater, and shallow-marine realms cannot be applied to vent ecosystems in isolation. While we do find functional redundancy, or convergence, among vent fauna across large scales, there is also dispersion, influencing the vulnerability and resilience of regional species pools.

Although scientists have called for the identification of 'representative' vent fields and regions for conservation and management plans (Dunn et al., 2018), the lack of spatial congruence among trait, taxonomic, and environmental uniqueness among vent regions of the globe suggests that this will not be possible using traditional measures. Instead we advocate for a holistic view, incorporating a variety of dimensions of uniqueness, assessed on a range of spatial scales. We believe this would likely yield a comprehensive understanding of priority areas for management, in a scenario where demand for minerals means that venting regions cannot be permanently and indefinitely protected. Unique functional, taxonomic, or environmental features of the global deep-sea hydrothermal-vent ecosystem may be left unprotected if these different dimensions are not quantified and compared in a unified framework for conservation and management.

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Chapter Six: Synthesis

1. THESIS SUMMARY

This thesis aimed to investigate the biodiversity of deep-sea hydrothermal-vent life from a new perspective. We used the traits of species, as well as the species themselves, to establish whether a trait-based approach is useful and suitable for vent ecological research. The research presented in this thesis:

- Identified traits for which relevant and appropriate information were available for vent species (Aim 1 and Chapters 2 and 3)
- Produced a trait dataset for some of the most intensively sampled and well-known vent fields on the Juan de Fuca Ridge (Aim 2, Chapter 2)
- Tested the hypothesis that rare species contribute more than common species to the functional uniqueness of an ecosystem (Aim 3, Chapter 2)
- Built a database of traits for vent species across the globe, to facilitate trait-based ecology across vents and other ecosystems and to share and document expert knowledge (Aim 4, Chapter 3)
- Identified and mapped environmental variables that might influence the ecology of vents and the dissimilarity among vent biogeographic provinces (Aim 5, Chapter 4)
- Completed the first, global-scale, trait-based study of hydrothermal vents, combining trait, environmental, and taxonomic findings to map the relative uniqueness of well-studied vent regions (Aim 6, Chapter 5)

Here, we show that vent ecosystems host species with unique trait combinations, which, on the community scale, enable them to pack into the plentiful niche space offered across the strong environmental gradients, or zones, at vents (Chapter 2). This distinctiveness is also evident at the global scale in the traits, distributions, and habitats unique to different regions (Chapters 4 and 5). However, some species with contrasting evolutionary histories share traits and appear functionally redundant within a global species pool (Chapter 5). In addition to revealing the uniqueness of vent ecosystems (Chapters 2 and 5), a trait-based approach has enabled us to compare vents with other ecosystems, using species traits as a common 'biological currency'. For instance, we have been able to test the hypothesis, established in reef, rainforest, and alpine communities, that rare species contribute more than common species to the functional uniqueness of communities (Chapter 2; Chapman et al., 2018). We found that common species, as well as rare, contributed uniqueness, highlighting the importance of the 'wild', untouched nature of vents in their present form (Chapter 2; Chapman et al., 2018). We have also built a database of vent species traits, with databases of traits for other taxonomic groups and ecosystems in mind (Chapter 3, in review for an open-access publication and data release in *Global Ecology and Biogeography*). This database (Chapter 3) should therefore facilitate cross-ecosystem comparisons. This would enable vents to become one of the ecosystems ecologists and conservationists use to test ecological theories, to trial trait-based methods, and to study wild systems before the first human impacts are realised.

2. A TRAIT-BASED APPROACH TO THE BIODIVERSITY OF HYDROTHERMAL-VENT ECOSYSTEMS: IMPLICATIONS FOR THE STUDY AND PROTECTION OF HYDROTHERMAL VENTS AND OTHER SYSTEMS

2.1 Hydrothermal vents as key study systems for ecologists and conservation scientists: challenging the view that vents are data-poor systems

My thesis demonstrates both the potential and limitations of working to understand ecological and conservation science principles using vents as a study system. For example, we have built a global trait database for vent fauna, but it has missing data (Chapter 3). There is also presently a trade-off between the spatial resolution of species distribution information and the number of species that can be included at each scale. The database can be used for research on the vent-field scale, though this currently decreases the number of vent fields and species that can be studied. In Chapter Five, we increase the number of species and regions that can be analysed by setting the regional species pool as our finest spatial resolution.

In assembling the sFDvent database, we have increased the number of vent species that have been recorded with accompanying trait, taxonomy, and location information. We have documented knowledge otherwise stored only in the expert knowledge of vent biologists and ecologists who have visited vent fields and studied the fauna. Moreover, as demonstrated in Chapter Four, large-scale environmental characteristics can likely influence the biogeography of vent ecosystems. Thus, investigating macroecological trends using regional species pools is appropriate for functional biogeographic work. Still, we expect the spatial resolution of the 'living' sFDvent database to increase with time, facilitating smaller-scale studies of trait-based community-assembly patterns. We therefore suggest that smaller-scale community and fluid-composition data, already collected across numerous vent fields, should be synthesised and released in a readily accessible format for such purposes.

Ecological research is, however, always limited by sampling bias (e.g., through differences in: equipment or methodology used; detectability; sampling intensity; and spatial bias; Kotze et al., 2012; Tyler et al., 2012). Thus, we would argue that the data available for vent ecosystems are no less appropriate for ecological research than data compiled across terrestrial and marine realms. In assuming vent data are too limiting to use in some statistical tests and large-scale, or cross-ecosystem, analyses (e.g., Gauthier et al., 2010), vent research to date has mostly been conducted by those specialising in the study of vent ecosystems. Here, we argue that vents are compelling ecosystems for broader ecologists and conservation scientists. The limitations inherent in vent research, while compounded by difficulties in accessing, repeat sampling, and finding vent fields, are also common in other fields of ecological research. As an example, the PREDICTS project (Hudson, Newbold et al., 2016) worked to assemble a global-scale database on the impacts of human pressures on local biodiversity. These data, with more than 50,000 species across clades and greater than 32,000 sites (Hudson, Newbold et al., 2016), have been used successfully to assess: how land uses, and the intensity of these uses, have affected terrestrial biodiversity (Newbold et al., 2016); the relative biodiversity of sites within and outside protected areas across the globe (Gray et al., 2016); the responses of bee communities to land-use change (De Palma et al., 2016); and, among other topics, how traits influence responses to land-use intensity (Newbold et al., 2014). These research areas have all been explored despite biases in the intensity and spatial distribution of sampling, as well as differences in the methods used to sample and measure biodiversity (Phillips et al., 2017). The PREDICTS example therefore demonstrates that the limitations constraining vent ecological research to date, particularly on the large scale, are shared across systems, databases, and taxa, and do not have to be restrictive (**Figure 41;** see also: Kattge et al., 2011; Tedesco et al., 2017; Dornelas et al., 2018; and GBIF.org, 2018). Indeed, perhaps the future challenges for macroecological research introduced by the increasing use of drones and camera traps in terrestrial, freshwater, and shallow-marine realms (MacNeil et al., 2008; Kotze et al., 2012), could be addressed using research methods such as those applied in vent ecosystems, where data and sampling limitations associated with remotely operated equipment have been present since the earliest phases of fieldwork.

Figure 41 (overleaf): Similarities between terrestrial ecosystems and deep-sea hydrothermal vents. Here, we highlight some examples to illustrate how terrestrial ecosystems, and how they are studied, are similar to hydrothermal vents. The main differences among these systems and approaches are spatial scales, where terrestrial ecosystem processes and methodologies tend to operate on larger scales than at deep-sea hydrothermal vents, which are like miniature ecoregions in terms of the habitat and physico-chemical heterogeneity they comprise. First, we compare tropical rainforests (top left; source: Morberg, 2011) with tubeworm bushes (top right; source: Ocean Networks Canada, 2011), emphasizing the habitat complexity present in each. Similar ecological processes can be studied in each of these ecosystems (e.g., trophic levels, access to nutritional sources, energy availability and gradients, and competition). Next, we show plant succession following the 1980 eruption of Mount St. Helens in the U.S. (middle left; reproduced and cropped from Dale and Denton (2018, pp. 157, Figure 8.6) with permission from Springer Nature), which is comparable to vent community succession following the 1998 eruption of Axial Volcano on the Juan de Fuca Ridge, represented in diagrammatic form (middle right; after Marcus et al., 2009). The ecological processes involved in Mount St. Helens and the deep Northeast Pacific Ocean are comparable. Finally, we compare methodologies common across terrestrial and vent ecosystems, showing an image from a remotely operated drone above a forest (bottom left; source: Lee, 2018) and a view from a Remotely Operated Vehicle (ROV) of Grotto vent, offshore of western Canada (bottom right; source: Ocean Networks Canada, 2010).

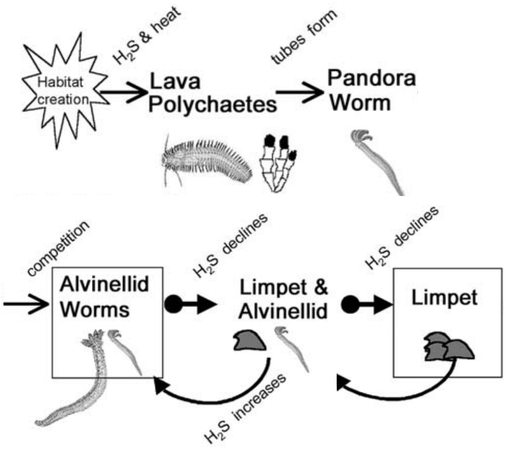
HABITAT
COMPLEXITY

ENERGY
GRADIENTS

DISTURBANCE
ECOLOGY

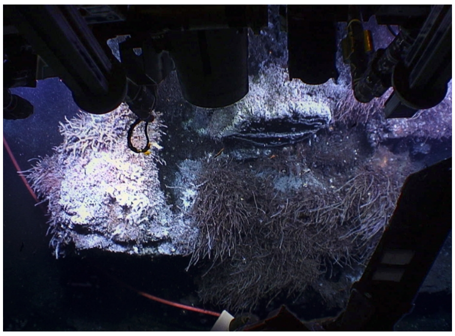
SUCCESSION

COMMUNITY
ASSEMBLY



REMOTELY-
OPERATED
VEHICLES

IMAGE ANALYSIS

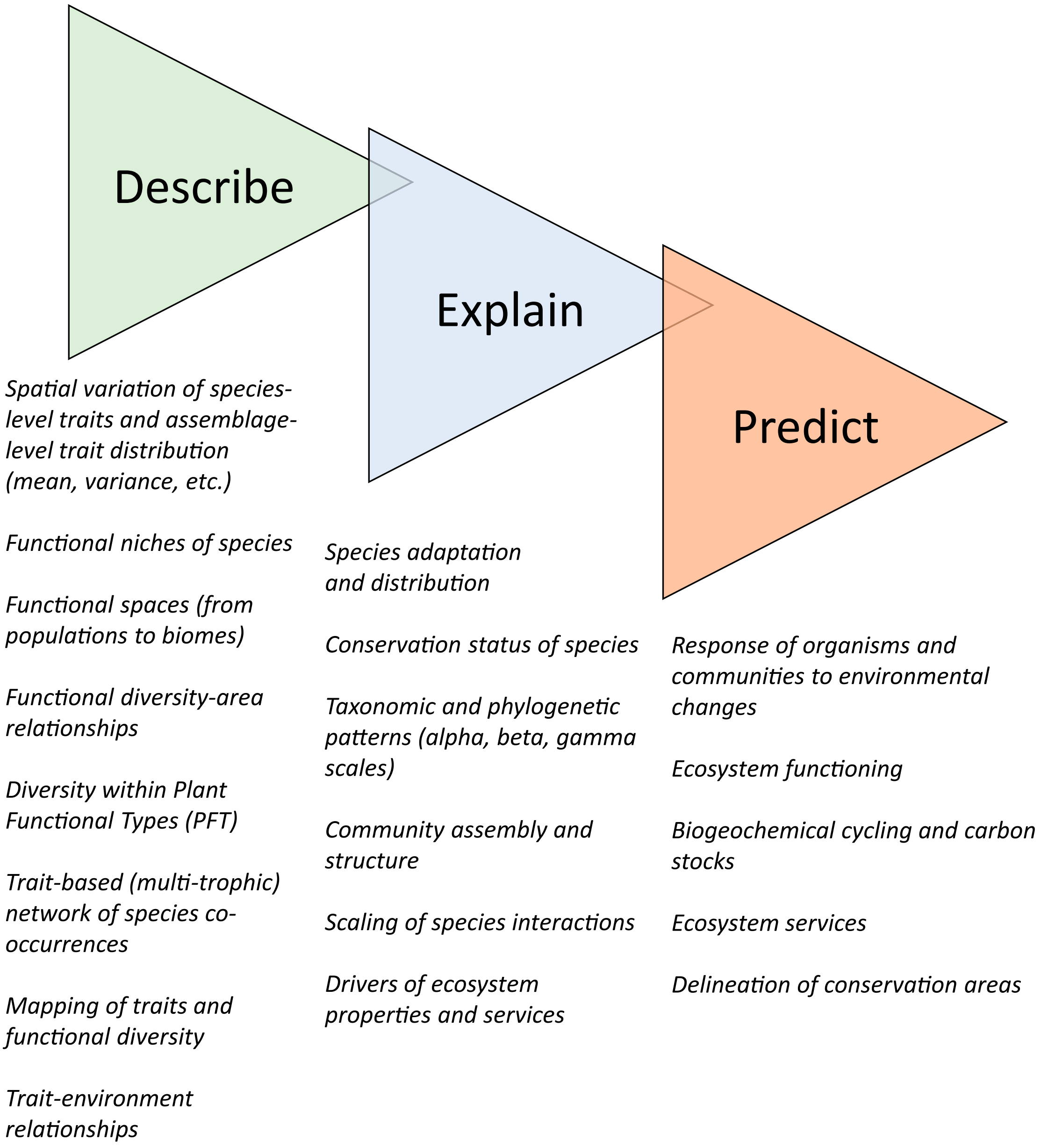


2.2 Testing ecological theories with vents as model systems

In using a trait-based approach to study the biodiversity of deep-sea hydrothermal vents, we have found that vents tend to buck the trends set in other ecosystems. For example, we show, contrary to other ecosystems, that common and rare species both contribute to functional uniqueness in vent communities (Chapter 2; Chapman et al., 2018), and global taxonomic, functional, and environmental uniqueness patterns are not spatially congruent (Chapter 5). These differences may, as argued in Chapter Two, result from vents being untouched ecosystems, relative to most other environments on Earth (Chapman et al., 2018). In addition, vents have plentiful niche space, which, as demonstrated chemosynthetic wood-fall environments (McClain et al., 2018), shapes resource use and affects community dynamics. Vent species also adapt to, or find microhabitats within, strong physico-chemical gradients on small scales. On large scales, too, there are distinctive environmental conditions at depth, affecting the ambient waters and vent fluids of deep-sea hydrothermal-vent ecosystems (Chapter 4).

With these distinctive attributes influencing vent ecology, it could be argued that vents are simply too unique to include in general ecological and conservation-science research. Conversely, as shown in **Figure 41**, there are many similarities between vents and other ecosystems that make them compelling study systems for a broad range of ecological research questions. For instance, resource use, the impacts of substratum heterogeneity, microclimate effects, and the relative mobility of organisms are just some areas that have been investigated in tropical rainforest ecosystems (Lowman and Moffett, 1993). These research topics could also be explored in densely packed vent communities, which are similarly complex in habitat and community structuring, environmental heterogeneity, and the influence of energy gradients (**Figure 41**). In addition, the extreme physico-chemical environment in which vent fauna thrive has been likened to the deserts bees and ants are adapted to survive in (McMullin et al., 2000). Oxygen limitation, too, is not unique to vent ecosystems, with anoxia an issue handled by nematodes and goldfish, among other taxonomic groups (McMullin et al., 2000). Fire has also been the subject of much trait-based research, enabling ecologists to study the traits required to survive in fire-prone ecosystems (Allen, 2008; Ames et al., 2017) and how fire frequency shapes functional diversity (Loiola et al., 2010; Giordani et al., 2016). In addition, terrestrial volcanic eruptions, such as that of Mount St. Helens in 1980, have enabled ecologists to study the impacts of disturbance on community-assembly processes like succession (Moral et al., 1995). In the same way as fires and volcanoes on land shape species and their traits, submarine volcanic eruptions are known to affect community assembly, and the traits of pioneer coloniser species, at vents (Tunnicliffe et al., 1997; Marcus et al., 2009; Bayer et al., 2011; Gollner et al., 2013). Components of island biogeographic theory might also be explored at vents, as vent fields differ in size and can be separated by large distances, shaped by plate tectonics (Hessler and Kaharl, 1995), like islands (Whittaker et al., 2017). Species-area relationships (Whittaker et al., 2017) could thus be investigated at vents, should data on vent-field sizes be collected in future. There are also similarities between the island-like spatial configuration of vents and reefs, suggesting that comparing these systems will also yield ecological insights (e.g., Whittaker and Fernández-Palacios, 2007). In summary, we propose that vents should be included in comparative studies, as suggested for other marine and terrestrial ecosystems by Webb (2012).

While the aforementioned ideas suggest that vents can be used as model, case-study systems to test ecological theories, they will be best achieved if datasets (e.g., as provided with Chapters 3 and 4) continue to be updated and developed. From a trait-based perspective, the data in this thesis have facilitated the descriptive stage of the Violle et al. (2014) model of functional biogeography (**Figure 42**). We have also begun to identify possible links between trait, taxonomic, and environmental patterns, forming part of the 'explain' phase of the functional biogeography of vents. If the sFDvent database, and the availability of data on species distributions, habitats (including physico-chemical conditions), and phylogeny, continue to grow, we may be able to use traits to make predictions about vent species pools on a variety of scales (e.g., **Figure 43**). Thereafter, we might also be able to determine how we expect vent communities to respond to scenarios of anthropogenically-induced change.



Spatial variation of species-level traits and assemblage-level trait distribution (mean, variance, etc.)

Functional niches of species

Functional spaces (from populations to biomes)

Functional diversity-area relationships

Diversity within Plant Functional Types (PFT)

Trait-based (multi-trophic) network of species co-occurrences

Mapping of traits and functional diversity

Trait-environment relationships

Species adaptation and distribution

Conservation status of species

Taxonomic and phylogenetic patterns (alpha, beta, gamma scales)

Community assembly and structure

Scaling of species interactions

Drivers of ecosystem properties and services

Response of organisms and communities to environmental changes

Ecosystem functioning

Biogeochemical cycling and carbon stocks

Ecosystem services

Delineation of conservation areas

Figure 42: The components of functional biogeography. Reproduced from Violle et al. (2014, pp. 13692, Figure 2).

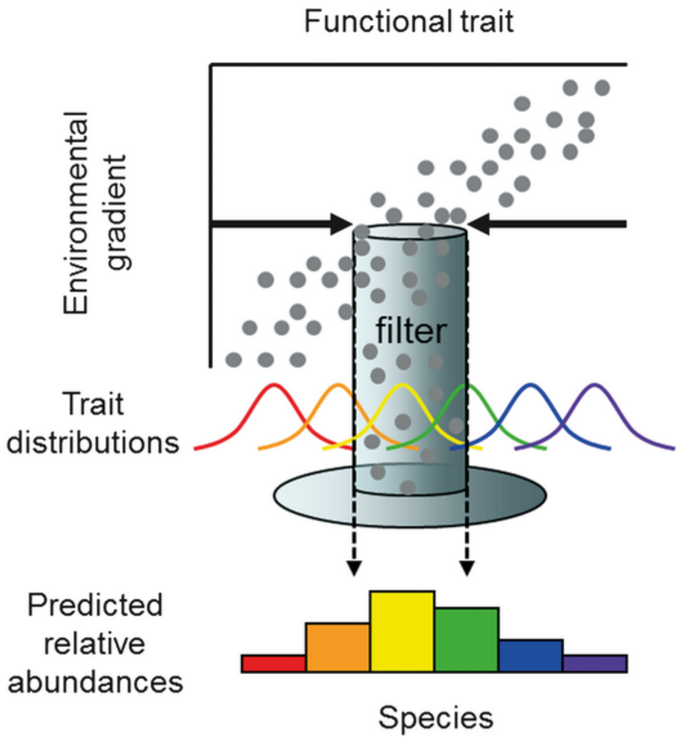


Figure 43: An illustration of the use of traits in a predictive framework, as proposed for the TraitSpace model of Laughlin et al. (2012). Reproduced (and cropped) from Laughlin et al. (2012, pp. 1292, Figure 1) with permission from Wiley.

2.3 Managing the protection of deep-sea hydrothermal-vent ecosystems: findings and future work

The greatest anthropogenic threat to vent ecosystems today is the proposed commercial-scale mining of polymetallic sulfides. Mining of vents will be similar in appearance to terrestrial open-cut mining, removing surface sulfides as well as material from below the Earth's crust (Van Dover et al., 2018). Impacts will likely include: the physical destruction of vent substrata, such as sulfide chimneys (**Figure 44**), and the changes to hydrothermal-fluid circulation and loss of fauna this will likely cause; sediment-plume production, which may smother filter-feeding species; and pollution, from equipment and wastewater (Ramirez-Llodra et al., 2011; Van Dover, 2014; Jones et al., 2018). The impacts are uncertain, though, with some scientists arguing that mining disturbances at active vents will be analogous to natural catastrophic eruptions (Ardron et al., 2011). Contrarily, the cumulative nature, scale, intensity, duration, and frequency of mining will likely differentiate its impacts from those of natural disturbances (**Figure 45**; Van Dover, 2014). In general, as there is no precedent, the impacts of mining on vent ecosystems are relatively unknown; yet, they are expected to be severe, at least on local scales (Boschen et al., 2013; Van Dover et al., 2018).

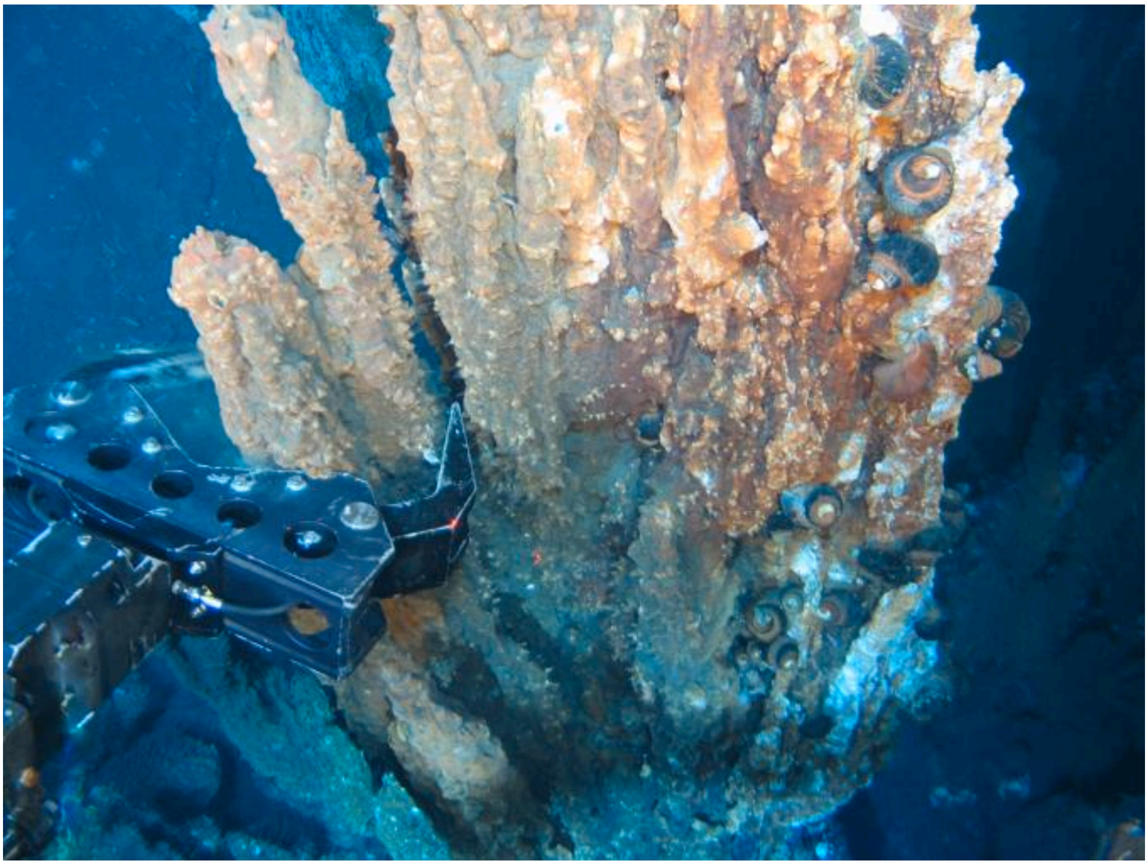


Figure 44: Extraction of a section of sulfide from a deep-sea hydrothermal-vent chimney. Image courtesy of Nautilus Minerals.

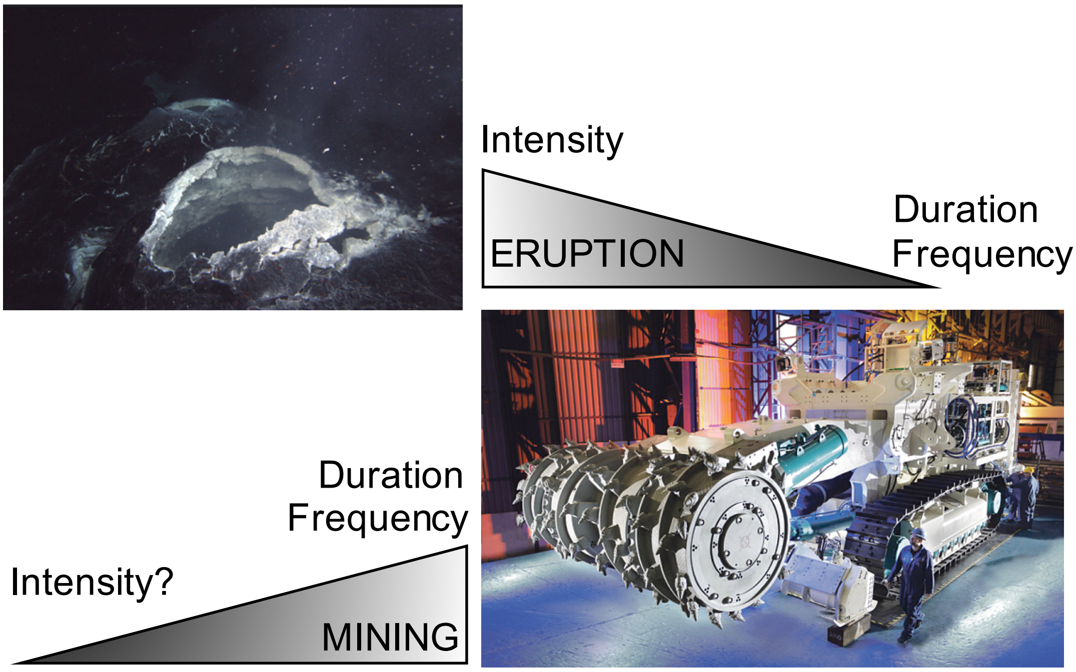


Figure 45: An illustration of the differences in intensity, duration, and frequency of impacts from volcanic eruptions, such as that of Axial Seamount in 1998 and 2011 (image source: Chadwick, 2011), and deep-sea mining (image courtesy of Nautilus Minerals), respectively.

With this in mind, the work presented in this thesis provides several key insights into how best to design protection measures for vent ecosystems. For instance, in Chapter Two, we show that both rare and common species make unique trait contributions to the functional distinctiveness of vent communities on the Juan de Fuca Ridge (Chapman et al., 2018). At the World Conference on Marine Biodiversity (WCMB, 2018), researchers shared work applying our methodology and R script to test the same principle in Manus Basin vent communities (P. Turner, pers. comm., May 2018). They also found rare and common species contributing to functional uniqueness (P. Turner, pers. comm., May 2018). This is a key finding for conservation and management purposes, suggesting rare and common species should both be protected under management schemes, rather than prioritising rare species, as is common in conservation practice given an assumed higher likelihood of rare-species extinctions (though see Gaston and Fuller, 2008).

Furthermore, in Chapter Five, we show that different priority regions would be identified using taxonomic, trait, and environmental measures of uniqueness. The lack of congruence among these measures makes conservation decisions more difficult, as there is no single-best metric capturing the relative uniqueness of vent ecosystems across the globe. Many conservation strategies have been designed using principles developed in the terrestrial and shallow-marine realms. Accordingly, it is likely that without this new insight, we would have assumed species richness to be a good proxy for trait and environmental uniqueness, representing overall biodiversity (Brooks et al., 2006; Parravicini et al., 2014). As this is not the case for the relatively well-sampled vent regions we investigated (Chapter 5), we emphasize the importance of using different measures of biodiversity when prioritising ecosystems for protection (see also Fleishman et al., 2006). Different biodiversity metrics should also be used when comparing pre- and post-disturbance sites during monitoring.

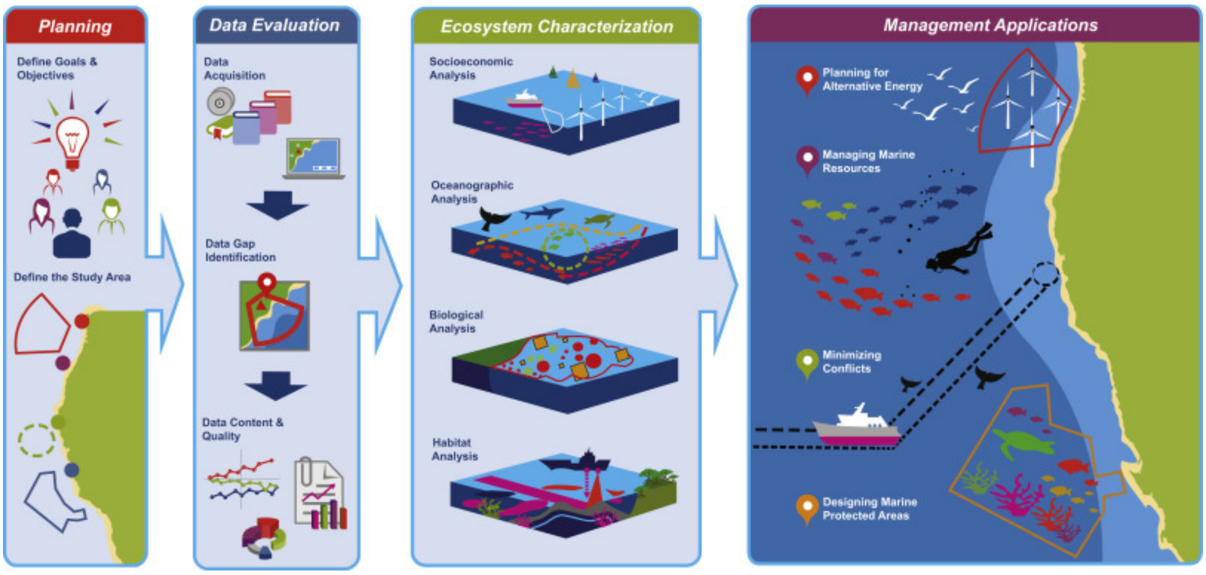


Figure 46: The NOAA Biogeographic Assessment Framework for marine spatial planning. Reproduced from Caldow et al. (2015, pp.425, Figure 1) with permission from Elsevier.

In this thesis, we have, in effect, conducted analyses suggested in NOAA's Biogeographic Assessment Framework for marine spatial planning (Caldow et al., 2015; **Figure 46**). We have characterised the broad-scale biology, habitat, and oceanography of vent ecosystems, and we have summarised some of the socioeconomic aspects expected in years to come (Chapters 4 - 6; Caldow et al., 2015). Through this work, it becomes apparent that vents are a valuable untouched system that can be used to advance biological and ecological understanding. For too long, vents have been geographically and literarily isolated. Yet, if we examine the habitat characteristics and fauna of deep-sea hydrothermal-vent ecosystems, we can see that, if they were on land, visible to the human eye, they would probably be protected and perhaps even Red Listed (IUCN, 2018). For instance, 'IUCN Category V Protected Areas', designed to protect seascapes used by people, have essential and desirable characteristics such as: distinct scenic quality (**Figure 47**; Phillips, 2002); unique land-use patterns (Phillips, 2002), with vents globally distinct in having no current human use beyond scientific research; research suitability (Phillips, 2002), which we demonstrate in this thesis; and educational importance (Phillips, 2002), emphasized through various outreach activities taking place across the globe (e.g., Ocean Networks Canada and the Ocean Exploration Trust, among other initiatives). Deep-sea hydrothermal vents meet many of the criteria for IUCN Category V Protected Areas, which, under Principle 9, should not contain economic activities that could take place elsewhere (Phillips, 2002). This, and other suggestions for the Red Listing of ecosystems (Keith et al., 2013), therefore provides support for recent calls to prohibit the mining of active deep-sea hydrothermal vents (Van Dover et al., 2018).

3. CONCLUSION

In using a trait-based approach to study the biodiversity of hydrothermal-vent ecosystems, we have broken down the terminological barriers separating vent ecosystems from other environments on Earth. We have also been able to use traits to compare taxonomically and spatially distinct regions. In identifying similarities and redundancies among species, through their traits, we have, in fact, revealed the uniqueness of vent ecosystems - one of the reasons many of us find them utterly fascinating. In placing vents in a broader ecological context, alongside coral reefs and tropical rainforests, we have also highlighted the importance of vents as untouched ecosystems. This 'wild' status is set to change by as soon as 2020, emphasizing an urgent need to focus research efforts, and associated funding, on these ecosystems. We need to study and protect these untouched ecosystems before they are damaged, to inform conservation practices through an improved understanding of biodiversity in wilderness areas. I hope, through the work presented in this thesis, we have ensured that the enchantment of vents remains in those already hooked, and also captures the scientific imaginations of those yet to explore these beautiful, unusual ecosystems.

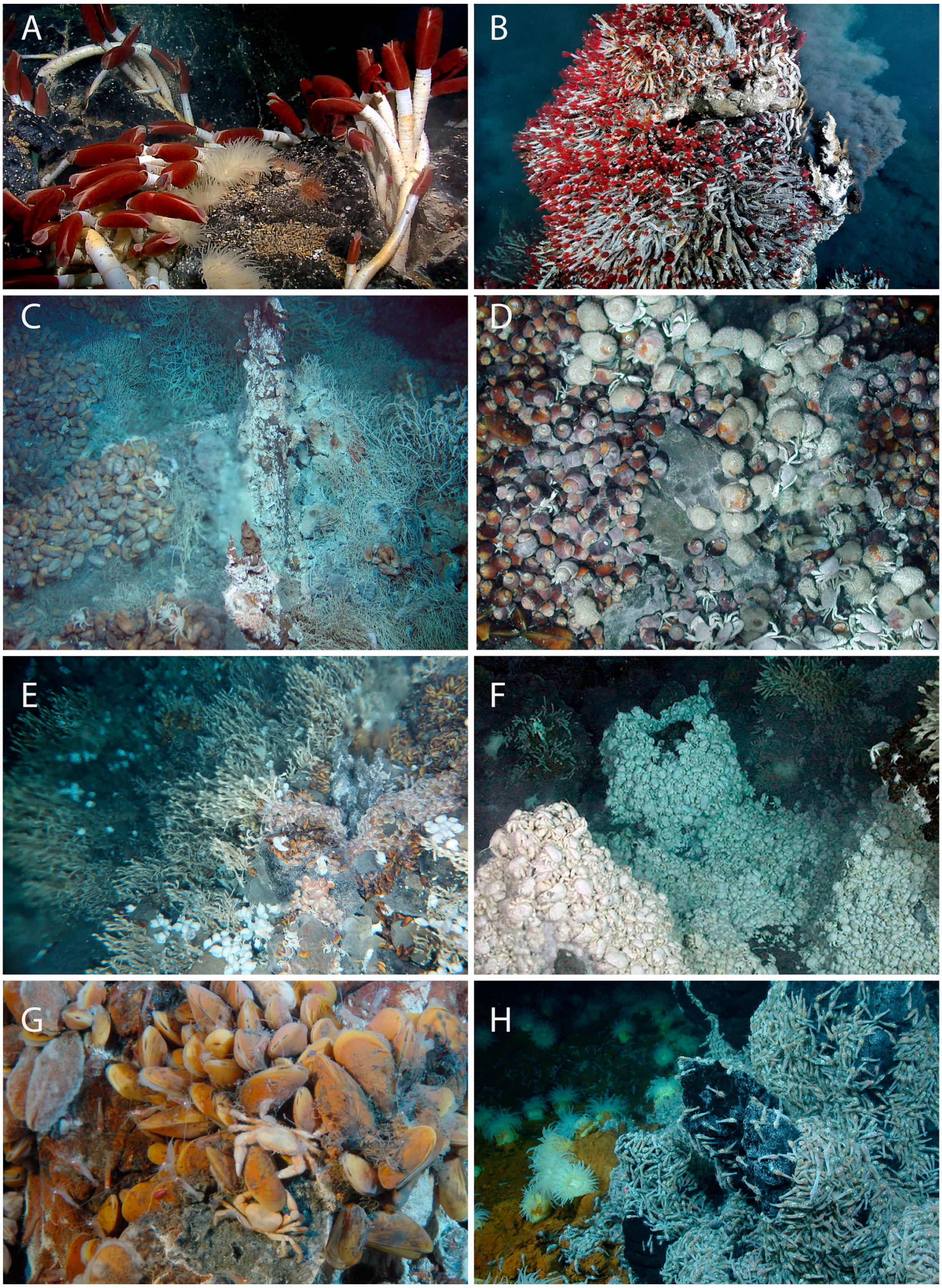


Figure 47: Images depicting the typical fauna and biodiversity of vents across the globe, highlighting the distinct scenic quality of these systems. Regions are depicted as follows: A) Galapagos Spreading Centre; B) Juan de Fuca Ridge; C) New Hebrides Volcanic Arc; D) Lau Basin; E) Central Indian Ridge; F) East Scotia Ridge; G) Mid-Atlantic Ridge; and H) Mid-Cayman Rise. Reproduced from Van Dover et al. (2018, pp. 21, Figure 1, wherein full image credits are provided, in addition to further information on the dominant species shown in each of the images).

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Appendix A Supporting Information to Accompany Chapter Two

Appendix A.1

Appendix A.1 contains Supporting **Tables 15 - 20** as well as **Figures 48** and **49**. **Table A.1.1** (traits matrix used in this study with a supporting key and rationale, references, and species list) is provided as a separate Excel file on the USB storage device that accompanies this thesis.

Table 15: A summary of eight studies, focusing on findings or methods assessing the contributions of rare species to diversity using a functional trait-based approach.

Taxa	Metric(s)	Number of Species	Location	Spatial scale	Goal	Major finding	Reference
Forest ants (Formicidae)	FD (Petchey and Gaston 2002, 2006) and FAD (Walker et al., 1999)	99	Secondary successional gradient in Atlantic Forest, Brazil	Landscape	To identify the relationship between species diversity and functional diversity.	Recruitment of rare species was the main driver of increasing functional diversity and rare species were more functionally unique than common species.	Bihn et al., 2010
Rocky shore community	Species richness and biomass	<30 (~24)	Rocky intertidal plots, MA, USA	Local	To determine whether realistic declines in rare species can impact higher trophic levels, using a diversity loss experiment.	Rare species disproportionately impact the diversity and abundance of species from higher trophic levels (‘cornerstone species’, shaping the community).	Bracken and Low, 2012

Soft-sediment macrofauna	Rarity expressed as range size. Biological traits related to rarity in percentage terms (e.g. ‘n’ % of the unique species had body size ‘x’).	351	Hauraki Gulf, North Island, New Zealand	Multiple scales across 60 kilometres	To assess the contribution of rare species to biodiversity.	Restricted-range species might improve community resilience as they shared traits in common with the total observed species pool.	Ellingsen et al., 2007
Tropical tree seedlings	Relative positions of species along the breadth of trait space, assessed using Principal Component Analysis (PCA).	142 from China, 53 from Puerto Rico	Tropical rainforests in China and Puerto Rico	Regional (218 and 200 plots)	To determine where rare and common species fit in trait space, focusing on intraspecific trait variation.	Common species tend to occupy central positions in trait space, whereas rare species have more variance in their traits and are found in the periphery of trait space.	Umaña et al., 2015
Tall-grass prairie communities	Convex hull volume (functional trait volume - FTV) and rarity defined similarly to Rabinowitz (1981) - geographic range, habitat specificity, and local abundance.	248 (46 with trait data)	Cedar Creek Ecosystem Science Reserve, Minnesota, USA	Local (1m^2 plots), subsampling from a subset (46 of 248 species with trait data)	To assess the influence of rare species on grassland ecosystem functioning via rare and common species contributions to community functional diversity.	Rare species contribute to ecosystem functioning by adding redundancy and uniqueness.	Jain et al., 2014

Species-rich tropical assemblages of (i) stream fish, (ii) rainforest trees, and (iii) birds	Local abundance, geographic range, and habitat breadth combined into a rarity metric. Functional richness (FRic - convex hull volume trait space filled), functional specialization (FSpe - the position of the species within the functional trait space), and functional originality (FOri - the mean distance between a species and its nearest neighbour in trait space) used to define functional structure.	395 fish, 262 trees, and 86 birds	Brazilian Amazon (stream fish), French Guiana (rainforest trees), and the Australian Wet Tropics (birds)	Regional scale, simulating species losses from regional assemblages	To investigate how extinctions affect the functional structure of species assemblages, on local and regional scales.	Rare species extinction had a disproportionate impact on assemblage functional richness, specialization, and originality.	Leitão et al., 2016

Coral reef fish, alpine plants, and tropical trees	Rarity defined on local and regional scales according to relative abundance and relative occupancy. Functional distinctiveness and vulnerability measured.	846 fish (633 used), 2,535 alpine plants for abundance data, and 662 tropical trees	South Pacific reef fish (633 species of 846 used in analysis), alpine plants from National Alpine Botanical Conservatory records, and tropical trees in French Guiana.	Multiple scales	To determine whether distinct trait combinations were supported by rare species.	The most vulnerable functions (with poorly-insured trait values) and unique traits were supported by rarer species, on local and regional scales.	Mouillot et al., 2013
Alpine plants	FRi index - functional richness (Mason et al., 2005); FDvar index - richness and divergence (Mason et al., 2003); FRO index - evenness (Mouillot et al., 2005); and FDiv - functional divergence (Villéger et al., 2008).		Alpine granite gravel fields in South Island, New Zealand	Regional (90 plots per location)	To determine whether two geographically distinct sites hosting a rare ecosystem share community-assembly mechanisms.	Rare species contributed to trait diversity and divergence, so should be incorporated into models of community assembly as a source of local trait diversity in species-poor communities with strong environmental filters.	Richardson et al., 2012

Table 16: Outcomes of binomial tests used to determine whether there was a significant difference between the proportion of communities a species made a unique trait combination (UTC) contribution to, based on sample data, and the proportion expected given randomly assembled, artificial communities. The richness bins used in these tests are shown in **Figure 16** as dotted boxes.

Species	Richness Bin	Number of Successes	Number of Trials	Probability of Success	Alternative Hypothesis	p-value
Paralvinella palmiformis	6 to 22	1	54	0.01851852	True probability of success is not equal to 0.4077181	4.111e-11
Paralvinella pandorae	6 to 22	35	38	0.9210526	True probability of success is not equal to 0.4338624	3.313e-10
Provanna variabilis	9 to 19	1	39	0.02564103	True probability of success is not equal to 0.4646465	1.018e-09
Depressigyra globulus	9 to 19	12	50	0.24	True probability of success is not equal to 0.5190563	9.014e-05
Amphisamytha carldarei	4 to 19	5	57	0.0877193	True probability of success is not equal to 0.5190563	6.524e-12
Protomystides verenae	14 to 19	6	21	0.2857143	True probability of success is not equal to 0.4990548	0.07836
Sericosura verenae	12 to 19	16	19	0.8421053	True probability of success is not equal to 0.4638554	0.0009265
Parougia wolfi	12 to 19	11	30	0.3666667	True probability of success is not equal to 0.4834308	0.2728

Table 17: Parameter estimates for linear models testing the relationship between rarity (in terms of: maximum relative abundance - 'Abundance', number of samples within which a species was found - 'Occupancy', number of vent fields a species was sampled in - 'Geographic Extent', and a Rarity Index - calculated *sensu* Leitão et al. 2016, without log transformation) and functional distinctiveness, shown in **Figure 14**.

Rarity Metric	p-value	Slope	Intercept	Relationship
Abundance	0.457	0.03329	0.32513	Not significant
Occupancy	0.827	0.0001609	0.3296457	Not significant
Geographic Extent	0.938	0.0004169	0.3312752	Not significant
Rarity Index	0.688	0.01958	0.32591	Not significant

Table 18: Summary of species traits for the three simulated groups introduced in **Figure 16**: 'Rapidly Redundant', 'Redundant with Richness', and 'Always Unique'. Note that the greyscale used on this table matches the colour scheme of the plots in **Figure 16**, for ease of comparison.

Scenario	Trait similarities
Always Unique	No traits are common in all 12 species of the 'Always Unique' group, but it is the only group within which some species have nutritional symbionts. This group also has the highest number of species forming 3D structures and the broadest spread of trophic levels and mobilities. • ⅓ of the species form 3D structures • ½ of the species have low mobility (4 species have medium and 2 high) • There is a relatively even split amongst the trophic level indicator groups, apart from scavenging, which is only fulfilled by *Munidopsis alvisca* • Only 3 of these species has nutritional symbionts (*Idas washingtonius, Calyptogena starobogatovi,* and *Lepetodrilus fucensis*) • ½ of the species have large body sizes, with the remainder evenly split between small and medium sizes
Redundant with Richness	• None of these species have nutritional symbionts • Only *Amphisamytha carldarei* and *Paralvinella pandorae* form 3D structures • Low or medium mobility • Mostly primary consumers / detritivores, with *Protomystides verenae* and *Parougia wolfi* the only higher level consumers in this group • The majority of species in this group are medium in size

Rapidly Redundant	• Do not form 3D structures or have nutritional symbionts • Low or high mobility • Medium or large estimated maximum body size • Primary consumer / detritivore and higher consumer trophic level indicators

Table 19: Analysis of traits affecting the functional distinctiveness of each of the 37 species included in our study, with significant p-values shown in bold. This table, produced following the distance-based redundancy analysis (db-RDA - formula: FDistinct ~ Mobility + Forms3DStructure + TrophicIndicator + NutritionalSymbionts + logMaxBodySize) shown in **Figure 17**, was completed using an ANOVA by terms, with 200 permutations.

	Degrees of Freedom	Sum of Squares	F	p-value
Mobility	1	0.002262	2.2116	0.162
Forms 3D Structure	1	0.145567	142.3293	**0.001**
Trophic Indicator	1	0.000226	0.2214	0.630
Nutritional Symbionts	1	0.085740	83.8333	**0.001**
log Max. Body Size	1	0.000275	0.2689	0.595
Residual	31	0.031705		

Table 20: Trait-based approaches identify features of hydrothermal-vent communities that clarify assemblage structure and key roles.

Trait Feature	Species	Commonness	Consequence or Interpretation
Nutritional Symbionts	*Lepetodrilus fucensis*	Very common	Access to nutritional resources; competitive dominance
Nutritional Symbionts	Bivalves (*Calyptogena starobogatovi* and *Idas washingtonius*)	Very rare	Access to nutritional resources; small discrete niche
Forms a 3D Structure	*Lepetodrilus fucensis*	Very common	Space acquisition; habitat alteration
Contributes a UTC in more communities than expected	*Paralvinella palmiformis*	Common	Good competitor with congener
Contributes a UTC in fewer communities than expected	*Paralvinella pandorae*	Very common	Poor competitor with congener
High Redundancy	*Buccinum thermophilum* and *Nereis piscesae*	Rare	Replacement by other common predators
Contributes a UTC in a low proportion of communities	*Amphisamytha carldarei*	Very common	Specific habitat requirements
Contributes a UTC in a low proportion of communities	*Provanna variabilis*	Very common	Specific habitat requirements

Contributes a UTC in a low proportion of communities	*Depressigyra globulus*	Common	Specific habitat requirements
Contributes a UTC in a high proportion of communities	*Sericosura verenae*	Common	Unique niche

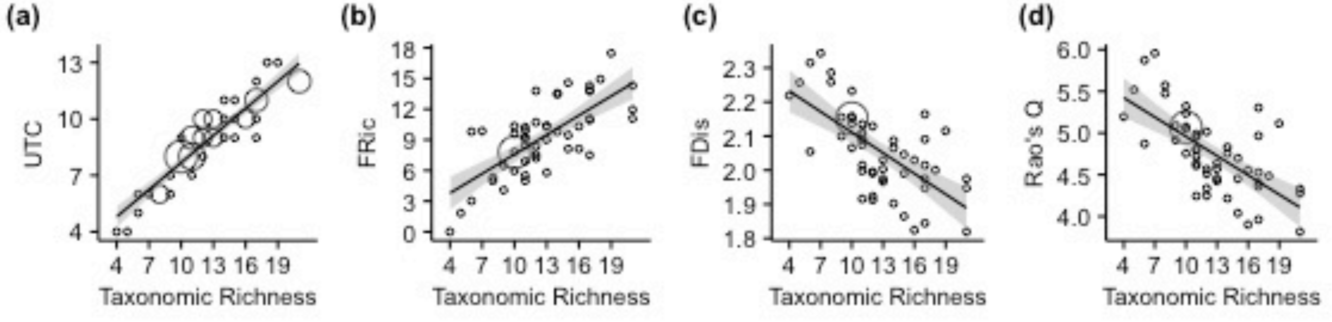
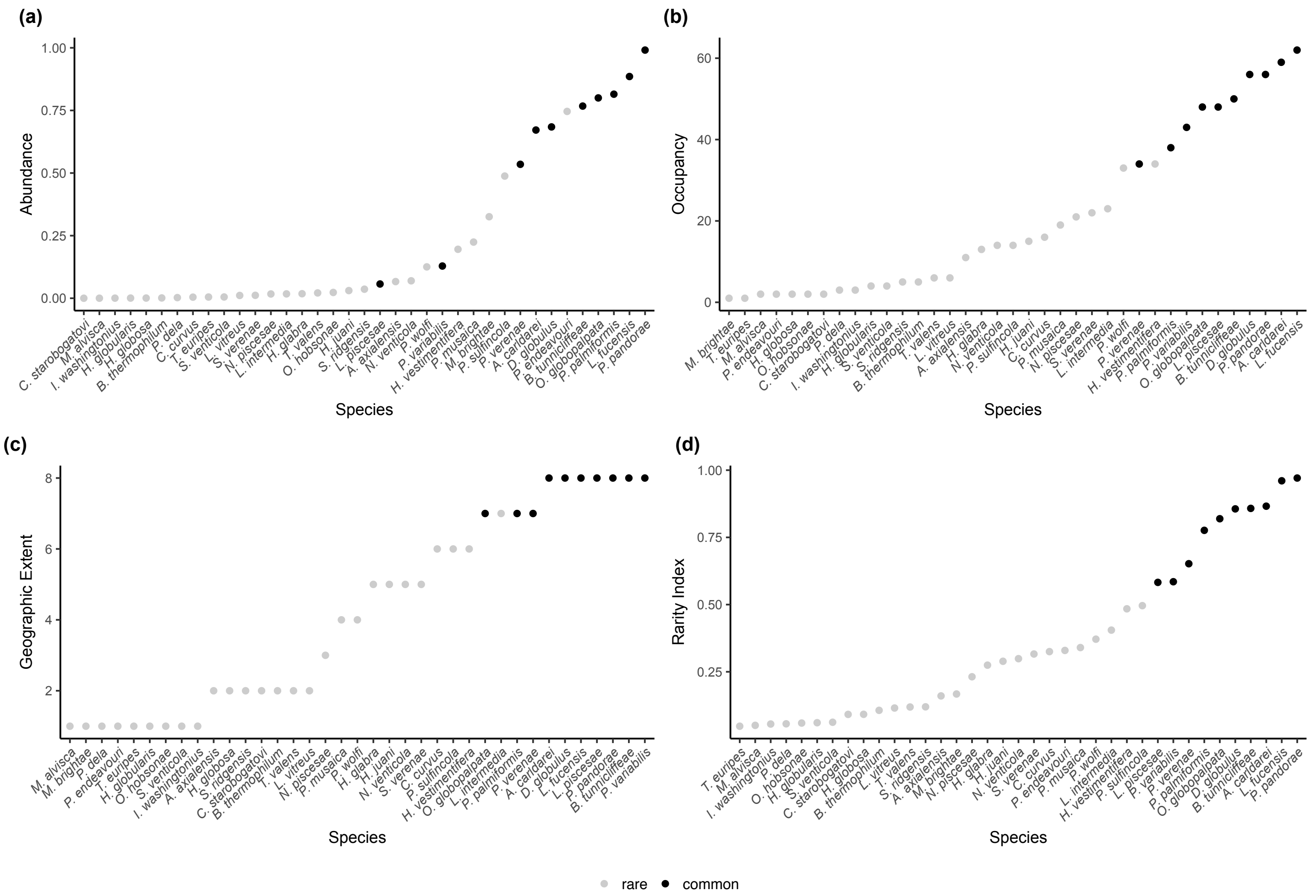


Figure 48: The relationship between functional diversity (measured in (a) using the number of unique trait combinations (UTC), in (b) as functional richness (FRic), in (c) as functional dispersion (FDis), and in (d) as Rao's quadratic entropy (Rao's Q)) and taxonomic (species) richness. The relationships presented in panels (a) to (d) were computed using linear models in R, with solid best-fitting lines and shaded confidence intervals. Circle sizes are relative to the number of samples with the given richness and metric value. All relationships are significant (p-value < 0.05), with the following slope values: (a) 0.48, (b) 0.63, (c) -0.02, and (d) -0.08.

Figure 49 (overleaf)**:** An overview of the rarity of each species (with rare species - those with a rarity index value less than 0.5 - represented by grey dots, and common species - with a rarity index value greater than 0.5 - shown with black dots). Each panel represents a different facet of rarity focused on in our study: (a) abundance (maximum relative abundance), (b) occupancy (the number of samples a species was observed in), (c) geographic extent (the number of vent fields a species was sampled in), and (d) a combined Rarity Index, calculated as described in Leitão et al. (2016) without log transformation.


(a)
Abundance
1.00
0.75
0.50
0.25
0.00
C. starobogatovi
M. alvisca
I. washingtonius
H. globularis
H. globosa
B. thermophilum
P. dela
C. curvus
T. euripes
S. venticola
L. vitreus
S. verenae
N. piscesae
L. intermedia
H. glabra
T. valens
O. hobsonae
H. juani
S. ridgensis
L. piscesae
A. axialensis
N. venticola
P. wolfi
P. variabilis
H. vestimentifera
P. musaica
M. brightae
P. sulfincola
P. verenae
A. carldarei
D. globulus
P. endeavouri
B. tunnicliffeae
O. globopalpata
P. palmiformis
L. fucensis
P. pandorae
Species
(b)
Occupancy
60
40
20
0
M. brightae
T. euripes
M. alvisca
P. endeavouri
H. globosa
O. hobsonae
C. starobogatovi
P. dela
I. washingtonius
H. globularis
S. venticola
S. ridgensis
B. thermophilum
T. valens
L. vitreus
A. axialensis
H. glabra
N. venticola
P. sulfincola
H. juani
C. curvus
P. musaica
N. piscesae
S. verenae
L. intermedia
P. wolfi
P. verenae
H. vestimentifera
P. palmiformis
P. variabilis
O. globopalpata
L. piscesae
B. tunnicliffeae
D. globulus
P. pandorae
A. carldarei
L. fucensis
Species
(c)
Geographic Extent
8
6
4
2
M. alvisca
M. brightae
P. dela
P. endeavouri
T. euripes
H. globularis
O. hobsonae
S. venticola
I. washingtonius
A. axialensis
H. globosa
S. ridgensis
C. starobogatovi
B. thermophilum
T. valens
L. vitreus
N. piscesae
P. musaica
P. wolfi
H. glabra
H. juani
N. venticola
S. verenae
C. curvus
P. sulfincola
H. vestimentifera
O. globopalpata
L. intermedia
P. palmiformis
P. verenae
A. carldarei
D. globulus
L. fucensis
L. piscesae
P. pandorae
B. tunnicliffeae
P. variabilis
Species
(d)
Rarity Index
1.00
0.75
0.50
0.25
T. euripes
M. alvisca
I. washingtonius
P. dela
O. hobsonae
H. globularis
S. venticola
C. starobogatovi
H. globosa
B. thermophilum
L. vitreus
T. valens
S. ridgensis
A. axialensis
M. brightae
N. piscesae
H. glabra
H. juani
N. venticola
S. verenae
C. curvus
P. endeavouri
P. musaica
P. wolfi
L. intermedia
H. vestimentifera
P. sulfincola
L. piscesae
P. variabilis
P. verenae
P. palmiformis
O. globopalpata
D. globulus
B. tunnicliffeae
A. carldarei
L. fucensis
P. pandorae
Species
● rare
● common

Appendix A.2

Appendix A.2 is provided as a separate R script file on the USB storage device that accompanies this thesis. It is the R script used for computing the proportion of communities each species contributes a UTC in, using observed (sample) data and artificially assembled communities, and a distance-based redundancy analysis using traits.

Appendix A.3

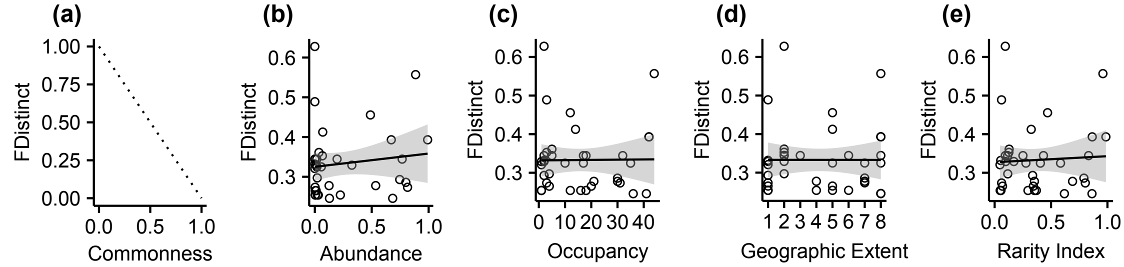


Figure 50: The relationship between rarity and functional distinctiveness, as computed using the 'distinctiveness' function of the 'funrar' functional rarity package and data from tubeworm grab samples only. Panel (a) outlines the expected linear relationship between rarity and distinctiveness, whereby more common species offer less functional distinctiveness than rare species. Panel (b) shows the observed relationships between the maximum relative abundance of each species included in this study and their functional distinctiveness relative to all other species in the community. Panel (c) delineates the relationship between the occupancy of each species (measured as the number of samples within which the species was observed) and its functional distinctiveness. Panel (d) demonstrates the relationship between the geographic extent of a species (quantified as the number of vent fields within which the species was observed) and its functional distinctiveness. Finally, Panel (e) shows the relationship between the Rarity Index (calculated as described in Leitão et al., 2016, without log transformation) and functional distinctiveness. Note that the relationships shown in (b), (c), (d), and (e) are relatively flat, contrary to the expectation presented in (a), suggesting that rare and common species contribute functional distinctiveness. This suggests that the results presented in Chapter Two are not simply an outcome of sampling method.

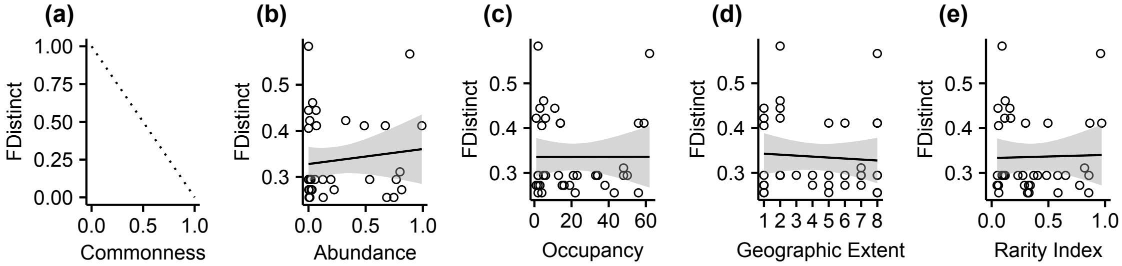


Figure 51 (caption continues overleaf)**:** The relationship between rarity and functional

distinctiveness, as computed using the 'distinctiveness' function of the 'funrar' functional rarity package and binary trait data. Panel (a) outlines the expected linear relationship between rarity and distinctiveness, whereby more common species offer less functional distinctiveness than rare species. Panel (b) shows the observed relationships between the maximum relative abundance of each species included in this study and their functional distinctiveness relative to all other species in the community. Panel (c) delineates the relationship between the occupancy of each species (measured as the number of samples within which the species was observed) and its functional distinctiveness. Panel (d) demonstrates the relationship between the geographic extent of a species (quantified as the number of vent fields within which the species was observed) and its functional distinctiveness. Finally, Panel (e) shows the relationship between the Rarity Index (calculated as per Leitão et al., 2016, without log transformation) and functional distinctiveness. Note that the relationships shown in (b), (c), (d), and (e) are relatively flat, contrary to the expectation presented in (a), suggesting that rare and common species contribute functional distinctiveness. This suggests that the results presented in Chapter Two are not simply the result of the number of modalities per trait.

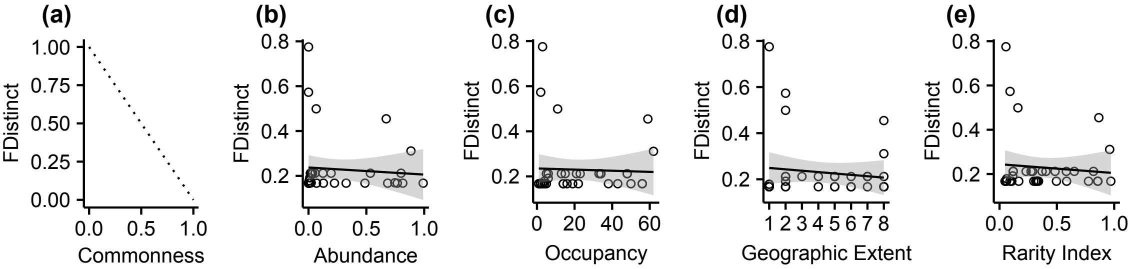
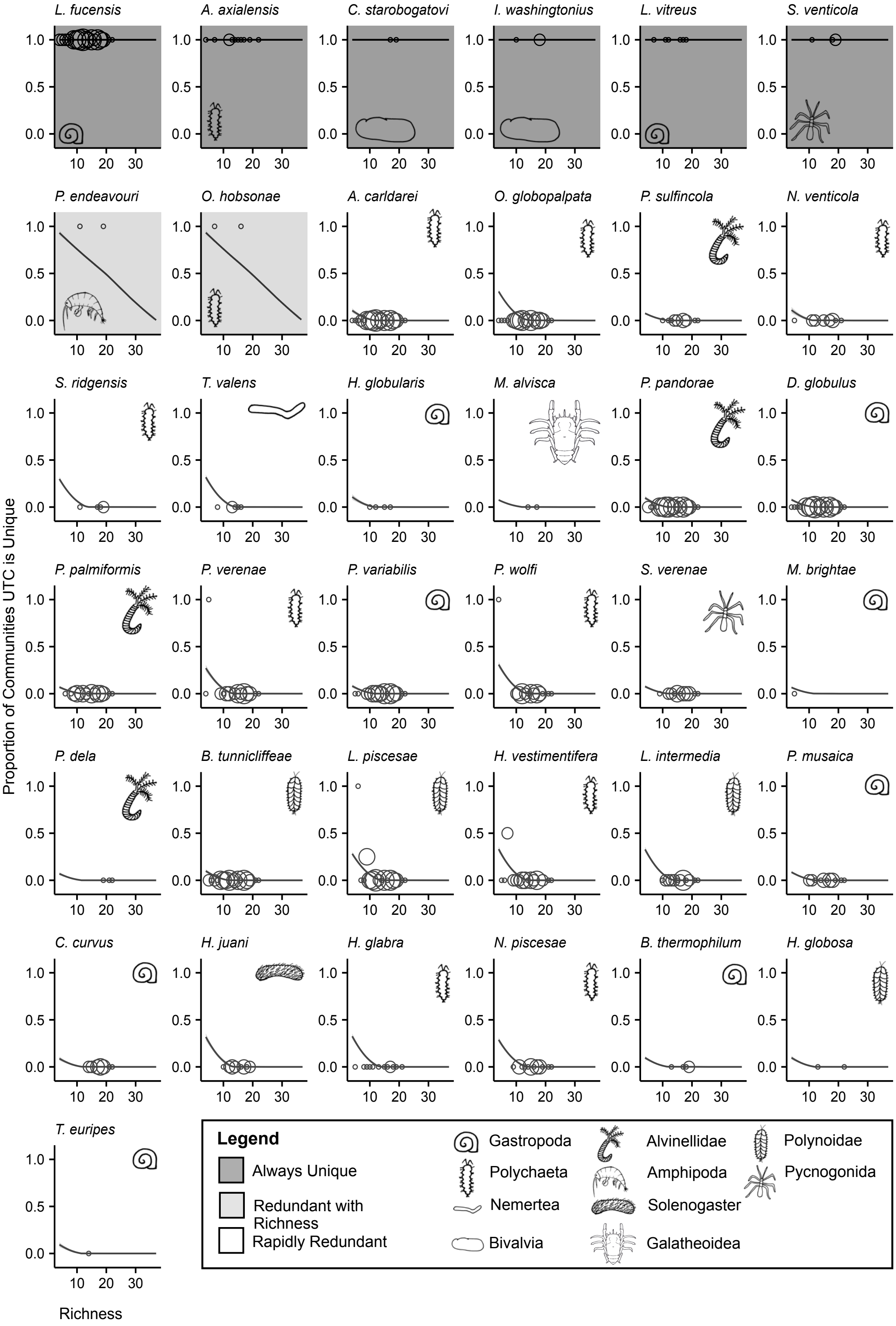


Figure 52 (caption continues overleaf): The relationship between rarity and functional distinctiveness, as computed using the 'distinctiveness' function of the 'funrar' functional rarity package and different ecologically meaningful traits to those presented in the main manuscript. The traits used for this analysis were: 'Chemosynthetic Endemic' (whether a species is endemic to chemosynthetic environments or not), 'Diet' (the nutritional source of a species, be it mixed in source or predominantly from the water column via suspension feeding, etc.), and 'Symbionts' (whether a species has endosymbionts, epibionts, or neither). The traits matrix is presented in **Table A.3.1**. Panel (a) outlines the expected linear relationship between rarity and distinctiveness, whereby more common species offer less functional distinctiveness than rare species. Panel (b) shows the observed relationships between the maximum relative abundance of each species included in this study and their functional distinctiveness relative to all other species in the community. Panel (c) delineates the relationship between the occupancy of each species (measured as the number of samples within which the species was observed) and its functional distinctiveness. Panel (d) demonstrates the relationship between the geographic extent of a species (quantified as the number of vent fields within which the species was observed) and its functional distinctiveness. Finally, Panel (e) shows the relationship between the Rarity Index (calculated according to Leitão et al., 2016, without log transformation) and functional distinctiveness. Note that the relationships

shown in (b), (c), (d), and (e) are relatively flat, contrary to the expectation presented in (a), suggesting that rare and common species contribute functional distinctiveness. This suggests that the results presented in Chapter Two are not only an outcome of trait selection.

Figure 53 (overleaf)**:** The proportion of communities within which each species makes a unique trait combination (UTC) contribution. Each panel in this figure shows the proportion of communities a species (named at the top of each panel) makes a unique contribution to (y-axis), relative to species richness (x-axis). Solid lines in each panel depict the relationships identified using artificial, randomly assembled communities of 4 to 37 species in richness (mean values based on communities that were randomly assembled 1,000 times per level of richness - see Methods in Chapter Two). Circles in each panel are observations from sample data, with circle size relative to the number of samples with the given result. Each panel is shaded according to the groups listed in the legend, that are assigned based on the shape of the relationship between species richness and UTC contributions revealed in the randomly assembled communities. Cartoon inserts illustrate the taxonomic group of each species, as outlined in the Legend. Species names have been shortened, but are given in full in **Table A.3.1**.


L. fucensis
A. axialensis
C. starobogatovi
I. washingtonius
L. vitreus
S. venticola
P. endeavouri
O. hobsonae
A. carldarei
O. globopalpata
P. sulfincola
N. venticola
S. ridgensis
T. valens
H. globularis
M. alvisca
P. pandorae
D. globulus
P. palmiformis
P. verenae
P. variabilis
P. wolfi
S. verenae
M. brightae
P. dela
B. tunnicliffeae
L. piscesae
H. vestimentifera
L. intermedia
P. musaica
C. curvus
H. juani
H. glabra
N. piscesae
B. thermophilum
H. globosa
T. euripes
1.0
0.5
0.0
10
20
30
Proportion of Communities UTC is Unique
Richness
Legend
Always Unique
Redundant with Richness
Rapidly Redundant
Gastropoda
Polychaeta
Nemertea
Bivalvia
Alvinellidae
Amphipoda
Solenogaster
Galatheoidea
Polynoidae
Pycnogonida

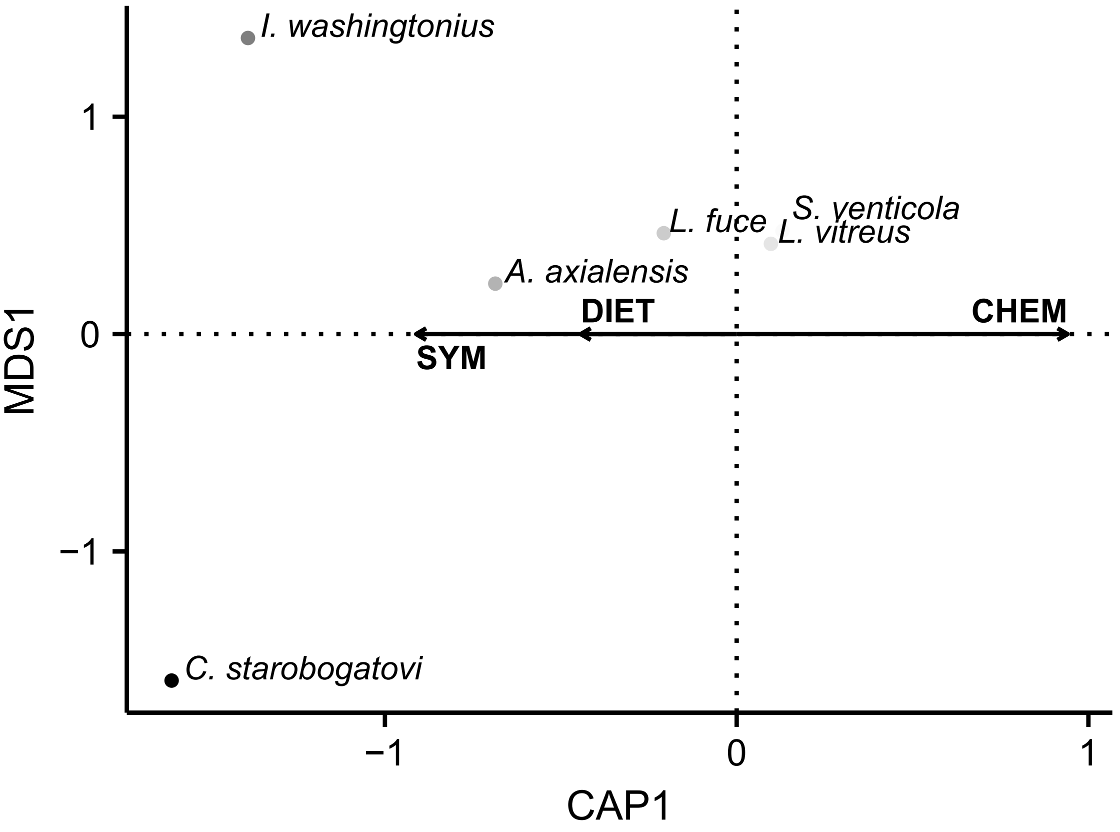


Figure 54: Distance-based redundancy analysis (dbRDA – formula: FDistinct ~ Chemosynthetic Endemic + Diet + Symbionts) of Gower distances showing the functional distinctiveness of each of the species relative to one another and the potential traits driving distinctiveness differences (labelled in bold next to arrows, with trait names shortened as follows: SYM - Symbionts, DIET - Diet, CHEM - Chemosynthetic Endemic). All traits were significant in this model, based on an ANOVA by terms with 200 permutations. Functional distinctiveness is colour-coded, with the most functionally distinct species (*Calyptogena starobogatovi*) shown in black and the point colours becoming lighter with decreasing functional distinctiveness. The species labelled on this plot belong to the 'always unique' group (see **Figure 53**), though the functional distinctiveness of all 37 species was driven by the same traits. Species names have been shortened but are given in full in **Table A.3.1** (particularly, note that *Lepetodrilus fucensis* has been shortened to *L. fuce* for display purposes).

In **Appendix A.3**, we test the robustness of the methods and results presented in Chapter Two. We test the hypothesis that rare species over-contribute to functional diversity using: (i) only samples from tubeworm grabs (excluding suction samples, to test whether including samples compiled from mixed sampling methods might have affected our results - **Figure 50**); (ii) traits scored in binary (ensuring that the number of modalities per trait were equal, to see whether having different numbers of modalities per trait might have influenced our results - **Figure 51**); and (iii) different ecologically meaningful traits to those presented in Chapter Two (to determine how trait selection might have affected our findings - **Figure 52**).

The traits used in (iii) were: 'Chemosynthetic Endemic' (whether a species is endemic to vent environments ('Yes') or not ('No'), 'Diet' (the nutritional source of a species, scored as follows: 0 - mixed sources, 1 - detritivore, 2 - rock and sediment surfaces, 3 - suspension feeding (from the water column), 4 - other meiofauna and macrofauna, and 5 - symbiont), and 'Symbionts' (whether a species has endosymbionts (2), epibionts (1), or neither (0) - note that this has different modalities to the 'Nutritional Symbionts' trait used in the main body of Chapter Two). The trait matrix used for (iii) is available in **Table A.3.1**.

The methods for each analysis conducted on these input datasets are as described for sample data in the Methods in Chapter Two. The outcomes of these tests are shown in **Figure 50**, **Figure 51**, and **Figure 52** respectively, and can be compared to **Figure 14**, shown in the main body of Chapter Two.

For (iii), we also test the relative contributions of species to functional diversity using the UTC approach on sampled and artificially assembled assemblages described in Chapter Two and assess the relative functional distinctiveness of the species using a distance-based redundancy analysis of Gower distances (**Figure 53** and **Figure 54**, which can be compared to **Figure 15** and **Figure 17** in Chapter Two).

Finally, we ran linear models to identify whether a single trait significantly influenced the patterns identified in Chapter Two (e.g., using the db-RDA presented in **Figure 17**). No single trait was significantly related to functional distinctiveness (all p-values were greater than 0.05).

Table A.3.1 (species traits matrix used in Appendix A.3, with supporting key and references) is provided as a separate Excel file on the USB storage device that accompanies this thesis.

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Appendix B Supporting Information to Accompany Chapter Three

Appendix B.1

Scopus Search Information

i) Scopus search referenced in the Introduction:

Scopus search: 'trait' AND 'database' in agricultural, biological, environmental, and earth sciences.

Results: 53 titles published since 2000, which were then manually filtered for relevance, to ensure they were describing trait databases being released, resulting in 25 records, 6 of which were published in 2017.

An Excel file (**Table B.1.1**) containing the exported records is provided on the USB storage device accompanying this thesis for reference.

ii) Scopus search referenced in the Discussion:

Scopus search 1: 'hydrothermal vent' AND 'annelid' OR 'worm' OR 'polychaete'

Search 1 results: 602 records

Scopus search 2: 'hydrothermal vent' AND 'mollusc' OR 'mollusk' OR 'snail' OR 'gastropod' OR 'bivalve' OR 'clam' OR 'mussel' OR 'limpet' OR 'whelk'.

Search 2 results: 900 records

Scopus search 3: 'hydrothermal vent' AND 'arthropod' OR 'amphipod' OR 'decapod' OR 'shrimp' OR 'copepod'.

Search 3 results: 369 records

Scopus search 4: 'hydrothermal vent' AND 'Pacific'.

Search 4 results: 1947 records

Scopus search 5: ‘hydrothermal vent’ AND ‘Atlantic’.

Search 5 results: 1103 records

Scopus search 6: ‘hydrothermal vent’ AND ‘Indian Ocean’

Search 6 results: 202 records

Scopus search 7: ‘hydrothermal vent’ AND ‘East Pacific’

Search 7 results: 855 records

Scopus search 8: ‘hydrothermal vent’ AND ‘West Pacific’

Search 8 results: 119 records

Appendix B.2

Summary of Decisions Made by the sFDvent Working Group During Database Design and Testing

Defining ‘trait’:

Our working group decided to focus on species traits (e.g., trophic level, maximum body size, etc.), rather than individual traits capturing variation within species and populations, given the availability of information regarding populations of vent species.

Trait selection:

Looking to existing databases to ensure cross-ecosystem compatibility with sFDvent, we suggested the following traits (within categories, as underlined), before reducing these in number to those which could be scored for many of the species across the globe, given the current state of knowledge for vent species:

Ecosystem Engineer:

- Foundation species (note that the group deemed this to be a binary – yes or no – trait scored according to whether a species provided a physical structure from which other species could benefit).
- Early coloniser (i.e., whether a species is present at an early successional stage)

- Habitat builder (capturing habitat complexity as a shape descriptor)
- Host / guest (in terms of symbiosis)
- Body form

Species Associations / Interaction Strengths:

- Using other organisms as a substratum (yes or no)
- Strong species dependency? (yes/no with host/guest also described)

Biogeography / Geographic Distribution:

- Geographic range size (latitudes and longitudes)
- Patchiness or occupancy
- Depth (e.g., vertical range size)

Generalist / Specialist:

- Basalt or sulfide (rock type most commonly occupied)

Habitat Use:

- Gregariousness (or 'aggregated' with yes or no)
- Substratum (soft or hard, basalt or sulphide)
- Zonation (e.g., at and/or from a vent chimney)

Adult Mobility:

- Mobility, captured as per Faulwetter et al. (2017): sessile/mobile, crawler, burrower, swimmer, non-motile or semi-motile, zoochory

Trophic Structure:

- Trophic level
- Feeding mode (capturing the 'messiness' of feeding and, thus, whether a species enables access to food by other organisms)
- Food source / nutritional supply (origin of the food – e.g., water column and therefore possibly the sea surface, or at depth)

Morphology:

- Maximum body size
- Maximum possible abundance / biomass / dominance achieved (or an estimator of the relative abundance curve for a species)

Life History:

- Life span (1, 10, 100)
- r- or K- selected ("weediness")
- Larval dispersal and other reproductive traits

Energy / Holobiont:

- Type of symbiont
- Source
- Location of symbiont
- Type of bacteria
- Transmission

Physiology:

- Fundamental temperature range

Parasite Host:

- Parasite host (yes or no)

Refinements after testing:

Our working group tested the trait database design to determine whether the traits, modalities, and setup worked well when scoring using Google Sheets (selected to facilitate population by collaborators from institutes across the globe). We deem the following features important for the user-friendly setup of a trait database, to encourage scoring:

- Column order (i.e. a database should be set up with the traits that are easiest to score to the left, progressing to the hardest on the right, to encourage contributions).
- Ranges should be given as numbers (e.g., for relative adult mobility, scores ranged from 1 for sessile to 4 for the most mobile).
- References should be required for each score, to ensure that every score has a traceable origin (even if the origin is 'expert opinion').
- Fixed, drop-down options should be given to ensure quality and consistency of entries.
- The taxon names should be 'frozen', to enable the user to view the taxon at all times when scoring.
- A certainty score of '0' should be allowed, to ensure that lack of knowledge is captured in these cells, as blank cells could otherwise represent: i) lack of knowledge, or ii) a missed entry.

Appendix B.3

sFDvent Data Files

Appendix B.3 describes **Tables B.3.1, B.3.2, B.3.3, B.3.4**, and **B.3.5,** which are all provided as separate Excel files on the USB storage device that accompanies this thesis. A tutorial video (**Video B.3.1**) is also described here but provided as a separate .mov file on the USB storage device. References cited in all files are provided in **Appendix B.7**.

Video B.3.1 is a copy of a narrated tutorial sent to all contributors as part of the online, personalised Google Sheets populated to create **Table B.3.3**. This video could be used as a guide by future contributors to the database.

Table B.3.3 is a copy of raw data contributions, compiled from the personalised files sent to each sFDvent contributor. This dataset includes traits that were removed from the error-checked, quality-controlled dataset due to lack of coverage and would require appropriate processing for each user's research question before it could be used in an analysis.

Table B.3.4 is a clean version of **Table B.3.3**, processed according to the decision rules documented in **Table B.3.5**. **Table B3.5** also outlines the processing steps undertaken to take the raw data file (**Table B.3.3**) to the recommended file that was sent to all contributors to conduct final error-checks on. First, individual contributor sheets were joined together manually, as the number of columns per trait differed in each sheet because contributors could provide more than one score per trait per species. These data form the raw database (**Table B.3.3**). Next, empty columns, NAs, and other missing data descriptors (e.g., -) were removed, before duplicates were identified and managed as documented in **Table B.3.5**. The names of taxa were then checked using the 'Match taxa' WoRMS database tool (Horton et al., 2017). Any taxa that were not identified to species level and could not be traced to a taxonomist by observed location or literary source were then removed, to avoid artificial inflation of diversity in analyses conducted using the database. The average certainty score and percentage of scored species were then calculated for each trait. Traits with fewer than 50% of species scored and/or an average certainty score below 2.3 were removed.

Consequently, these data were copied into a Google Sheet document shared with all contributors for error-checking and final gap filling. These clean data form the recommended dataset in **Table B.3.2** and thus represent data approved by expert deep-sea researchers and the state of knowledge on vent species traits across the globe. This dataset can be linked with location information (also provided by deep-sea expert contributors) and other, well-known databases as shown in **Figure 21**. **Table 3** summarises traits, modalities (or scoring options), and associated rationale.

Tables B.3.2 and **B.3.4** also contain location information for the species in the sFDvent database. This was collected as ancillary data and therefore has not been standardised, and may not represent the full extent of current knowledge. However, there has not yet been a single repository for data on vent species distributions. Instead, there are separate sources of information, such as:

ChEssBase - geo- and literary-referenced species lists for fauna from chemosynthesis-based ecosystems, now accessible using OBIS - the Ocean Biogeographic Information System (Baker et al., 2010; OBIS, 2017); the InterRidge Vents Database, comprising a list of hydrothermal-vent-field locations and ancillary data (Beaulieu, 2015); species-presence data available in the supplementary data supporting Bachraty et al. (2009); and information published in the renowned handbook of deep-sea hydrothermal-vent fauna produced by Desbruyères et al. (2006) (though note that this book also includes non-vent fauna observed in the periphery of vent fields). To begin to resolve this, location information was compiled to meet a wider sFDvent-working-group aim using Desbruyères et al. (2006) and expert knowledge and can be linked to each taxon using the 'Taxon' column and any name updates that can be traced using the AphiaID for the taxon. The location information, however, varies in spatial scale due to disparities in data availability on species observations across the globe. Hence, for the spatial coverage data presented in this paper, we re-classified location information into i) ocean, and ii) region, controlled vocabularies as per the InterRidge Vents Database (Beaulieu, 2015). In addition, the taxa presented in sFDvent have been checked using the WoRMS 'Match Taxa' function (Horton et al., 2017), to ensure sFDvent taxonomy is up-to-date (and associated 'AphiaIDs' are provided in **Table B.3.2** for the highest taxonomic level possible). As we are launching sFDvent eight years after version 3 of ChEssBase was released (Baker et al., 2010), the updated species list provided as part of the database can be considered complementary to ChEssBase for taxonomic and geographic information on vent species.

Table B.3.2 is the clean dataset that we recommend for use and refer to for coverage and certainty values, etc. in the main manuscript. Here, 'Taxon' refers to the taxonomic identity assigned by contributors, while 'UniqueID' is an identifier created using letters from the taxon and the entry number, to make it easier to work with the data and reference a taxon. A glossary to support the traits and modalities given in **Tables B.3.2** and **B.3.3** is provided in **Table B.3.1**.

Appendix B.4

Usage Notes

Version 1 of the sFDvent database accompanies Chapter Three in two parts:

1. A data file comprising the processed and cleaned dataset that has been approved and recommended for use, given in **Table B.3.2** and also hosted at a doi to be confirmed on acceptance of the version of Chapter Three currently in review. References associated with the scores in this dataset are provided in **Appendix B.7**. While traits have been binned in this dataset to improve accessibility and reduce bias, we recommend that each user bins traits and/or processes the dataset as appropriate for the study being conducted.
2. A data file containing all raw data contributions as a static release, given in **Table B.3.3** and also hosted at a doi to be confirmed on acceptance of the version of Chapter Three currently in review. References associated with raw data entries can also be found in the full reference list provided in **Appendix B.7**. These raw data would need to be processed before use and we recommend: i) checking for collinearity among traits when selecting from these traits for a given study; ii) conducting error checks using the recommended dataset and/or literary sources; and iii) considering weighting or processing data according to given certainty scores (giving particular attention to certainty scores of '0', which have been given to show that the trait score should be removed and was randomly filled to demonstrate a lack of knowledge rather than an otherwise empty cell).

We also provide a metadata file for use in conjunction with trait data to determine which traits, species, and/or data files are most appropriate for a given research question. We do not recommend using the location metadata in isolation, as they were collected as ancillary data with the trait database, so may not represent the full extent of current knowledge.

Please note that references to 'Handbook', or the 'Handbook of Hydrothermal Vent Fauna', or similar, refer to Desbruyères et al. (2006). Any references that are unclear can be sought from the contributor. It is also worth noting when using the sFDvent trait database that a score with reference 'expert opinion' may be more accurate or higher quality than some older, literary sources and it should not always be assumed that an expert opinion is an estimate or less accurate than a literary source. For vent species, the current state of knowledge is not always otherwise captured in publications or cruise reports, given the observational nature of work conducted using Remotely Operated Vehicles (ROVs). For instance, an expert can learn a considerable amount about a species through hours of observation during a ROV dive that is not officially documented or further investigated (as sample numbers are governed by ROV storage capacity) but could form the basis for a trait score; sFDvent captures this knowledge, of particular importance for rare or less well-studied species.

Citation:

We ask that the sFDvent database is cited in all outputs using and/or developing the data, giving: i) the recommended citation for this paper, and ii) the sFDvent database doi. When an accompanying website is released for updated database versions at a later date, this should be referred to for up-to-date recommended citations so we ask all users to search 'sFDvent' online before citing.

We also ask all users of the sFDvent database to provide a copy of the data used for the analyses initiated with sFDvent data (i.e. including any modifications or corrections made) to abates@mun.ca, so the sFDvent database can be updated and improved accordingly and, thus, best represent the current state of knowledge of the species traits of deep-sea chemosynthetic fauna.

We propose that future versions of sFDvent should be released on a five-year cycle, to ensure that each version captures a substantial contribution to the state of knowledge of trait data for deep-sea vent species, given typical research cruise timeframes. A workflow for the cycle is proposed and illustrated in **Figure 23**. During this process, the database may expand to include other chemosynthesis-based ecosystems, such as whale falls, wood falls, and cold seeps, and, eventually, individual-level (intraspecific) traits. We would also recommend, for the maintenance of this regular workflow of sFDvent, that any issues or updates are flagged and provided by users by completing the table below and returning it to: abates@mun.ca.

Contributor Name	Taxon ID No.	Genus	Species	Trait / Column	Current Score	Proposed Change	Rationale / Support for Change	Other

We also propose that any future cruise-log designers should consider storing behavioural observations with geo-referenced trait 'tags', to facilitate inclusion in databases such as sFDvent. This would ensure that key ecological observations are not lost in modern-day, deep-sea equivalents of personal, hand-written field notebooks.

Appendix B.5

Extended Results - Trait-by-trait

Trait-specific descriptions

Relative adult mobility: Relative adult mobility ranges from 1 to 4, with the majority of taxa scoring 3. Taxa in the Arthropoda and Chordata phyla have the highest mobility scores (with mean scores of 3.3 and 3.9, respectively) and the lowest scores are assigned to taxa in the Cnidaria and Porifera (with respective mean scores of 1.1 and 1). Average mobility is similar (3) across all oceans except the Arctic, Southern, and Mediterranean oceans, which have a mean relative adult mobility of 2.

Depth range: Depth ranges vary in the sFDvent database from 0 to 500 metres to > 5000 metres, with the most common depth records ranging from 2000 to 3000 metres. *Sirsoe hessleri, Acharax johnsoni, Coryphaenoides armatus,* and *Abyssorchomene distinctus* species have the deepest recorded ranges (> 5000 m) and 7 taxa have only the shallowest range (0 - 500 m: 4 molluscs and 3 arthropods).

Maximum body size: Estimated maximum body size ranges from 1 mm to 1000 mm, with 100 mm the most common body size class in the database (41% of taxa scored for body size) and 10 mm also common (40% of taxa with body size scores). More species had a score of 1000 mm as an estimated maximum body size (10%) than 1 mm (8%). The phylum Chordata hosts the largest species on average (mean estimated maximum body size 700 mm) and Acanthocephala, Foraminifera, and Nematoda the smallest (mean estimated maximum body size 1 mm). The Mediterranean has the highest mean estimated maximum body size (505), while the Arctic Ocean has the lowest (49).

Substratum preference: The majority of species are found on hard substrata (81% of species scored for this trait), while the fewest are associated with the water column (6% of species with a substratum preference score). Hard substrata are most often associated with arthropods (146 taxa) and soft substrata with molluscs (27 taxa).

Foundation species: Species are not commonly foundation species (84% scored 'No' and 16% 'Yes' for this trait).

Abundance: Overall, 'High' and 'Low' abundance scores were relatively evenly split across all taxa and oceans.

Gregariousness: Gregariousness is most often scored as 'Solitary' (44% of species with a Gregariousness score) and least often 'Always' (26% of species scored for this trait) but Arctic Ocean, Indian Ocean, and Southern Ocean taxa are more gregarious than taxa in other ocean basins.

Habitat Complexity: Habitat Complexity has scoring options: 'dense bush forming', 'open bush forming', 'bed forming (> 10 cm)', 'mat forming (< 10 cm)', 'burrow forming', and 'does not add'. The majority of species in the sFDvent database do not add habitat complexity (77% of taxa scored for Habitat Complexity), while 'dense bush forming' is the least common score for this trait (2% of species scored for the Habitat Complexity trait - all annelids).

Trophic mode: The most common trophic mode is 'Bacterivore' (39% of species scored with a Trophic Mode) and the least common (excluding 'Omnivore', only assigned to one species) is 'Carnivore - scavenger' (8% of species scored), despite 'Carnivore - other' being the second most common mode (29% of scored species). Scavenging carnivores are mostly from the Arthropoda phylum, while other carnivores were most commonly annelids and bacterivores and/or detritivores most commonly molluscs.

Nutritional source: Nutritional source is most commonly 'Sediment or rock surface' (41% of species scored for this trait), and least often 'Water column' (8% of scored species), with arthropods more often dependent on fauna and/or the water column and molluscs more often dependent on sediment or rock surfaces and/or symbionts.

Chemosynthesis-obligate: 'Chemosynthesis-obligate' is a trait specific to chemosynthesis-based ecosystems (CBEs), with scoring options of 'Vent', 'Other CBE', and 'No' used to represent the least restricted score for the species (e.g., a species found at vents but also in non-chemosynthetic ecosystems is given a score of 'No', as this score best demonstrates that this species is not tied to vents or chemosynthesis-based ecosystems). The most common score in the database is 'Vent' (74% of taxa, though we note that this might change in future versions of the database as more meiofauna, of less than 1 mm body size, are included) and the least common is 'Other CBE' (10%). The Arthropoda are predominantly vent-obligate (though also the phylum most often scored 'No'), while molluscs are most often also found in other CBEs, and the Chordata are mostly also found in non-vent environments.

Zonation from vent: 'Zonation from a vent' is a vent-specific trait with three modalities - 'High', 'Medium', and 'Low' - and the majority of taxa in the database are found in the 'Medium' zone (49% of species scored for this trait).

Position of symbiont: Position of symbiont has three modalities: 'Endosymbiont', 'Episymbiont', and 'None'. Of these modalities, most taxa do not have symbionts (80% of the species scored for this trait score 'None'), while 16% have endosymbionts and 4% have episymbionts, according to trait scores. Arthropods, molluscs, and annelids are the only taxonomic groups containing taxa with episymbionts and endosymbionts, though many taxa within these phyla do not have symbionts. All ocean basins host taxa with and without symbionts and there is a relatively consistent split in the proportion of taxa with each symbiont position (~75% without symbionts, ~19% with endosymbionts, and ~7% with epibionts, when the Mediterranean is excluded, given it only has two taxonomic records). The Southern Ocean has an above average proportion of symbiont-hosting species (44% have endosymbionts, 11% have episymbionts, and 44% are without symbionts, though we note that there is a low total number of taxa).

Appendix B.6

Comparative Review of Faunal Trait Databases

The Excel file **Table B.6.1** is provided on the USB storage device accompanying this thesis to support **Table 5**. It comprises information collated during a comparative review of animal trait databases, seeking to identify a 'common terminology' for traits across ecosystems and taxa.

Appendix B.7

Database Reference List

This reference list is provided on the USB storage device that accompanies this thesis. It comprises a reference list for all literary sources given as references for trait scores and/or comments in the sFDvent raw and recommended datasets (**Tables B.3.3** and **B.3.2**, respectively). These references are not listed again in the overall List of References for this thesis, unless referenced elsewhere in the thesis. They are provided in the same format as the publication in review.

Appendix B.8

The sFDvent Working Group was funded by the Synthesis Centre (sDiv) of the German Centre for Integrative Biodiversity Research (iDiv), following our response to a funding call. On the USB storage device that accompanies this thesis, I provide copies of the funding proposal I wrote (**Appendix B.8.1**), with support from Dr Amanda Bates, following guidance, and using text excerpts, from Dr Amanda Bates' previous funding application to SCOR (**Appendix B.8.2**).

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Appendix C Supporting Information to Accompany Chapter Four

Appendix C.1

Extraction and processing of environmental variables

First, we subset data from the InterRidge Vents Database (version 3.4; Beaulieu, 2015) to identify active, confirmed vent fields for which we could extract environmental data. The vent-field scale was selected for this global-scale analysis because vents have been unevenly sampled across the globe (preventing the use of vent-site locations for our purposes) and vent-field locations could be extracted with confidence using the InterRidge Vents Database (version 3.4; Beaulieu, 2015). As data were not available on vent-field area and shape, all variables were extracted for the longitude and latitude recorded for each vent field in the database; the data presented in this chapter therefore represent average environmental records based on extractions at point locations. Next, we processed the environmental data to facilitate extraction as described for each variable under each sub-heading below. While some environmental data were originally processed and extracted from the World Ocean Atlas dataset (Boyer et al., 2013), we used data freely-available from the BioORACLE dataset (Tyberhein et al., 2012; Assis et al., 2017) for the results presented in this chapter, as the processing is then consistent among many oceanographic variables (e.g., salinity, temperature, dissolved oxygen, etc.). A Microsoft Excel file accompanies this appendix (labeled **Table C.5.1**), so other researchers can also use the environmental data, extracted for active, confirmed vent fields (and subset to remove fields shallower than 200 m), listed below. This is provided on the USB storage device that accompanies this thesis.

Seafloor Age

We accessed NetCDF data on seafloor age from earthbyte.org (described in Müller et al., 2008). We imported the data using the 'raster' function of the 'raster' package (Hijmans, 2017) in R, before extracting for InterRidge vent field locations (latitude and longitude) using the 'extract' function (also in the 'raster' package).

Proximity to nearest vent field

We computed these proximities using locations of active, confirmed vent fields (longitude and latitude) in the InterRidge Vents Database (Beaulieu, 2015), which we read into ArcMap GIS software (ESRI, 2014) and assigned geographic coordinate system WGS 1984, before exporting as a shapefile for processing. We computed the geodesic distance between each vent field and its nearest vent field using the 'Near' function within the 'Proximity' toolset of the 'Analysis Tools' in ArcToolbox (ESRI, 2014). We then exported the results to the vent-field attribute table, which we converted to an Excel file using the 'Table to Excel' function in 'Conversion Tools', so it could be read into R (R Core Team, 2017), and converted from metres to kilometres, before analysis.

Seafloor roughness

We sourced seafloor roughness data from earthbyte.org (Whittaker et al., 2008) in NetCDF format, which could be read into R as raster data using the 'raster' function (package: 'raster'; Hijmans, 2017). We rotated these data in R prior to extraction ('rotate' function, 'raster' package; Hijmans, 2017), to re-project from a 0-360 degree grid to a -180 to 180 degree grid (to match that of the InterRidge Vents Database (Beaulieu, 2015)).

Proximity to nearest seep

Location data for seeps (as known in 2010) were provided by Dr Maria Baker, as produced by Dr Baker and Dr Daphne Cuvelier to create maps for the ChEss project (presented in German et al., 2011). We read these data into ArcMap GIS software (ESRI, 2014) with InterRidge Vents Database vent field locations (Beaulieu, 2015) and assigned both datasets the geographic coordinate system WGS 1984, before exporting as shapefiles for processing. We computed the geodesic distance between each vent field and its nearest seep using the 'Near' function within the 'Proximity' toolset of the 'Analysis Tools' in ArcToolbox (ESRI, 2014). We added the results to the attribute table for the vent-field location data, before converting this to an Excel file using the 'Table to Excel' function in 'Conversion Tools' so it could be read into R (R Core Team, 2017), and converted from metres to kilometres, before analysis.

Full spreading rate (mm per year)

These data were available in the InterRidge Vents Database (Beaulieu, 2015), so were simply extracted from the database for active, confirmed vents.

Storm intensity

We downloaded tropical cyclone wind-speed buffers footprint data, referred to as 'storm intensity' in this chapter, as a GeoTiff from the Global Risk Data Platform for the years 1970-2009 (UNEP/DEWA/GRID-Europe, 2015). The scale of the data ranges from 0 to 5, representing the estimated maximum Saffir-Simpson category of tropical cyclone that passed over an area between 1970 and 2009. We converted the GeoTiff to a raster using the 'brick' and 'plotRGB' functions of the 'raster' and 'rgdal' packages in R (Bivand et al., 2017; Hijmans, 2017), before using the 'extract' function (Hijmans, 2017) to extract the data for vent-field locations, then mapping using ArcMap GIS software (ESRI, 2014).

Sediment Thickness

Gridded global sediment thickness data were available via ngdc.noaa.gov as described in Whittaker et al. (2013). We: i) imported the data as raster data using the 'raster' function of the 'raster' package (Hijmans, 2017); ii) re-projected to the required extent (-180 to 180 degrees) using the 'rotate' function (Hijmans, 2017); and then iii) extracted for the InterRidge vent field locations using function 'extract' (Hijmans, 2017).

Tidal form factor

Tidal form factor data, extracted into a .csv file for vent fields from data presented in Haigh (2017) by Dr Ivan Haigh, were mapped for each vent field on the following scale: <0.25, for semidiurnal tides; 0.25 – 0.3 for areas where the tide varies between diurnal and semidiurnal; and >3 for diurnal (though no vent fields were found in locations with diurnal tides).

Tidal range

Tidal range data, extracted into a .csv file for vent fields from data presented in Haigh (2017) by Dr Ivan Haigh, were mapped for each vent field using Arcmap (ESRI, 2014).

Total organic carbon in sediments (TOC)

We downloaded TOC data in ASCII format as per the organic carbon content of sediments (calcite) described in Seiter et al. (2004a) and forming part of the global data compilation described in Seiter et al. (2004b). Using R (R Core Team, 2017), we rasterised these data using the 'raster' function of the 'raster' package (Hijmans, 2017) before extraction using function 'extract'.

Turbidity

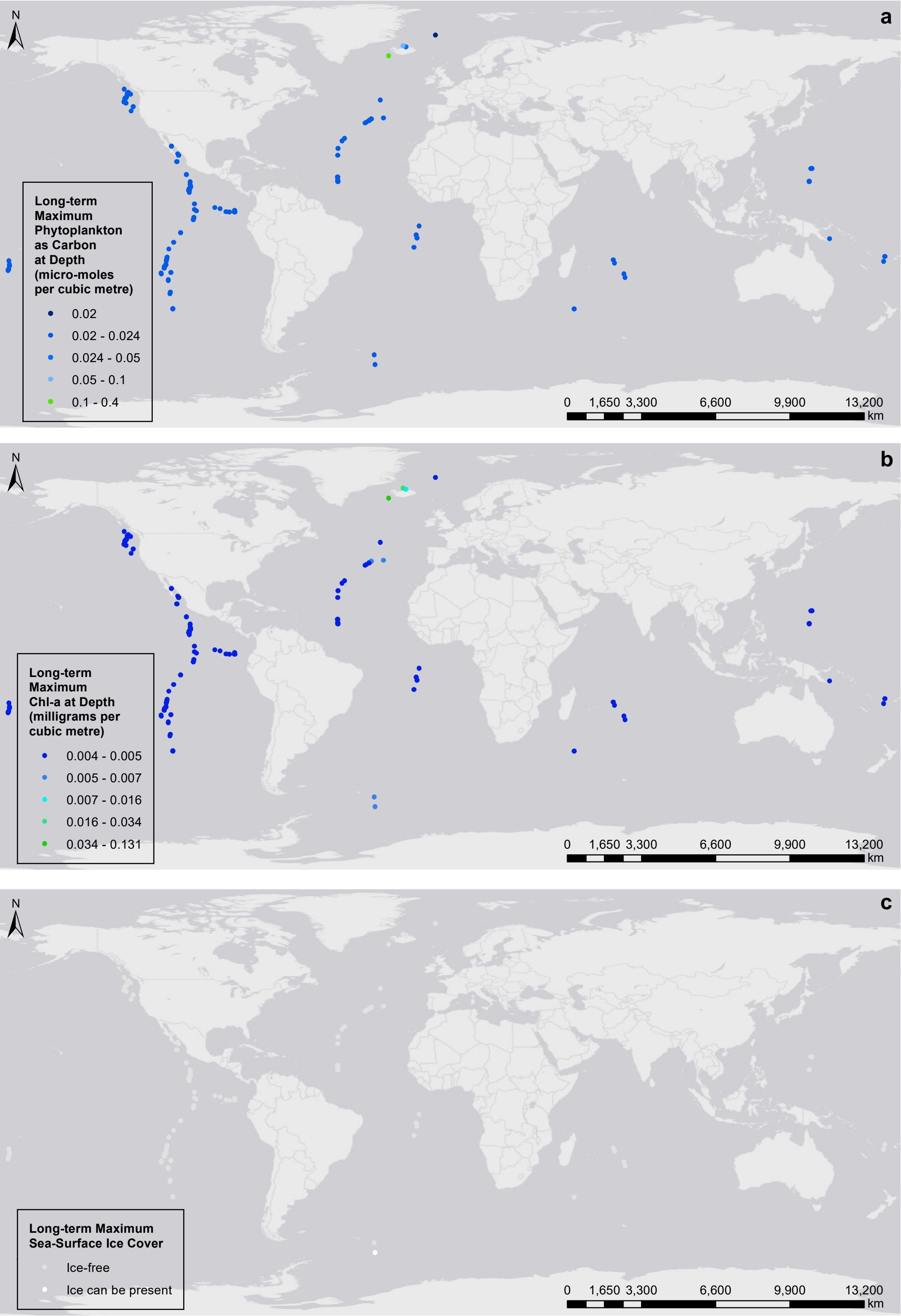
Turbidity data were available in NetCDF format from the NASA Goddard Space Flight Center, Ocean Biology Processing Group (2014) via oceandata.sci.gsfc.nasa.gov. We imported these as raster data using the 'raster' function of the 'raster' package (Hijmans, 2017) before extracting using the 'extract' function (Hijmans, 2017).

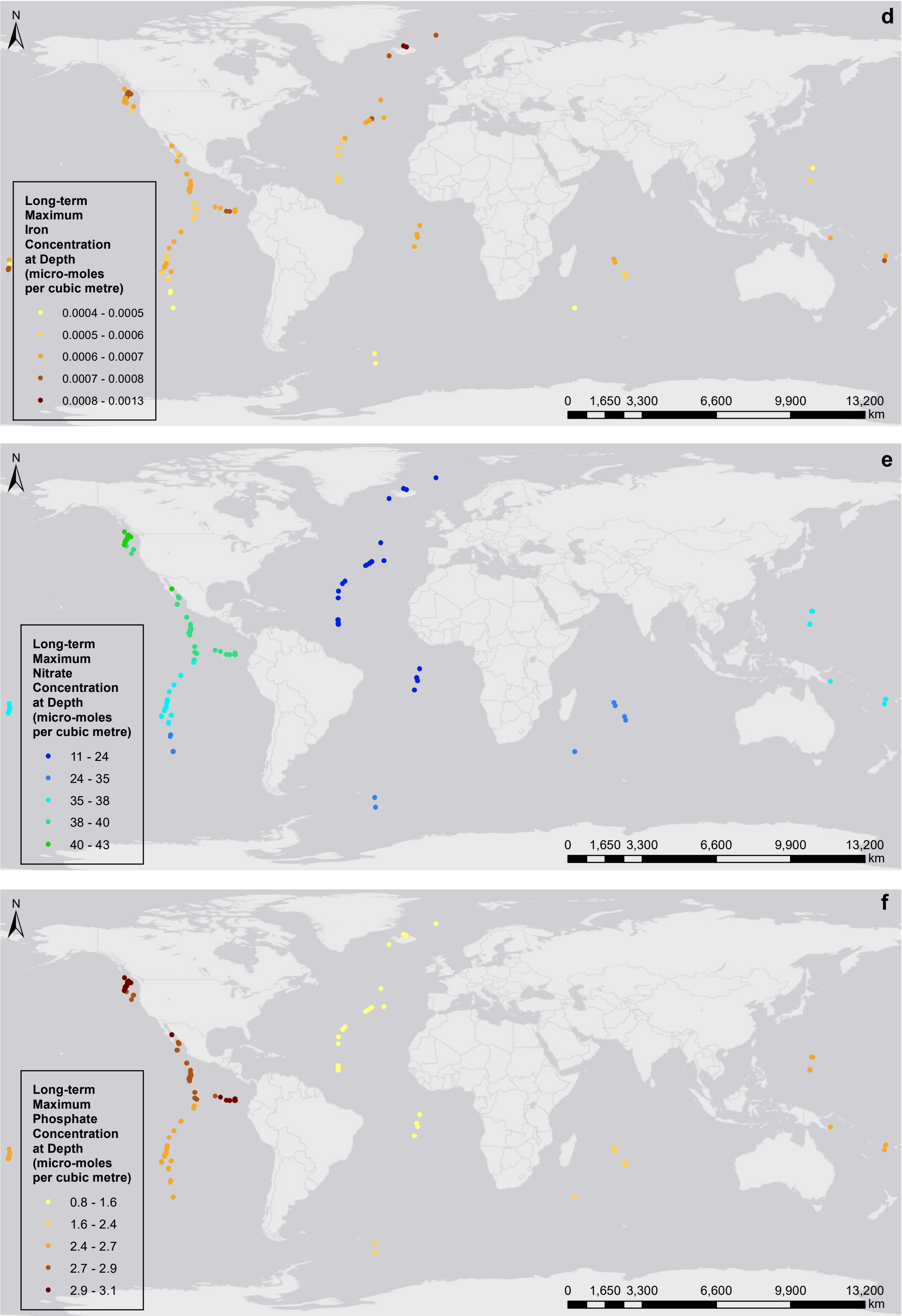
Environmental variables extracted from BioORACLE

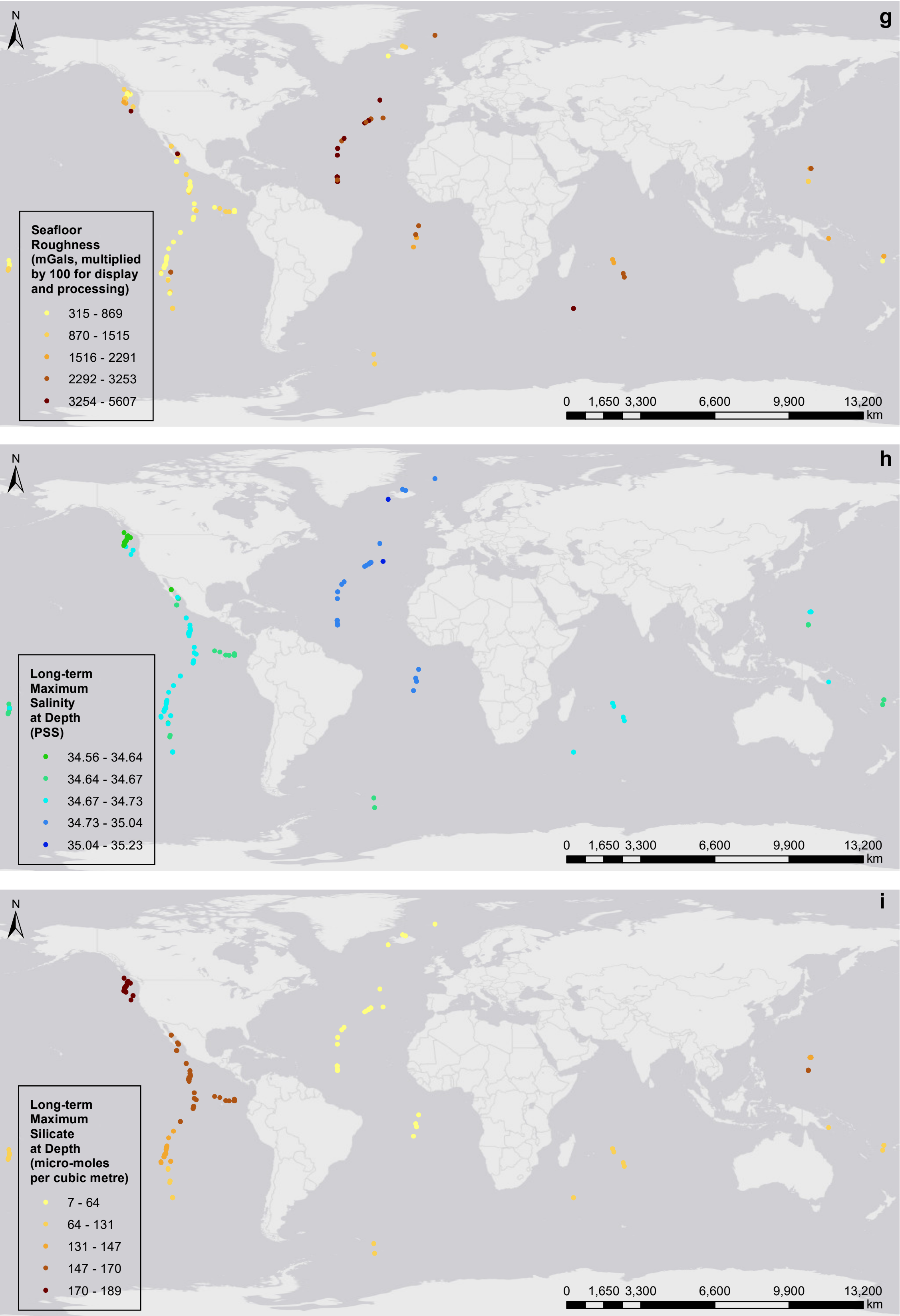
We pulled the following variables from the BioORACLE database (Tyberhein et al., 2012; Assis et al., 2017) using the 'sdmpredictors' R package (Bosch, 2017; R Core Team, 2017): chlorophyll-a concentration at the sea surface; maximum seafloor depth; average seafloor depth; long-term maximum mass concentration of chlorophyll in seawater at maximum depth; long-term maximum sea water velocity at maximum depth; long-term maximum mole concentration of dissolved oxygen (molecular) in seawater at maximum depth; long-term maximum mole concentration of dissolved iron in seawater at maximum depth; long-term maximum mole concentration of phosphate in seawater at maximum depth; long-term maximum mole concentration of nitrate in seawater at maximum depth; long-term maximum sea water temperature at maximum bottom depth; long-term maximum mole concentration of phytoplankton (as carbon) in seawater at maximum depth; long-term maximum mole concentration of silicate in seawater at maximum bottom depth; and long-term maximum sea ice concentration. We then extracted each variable for all vent-field locations using the 'raster' package (Hijmans, 2017).

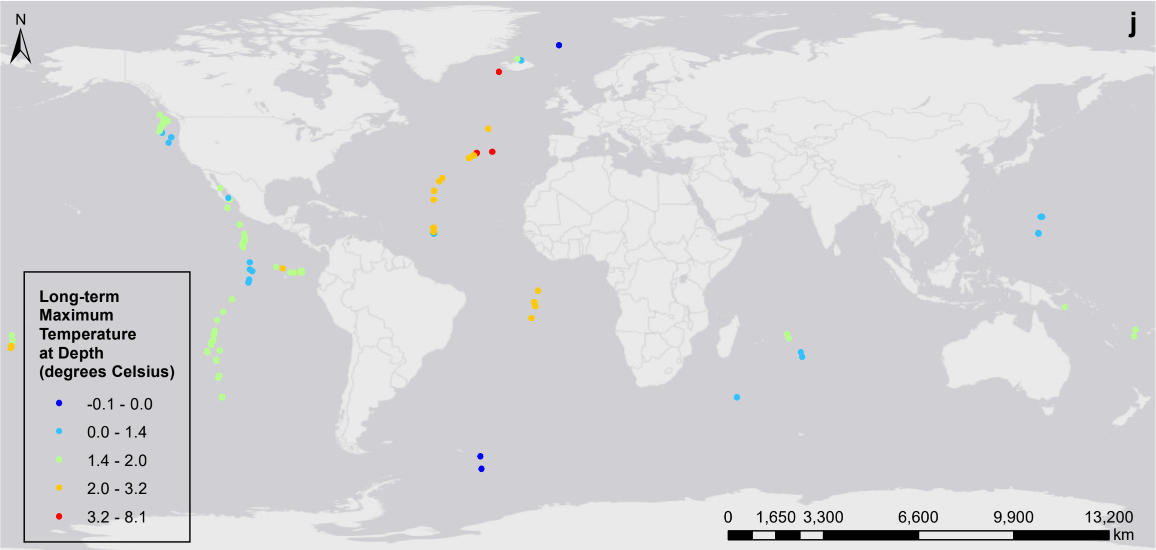
Appendix C.2

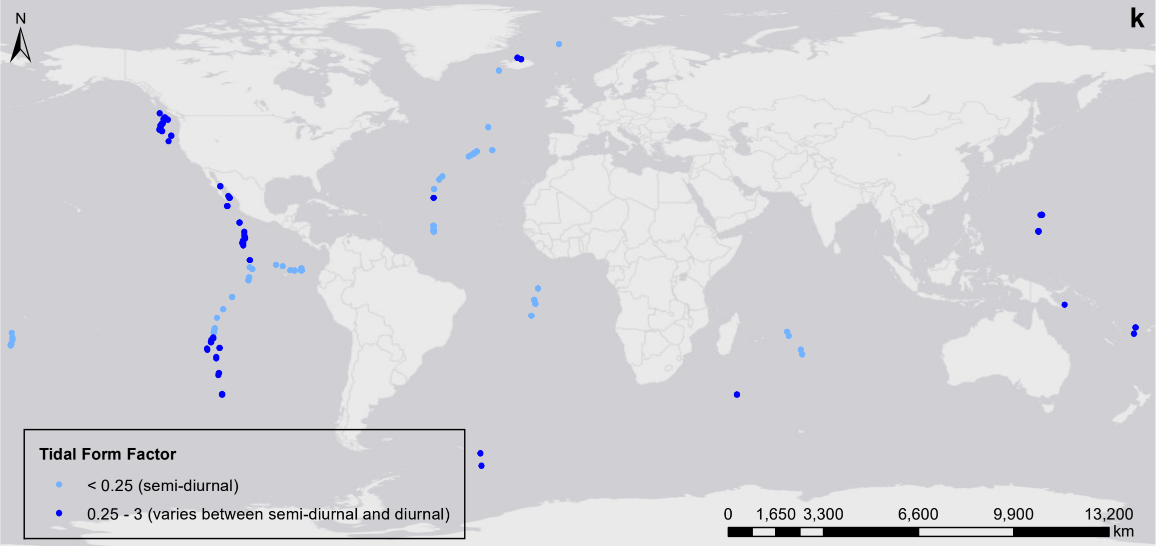
Figure 55 (overleaf): Global maps of environmental variables of potential influence on deep-sea hydrothermal-vent ecosystems. These maps supplement those shown in **Figure 27** as follows: a) long-term carbon in phytoplankton at depth (micromoles per cubic metre); b) long-term maximum chlorophyll at depth (milligrams per cubic metre); c) long-term maximum ice cover at the sea surface; d) long-term maximum iron concentration at depth (micromoles per cubic metre); e) long-term maximum nitrate concentration at depth (micromoles per cubic metre); f) long-term maximum phosphate concentration at depth (micromoles per cubic metre); g) seafloor roughness (mGals, multiplied by 100 for display and processing purposes); h) long-term maximum salinity at depth (PSS - practical salinity scale); i) long-term maximum silicate at depth (micromoles per cubic metre); j) long-term maximum temperature at depth (degrees Celsius); k) tidal form factor; l) turbidity (Kd); and m) names of the active, confirmed vent fields for which environmental data are extracted and presented in **Appendix C.5** (though note that not all field names can be presented).

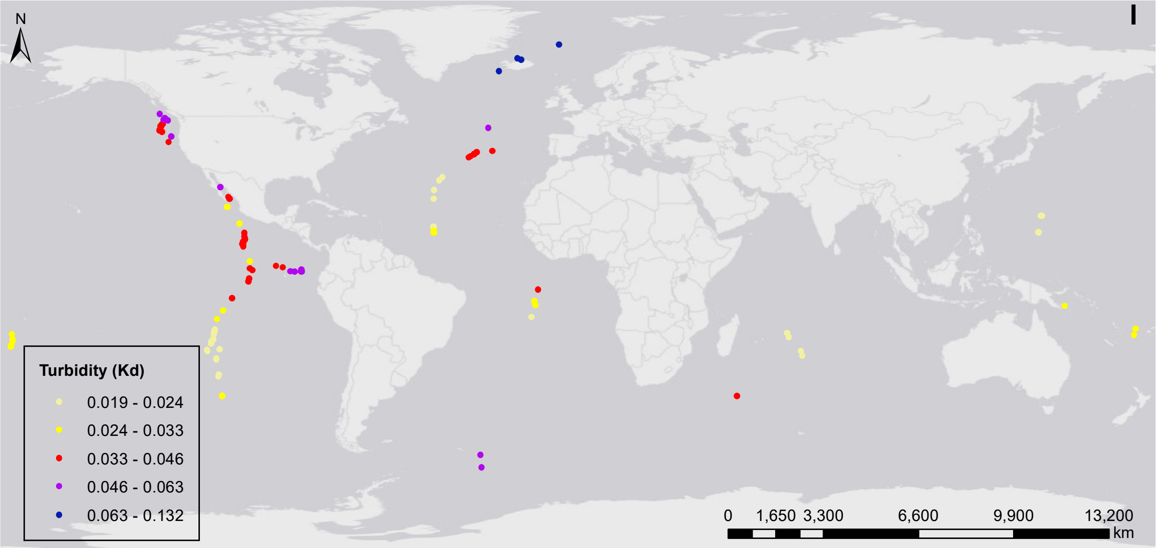

a
N
Long-term Maximum Phytoplankton as Carbon at Depth (micro-moles per cubic metre)
● 0.02
● 0.02 - 0.024
● 0.024 - 0.05
● 0.05 - 0.1
● 0.1 - 0.4
0 1,650 3,300 6,600 9,900 13,200 km
b
N
Long-term Maximum Chl-a at Depth (milligrams per cubic metre)
● 0.004 - 0.005
● 0.005 - 0.007
● 0.007 - 0.016
● 0.016 - 0.034
● 0.034 - 0.131
0 1,650 3,300 6,600 9,900 13,200 km
c
N
Long-term Maximum Sea-Surface Ice Cover
● Ice-free
● Ice can be present
0 1,650 3,300 6,600 9,900 13,200 km

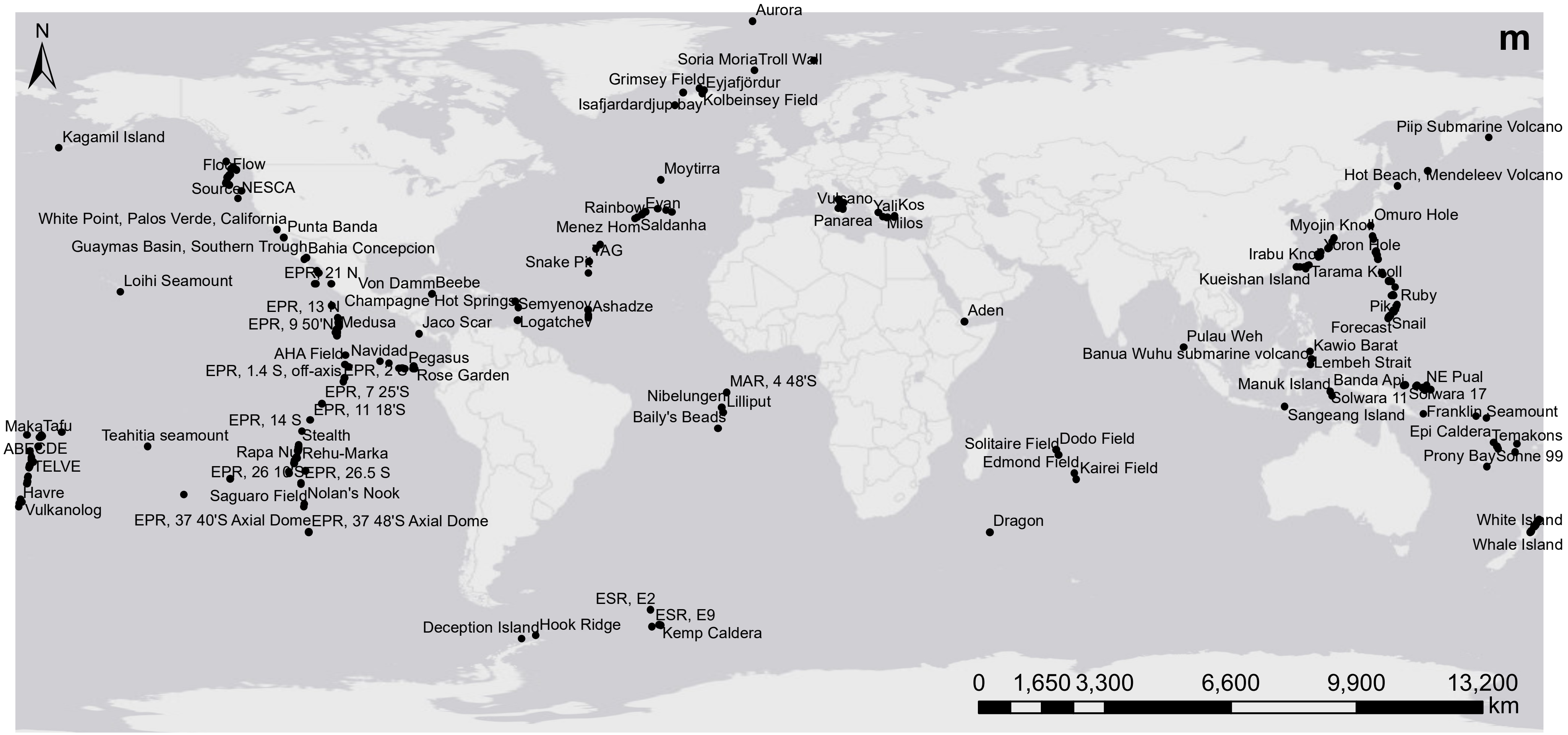

d
N
Long-term Maximum Iron Concentration at Depth (micro-moles per cubic metre)
● 0.0004 - 0.0005
● 0.0005 - 0.0006
● 0.0006 - 0.0007
● 0.0007 - 0.0008
● 0.0008 - 0.0013
0 1,650 3,300 6,600 9,900 13,200
km
e
N
Long-term Maximum Nitrate Concentration at Depth (micro-moles per cubic metre)
● 11 - 24
● 24 - 35
● 35 - 38
● 38 - 40
● 40 - 43
0 1,650 3,300 6,600 9,900 13,200
km
f
N
Long-term Maximum Phosphate Concentration at Depth (micro-moles per cubic metre)
● 0.8 - 1.6
● 1.6 - 2.4
● 2.4 - 2.7
● 2.7 - 2.9
● 2.9 - 3.1
0 1,650 3,300 6,600 9,900 13,200
km


g
N
Seafloor Roughness (mGals, multiplied by 100 for display and processing)
● 315 - 869
● 870 - 1515
● 1516 - 2291
● 2292 - 3253
● 3254 - 5607
0 1,650 3,300 6,600 9,900 13,200 km
h
N
Long-term Maximum Salinity at Depth (PSS)
● 34.56 - 34.64
● 34.64 - 34.67
● 34.67 - 34.73
● 34.73 - 35.04
● 35.04 - 35.23
0 1,650 3,300 6,600 9,900 13,200 km
i
N
Long-term Maximum Silicate at Depth (micro-moles per cubic metre)
● 7 - 64
● 64 - 131
● 131 - 147
● 147 - 170
● 170 - 189
0 1,650 3,300 6,600 9,900 13,200 km


N
j
Long-term Maximum Temperature at Depth (degrees Celsius)
-0.1 - 0.0
0.0 - 1.4
1.4 - 2.0
2.0 - 3.2
3.2 - 8.1
0 1,650 3,300 6,600 9,900 13,200
km


N
k
Tidal Form Factor
< 0.25 (semi-diurnal)
0.25 - 3 (varies between semi-diurnal and diurnal)
0 1,650 3,300 6,600 9,900 13,200
km


N
l
Turbidity (Kd)
0.019 - 0.024
0.024 - 0.033
0.033 - 0.046
0.046 - 0.063
0.063 - 0.132
0 1,650 3,300 6,600 9,900 13,200
km


m
N
Aurora
Soria Moria
Troll Wall
Grimsey Field
Eyjafjördur
Isafjardardjup bay
Kolbeinsey Field
Kagamil Island
Flo Flow
Source
NESCA
White Point, Palos Verde, California
Punta Banda
Guaymas Basin, Southern Trough
Bahia Concepcion
Loihi Seamount
EPR, 21 N
Von Damm
Beebe
Champagne Hot Springs
EPR, 13 N
EPR, 9 50'N
Medusa
Jaco Scar
AHA Field
Navidad
Pegasus
EPR, 1.4 S, off-axis
EPR, 2 S
Rose Garden
EPR, 7 25'S
EPR, 11 18'S
EPR, 14 S
Stealth
MakaTafu
Teahitia seamount
ABECDE
TELVE
Rapa Nui
Rehu-Marka
EPR, 26 10'S
EPR, 26.5 S
Havre
Vulkanolog
Saguaro Field
Nolan's Nook
EPR, 37 40'S Axial Dome
EPR, 37 48'S Axial Dome
Moytirra
Rainbow
Evan
Menez Hom
Saldanha
Snake Pit
TAG
Semyenov
Ashadze
Logatchev
MAR, 4 48'S
Nibelungen
Lilliput
Baily's Beads
Vulcano
Panarea
Yali
Kos
Milos
Aden
Solitaire Field
Dodo Field
Edmond Field
Kairei Field
Dragon
ESR, E2
ESR, E9
Kemp Caldera
Deception Island
Hook Ridge
Piip Submarine Volcano
Hot Beach, Mendeleev Volcano
Omuro Hole
Myojin Knoll
Yoron Hole
Irabu Knoll
Tarama Knoll
Kueishan Island
Ruby
Pika
Snail
Forecast
Pulau Weh
Banua Wuhu submarine volcano
Kawio Barat
Lembeh Strait
Manuk Island
Banda Api
NE Pual
Solwara 17
Solwara 11
Sangeang Island
Franklin Seamount
Epi Caldera
Temakons
Prony Bay
Sonne 99
White Island
Whale Island
0
1,650
3,300
6,600
9,900
13,200
km

Appendix C.3

Clusters based on environmental similarity (determined using the Partitioning Around Medoids approach and plotted in **Figure 28**), with associated location and tectonic-setting information. Here, we selected 11 coherent clusters. Clusters are coloured in this table as per the cluster colours in **Figure 28**. Tectonic settings are abbreviated according to the InterRidge Vents Database (version 3.4, Beaulieu, 2015), with BASC meaning back-arc spreading centre and MOR an abbreviation of mid-ocean ridge. In Region: N EPR refers to the North East Pacific Rise; S EPR is the South East Pacific Rise; JdF Ridge is the Juan de Fuca Ridge; N MAR refers to the northern Mid-Atlantic Ridge and S MAR the southern portion; CIR is the Central Indian Ridge; and SWIR is the South West Indian Ridge. After the table, we provide: a) a field-labelled copy of **Figure 28**, for reference, and b) a silhouette plot. Negative silhouette widths suggest that we should have less confidence in cluster assignments for the 6 fields marked with an asterisk (*) in the table below. We note a possible alternative, neighbouring cluster in superscript for these clusters.

Cluster	Vent Field	Ocean	Tectonic Setting	Region
1	13 N Ridge Site	N. Pacific	BASC	Mariana Trough
1	Alice Springs Field	N. Pacific	BASC	Mariana Trough
1	Mariana Mounds	N. Pacific	BASC	Mariana Trough
1	Mariana Trough, unnamed	N. Pacific	BASC	Mariana Trough
1	Pika	N. Pacific	BASC	Mariana Trough
1	Snail	N. Pacific	BASC	Mariana Trough
1	ESR, E2 ^{*9}	S. Atlantic	BASC	East Scotia Ridge
1	Franklin Seamount ^{*4}	S. Pacific	BASC	Woodlark Basin
1	EPR, 37 40'S Axial Dome ^{*4}	S. Pacific	MOR	Pacific-Antarctic Ridge
1	EPR, 37 48'S Axial Dome ^{*4}	S. Pacific	MOR	Pacific-Antarctic Ridge
2	ABE	S. Pacific	BASC	Lau Basin
2	CDE	S. Pacific	BASC	Lau Basin
2	CLSC, A3	S. Pacific	BASC	Lau Basin
2	Hine Hina	S. Pacific	BASC	Lau Basin
2	Kilo Moana	S. Pacific	BASC	Lau Basin
2	Mariner	S. Pacific	BASC	Lau Basin
2	Misiteli	S. Pacific	BASC	Lau Basin

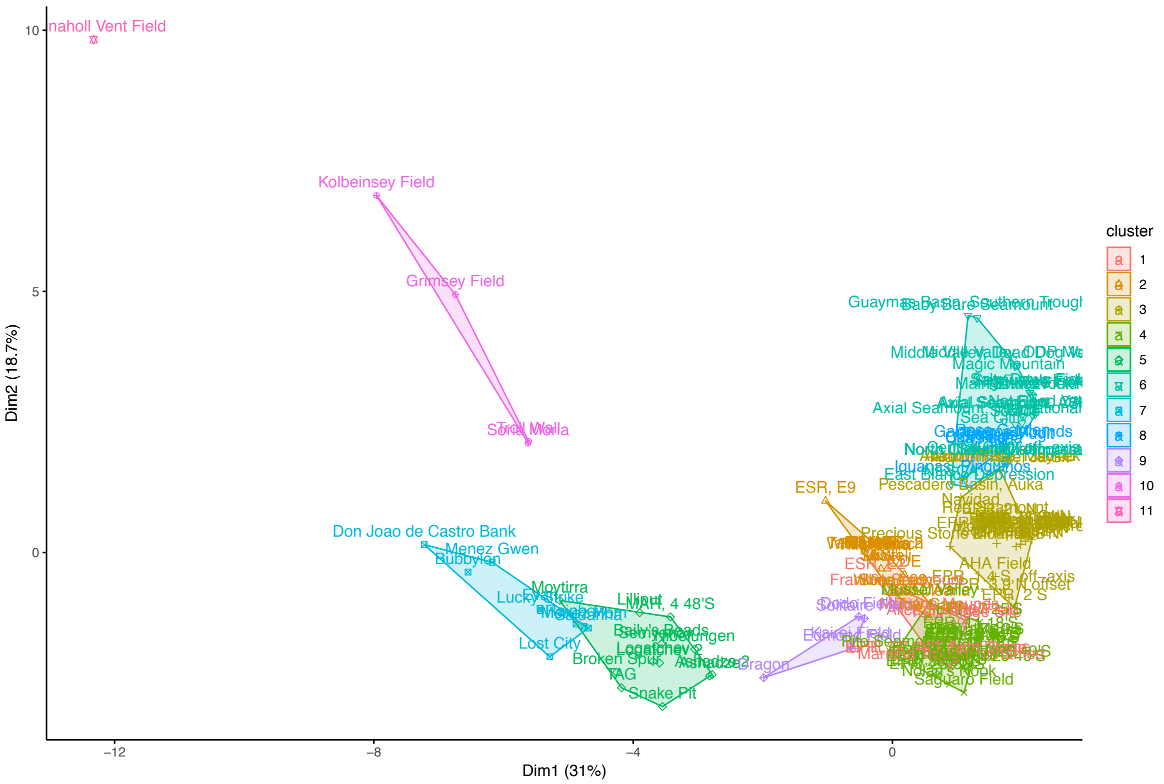
2	Si'iSi'i	S. Pacific	BASC	Lau Basin
2	Tahi Moana 2	S. Pacific	BASC	Lau Basin
2	TELVE	S. Pacific	BASC	Lau Basin
2	Tow Cam	S. Pacific	BASC	Lau Basin
2	Tu'i Malila	S. Pacific	BASC	Lau Basin
2	Vai Lili	S. Pacific	BASC	Lau Basin
2	White Church	S. Pacific	BASC	Lau Basin
2	Sonne 99	S. Pacific	BASC	North Fiji Basin
2	White Lady	S. Pacific	BASC	North Fiji Basin
2	ESR, E9 *1	Southern	BASC	East Scotia Ridge
3	Navidad *8	N. Pacific	MOR	Galapagos Rift
3	Precious Stone Mountain	N. Pacific	MOR	Galapagos Rift
3	Alarcon Rise, Ja Sit	N. Pacific	MOR	Gulf of California
3	Alarcon Rise, Meyibo	N. Pacific	MOR	Gulf of California
3	Alarcon Rise, Tzab-ek	N. Pacific	MOR	Gulf of California
3	Pescadero Basin, Auka	N. Pacific	MOR	Gulf of California
3	AHA Field	N. Pacific	MOR	N EPR
3	EPR, 10 02'N	N. Pacific	MOR	N EPR
3	EPR, 10 44.6'N	N. Pacific	MOR	N EPR
3	EPR, 11 17'N	N. Pacific	MOR	N EPR
3	EPR, 11 24'N	N. Pacific	MOR	N EPR
3	EPR, 11 42'N	N. Pacific	MOR	N EPR
3	EPR, 13 N	N. Pacific	MOR	N EPR
3	EPR, 13 N, Marginal High	N. Pacific	MOR	N EPR
3	EPR, 21 N	N. Pacific	MOR	N EPR
3	EPR, 3.9 N offset	N. Pacific	MOR	N EPR
3	EPR, 8 38'N	N. Pacific	MOR	N EPR
3	EPR, 9 17'N	N. Pacific	MOR	N EPR
3	EPR, 9 30'N	N. Pacific	MOR	N EPR
3	EPR, 9 33'N	N. Pacific	MOR	N EPR
3	EPR, 9 40'N	N. Pacific	MOR	N EPR
3	EPR, 9 47'N	N. Pacific	MOR	N EPR
3	EPR, 9 50'N	N. Pacific	MOR	N EPR
3	Feather Duster	N. Pacific	MOR	N EPR

3	Medusa	N. Pacific	MOR	N EPR
3	Mounds and Microbes	N. Pacific	MOR	N EPR
3	Red Seamount	N. Pacific	MOR	N EPR
3	Teotihuacan	N. Pacific	MOR	N EPR
3	EPR, 1.4 S, off-axis	S. Pacific	MOR	S EPR
3	EPR, 2 S	S. Pacific	MOR	S EPR
4	Mussel Valley	S. Pacific	BASC	North Fiji Basin
4	Animal Farm	S. Pacific	MOR	S EPR
4	EPR, 11 18'S	S. Pacific	MOR	S EPR
4	EPR, 14 S	S. Pacific	MOR	S EPR
4	EPR, 17 12'S	S. Pacific	MOR	S EPR
4	EPR, 17 34'S	S. Pacific	MOR	S EPR
4	EPR, 17 44'S	S. Pacific	MOR	S EPR
4	EPR, 18 10'S	S. Pacific	MOR	S EPR
4	EPR, 18 15'S	S. Pacific	MOR	S EPR
4	EPR, 18 26'S	S. Pacific	MOR	S EPR
4	EPR, 18 32'S	S. Pacific	MOR	S EPR
4	EPR, 20 06'S	S. Pacific	MOR	S EPR
4	EPR, 21 25'S	S. Pacific	MOR	S EPR
4	EPR, 23 30'S	S. Pacific	MOR	S EPR
4	EPR, 23 50'S	S. Pacific	MOR	S EPR
4	EPR, 26 10'S	S. Pacific	MOR	S EPR
4	EPR, 26.5 S	S. Pacific	MOR	S EPR
4	EPR, 7 25'S	S. Pacific	MOR	S EPR
4	EPR, Ridge 1, 20 40'S	S. Pacific	MOR	S EPR
4	EPR, Ridge 3, 20 40'S	S. Pacific	MOR	S EPR
4	Nolan's Nook	S. Pacific	MOR	S EPR
4	Pito Seamount	S. Pacific	MOR	S EPR
4	Rapa Nui	S. Pacific	MOR	S EPR
4	Rehu-Marka	S. Pacific	MOR	S EPR
4	Saguaro Field	S. Pacific	MOR	S EPR
4	Stealth	S. Pacific	MOR	S EPR
5	Ashadze	N. Atlantic	MOR	N MAR
5	Ashadze 2	N. Atlantic	MOR	N MAR
5	Broken Spur	N. Atlantic	MOR	N MAR
5	Logatchev	N. Atlantic	MOR	N MAR
5	Logatchev 2	N. Atlantic	MOR	N MAR
5	Moytirra	N. Atlantic	MOR	N MAR
5	Semyenov	N. Atlantic	MOR	N MAR

5	Snake Pit	N. Atlantic	MOR	N MAR
5	TAG	N. Atlantic	MOR	N MAR
5	Baily's Beads	S. Atlantic	MOR	S MAR
5	Lilliput	S. Atlantic	MOR	S MAR
5	MAR, 4 48'S	S. Atlantic	MOR	S MAR
5	Nibelungen	S. Atlantic	MOR	S MAR
6	Magic Mountain	N. Pacific	MOR	Explorer Ridge
6	NESCA	N. Pacific	MOR	Gorda Ridge
6	Sea Cliff	N. Pacific	MOR	Gorda Ridge
6	Guaymas Basin, Southern Trough	N. Pacific	MOR	Gulf of California
6	Axial Seamount, ASHES	N. Pacific	MOR	JdF Ridge
6	Axial Seamount, CASM	N. Pacific	MOR	JdF Ridge
6	Axial Seamount, International District	N. Pacific	MOR	JdF Ridge
6	Baby Bare Seamount	N. Pacific	MOR	JdF Ridge
6	Central Cleft, off-axis	N. Pacific	MOR	JdF Ridge
6	East Blanco Depression	N. Pacific	MOR	JdF Ridge
6	Floc	N. Pacific	MOR	JdF Ridge
6	Flow	N. Pacific	MOR	JdF Ridge
6	High-Rise Field	N. Pacific	MOR	JdF Ridge
6	Main Endeavour Field	N. Pacific	MOR	JdF Ridge
6	Middle Valley, Dead Dog Vent Field	N. Pacific	MOR	JdF Ridge
6	Middle Valley, ODP Mound	N. Pacific	MOR	JdF Ridge
6	Mothra Field	N. Pacific	MOR	JdF Ridge
6	North Cleft, high temperature	N. Pacific	MOR	JdF Ridge
6	North Cleft, low temperature	N. Pacific	MOR	JdF Ridge
6	Not Dead Yet	N. Pacific	MOR	JdF Ridge
6	Salty Dawg Field	N. Pacific	MOR	JdF Ridge
6	Sasquatch Field	N. Pacific	MOR	JdF Ridge
6	Source	N. Pacific	MOR	JdF Ridge
6	South Cleft	N. Pacific	MOR	JdF Ridge
7	Bubbylon	N. Atlantic	MOR	N MAR
7	Evan	N. Atlantic	MOR	N MAR
7	Lost City	N. Atlantic	MOR	N MAR
7	Lucky Strike	N. Atlantic	MOR	N MAR

7	Menez Gwen	N. Atlantic	MOR	N MAR
7	Menez Hom	N. Atlantic	MOR	N MAR
7	Rainbow	N. Atlantic	MOR	N MAR
7	Saldanha	N. Atlantic	MOR	N MAR
7	Don Joao de Castro Bank	N. Atlantic	MOR	Terceira Rift
8	Calyfield	N. Pacific	MOR	Galapagos Rift
8	Galapagos Mounds	N. Pacific	MOR	Galapagos Rift
8	Iguanas-Pinguinos	N. Pacific	MOR	Galapagos Rift
8	Pegasus	N. Pacific	MOR	Galapagos Rift
8	Rose Garden	N. Pacific	MOR	Galapagos Rift
8	Tempus Fugit	N. Pacific	MOR	Galapagos Rift
8	Uka Pacha	N. Pacific	MOR	Galapagos Rift
9	Dodo Field	Indian	MOR	CIR
9	Edmond Field	Indian	MOR	CIR
9	Kairei Field	Indian	MOR	CIR
9	Solitaire Field	Indian	MOR	CIR
9	Dragon	Indian	MOR	SWIR
10	Grimsey Field	Arctic	MOR	Kolbeinsey Ridge
10	Kolbeinsey Field	Arctic	MOR	Kolbeinsey Ridge
10	Soria Moria	Arctic	MOR	Mohns Ridge
10	Troll Wall	Arctic	MOR	Mohns Ridge
11	Steinaholl Vent Field	N. Atlantic	MOR	Reykjanes Ridge

a)



cluster
1
2
3
4
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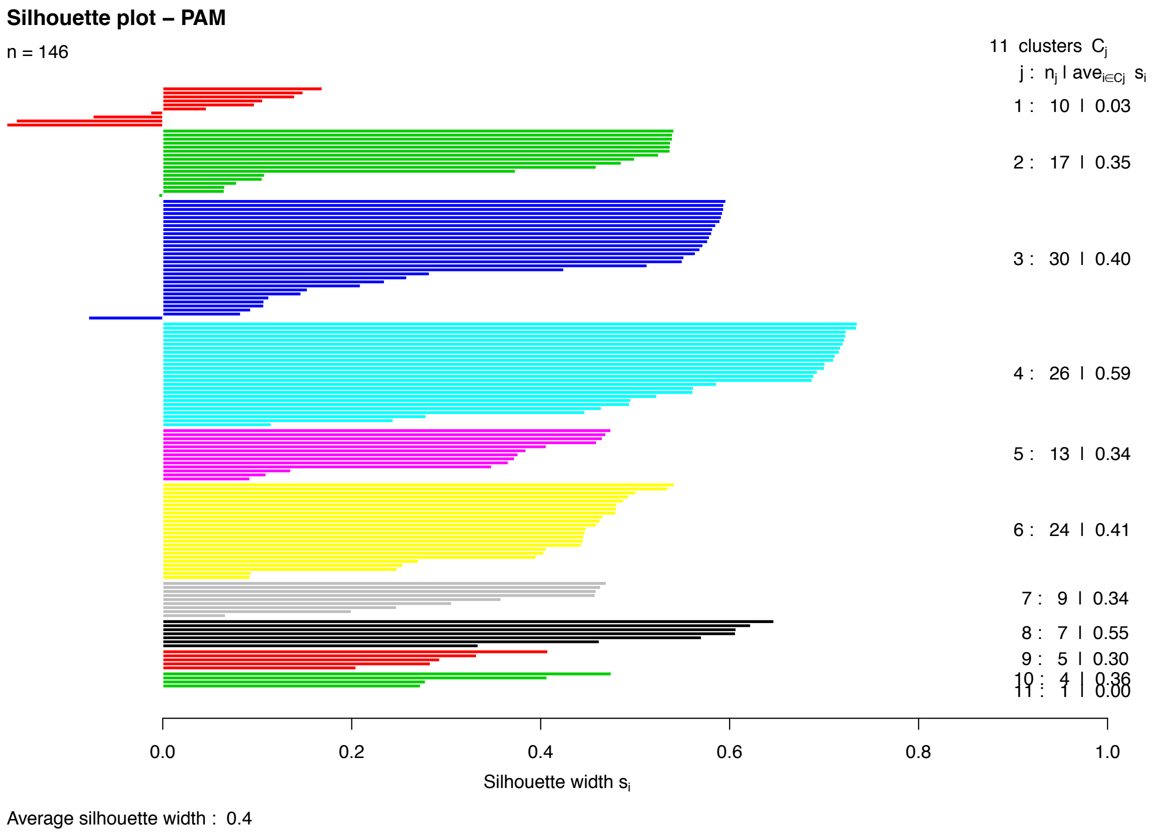
11
naholl Vent Field
Kolbeinsey Field
Grimsey Field
Soria Moria
Troll Wall
Don Joao de Castro Bank
Menez Gwen
Bubbylon
Lucky Strike
Moytirra
Lost City
Lilliput
MAR, 4 48'S
Broken Spur
TAG
Snake Pit
Logatchev
Ashadze 2
Dragon
Guaymas Basin, Southern Trough
Baby Bare Seamount
Middle Valley
Magic Mountain
Axial Seamount
Sea Cliff
Pescadero Basin, Auka
ESR, E9
East Diamante
Navidad
Precious Stone
AHA Field
EPR, 4 S, off-axis
Saguaro Field
Kairei Field
Solitaire Field
Dodo Field
Mussel Valley
Nolan's Rock
Dim2 (18.7%)
Dim1 (31%)
10
5
0
−12
−8
−4
0

b)



Silhouette plot – PAM
n = 146
11 clusters C_j
j : n_j | $ave_{i \in Cj}$ s_i
1 : 10 | 0.03
2 : 17 | 0.35
3 : 30 | 0.40
4 : 26 | 0.59
5 : 13 | 0.34
6 : 24 | 0.41
7 : 9 | 0.34
8 : 7 | 0.55
9 : 5 | 0.30
10 : 4 | 0.36
11 : 1 | 0.00
0.0
0.2
0.4
0.6
0.8
1.0
Silhouette width s_i
Average silhouette width : 0.4

Appendix C.4

Clusters based on environmental similarity (according to a hierarchical cluster analysis using the 'Ward D2' agglomeration method, plotted in **Figure 29**), with associated location and tectonic-setting information. Clusters are coloured in this table as per the cluster colours in **Figure 29**. Tectonic settings are abbreviated according to the InterRidge Vents Database (version 3.4, Beaulieu, 2015), with BASC meaning back-arc spreading centre and MOR an abbreviation of mid-ocean ridge. In Region: N EPR refers to the North East Pacific Rise; S EPR is the South East Pacific Rise; JdF Ridge is the Juan de Fuca Ridge; N MAR refers to the northern Mid-Atlantic Ridge and S MAR the southern portion; CIR is the Central Indian Ridge; and SWIR is the South West Indian Ridge. Based on a silhouette-width plot (presented below the table), we have lower confidence in the clusters assigned to two fields, as marked with an asterisk (*) in the table below; the alternative, neighbouring cluster is given in superscript.

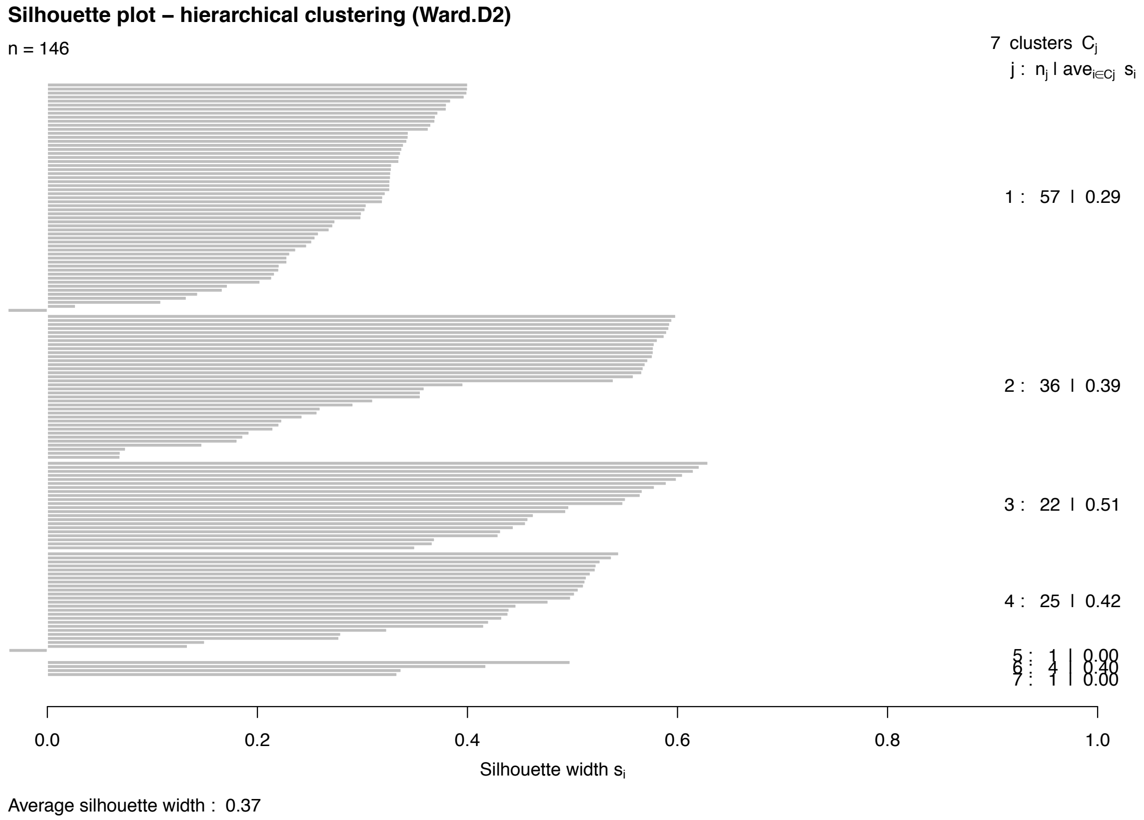
Cluster	Vent Field	Ocean	Tectonic Setting	Region
1	Dodo Field	Indian	MOR	CIR
1	Edmond Field	Indian	MOR	CIR
1	Kairei Field	Indian	MOR	CIR
1	Solitaire Field	Indian	MOR	CIR
1	Dragon	Indian	MOR	SWIR
1	13 N Ridge Site	N. Pacific	BASC	Mariana Trough
1	Alice Springs Field	N. Pacific	BASC	Mariana Trough
1	Mariana Mounds	N. Pacific	BASC	Mariana Trough
1	Mariana Trough, unnamed	N. Pacific	BASC	Mariana Trough
1	Pika	N. Pacific	BASC	Mariana Trough
1	Snail	N. Pacific	BASC	Mariana Trough
1	ESR, E2	S. Atlantic	BASC	East Scotia Ridge
1	ABE	S. Pacific	BASC	Lau Basin
1	CDE	S. Pacific	BASC	Lau Basin
1	CLSC, A3	S. Pacific	BASC	Lau Basin
1	Hine Hina	S. Pacific	BASC	Lau Basin
1	Kilo Moana	S. Pacific	BASC	Lau Basin
1	Mariner	S. Pacific	BASC	Lau Basin
1	Misiteli	S. Pacific	BASC	Lau Basin
1	Si'iSi'i	S. Pacific	BASC	Lau Basin
1	Tahi Moana 2	S. Pacific	BASC	Lau Basin
1	TELVE	S. Pacific	BASC	Lau Basin
1	Tow Cam	S. Pacific	BASC	Lau Basin
1	Tu'i Malila	S. Pacific	BASC	Lau Basin

1	Vai Lili	S. Pacific	BASC	Lau Basin
1	White Church	S. Pacific	BASC	Lau Basin
1	Mussel Valley	S. Pacific	BASC	North Fiji Basin
1	Sonne 99	S. Pacific	BASC	North Fiji Basin
1	White Lady	S. Pacific	BASC	North Fiji Basin
1	Franklin Seamount	S. Pacific	BASC	Woodlark Basin
1	EPR, 37 40'S Axial Dome	S. Pacific	MOR	Pacific-Antarctic Ridge
1	EPR, 37 48'S Axial Dome	S. Pacific	MOR	Pacific-Antarctic Ridge
1	Animal Farm	S. Pacific	MOR	S EPR
1	EPR, 11 18'S	S. Pacific	MOR	S EPR
1	EPR, 14 S	S. Pacific	MOR	S EPR
1	EPR, 17 12'S	S. Pacific	MOR	S EPR
1	EPR, 17 34'S	S. Pacific	MOR	S EPR
1	EPR, 17 44'S	S. Pacific	MOR	S EPR
1	EPR, 18 10'S	S. Pacific	MOR	S EPR
1	EPR, 18 15'S	S. Pacific	MOR	S EPR
1	EPR, 18 26'S	S. Pacific	MOR	S EPR
1	EPR, 18 32'S	S. Pacific	MOR	S EPR
1	EPR, 20 06'S	S. Pacific	MOR	S EPR
1	EPR, 21 25'S	S. Pacific	MOR	S EPR
1	EPR, 23 30'S	S. Pacific	MOR	S EPR
1	EPR, 23 50'S	S. Pacific	MOR	S EPR
1	EPR, 26 10'S	S. Pacific	MOR	S EPR
1	EPR, 26.5 S	S. Pacific	MOR	S EPR
1	EPR, 7 25'S [*2]	S. Pacific	MOR	S EPR
1	EPR, Ridge 1, 20 40'S	S. Pacific	MOR	S EPR
1	EPR, Ridge 3, 20 40'S	S. Pacific	MOR	S EPR
1	Nolan's Nook	S. Pacific	MOR	S EPR
1	Pito Seamount	S. Pacific	MOR	S EPR
1	Rapa Nui	S. Pacific	MOR	S EPR
1	Rehu-Marka	S. Pacific	MOR	S EPR
1	Saguaro Field	S. Pacific	MOR	S EPR
1	Stealth	S. Pacific	MOR	S EPR
2	Calyfield	N. Pacific	MOR	Galapagos Rift
2	Galapagos Mounds	N. Pacific	MOR	Galapagos Rift
2	Iguanas-Pinguinos	N. Pacific	MOR	Galapagos Rift
2	Navidad	N. Pacific	MOR	Galapagos Rift
2	Pegasus	N. Pacific	MOR	Galapagos Rift
2	Precious Stone Mountain	N. Pacific	MOR	Galapagos Rift

2	Rose Garden	N. Pacific	MOR	Galapagos Rift
2	Tempus Fugit	N. Pacific	MOR	Galapagos Rift
2	Uka Pacha	N. Pacific	MOR	Galapagos Rift
2	Alarcon Rise, Ja Sit	N. Pacific	MOR	Gulf of California
2	Alarcon Rise, Meyibo	N. Pacific	MOR	Gulf of California
2	Alarcon Rise, Tzab-ek	N. Pacific	MOR	Gulf of California
2	AHA Field	N. Pacific	MOR	N EPR
2	EPR, 10 02'N	N. Pacific	MOR	N EPR
2	EPR, 10 44.6'N	N. Pacific	MOR	N EPR
2	EPR, 11 17'N	N. Pacific	MOR	N EPR
2	EPR, 11 24'N	N. Pacific	MOR	N EPR
2	EPR, 11 42'N	N. Pacific	MOR	N EPR
2	EPR, 13 N	N. Pacific	MOR	N EPR
2	EPR, 13 N, Marginal High	N. Pacific	MOR	N EPR
2	EPR, 21 N	N. Pacific	MOR	N EPR
2	EPR, 3.9 N offset	N. Pacific	MOR	N EPR
2	EPR, 8 38'N	N. Pacific	MOR	N EPR
2	EPR, 9 17'N	N. Pacific	MOR	N EPR
2	EPR, 9 30'N	N. Pacific	MOR	N EPR
2	EPR, 9 33'N	N. Pacific	MOR	N EPR
2	EPR, 9 40'N	N. Pacific	MOR	N EPR
2	EPR, 9 47'N	N. Pacific	MOR	N EPR
2	EPR, 9 50'N	N. Pacific	MOR	N EPR
2	Feather Duster	N. Pacific	MOR	N EPR
2	Medusa	N. Pacific	MOR	N EPR
2	Mounds and Microbes	N. Pacific	MOR	N EPR
2	Red Seamount	N. Pacific	MOR	N EPR
2	Teotihuacan	N. Pacific	MOR	N EPR
2	EPR, 1.4 S, off-axis	S. Pacific	MOR	S EPR
2	EPR, 2 S	S. Pacific	MOR	S EPR
3	Ashadze	N. Atlantic	MOR	N MAR
3	Ashadze 2	N. Atlantic	MOR	N MAR
3	Broken Spur	N. Atlantic	MOR	N MAR
3	Bubbylon	N. Atlantic	MOR	N MAR
3	Evan	N. Atlantic	MOR	N MAR
3	Logatchev	N. Atlantic	MOR	N MAR
3	Logatchev 2	N. Atlantic	MOR	N MAR
3	Lost City	N. Atlantic	MOR	N MAR
3	Lucky Strike	N. Atlantic	MOR	N MAR

3	Menez Gwen	N. Atlantic	MOR	N MAR
3	Menez Hom	N. Atlantic	MOR	N MAR
3	Moytirra	N. Atlantic	MOR	N MAR
3	Rainbow	N. Atlantic	MOR	N MAR
3	Saldanha	N. Atlantic	MOR	N MAR
3	Semyenov	N. Atlantic	MOR	N MAR
3	Snake Pit	N. Atlantic	MOR	N MAR
3	TAG	N. Atlantic	MOR	N MAR
3	Don Joao de Castro Bank	N. Atlantic	MOR	Terceira Rift
3	Baily's Beads	S. Atlantic	MOR	S MAR
3	Lilliput	S. Atlantic	MOR	S MAR
3	MAR, 4 48'S	S. Atlantic	MOR	S MAR
3	Nibelungen	S. Atlantic	MOR	S MAR
4	Magic Mountain	N. Pacific	MOR	Explorer Ridge
4	NESCA	N. Pacific	MOR	Gorda Ridge
4	Sea Cliff	N. Pacific	MOR	Gorda Ridge
4	Guaymas Basin, Southern Trough	N. Pacific	MOR	Gulf of California
4	Pescadero Basin, Auka *2	N. Pacific	MOR	Gulf of California
4	Axial Seamount, ASHES	N. Pacific	MOR	JdF Ridge
4	Axial Seamount, CASM	N. Pacific	MOR	JdF Ridge
4	Axial Seamount, International District	N. Pacific	MOR	JdF Ridge
4	Baby Bare Seamount	N. Pacific	MOR	JdF Ridge
4	Central Cleft, off-axis	N. Pacific	MOR	JdF Ridge
4	East Blanco Depression	N. Pacific	MOR	JdF Ridge
4	Floc	N. Pacific	MOR	JdF Ridge
4	Flow	N. Pacific	MOR	JdF Ridge
4	High-Rise Field	N. Pacific	MOR	JdF Ridge
4	Main Endeavour Field	N. Pacific	MOR	JdF Ridge
4	Middle Valley, Dead Dog Vent Field	N. Pacific	MOR	JdF Ridge
4	Middle Valley, ODP Mound	N. Pacific	MOR	JdF Ridge
4	Mothra Field	N. Pacific	MOR	JdF Ridge
4	North Cleft, high temperature	N. Pacific	MOR	JdF Ridge
4	North Cleft, low temperature	N. Pacific	MOR	JdF Ridge
4	Not Dead Yet	N. Pacific	MOR	JdF Ridge
4	Salty Dawg Field	N. Pacific	MOR	JdF Ridge
4	Sasquatch Field	N. Pacific	MOR	JdF Ridge
4	Source	N. Pacific	MOR	JdF Ridge

4	South Cleft	N. Pacific	MOR	JdF Ridge
5	ESR, E9	Southern	BASC	East Scotia Ridge
6	Grimsey Field	Arctic	MOR	Kolbeinsey Ridge
6	Kolbeinsey Field	Arctic	MOR	Kolbeinsey Ridge
6	Soria Moria	Arctic	MOR	Mohns Ridge
6	Troll Wall	Arctic	MOR	Mohns Ridge
7	Steinaholl Vent Field	N. Atlantic	MOR	Reykjanes Ridge



Appendix C.5

This appendix is provided as a separate Microsoft Excel file (**Table C.5.1**) on the USB storage device provided with this thesis and contains the environmental data extracted for each vent field.

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Appendix D Supporting Information to Accompany Chapter Five

Appendix D.1

Abbreviations used in figures and tables and support for the environmental variables included in our analyses in Chapter Five.

Table 21: Abbreviations used in figures and tables.

Abbreviation	Region Name
NFiji	North Fiji Basin
JdF	Juan de Fuca Ridge
Lau	Lau Basin
Mariana	Mariana Arc
Manus	Manus Basin
S.MAR	South Mid-Atlantic Ridge
ESR	East Scotia Ridge
N.MAR	North Mid-Atlantic Ridge
CIR	Central Indian Ridge
SEPR	South East Pacific Rise
NEPR	North East Pacific Rise
GoC	Gulf of California
Okinawa	Okinawa Trough
Kermadec	Kermadec Arc
MohnsRidge	Mohns Ridge
SWIR	South West Indian Ridge

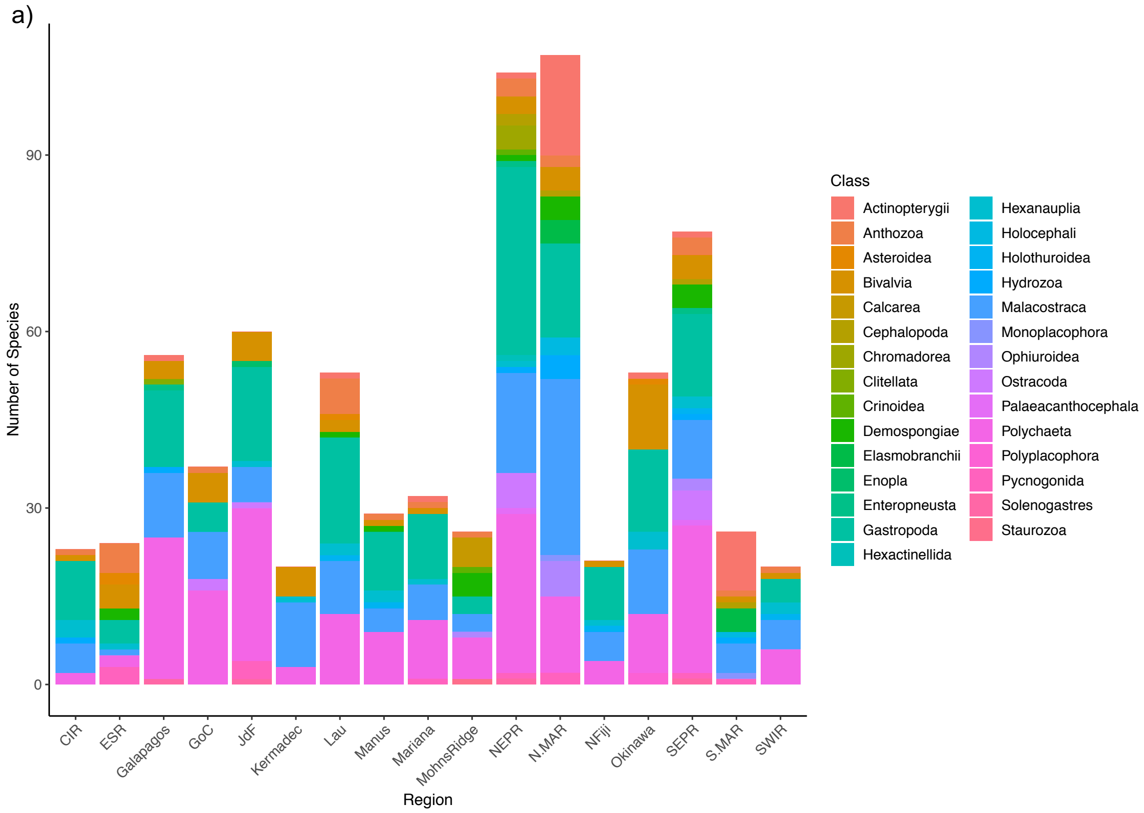
Table 22 (overleaf): Rationale for the environmental variables included in our analyses. Note that correlations were computed on the vent-field data provided in Chapman et al. (in prep. - Chapter 4) to increase the statistical power and ensure correlations and associated decisions remained relevant from preliminary multivariate analyses through to uniqueness computation (which was conducted on vent fields and then averaged per region). Correlations referred to in this table are Spearman's rank correlation coefficients (most appropriate for these data, as not all variables are normally distributed). We opted to exclude variables for this study, rather than include, where possible, to ensure that environmental uniqueness was a relatively conservative measure, rather than inflated by the inclusion of many similar variables.

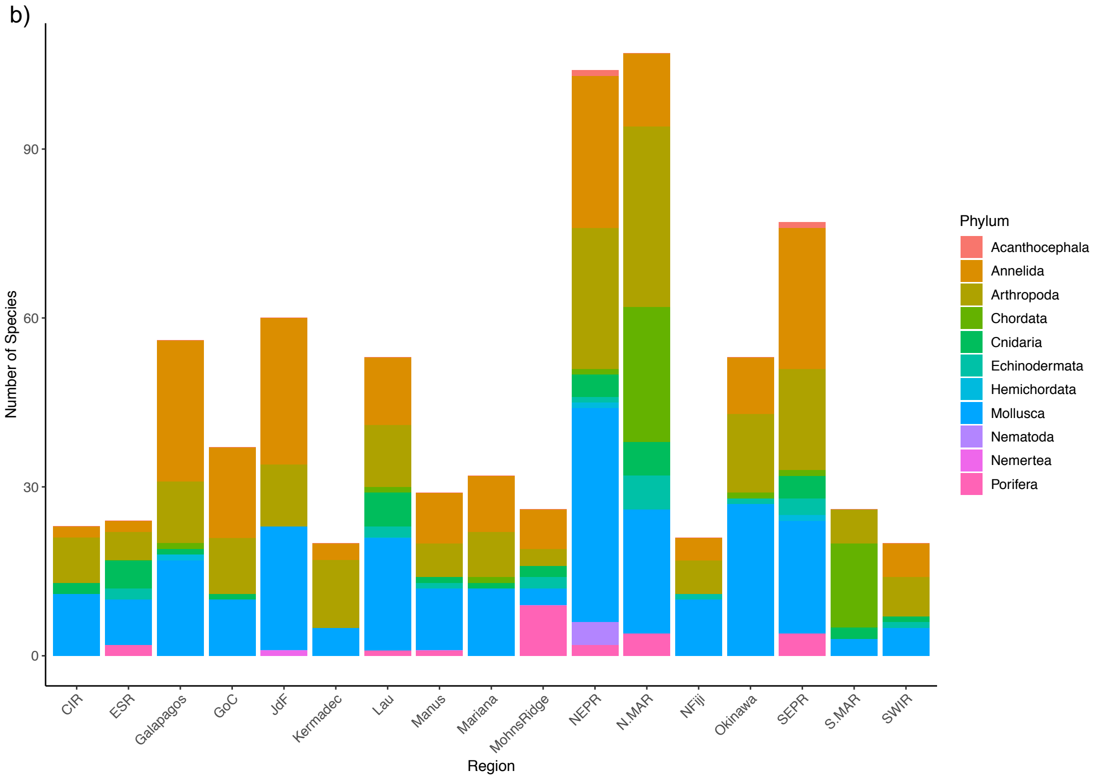
Environmental Variable	Name in Figures	Included / Excluded	Rationale
Turbidity	-	Excluded	Significantly ($p < 0.05$) correlated with many other variables and not a key driver variable separating fields, based on analyses presented in Chapman et al. (in prep. - Chapter 4).
Tidal range	TIDALRANGE	Included	Not significantly or strongly related to other variables.
Tidal form factor	-	Excluded	Too similar in influence to tidal range, and less strong of an influence based on analyses presented in Chapman et al. (in prep. - Chapter 4).
Total organic carbon (TOC) in sediments	TOC	Included	Significantly ($p < 0.05$) and strongly ($R > 0.5$ or < -0.5) correlated with nutrients (e.g., nitrate, silicate, etc.) and dissolved oxygen, so others removed as captured in this variable.
Silicate, nitrate, and phosphate (long-term maximum at depth)	-	Excluded	*See above.*
Dissolved oxygen (long-term maximum at depth)	-	Excluded	*See above.*
Full spreading rate (mm per year)	SPREADING	Included	Fundamental in shaping the number of vent fields in a region, fluid chemistry, and other environmental processes shaping the habitat of vent fauna. Significantly ($p < 0.05$) and strongly related to seafloor roughness ($R = -0.6$) and proximity to nearest seep ($R = 0.6$), which were removed.
Proximity to nearest seep (km)	-	Excluded	*See above.*
Proximity to nearest vent	PROXVENT	Included	No significant, strong correlations with other included variables.
Seafloor roughness	-	Excluded	Significantly ($p < 0.05$) and strongly ($R = -0.6$) correlated with spreading rate.
Sediment thickness (mm)	-	Excluded	Significantly ($p < 0.05$) correlated with spreading rate, and many other included variables.

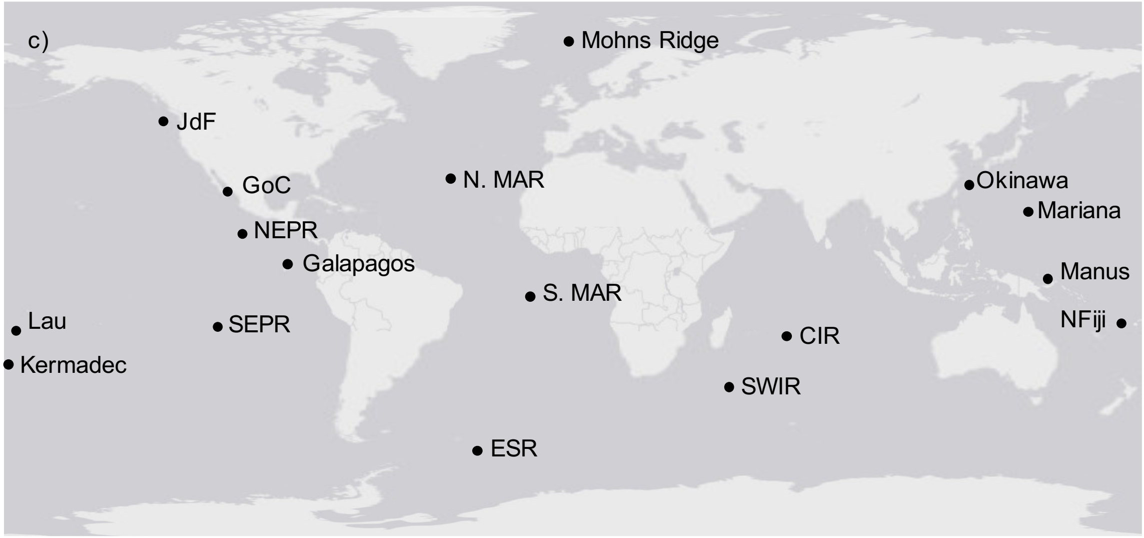
Salinity (long-term maximum at depth)	SALINITY	Included	Correlated with nutrients and temperature so could be included, as nutrients and temperature were removed and no correlated variables remained.
Temperature (long-term maximum at depth)	-	Excluded	Correlated with salinity and mean depth, among other - now excluded - variables ($R = 0.8$ for salinity and $R = 0.5$ for mean depth, with $p < 0.05$ for both).
Long-term maximum mole concentration of phytoplankton (as carbon) at maximum depth	CARBONPHYTO	Included	Stronger influence on vent-field dissimilarity in Chapman et al. (in prep. - Chapter 4) than long-term maximum chlorophyll at depth, with which it was strongly ($R = 0.997$) and significantly ($p < 0.05$) correlated.
Long-term maximum chlorophyll at depth	-	Excluded	*See above.*
Mean depth	DEPTHmean	Included	Strong ($R = 0.5$), significant ($p < 0.05$) correlation with temperature only, which was removed.
Tropical storm intensity	-	Excluded	This variable would bias results as it mostly applies to regions in the tropics.
Ice cover	-	Excluded	This variable would bias results as it only applies to polar regions.
Seafloor age (Ma)	-	Excluded	Data unavailable for the Manus Basin and Okinawa Trough regions.
Average sea-surface Chl-a	-	Excluded	Significantly ($p < 0.05$) related to TOC and phytoplankton at depth, among other variables.
Current velocity (long-term maximum at depth)	-	Excluded	Significantly ($p < 0.05$) related to TOC, spreading rate, and salinity, among other included variables.
Iron (long-term maximum at depth)	-	Excluded	Significantly ($p < 0.05$) related to TOC, phytoplankton at depth, and salinity, among other variables.

Appendix D.2

Figure 56 (below and overleaf)**:** Taxonomic composition of the regional species pools included in this study (Classes in (a) and Phyla in (b)) and a map depicting the locations of regions studied (c). Some region names have been abbreviated as follows: CIR - Central Indian Ridge; ESR - East Scotia Ridge; GoC - Gulf of California; JdF - Juan de Fuca Ridge; Kermadec - Kermadec Arc; Lau - Lau Basin; Manus - Manus Basin; Mariana - Mariana Arc; MohnsRidge - Mohns Ridge; NEPR - North East Pacific Rise; N.MAR - North Mid-Atlantic Ridge; NFiji - North Fiji Basin; Okinawa - Okinawa Trough; SEPR - South East Pacific Rise; S.MAR - South Mid-Atlantic Ridge; and SWIR - South West Indian Ridge.




b)
Number of Species
0
30
60
90
Region
CIR
ESR
Galapagos
GoC
JdF
Kermadec
Lau
Manus
Mariana
MohnsRidge
NEPR
N.MAR
NFiji
Okinawa
SEPR
S.MAR
SWIR
Phylum
Acanthocephala
Annelida
Arthropoda
Chordata
Cnidaria
Echinodermata
Hemichordata
Mollusca
Nematoda
Nemertea
Porifera


c)
Mohns Ridge
JdF
GoC
N. MAR
Okinawa
Mariana
NEPR
Galapagos
Manus
S. MAR
Lau
SEPR
NFiji
CIR
Kermadec
SWIR
ESR

Appendix D.3

Updating the taxonomic biogeography of deep-sea hydrothermal-vent fauna

To quantify the relative uniqueness of vent regions across the globe, we also updated the global taxonomic biogeography of deep-sea hydrothermal-vent fauna (**Figure 31** and **Figure 32**). Using this dimension of diversity alone, we can compare our new understanding of the relationships among geographically isolated vent regions to the predictions made using biogeographic models created when fewer vent regions had been sampled sufficiently to include in a multivariate analysis. In some cases, the addition of new regions has not challenged long-held views of vent biogeography. For example, the Manus, Lau, and North Fiji Basins of the West Pacific are mature back-arc basin systems for which similarity and gene flow have been documented previously (Vrijenhoek, 1997; Tunnicliffe et al., 1998; Desbruyères et al., 2006). Kermadec Arc is most similar to these basins, though more separated from them than they are to one another (**Figure 32**), which likely reflects the more geologically recent connection of this region to the West Pacific (Tunnicliffe et al., 1998). The taxonomic affinity between the Juan de Fuca Ridge and Gulf of California is stronger than that between the Juan de Fuca Ridge and the East Pacific Rise regions (**Figure 32**). This is no surprise, given previous work highlighting the tectonic histories that drove geographic isolation of these species pools (Tunnicliffe, 1988; Hessler and Lonsdale, 1991; Tunnicliffe et al., 1998). The taxonomic similarity we find among East Pacific Rise regions and the Galapagos (**Figure 32**) also echoes expectations in Tunnicliffe (1988) and Vrijenhoek (1997).

In including relatively recently sampled regions in this study, we can test biogeographic predictions made using previous models. The most recently sampled regions we include are the East Scotia Ridge (Rogers et al., 2012), the Indian Ocean regions (Hashimoto et al., 2001; Watanabe and Beedessee, 2015; Copley et al., 2016), and Mohns Ridge (also referred to as Mohn Ridge, and Mohn's Ridge, in other work; Schander et al., 2010; Kongsrud and Rapp, 2012). While the dissimilarity of the East Scotia Ridge relative to other regions (**Figure 32**) is as recorded in Rogers et al. (2012), the Mid-Atlantic Ridge connection to this region is new. This may be an artefact of the number of groups chosen during hierarchical-agglomerative clustering, but it aligns with the expectations of Rogers et al. (2012), who predicted the East Scotia Ridge to be more similar to the southern Mid-Atlantic Ridge if larval transport could take place between these two areas. Meanwhile, Mohns Ridge is also relatively isolated (**Figure 32**), in line with the expectations of these researchers (Rogers et al., 2012), likely due to the oceanographic current and thermal 'barriers' created by the Polar Front, as well as the similarity of Mohns Ridge vent fauna to surrounding non-endemic Arctic fauna, given the shallow depth of vents in this region and their proximity to continental shelves and seeps (Schander et al., 2010). The Indian Ocean has been subject of many vent biogeography discussions (Tunnicliffe et al., 1998; Van Dover et al., 2001; Moalic et al., 2012), wherein Pacific and Atlantic Ocean connections have been debated. For example, the Central Indian Ridge has been shown to be dissimilar from Southwest Pacific vents by Watanabe and Beedessee (2015), while Bachraty et al. (2009) join these regions in their biogeographic model. Here, based on taxonomic composition, we join the South West Indian Ridge (SWIR) and Central Indian Ridge (CIR; **Figure 32**), though they are more taxonomically similar to West Pacific vents than East Pacific, as per the findings of Watanabe and Beedessee (2015), based on the CIR. We do not find support for the connections between Indian Ocean vents and those of the Mid-Atlantic Ridge or East Scotia Ridge identified through phylogenetic analyses (Roterman et al., 2013; Chen et al., 2015; Herrera et al., 2015; Vereshchaka et al., 2015), but the grouping of SWIR and CIR regions is consistent with other taxonomy-based biogeographic studies (Copley et al., 2016; Chen et al., 2017; Zhou et al., 2018) and this may be an artefact of clustering at the species, rather than genus or other higher taxonomic levels (Van Dover et al., 2001).

While our updated taxonomic biogeography of deep-sea hydrothermal-vent species pools is generally geographically constrained, we can identify transoceanic similarities by clustering regions according to environmental characteristics (**Figure 33**); these similarities may be particularly relevant in limiting trait similarity among fauna (Heino et al., 2013). Here, the North Fiji Basin is more similar to the Galapagos than the closer Lau Basin or Juan de Fuca Ridge - closer to the Galapagos (**Figure 33**). Mariana Arc and Manus Basin regions are environmentally similar (**Figure 33**), despite being some of the furthest apart of all West Pacific regions in terms of dispersal distance (Hessler and Lonsdale, 1991). The southern Mid-Atlantic Ridge is more environmentally similar to the East Scotia Ridge than the North Mid-Atlantic Ridge, which is similar to the Central Indian Ridge according to the environmental variables included in our cluster analysis (**Figure 33**). If larval transport does take place between southern Mid-Atlantic Ridge and East Scotia Ridge regions (Rogers et al., 2012), this may suggest that recruitment and colonisation is more likely, though our study is constrained in representing average environmental conditions for vent fields, averaged across vent regions. The North and South East Pacific Rise (NEPR and SEPR) regions are most similar in our analysis (**Figure 33**), rather than the SEPR being connected to the West Pacific, as expected by Mironov et al. (1998), who consider the importance of large-scale oceanographic drivers of taxonomic similarity explicitly. This suggests that the inclusion of large-scale oceanographic current models might be beneficial in future, similar analyses of environmental similarity among vent ecosystems. The separation of Gulf of California and SWIR regions (**Figure 33**) is as expected, given the notably different substrata and associated conditions at vent fields studied in these regions to date (Copley et al., 2016; Goffredi et al., 2017; Zhou et al., 2018). While we do not explicitly compare these regions in terms of substratum or physico-chemical conditions, we have captured their environmental dissimilarity relative to other regions using other environmental indicators, demonstrating the utility of including available environmental data in vent biogeographic studies.

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Appendix E Peer-reviewed publications, presentations, fieldwork, training, working group meetings, and outreach activities

Peer-reviewed publications published, accepted, and in review during my PhD include:

- Chapman, A. S. A., Tunnicliffe, V., and Bates, A. E. (2018). Both rare and common species make unique contributions to functional diversity in an ecosystem unaffected by human activities, *Diversity and Distributions*, 24, 5, 568 - 578, doi: 10.1111/ddi.12712. (Chapter 2)
- McClain, C. R., Nunnally, C., Chapman, A. S. A., and Barry, J. P. (2018) Energetic increases lead to niche packing in deep-sea wood falls, *Biology Letters*, 14, 9, doi: 10.1098/rsbl.2018.0294.
- Jones, D. O. B., Amon, D. J., and Chapman, A. S. A. (2018) Mining deep-ocean mineral deposits: what are the ecological risks? *Elements*, 14, 325 - 330, doi: 10.2138/gselements.14.5.325.
- Chapman, A. S. A., Bates, A. E., et al. (in review with *Global Ecology and Biogeography*) sFDvent: a global trait database for deep-sea hydrothermal-vent fauna. (Chapter 3)

Presentations given during PhD candidature include:

- Chapman, A. S. A., Tunnicliffe, V., Bates, A. E., and the sFDvent Working Group (2018) 'Functional diversity and biogeography using 'sFDvent' - the first global trait database for hydrothermal vent species', oral presentation, World Conferences on Marine Biodiversity, Palais des Congrès de Montréal, Canada (peerj.com/preprints/26627).
- Chapman, A. S. A., Tunnicliffe, V., and Bates, A. E. (2018) 'Assessing the biodiversity of untouched hydrothermal vents', oral presentation, Student Conference on Conservation Science, University of Cambridge, UK (sccs-cam.org; awarded 2nd prize for 'Best Student Talk')
- Chapman, A. S. A., Tunnicliffe, V., and Bates, A. E. (2017) 'Contributions of rare and common species to the functional diversity of basalt-hosted tubeworm bush communities from the Juan de Fuca Ridge', oral presentation, 6th International Symposium on Chemosynthesis-Based Ecosystems (CBE6), Woods Hole Oceanographic Institution (WHOI), Boston, USA (goo.gl/N73K9Y; awarded 'Best Student Talk' by the Deep-Sea Biology Society)
- Chapman, A. S. A., et al. (2017) 'sFDvent: Building the first global functional trait database for hydrothermal vent species', poster, CBE6, WHOI, Boston, USA (goo.gl/1mkfr5)

- Chapman, A. S. A. (2016) 'Reshaping our view of hydrothermal vent biodiversity: integrating taxonomic identities, biogeographic provinces, and functional traits', seminar, German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Germany
- Chapman, A. S. A. et al. (2015) 'Hydrothermal vents: a step too far for functional trait metrics?', poster, British Ecological Society Annual Meeting, Edinburgh (also presented with associated 'lightning talk' at the Wessex Doctoral Training Network Student Conference at the University of Oxford in 2016)
- Chapman, A. S. A. et al. (2015) 'Hydrothermal vent biodiversity – a functional trait perspective', poster, Natural History Museum, London (session held as part of the NERC Advanced 'Introduction to Molecular Phylogenetics' Short Course)

Funding and awards applied for and gratefully received during PhD candidature include:

- 'sFDvent' Working Group funding from the German Centre for Integrative Biodiversity Research (iDiv) via its Synthesis Centre (~€29,500 awarded for two meetings following our response to a funding call via written proposal, with further grant later awarded for a third meeting in Montréal):
    - Co-Principal Investigator of the 'sFDvent' working group, building the first global-scale trait database for deep-sea hydrothermal vent species (https://www.idiv.de/?id=423). This involved co-leading and facilitating two working group meetings at iDiv to: i) design and build the database with expert deep-sea vent ecologists; and ii) compile, clean, and process database contributions and develop analyses and outputs with deep-sea vent ecologists and statisticians, including numerical ecologist Prof. Pierre Legendre.
    - Ongoing responsibilities include: co-ordinating and managing an international pool of 39 expert database contributors, as well as compiling, processing, quality control checking, and consistency checking the contributions to design and build the database.
- Student Training and Travel Grants / Awards from:
    - Deep-Sea Biology Society (£750), Marine Biological Association of the U.K. (£100), and InterRidge ($400) (for travel to CBE6 at WHOI, USA, 2017) and Deep-Sea Biology Society Award for 'Best Student Talk'
    - Intergovernmental Oceanographic Commission (IOC) funding (full support) to participate in the OBIS-INDEEP Training and Workshop in Belgium (2016)
    - Challenger Society for Marine Science (£500 to support a two-month trip to the University of Victoria, Canada, to gain laboratory experience with Prof. Verena

  - Tunnicliffe and to participate in a research cruise with the Canadian Department for Fisheries and Oceans in 2016)
  - British Ecological Society (£300 towards a Multivariate Statistics course in Scotland, 2016)

Training courses undertaken during PhD candidature include:

- 'Statistical Models for Wildlife Population Assessment and Conservation' (NERC-funded Advanced Training Short Course), University of Kent
- 'Introduction to Multivariate Ecological Statistics', University of Oxford
- 'Advances in Spatial Analysis of Multivariate Ecological Data: Theory and Practice', Scottish Centre for Ecology and the Natural Environment (SCENE), Loch Lomond National Park, Scotland
- Structural Equation Modelling, University of Southampton
- Mixed-effects modelling workshop, University of Southampton
- Public engagement and outreach, University of Southampton
- NERC-funded public engagement course, NERC, Swindon
- NERC Advanced Training Short Course: Molecular Phylogenetics, Natural History Museum, London
- 'Project Management and Leadership', HR Wallingford, Wallingford
- 'Building Research Collaborations', University of Southampton
- 'Media Communication', University of Southampton
- OBIS-INDEEP training and a workshop at the UNESCO-IOC Project Office for International Oceanographic Data and Information Exchange in Belgium.

Teaching and outreach during PhD candidature:

- Postgraduate Demonstrator, leading GIS tutorials and discussion sessions for Masters students on the 'Deep-Sea Ecology' course at the University of Southampton, assisting with undergraduate statistics sessions for the Dale Fort field course, and mentoring postgraduate and undergraduate students
- Massive Open Online Course facilitator for 'Exploring Our Oceans' on FutureLearn
- 'Scientist Ashore' for the Ocean Exploration Trust (2015)
- Science, Technology, Engineering, and Maths (STEM) Ambassador (volunteering at science-oriented events for schoolchildren, such as: Young Women in Science Day at the Winchester Science Centre and an event including 'Speed Networking' at Richard Taunton College, Southampton)

- EcoSchools Volunteer, National Oceanography Centre, Southampton
- Ocean and Earth Science Open Day Volunteer and Student Ambassador for University Open Days
- Volunteer at Southampton Boat Show (2015)
- ‘Science Uncovered’ deep-sea ecology display at the Natural History Museum, London

Research cruise participated in during PhD candidature:

- Research cruise from 2nd-16th August 2016 aboard *J. P. Tully*, aiming to survey and sample in Endeavour Marine Protected Area, as well as Middle Valley, offshore of western Canada. The P.I. for this cruise was Ben Grupe.

Working-group meetings led and participated in during PhD candidature:

- sFDvent Working Group meeting 1: 10th - 13th October 2016, German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Germany
- sFDvent Working Group meeting 2: 24th - 28th April 2017, German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Germany
- sFDvent Working Group writing meeting: 10th - 13th May 2018, Montréal, Canada

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