

Hydrothermal vent fauna of the western Pacific Ocean: Distribution patterns and biogeographic networks

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Abstract

Aim: Deep-sea hydrothermal vent habitats support a low-diversity fauna in which most species are unique to the ecosystem. To inform conservation planning around this vulnerable marine ecosystem, we examine species distributions over a wide area to assess the underlying beta-diversity components and to examine biogeographic patterns. We assess the concept of a highly connected fauna that would repopulate areas of local extinction from distal locations.

Location: Western Pacific Ocean from Japan to New Zealand.

Methods: We assemble a database of 295 confirmed species records for 11 western Pacific vent systems. The SET beta-diversity framework supports query of the distribution of pairwise pattern components in comparisons among vent systems. We build a network based in graph theory to examine connectivity among vent systems based on shared species similarity. A bipartite network revealed the relative role of each species in linkages among vent system nodes. We assess the importance of sampling bias and distance between systems.

Results: Overall, two-thirds of the taxa are restricted to a single basin or arc. The Mariana Trough system has the highest corrected weighted endemism for vent-specific species, followed by that of the Okinawa Trough. Species replacement is the dominant feature of beta-diversity. Eleven vent systems form seven network modules with stronger connectivity in the Southwest than Northwest Pacific. The Manus Basin vent system emerges as a network 'hub' reflecting its central geographic near the equator.

Main Conclusion: Two western Pacific biogeographic provinces arise, north and south of the equator that few species transcend. Local and regional conservation plans should consider the low network connectivity and high system endemism in management of hydrothermal vent ecosystems in the event of seabed mining. Species recruitment is unlikely to transcend vent system boundaries. We identify Okinawa Trough, Mariana Trough, Manus Basin, Feni-Tabar Arc and Kermadec Arc for development of conservation plans that initiate or expand protection.

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KEYWORDS

beta-diversity, biogeography, conservation, endemism, faunal distribution, hydrothermal vent, network connectivity, seabed mining, western Pacific

1 | INTRODUCTION

Ecosystems in the 'extreme' environment of hydrothermal vents have high perceived scientific and cultural values because of the unusual adaptations of the associated organisms (Turner et al., 2019). The animals that inhabit hydrothermal vents have unusual adaptations to heat variations, high concentration of toxic compounds, and food acquisition (Van Dover, 2000). The resultant community is relatively low diversity but forms isolated pockets of high biomass on the deep ocean floor (Tunncliffe, 1991). Despite the very small size of the vent habitat on the seafloor, vents have emerging value through metal-rich deposits and biological products (Van Dover et al., 2018). In the event of mining decisions that may disrupt active vent sites, better information on fundamental ecosystem properties is necessary to formulate strategies for mine site selection and/or conservation. Resource potential appears high in the volcanic arc-backarc settings of the western Pacific (Hannington et al., 2010) where several countries have issued mineral exploration licences. Reliable documentation of faunal diversity and its distribution are key components in developing conservation approaches.

Of the 304 active confirmed vent sites/fields listed in the InterRidge Vents Database 3.4 (Beaulieu & Szafranski, 2020), 44% occur in the western Pacific Ocean. In this region of complex tectonic plate interactions, nearly all hydrothermalism occurs on back-arc spreading ridges and volcanic arcs. Over 90% of all volcanic arcs are in the western Pacific where magmatic gas input strongly influences hydrothermal emissions, often at shallow depths (de Ronde & Stucker, 2015). Unlike the extensive mid-ocean spreading ridges of the Indian, Atlantic and east Pacific oceans, a back-arc ridge is confined by a small basin and is relatively short. The distribution of landmasses and bathymetric features constrains ocean circulation, thereby enhancing geographic isolation and barriers to dispersal among these back-arc basins (Mitarai et al., 2016). Potential connectivity among vent sites is limited by larval transport probability and habitat suitability for recruitment (Mullineaux et al., 2018). In a region where vent habitats range from 250 to 3600m depth, it is unlikely that many species span the full oceanographic and geological conditions available.

Past biogeographic studies of the western Pacific vent fauna are largely based on an early dataset (Desbruyères, 2006) that Bachraty et al. (2009) use in a global analysis to split the western Pacific into two northern and southern provinces. Rogers et al. (2012) extend the global dataset and propose four vent provinces in the western Pacific. In contrast, Moalic et al. (2012) use a network analysis approach to find one highly connected western Pacific province; they identify links into the eastern Pacific and the Indian Ocean through the Mariana Trough and Manus Basin nodes. In the last decade, scientific exploration has accelerated in most regions of the western

Pacific gathering faunal samples from many new sites from New Zealand to Japan. Improved molecular techniques have enhanced analyses of specimens from both new and old collections for genetic barcoding (e.g. Poitrimol et al., 2022; Stiller et al., 2020). In general, greater sampling tends to extend and infill species ranges in poorly sampled systems. For example, wider sampling on oceanic seamounts reveals broad ranges for most species (Rowden et al., 2010) where more limited data had suggested high endemism (Rogers, 1994). Thus, we might expect that the new records of vent fauna from the western Pacific would extend the ranges of many species and diminish 'distinctness' of localized regions in the western Pacific despite apparent barriers to interchange.

Our study presents an updated database of western Pacific vent fauna by compiling and verifying all available records; we also add some new records from recent samples. We use a combination of methods to assess patterns of diversity distribution and potential connections across the study area based on these records. This approach follows two recent studies: (i) Brunner et al. (2022) apply two complementary methods from graph theory to examine connections among 36 vent sites in the Northwest Pacific and identify priority sites for conservation, and (ii) Giguère and Tunncliffe (2021) examine the Mariana region of the Northwest Pacific to explore β -diversity patterns among vent sites. Our work supplements the data in these two studies with recent Northwest Pacific vent species reports and expands from these four vent systems to encompass an additional seven systems in the Southwest Pacific. The first objective of our present work is to determine whether connectivity is likely to support re-establishment of faunal assemblages removed by major habitat disturbance such as seabed mining. The second is to assess species ranges and biogeographic patterns of vent animals in the western Pacific.

2 | METHODS

2.1 | Region of study

We focus on 11 venting systems of the Northwest (NW) and Southwest (SW) Pacific: five on back-arc ridges (labelled as 'Trough' or 'Basin' in Figure 1) and six on volcanic arcs (labelled as 'Arc'). Here, a vent system is a geologically and/or geographically distinct venting region with distinct geophysical properties. Three arc/back-arc region pairs occur in our study: Mariana Arc/Mariana Trough, New Hebrides Arc/North Fiji Basin and Tonga-Tofua Arc/Lau Basin. Both the Izu-Bonin and Kermadec arcs are formed as the Pacific Plate subducts below the adjacent plate (Stern et al., 2003; Zellmer & Taylor, 2001), but neither has an associated rifting basin. While the Okinawa Trough does have a companion volcanic arc, it is the

FIGURE 1 The western Pacific vent systems. The Northwest Pacific hosts the northern four systems while the seven systems below the equator lie in the Southwest Pacific. Base map from GEBCO Compilation Group (2022).

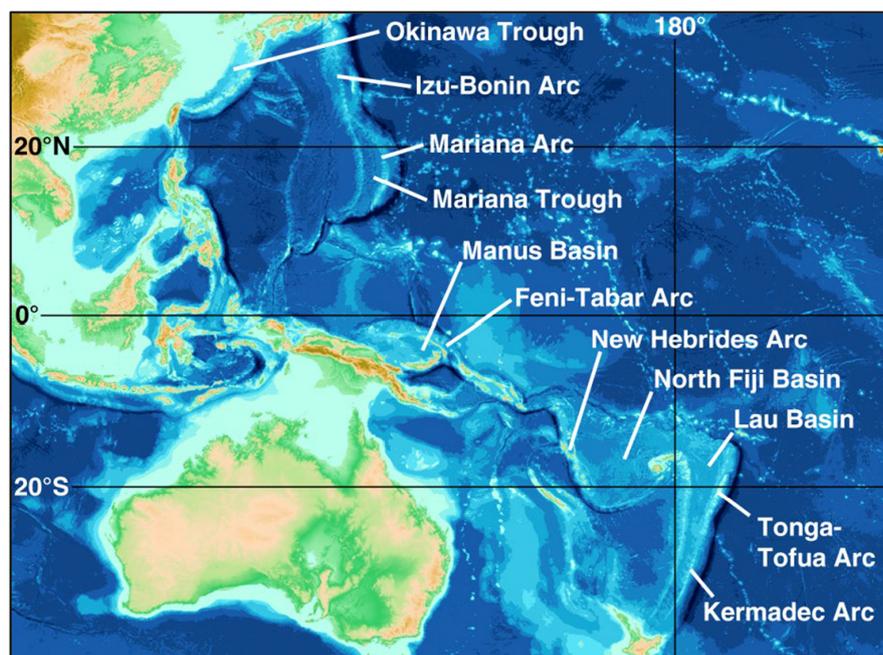


TABLE 1 Summary of species records for each vent system in this study.

Vent system	Species verified	Fraction unique to system ^a	Corrected weighted endemism	Additional records not used ^b	Vent sites contributing to report
Okinawa Trough	91	0.78	0.87	45	19
Izu-Bonin Arc	31	0.26	0.58	0	9
Mariana Arc	31	0.29	0.58	16	9
Mariana Trough	34	0.74	0.83	5	8
Manus Basin	48	0.35	0.52	1	3
Feni-Tabar Arc	17	0.65	0.77	1	1
New Hebrides Arc	12	0.00	0.24	1	2
North Fiji Basin	59	0.24	0.51	0	6
Lau Basin	70	0.33	0.56	3	8
Tonga-Tofua Arc	38	0.11	0.42	26	5
Kermadec Arc	36	0.44	0.66	25	9

Note: Systems are listed according to their geographic locations, from northwest to southeast.

^aRecorded in a single system.

^bDue to lack of resolution to species level or to a unique higher taxon.

incipient rifting back-arc that hosts most hydrothermalism (Ishibashi et al., 2015). The complex microplate tectonics around Manus Basin has current subduction located under New Britain (Wallace et al., 2009). Lastly, the nearby Feni-Tabar Arc is unusual as it is situated in an intra-plate setting isolated from the dynamics around New Guinea (Stracke & Hegner, 1998).

2.2 | Dataset

Information from vent sites within a system are combined; it was neither possible to determine within-site collection effort nor apply taxonomic corrections to original invalid records when literature corrections did not cover all taxon locations. The number of sites in each

system covered by the data is noted in Table 1. Species included are macrofauna (adults over 1 mm body size) and those collected within the influence of venting fluids to the extent that reports enable this distinction; where unclear, we include the record. Records of species that also inhabit non-chemosynthetic habitats are rare, but included when evident the species made substantial use of the vent habitat and was not merely peripheral.

The faunal lists are compiled initially from the primary literature. Search terms in both Google Scholar and Web of Science included the system name (sometimes with alternative designations such as back-arc basin OR spreading ridge), AND 'hydrothermal vent OR hot vent', AND 'new species OR new taxa' OR 'species list'. Date range was 1980 to December 2022. We first assessed original species descriptions and then examined subsequent

sources that record these species in other systems. Accepted sources are those from experts in the relevant taxonomic group, have identifications assisted by such expertise, or are verified with genetic information; in some cases, the morphology of a described species is sufficiently distinct to determine its identity with high confidence. There are reported species occurrences that we did not accept, many because the taxon was later corrected. However, there remain records we consider unverified, particularly where a misidentification is possible. The list for each vent system is presented in Supporting Information (Appendix I, Table S1) along with the sources for species description and location authority. Taxa identified only to genus level are included only when the genus appears in no other regional list, thus eliminating the possibility of a shared, but unverified, species. Taxa with a number or letter ('dark taxa') are deemed distinct where the location author has published DNA sequences in support of their genetic distinctness. Species of *Amphisamya* and *Shinkailepas* have unpublished sequences from the sources cited. Recent collections from our expeditions to Izu-Bonin Arc, New Hebrides Arc and Tonga-Tofua Arc are included to the extent that species verification is possible. Species information is tabulated in a site by species occurrence matrix (Appendix I, Table S2). For nine species, COI and 18S sequences are available at GenBank (accession numbers: Appendix I, Table S3). DNA from tissue material was extracted and sequenced by the Barcode of Life Database (BoLD) facility (boldsystems.org).

2.3 | Diversity

The α -diversity measure for a vent system is the number of verified species. Because of the common correlation between species richness and number of endemics (Gaston, 1998), we present a corrected weighted endemism measure (Crisp et al., 2001): the sum of proportions of the range of each species occurring within one system divided by richness for that system. β -diversity patterns across the western Pacific are assessed using the SET framework (meaning set theory) that uses the Jaccard family of indices (Schmera et al., 2020). This approach identifies which 'pairwise pattern components' dominate each system-system comparison; *species overlap* (O_j), *species richness difference* (D_j) and *species replacement* (R_j). Here, β -diversity = $(R_j + D_j) / (1 - O_j)$. The SET framework further decomposes β -diversity into the 'intersection of nestedness & β -diversity' (I_j) and the 'relative complement of nestedness in β -diversity' (RC_j). I_j and RC_j are identical to D_j and R_j , respectively, when $O_j > 0$. However, when there is no pairwise species overlap, $I_j = 0$ and $RC_j = 1$. We use the O_j , R_j and D_j nomenclature for clarity, but employ the preceding condition. Pairwise distances are assessed through agglomerative hierarchical clustering using the Jaccard index calculated using the *vegan* R package (Oksanen et al., 2019) that also generated an ordination plot. Output from the 'beta.div.comp' function in the 'adespatial' R package (Dray et al., 2018) is displayed on a simplex plot (Podani & Schmera, 2011) generated by the 'TernaryPlot' R function (Smith, 2017).

The Local Contribution to Beta Diversity (LCBD) metric ('beta.div' function in the 'adespatial' R package (Dray et al., 2018)) identifies the relative contribution of each system to overall β_j -diversity. For each pair of sites, the $\beta_{ratio} (I_j/\beta_j)$ reflects which component plays a dominant role in shaping β -diversity. To determine whether the pairwise distance values deviate from chance, we use the Raup-Crick dissimilarity index (β_{RC}) that controls for richness difference and identifies values beyond the 95% confidence intervals of a null model iteration. β_{RC} values are calculated using the 'raupcrick' function in the 'vegan' R package (R Core Team, 2020) and converted output values to a scale of negative one to positive one (Chase et al., 2011). A similar approach is described in more detail in a previous regional study (Giguère & Tunnicliffe, 2021).

2.4 | Network connectivity

We use methods from graph theory to formulate a similarity network of nodes connected by edges as applied to extant vent assemblages by Brunner et al. (2022). In our work, nodes are vent systems and edges represent undirected relationships based in faunal similarity. This network is a proxy for species connections that formed in the past and may continue today. First, we show a similarity network using pairwise similarity (1 - Sorensen coefficient) to weight the linkage between nodes; weak edges that did not pass a 'percolation threshold' (Rozenfeld et al., 2008) were removed ('sidier' R package (R Core Team, 2020)). A central assumption is that all vent systems are connected, at least indirectly. 'Betweenness centrality' ('igraph' R package (Csardi & Nepusz, 2006)) represents the relative role that each vent system plays in maintaining indirect connections among all vent systems. Second, a bipartite network complements the similarity network to examine the role of each species in the linkages among vent system nodes. A species node is connected to all vent system nodes at which it is present. With the 'rnetcarto' package in R (Doulcier & Stouffer, 2015), we maximize the 'Modularity' (Guimera & Amaral, 2005a) with an iterative grouping approach. The outcome is clusters of nodes (species and systems) that form 'modules' that maximize the within-module connections and minimize the between-module connections. Vent systems with distinctive species assemblages can be identified as well as apparent barriers to connectivity in a biogeographical sense (e.g. Kougioumoutzis et al., 2017).

The role of each node (vent system or species) as a network connector is determined by two factors that assess the strength of linkages (Guimera & Amaral, 2005a, 2005b). Within module degree (z) evaluates the relative role a node plays in connecting nodes within its module, while the participation coefficient (P) measures the role of a node in driving inter-module connectivity. Both metrics are derived using the 'rnetcarto' R package. We assign each vent system node one of the universal cartographic roles (Guimera & Amaral, 2005b; Olesen et al., 2007) as follows: 'Peripheral nodes' ($z_i < 2.5$ and $P_i < 0.62$), 'Module hubs' ($z_i > 2.5$ and $P_i < 0.62$), 'Connector nodes' ($z_i < 2.5$ and $P_i > 0.62$) and 'Network Hubs' ($z_i > 2.5$

and $P_i > 0.62$). More detail and references on methods are available in Brunner et al. (2022).

We explore the roles of three parameters in shaping the β -diversity outcomes. First, we assess the influence of sampling effort, recognizing that the extent of exploration and sampling is not consistent across vent systems. The number of vent sites (Table 1) that contribute to species records in a system can reflect thoroughness of exploration. Secondly, the number of expeditions to a vent system may influence the extent of sampling, thus species discovery. We created an expedition list for the northwest Pacific by extracting an inventory of biological samples from the DARWIN ('Data Research system for Whole cruise Information') database of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). After cross-referencing these samples with cruise numbers, they were partitioned to four vent systems under study; the American cruises for the Mariana Arc and back-arc were added from our work and Woods Hole Oceanographic Institution (WHOI) records. Similarly, the National Institute of Water and Atmospheric Research (NIWA) biological database in New Zealand provided expedition data for the Kermadec Arc. For the remaining systems, we began with the list of expeditions listed by Thaler and Amon (2019). First, we culled expeditions that did not have appropriate benthic collection equipment on board (e.g. water column surveys only) and then added expeditions acknowledged in species reports and those for which we retain collections. A data matrix for each variable represents the differences in number of sites or expeditions between each pair of vent systems.

Geographic distances between vent system pairs is the third potential driver of β -diversity representing a simple measure

of relative barriers to species dispersion. We determined the mid-point between most distal sites in each system and measured the distances between all systems. We assumed a mid-water pathway of 1000m depth (all but one inter-basin barrier is deeper than this depth) and mapped the shortest distance between mid-points with the following flow conditions: (i) entry into Okinawa Trough follows the northward Kuroshio via the southern extreme with exit via the Kerama Gap (Nakamura et al., 2013); (ii) exchange between Manus Basin and southwest Pacific systems is through Woodlark Basin except for Feni-Tabar (north of New Britain); and (iii) Lau Basin and Tonga-Tofua Arc connects northwestward through the North Fiji Passage while distance to/from Kermadec is assessed through South Fiji Basin (Simons et al., 2019). The distance-based Moran Eigenvector Map (dbMEM), which provides spatial variables for each system relative to all systems, is calculated directly from the resultant pairwise matrices following the methods of Legendre and Legendre (2012). See quantitative data for these parameters in Appendix I, Table S4.

We use Variance Partitioning (R 'vegan' package (Oksanen et al., 2015)) to determine the relative contributions of the three variables to the observed β -diversity patterns (represented by the Sorensen coefficient used in the species assemblage network) across the vent systems. This approach also examines joint contributions through interactions with one another (Borcard & Legendre, 2002). Each analytical approach outlined above derived outputs that contribute insights to the overall interpretation of the species patterns (Figure 2).

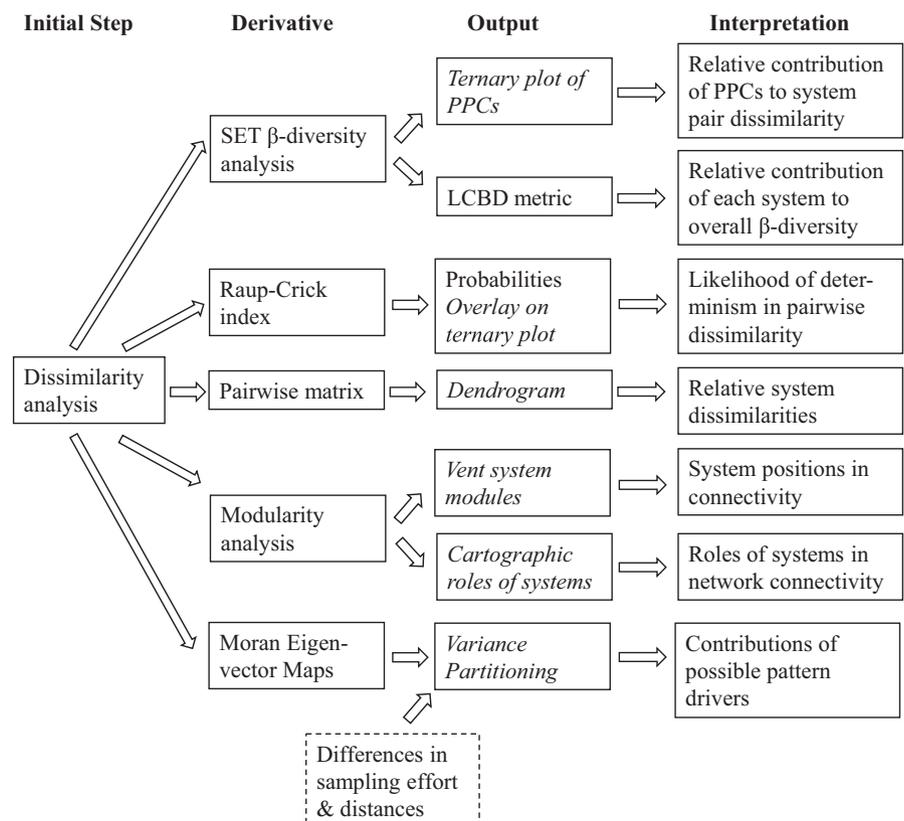


FIGURE 2 Workflow for the analyses and their contributions to the biogeographic interpretations in this study. LCBD, local contributions to betadiversity; PPC, pairwise pattern component. The outputs in italics are presented as figures.

3 | RESULTS

3.1 | Dataset

From a total of 456 records, we extracted 399 taxa designated as distinct 'species' (with or without complete identities). Of these, we can verify with high certainty 295 taxa that are either described species or unique at the taxonomic level known (Appendix I, Table S1). An additional 103 taxa are not included as they remain unidentified to species level and the lowest taxon noted occurs elsewhere (the unnamed species could be the same species as another record).

3.2 | Diversity

Richness values within vent systems range from 12 to 91 (Table 1). Overall, two-thirds of the taxa are restricted to a single basin or arc. The Okinawa Trough dominates this statistic with the highest species richness and uniqueness. In the remaining systems combined, this fraction drops to nearly one-third. There is strong relationship between number of species and number of endemics (Spearman $r = .68$; $p = .03$), however, using the corrected weighted endemism (CWE) measure, the relationship with richness is no longer significant ($r = .10$, $p = .79$). CWE remains highest for Okinawa Trough and Mariana Trough with Feni-Tabar Arc as the highest in the SW Pacific (Table 1). Figure 3 illustrates the species distribution among systems where only a few species transcend more than two systems. The broadest ranges are those of the alvinocaridid shrimp *Rimicaris variabilis* (Komai & Tsuchida, 2015) and the bathymodioline mussel *Bathymodiolus septemdiarum* Hashimoto & Okutani, 1994, both of which occur in NW and SW Pacific vent systems. Overall, the similarity among vent systems is low.

Clustering using Jaccard and Sorensen indices yields very similar results in which NW and SW Pacific vent systems separate into two clusters with the exception of the Feni-Tabar Arc system (Figure 4). Within each cluster, members of one pair of systems do not differ ($p > .05$): Izu-Bonin and Mariana Arcs (NW Pacific), Lau and North Fiji Basins (SW Pacific). An nMDS plot (Appendix II, Figure S1) illustrates

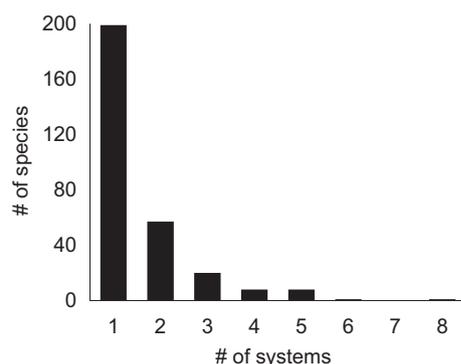


FIGURE 3 Number of species occurring in one or more vent systems. One species occurs in six (the shrimp *Rimicaris variabilis*) and one in eight (the mussel *Bathymodiolus septemdiarum*) systems.

tight clustering of the SW Pacific systems (except Feni-Tabar Arc) compared to the NW Pacific. Using 162 taxa at the genus level (Appendix II, Figure S2), the data-poor New Hebrides Arc separates first and the Mariana Trough aligns with the remaining SW Pacific systems.

A ternary plot (Figure 5) illustrates the relative contribution of pairwise pattern components to β -diversity. Here, for 70% of the possible system-system pairs, over half the species are replaced in each comparison. The dominance of replacement over richness difference among vent systems is reflected in the low mean β_{ratio} of 0.31 (SD 0.23). In turn, richness difference is more important than species overlap with a Nestedness ratio 0.78 (SD 0.24). Species overlap between systems is below 40% everywhere with the highest overlap between the Lau and North Fiji basins. As assessed by β_{RC} , most comparisons deviate significantly from the null model; the majority of the deviations are more different than expected (red points on Figure 5) indicating that deterministic factors may influence the pattern.

The LCBD metric identifies three sites that contribute most to high β -diversity: Okinawa Trough, Mariana Trough and Feni-Tabar Arc (all $p < .01$). For each, there is a high percentage of species unique to the system (Table 1).

3.3 | Network connectivity

The modularity analysis identifies seven modules: one containing four systems (Lau Basin, New Hebrides Arc, North Fiji Basin and Tonga-Tofua Arc), another containing two systems (Izu-Bonin Arc and Mariana Arc) and the remaining as five isolated systems. The similarity network in Figure 6 illustrates distances among these modules. There is a greater resemblance among SW Pacific systems compared to those of the NW Pacific systems (Figures 4 and 6). Nonetheless, all similarity levels are low. Manus Basin, occupying a central geographical position, has the highest betweenness centrality (Table 2), thus plays the strongest role in connecting all modules. The next highest value of betweenness centrality is for the Mariana Volcanic Arc; it shares five species with Manus Basin. In contrast, the betweenness centrality values for Okinawa Trough and the Feni-Tabar Arc (at the geographic extremes) are zero reflecting their negligible contribution to the overall network. Connections to the latter system are so weak that the percolation threshold algorithm disconnects it from the network rather than retaining a disproportionately large number of edges (Muñoz-Pajares, 2013). The overall low connectivity of distinct modules is reflected in the assigned cartographic roles in Figure 7, where Manus Basin achieves status as a 'network hub' (barely), and none is classified as a 'connector node'. Overall, this network is not well integrated and connections are weak. The relative proportion of module-endemics is highly variable, as reflected in the wide range of participation coefficients (Table 2).

The bipartite network (Figure 8), built from the species occurrence matrix, illustrates how few vent species (16) range across the equator in the western Pacific resulting in a clear north/south

FIGURE 4 Dissimilarity dendrogram of western Pacific vent systems based on Sorensen's index; the higher the split, the greater the dissimilarity. The highest split separates the NW Pacific (right) from the SW Pacific (left) systems. Here, colours identify systems with compositions that differ at a 5% level in a null model test (9999 iterations). The closest relationship is between Lau and North Fiji basins.

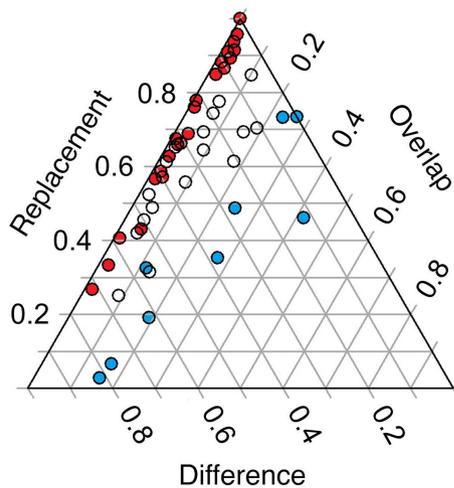
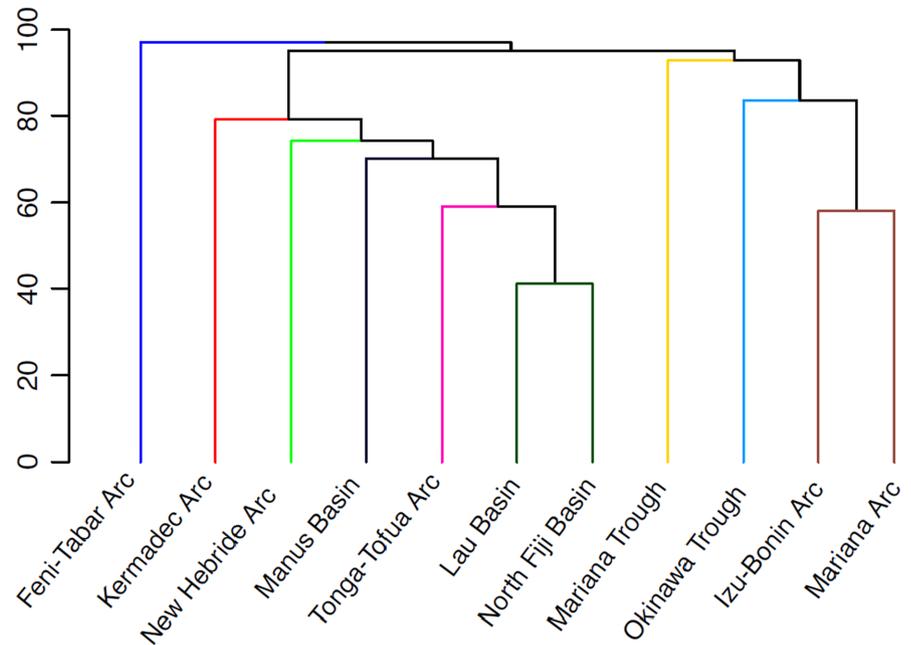


FIGURE 5 Ternary (simplex) plot to illustrate relative roles of three pairwise pattern components in the pairwise comparisons of assemblage composition in western Pacific vent systems. There are 55 between-system pairs represented. The components are read clockwise around the triangle: species *overlap* (proportion of species shared), species *richness difference* and species *replacement* (the proportion of species replaced in a pairwise comparison). Here, no pair shows more than 42% species overlap (Lau-N.Fiji), while 38 pairs have greater than 50% of the species replaced. Seven pairs that share no species (in accordance with the SET framework) lie at the top apex: three include Okinawa Trough and four include Feni-Tabar Arc. Red denotes pairs that are more different than expected in Raup-Crick null model simulations, while blue points are pairs more similar. Eight of the nine blue symbols are comparisons between systems of the Southwest Pacific.

separation. The key role of Manus Basin as a connector vent system is evident with its links on both sides of the equator. The few shared species of both NW Pacific Mariana Trough and SW Pacific Feni-Tabar Arc are nearly equally divided between other northwest

and southwest modules despite the high isolation of both vent systems. Overall, however, the module endemic species dominate the figure, emphasizing the restricted ranges of most species. Nine species emerge as 'connector nodes' (Table 3; Appendix II, Figure S3). The highest Participation value applies to the stalked barnacle, *Leucolepas longa* Southward & Jones, 2003, that is present in four modules. The roles of the remaining species are Peripheral ($n=58$) and Ultraperipheral ($n=228$) (Appendix II).

The three variables we used in the pairwise redundancy analysis (differences in number of vent sites and in number of expeditions, and distance between systems) explain only 28% of the module grouping with distance between systems contributing the greatest portion (22%; Figure 9).

4 | DISCUSSION

Active hydrothermal vents of the western Pacific fall within national jurisdictions. In 2006, United Nations General Assembly Resolution 61/105 designated hydrothermal vents as Vulnerable Marine Ecosystems recognizing the value of their biodiversity, such as endemic animals; thus, States are committed to making conservation efforts in this context (Van Dover et al., 2018). Positions of States with respect to seabed mining for minerals at active vents include: developing plans and tools for extraction (Japan), active exploration licences (Tonga), withdrawal of exploitation licences (PNG), and declaration of moratoria pending further research and other outcomes (PNG, Fiji, Vanuatu, New Zealand). For all these jurisdictions, our results can inform conservation policy related to management of mining impacts, to advancing research agenda and to instituting mining bans.

A key result of our work is the extent to which vent taxa are spatially constrained. The dominant pattern component of

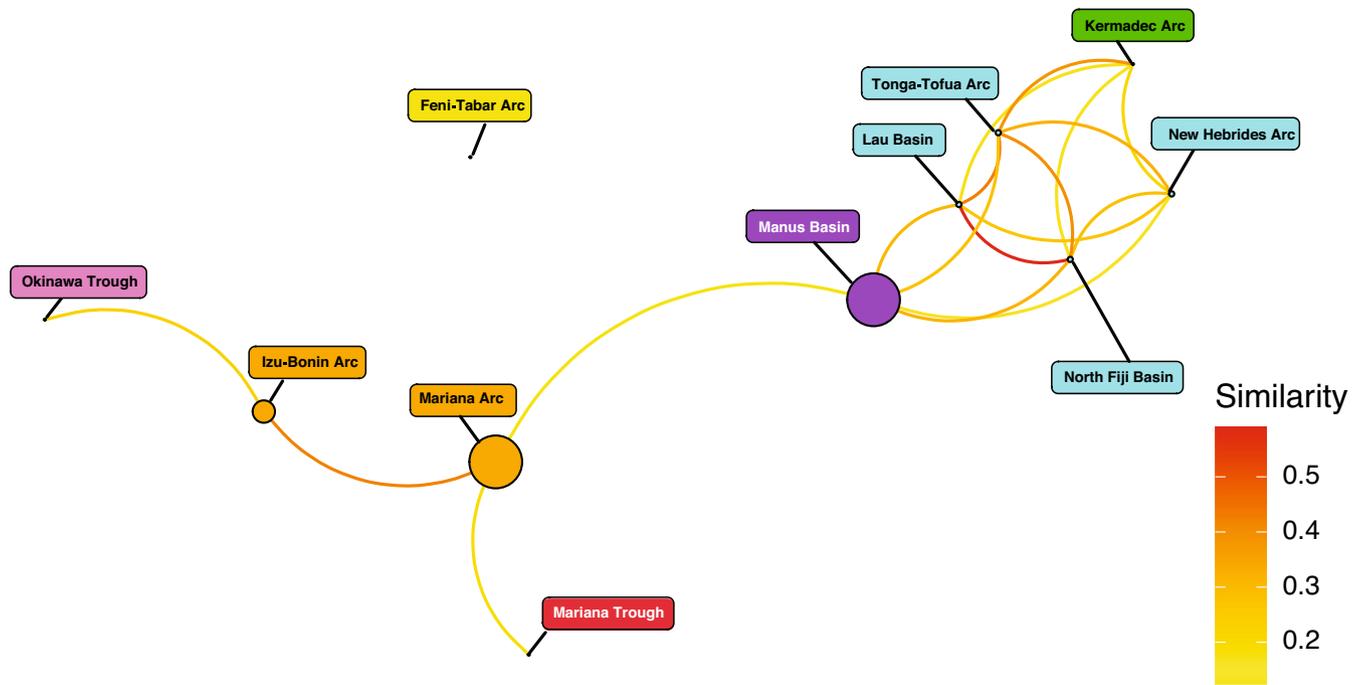


FIGURE 6 Modularity analysis of western Pacific vent systems detects seven modules indicated by colours. Coloured lines represent the Sorensen similarity value between vent systems based on species composition; values below 0.1 are not shown. The layout uses the Fruchterman and Reingold (1991) method, in which the distance between nodes is inversely proportionate to their shared edge weight. The size of each node is proportionate to its betweenness centrality (Table 2), a measure of the relative presence of a node in the pathways between all node pairs.

TABLE 2 Structural attributes of vent system nodes in the bipartite network.

Vent system	P_i	z_i	Cartographic role	Betweenness centrality
Okinawa Trough	0.37	8.43	Module Hub	0
Izu-Bonin Arc	0.18	4.88	Module Hub	8
Mariana Arc	0.47	3.73	Module Hub	20
Mariana Trough	0.16	5.57	Module Hub	0
Manus Basin	0.63	5.10	Network Hub	20
Feni-Tabar Arc	0.00	4.00	Module Hub	0
New Hebrides Arc	0.15	0.84	Peripheral	1.25
North Fiji Basin	0.22	5.44	Module Hub	1.25
Lau Basin	0.16	6.79	Module Hub	1.25
Tonga-Tofua Arc	0.41	2.75	Module Hub	1.25
Kermadec Arc	0.28	5.48	Module Hub	0

Note: P_i is the participation coefficient that is a measure of the linkages among modules while z_i represents within module degree of connectivity.

β -diversity is species replacement between systems; species overlap is very low. In the western Pacific, only 19 species inhabit four or more vent systems. Instead of greater homogeneity with increased exploration and taxonomic resolution, more regionalization is emerging: we now see high endemism at system and

regional scales. Species that are geographically constrained are vulnerable to extinction when environmental conditions change (Asaad et al., 2017). Thomas, Böhm, et al. (2022) determine that assessments of hydrothermal vent species for the IUCN Red List primarily rely on area of occupancy and extent of occurrence. These criteria are based on the geographic range plus ongoing or predicted decline in the range or population size of each species (IUCN, 2012). Among the 84 described vent-endemic mollusc species in the western Pacific, 32 are currently assessed as Critically Endangered, 25 as Endangered and 17 as Vulnerable on the IUCN Red List because some of the relevant States have plans to mine the vents (Thomas et al., 2021). Where resource exploitation affecting active vents occurs in the western Pacific, re-establishment of fully functional communities at compromised sites will be through recruits from the same system. Thus, careful local and regional assessments of potential population and species losses should accompany exploitation plans. For example, determining the sites within a system that are likely to be sources for colonizers is critical, as not all sites contain the lost species (Giguère & Tunnicliffe, 2021). Models of recovery times are useful tools (Suzuki et al., 2018), but need to be customized with species-specific larval times and habitat requirements.

Systems of particular conservation concern are those with high proportions of endemics that are revealed by our study to be: Okinawa Trough, Mariana Trough, Feni-Tabar Arc and Kermadec Arc. Our study also underscores the isolation of Okinawa Trough as recognized by Brunner et al. (2022); we find only a few additional

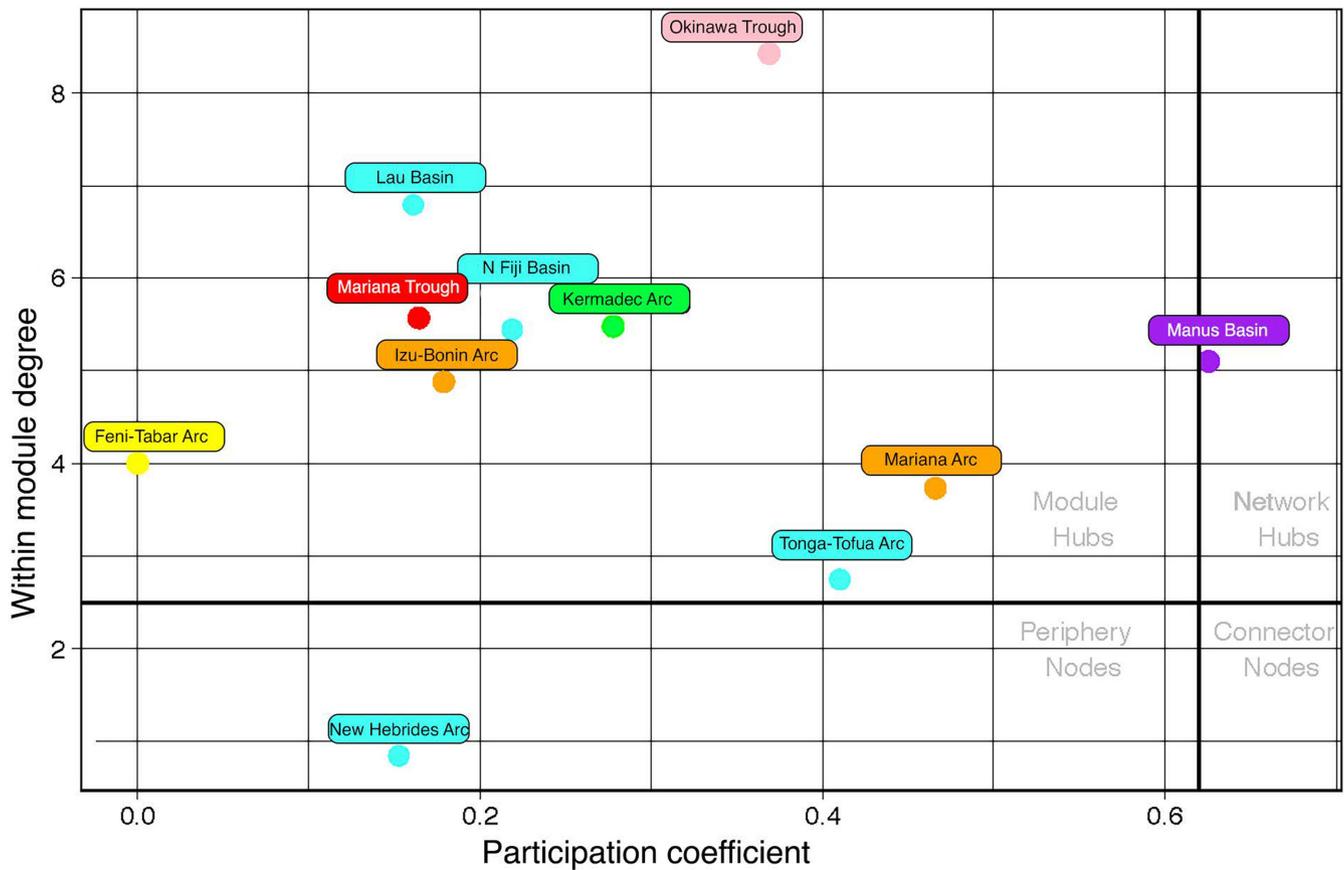


FIGURE 7 Cartographic roles of each western Pacific vent system based on participation coefficient and within module degree. The vertical axis is influenced strongly by species richness. Only Manus Basin approaches a role as a Network Hub in which both the within-module degree (z_i) and the participation coefficient (P_i) are high; the remaining systems are module hubs with the exception of the New Hebrides Arc which has a Peripheral role as both z_i and P_i are low.

species ranging into the SW Pacific. As mining plans advance here, so should plans to protect within-system vent sites that can provide recruits to disturbed areas. As part of the Mariana Trough falls in a United States Marine National Monument, we recommend extension of boundaries to encompass all vents given the isolated position of this system in the network. The Kermadec Arc is also vulnerable as it is a geographic endpoint in the vent system network. Of particular value here will be studies that address connectivity to adjacent systems to understand the extent of isolation of vent communities in this area where a moratorium on the issuance of mineral licences is due to end in April 2024. However, species that do occur in more than one system may not be able to provide recruits to cross the intervening barriers. For example, Watanabe et al. (2005) suggests that exchange is not possible for barnacles between Okinawa Trough and Izu-Bonin Arc, and Lee et al. (2019) propose incipient speciation may be underway in Manus Basin for a crab population where no exchange is detected with Lau or North Fiji.

The network structure highlights additional areas of conservation concern as it identifies locations that are pivotal in maintaining the vent system network and the pathways of connectivity. Modularity analysis detects a biogeographic boundary between NW and SW Pacific vent systems and emphasizes relative isolation of

large proportions of the fauna in most systems. Because the overall network is not tightly integrated, Manus Basin in Papua New Guinea (PNG) plays a key role as a network hub for the entire western Pacific. Moalic et al. (2012) also see a central network role for Manus Basin in their global study, but our new analysis reveals lower network connectivity in which only 5% of western Pacific species cross the equator, and none crosses the Pacific. The highest connectivity from SW to NW Pacific systems lies between the Manus Basin and the Mariana Arc (the latter falls in the USA Marine National Monument). While some vent populations appear isolated in Manus Basin, others have active gene exchange with systems further southwest (e.g. Yahagi et al., 2020) and may act as a sources for critical foundation species (e.g. Breusing et al., 2023). Upholding the moratorium that PNG recently declared on mining in its waters remains a conservation goal for which our study provides strong support.

Also in PNG's jurisdiction, Feni-Tabar Arc hosts gold-rich vent deposits at vents with high endemism. This system is an outlier unconnected to the similarity network with a participation coefficient of zero, but it also is one of three systems to make a significant local contribution to the overall β -diversity. While late Cenozoic geographic barriers to species interchange likely play a role in isolation, so may the hydrothermal environment. The geophysical structure

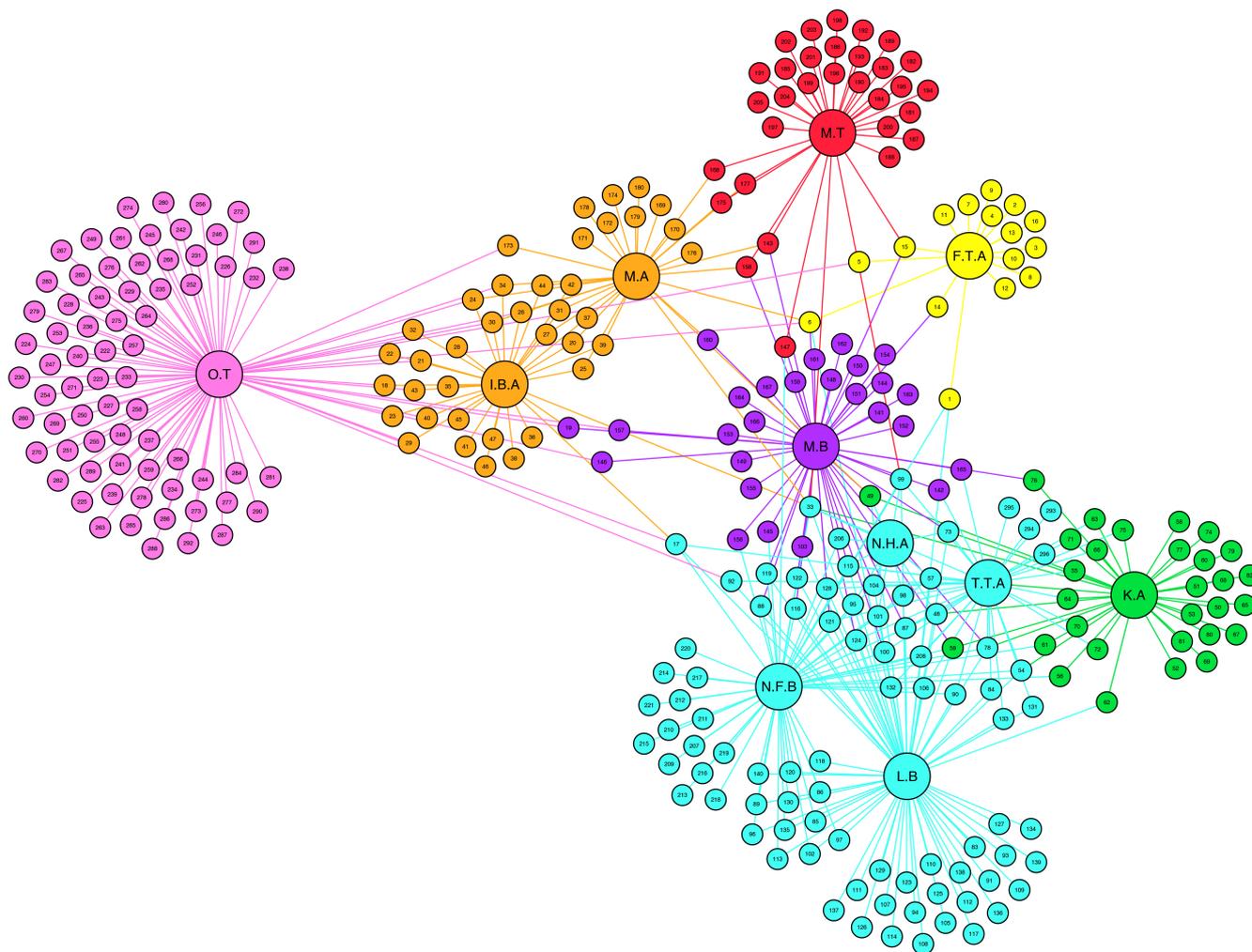


FIGURE 8 Bipartite Network combining western Pacific vent system modules with species nodes. Colours match the clusters identified in Figure 6 while numbers are unique species as listed in Appendix I, Table S5. A large number of species are shared by three modules of the Southwest Pacific while the linkages extending from the Manus Basin (M.B.) module emphasize its role in the connection pathway. Note the large proportions of endemics at Okinawa Trough (O.T.), Mariana Trough (M.T.), Feni-Tabar Arc (F.T.A.) and Kermadec Arc (K.A.). The multi-system modules are Izu-Bonin Arc (I.B.A.) and Mariana Arc (M.A.) in the northwest and New Hebrides Arc (N.H.A.), North Fiji Basin (N.F.B.), Lau Basin (L.B.) and Tonga-Tofua Arc (T.T.A.) in the southwest.

Species name	Animal type	ID key	P_i	z_i
<i>Leucolepas longa</i>	Stalked barnacle	6	0.80	-0.25
<i>Lamellibrachia juni</i>	Tubeworm	49	0.72	-0.18
<i>Levensteiniella raisae</i>	Scaleworm	143	0.67	-0.18
<i>Paralvinella hessleri</i>	Plume worm	147	0.67	-0.18
<i>Provanna nassariaeformis</i>	Snail	158	0.67	-0.18
<i>Branchipolynoe pettiboneae</i>	Scaleworm	19	0.67	-0.20
<i>Phymorhynchus wareni</i>	Large snail	15	0.67	-0.25
<i>Bathymodiolus septemdirum</i>	Mussel	33	0.66	0.05
<i>Munidopsis lauensis</i>	Squat lobster	59	0.63	-0.18

Note: These nine species are listed in order of high to low participation (P_i). Present are a barnacle (top), several polychaetes, two gastropods, a bivalve and a crustacean. The low within-module degree (z_i) means no species are considered 'Module Hubs'. ID Key refers to the numbers in Figure 8.

TABLE 3 The "Connector Species" in the western Pacific vent system network.

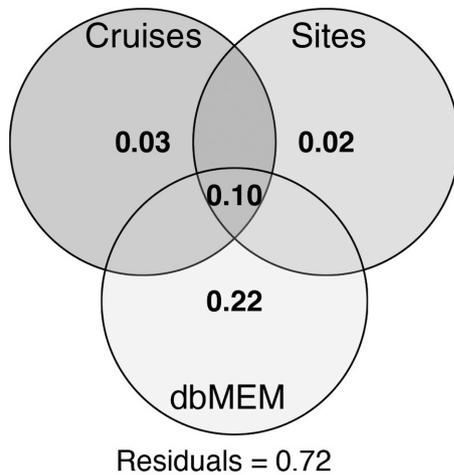


FIGURE 9 Variance Partitioning of vent system dissimilarity (Sorensen's coefficient) against sampling effort for the western Pacific, in the form of the number of cruises and sites sampled, as well as geographical distance in the form of a distance-based Moran's Eigenvector Map (dbMEM).

of the Feni-Tabar Arc is unusual in that the volcanoes lie in an intra-plate setting (a former forearc basin) (Stracke & Hegner, 1998). Krylova and Janssen (2006) note the high diversity of vesicomid clams here and propose its importance in dispersion of the group in the western Pacific. This unusual site may be an evolutionary source of some species shared elsewhere; further exploration and collection here are a high priority as are strategies to protect the area due to endemism levels that will likely expand with further sampling.

4.1 | The western Pacific network

Much has changed since the network analysis by Moalic et al. (2012). Their dataset lists 181 species for our study area where we now verify 295. Throughout these older lists, descriptions of new species have replaced taxa that were first designated as trans-Pacific or that were lumped species. Although collections have increased, many specimens remain taxonomically undetermined; for example, 50% of the total polychaete record is missing designations at species, genus or even family level. New exploration will likely alter the connectivity network identified in our study. The addition of a few gastropod records from Poitrimol et al. (2022) made a notable change in the overall linkages from Manus Basin.

Most species are peripheral or ultra-peripheral in the network. However, the barnacle *Leucolepas longa* Southward & Jones, 2003 stands out with an 80% participation in modules of the network from Okinawa Trough to Lau Basin. This species has lecithotrophic larvae competent for at least 45 days (Tunncliffe & Southward, 2004), thus may be capable of transiting from system to system. In our study, network connections indicate past, but not necessarily present, population connectivity. While *L. longa* may emerge at intermediate sites (as in genetic analyses of Watanabe et al. (2018)), it may also have gone extinct in parts of the network where other neolepadid

barnacles established instead. The nine 'connector' species in this network have many gaps in their distributions. While further exploration will fill some gaps, others may relate less to dispersal capabilities than to availability of suitable habitat, including absence of competitors (Mullineaux et al., 2018). The role of Woodlark Basin (south of Manus Basin) as a regional stepping-stone connecting SW Pacific sites (Boullart et al., 2022) will be clarified as faunal lists become available. In our network, the distance-based metric explains only 22% of the variance among systems. The Raup-Crick index of β -diversity identifies non-random differences between assemblages implicating deterministic factors in their formation (Chase et al., 2011); as 70% of our pairwise comparisons were non-random, both environmental and historical factors likely are relevant.

Our test of the influence of numbers of expeditions or of sites visited per system finds no evidence of sampling bias, as assessed through these variables. Nonetheless, better sampling would enhance interpretation. Minimal collection effort is reflected in the low species richness of the Feni-Tabar and New Hebrides arc vents. However, as only a third of species from the former vent system occurs elsewhere and no system-endemism emerged from the latter, the outcome likely reflects a real pattern.

A few species in our study inhabit other chemosynthetic-based ecosystems. One example, the vestimentiferan tubeworm *Lamellibrachia columna* Southward, 1991, has a disjunct vent range, but does occur at bridging methane seeps in the SW Pacific (McCowin et al., 2019; Tunncliffe & Cordes, 2020). Vent systems with sedimented sites often have more seep species, as noted by Watanabe et al. (2010) for the Okinawa Trough where at least 16 species here also occur in other habitats. As only one species in the Mariana Trough is currently also known at seeps (Chen et al., 2016), this system has a higher adjusted endemism, underscoring the recommendation for extended protection for this isolated system. In addition, our data do not encompass the global vent faunas. Nonetheless, there is no western Pacific species currently recorded at eastern Pacific vents. Three species widespread in the western Pacific do occur in the Indian Ocean: *Munidopsis lauensis* Baba & de Saint Laurent, 1992, *Bathymodiolus septemdierum* (Hashimoto & Okutani, 1994) and *Archinome jasoni* Borda et al., 2013; this last species is also known from vent sites in the Atlantic (Borda et al., 2013). A recent molecular study identifies a single widespread holothurian species shared with Indian Ocean vent fauna (Thomas, Sigwart, & Helyar, 2022) while He et al. (2023) report the Okinawa Trough *Shinkaia crosnieri* Baba and de Saint Laurent, 1992, at seeps in the Indian Ocean.

4.2 | Biogeographic regions of the western Pacific

In a global analysis of hydrothermal vents, we expect that the western Pacific will remain a distinct region, as the adjacent Indian Ocean vent fauna emerges as a separate biogeographic entity (Zhou et al., 2022). Our data assembly forms a strong basis to define regional species pools that underlie biogeographic provinces through

similarity and network modularity analyses (Wilson et al., 2009). Currently, SW Pacific vent systems form a tightly linked province compared to the NW Pacific province (Figure 10) where depth differences and tectonic setting may influence species distributions (Brunner et al., 2022; Giguère & Tunnicliffe, 2021; Watanabe et al., 2019). A key difference in our results from those of past studies (Bachraty et al., 2009; Desbruyères, 2006; Rogers et al., 2012) is that the Mariana Trough now aligns with the NW Pacific.

Contemporary oceanographic features strongly influence locations of biogeographic boundaries through environmental requirements and dispersability of component organisms. Watling et al. (2013) define global provinces of the lower bathyal zone (800 to 3500m) based on four oceanographic variables in which the region including Tonga-Tofua-Kermadec arcs and Lau Basin separates from the rest of the western Pacific; this distinction is upheld in a later analysis of cnidarian distributions (Watling & Lapointe, 2022). That depth zone encompasses the average depth of all our vent systems, but the boundary mismatch with our study suggests variables such as carbon flux and dissolved oxygen are irrelevant to vent fauna. The exceedingly low probability of propagule transport across the Equatorial Countercurrent inhibits connectivity between SW and NW Pacific vents (Mitarai et al., 2016). Metapopulation interactions

among systems in the SW Pacific are hindered by prevailing current directions and topographic barriers. As the trans-system species examined to date have differing pathways of gene flow, generalized patterns of connectivity are not evident (e.g. Breusing et al., 2023; Poitrimol et al., 2022).

Historical factors play an important role in current species distributions. North-south separation of vent systems began as spreading ridges in intervening basins went extinct at about 15 Ma (mid-Miocene) in the vicinity of the Philippine and Caroline plates (Lallemand, 2016; Sdrolias & Müller, 2006). In the SW Pacific, late Cenozoic microplate rearrangements were frequent as rifting initiated and stopped. Diversification of an ancestral fauna may have occurred on the Tonga-Tofua-Kermadec arc where volcanism dates to the mid-Eocene (~45 Ma) and was sustained through the Cenozoic (Duncan et al., 1985; Schellart et al., 2006), surely with associated hydrothermal activity as occurs today (de Ronde & Stucker, 2015). As the North Fiji Basin formed adjacent to the arc at ~10 Ma, fauna could readily populate; later, the northern end of the arc itself split to form the Lau Basin ~6 Ma (Crawford et al., 2003) creating another sink for nearby vent larvae. Subsequently, westward connections to the Manus Basin were likely fostered by vents in the Woodlark Basin (Boulart et al., 2022). Similarly, in the NW Pacific, the

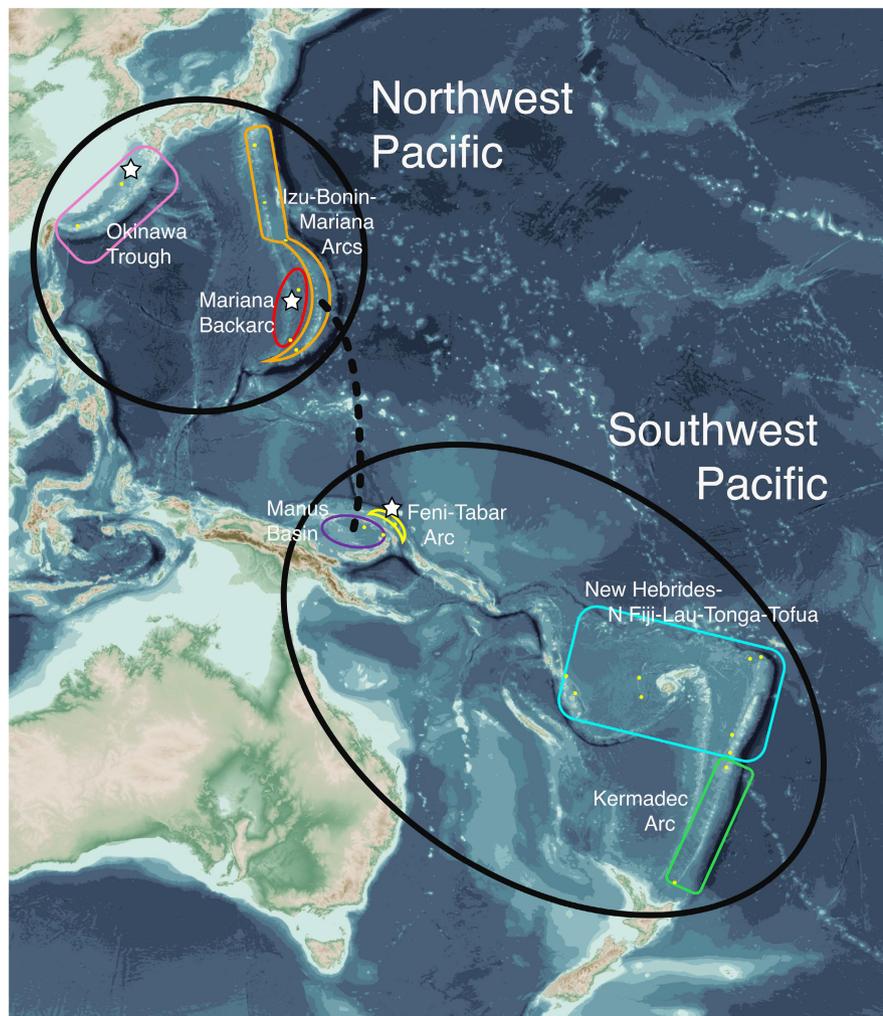


FIGURE 10 Summary of study outcomes. Black ellipses outline the vent provinces while the coloured shapes identify the network modules. The dotted black line represents the key linkage detected between the provinces. Stars indicate the three vent systems that contribute significantly to overall beta-diversity. The yellow dots are approximate locations of the geographic extremes of vent sites within each system for which we found data; overall, 72 sites were used.

Izu-Bonin-Mariana volcanic arc endured throughout the Cenozoic with considerable evidence of volcanism (Lallemand, 2016). Modern spreading initiated in the Mariana Trough at 3 Ma (Stern et al., 2003) presumably gathering recruits from the nearby arc, although few species exchange today. For the Okinawa Trough, the abundance of taxa unique to this vent system suggests a localized origin such as vents on the Ryukyu Arc and continental margin methane seeps.

We agree with Moalic et al. (2012) that the western Pacific played an important role in the evolution of vent faunas; we recommend further investigation into the early origination of arc faunas, in particular. The addition of more phylogeographic assessments may help determine diversification centres in the Pacific as illustrated for barnacles: the vent clade appears to originate in the NW Pacific and diversify further south before emerging in East Pacific Rise and Scotia Ridge vents in the late Miocene and, later, in the Indian Ocean (Herrera et al., 2015).

Species assemblage network analysis is highly effective in distinguishing distinct bioregions (Bloomfield et al., 2018). When combined with an examination of β -diversity patterns, evaluators have more information on the nature of diversity distribution and, to some extent, the drivers (Socolar et al., 2016). As mining plans advance in international waters in the Indian Ocean and Mid-Atlantic Ridge under the auspices of the International Seabed Authority, conservation of hydrothermal vent communities remains a top priority (Van Dover et al., 2018). The approach presented in this paper is one that can identify areas in need of special attention both to protect vulnerable sites and sites that serve as network hubs; it can be applied to other geographic regions in the future.

5 | CONCLUSIONS

The faunas of 11 western Pacific hydrothermal vent systems are characterized by a large number of system endemics and high β -diversity dominated by species replacement. These systems form a network that is poorly linked across the equator in which the Manus Basin emerges as a connection hub in the network. Few species extend beyond their basin or volcanic arc, thus disturbed communities will re-assemble by recruits within the vent system although system endemics could be lost. Four systems require conservation plans that focus on preservation of unique species in the event of disturbance such as mining: Mariana Trough, Okinawa Trough, Feni-Tabar Arc and Kermadec Arc. In addition, the central role of Manus Basin in linking this network that spans over 9000 km can be fostered with a sustained moratorium on mining here. We urge State jurisdictions to examine connectivity dynamics among vents in their jurisdiction and to consider consequences of conservation and exploitation scenarios of these unusual communities to vent systems beyond their borders. Continued support of exploration, systematic assessments and curation of hydrothermal vent collections is necessary to strengthen biogeographic assessments and conservation strategies. We expect two high-order provinces, Northwest Pacific

and Southwest Pacific, to remain well-defined in future global analyses of vent biogeography.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this study are available in the Supporting Information file Appendix I and are uploaded to Figshare (DOI: 10.6084/m9.figshare.24045732).

PEER REVIEW

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BIOSKETCH

The research team studies the communities found at hydrothermal vents in the Pacific. Among us, our field experiences and collections have spanned all (but one) of the vent systems documented in this paper. Together our expertise covers systematics, population connectivity, network analyses, community ecology and biogeographic patterns. Our interests in conservation approaches for active hydrothermal vents is fuelled by fascination with the unusual adaptations shown by most of these animals in these widespread, but locally limited, habitats. Our goal is to provide the science-based recommendations that can support management efforts.

Author Contributions: VT and OB conceived the study. All authors contributed data; TG created the database that was reviewed by CC. OB, TG and VT contributed analyses. VT wrote the manuscript and all authors contributed to edits.

SUPPORTING INFORMATION

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

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