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Adrien Tran Lu Y, Stéphanie Ruault, Claire Daguin-Thiébaud, Anne-Sophie Le Port, Marion Ballenghien, Jade Castel, Pierre-Alexandre Gagnaire, Nicolas Bierne, Sophie Arnaud-Haond, Camille Poitrimol, et al.

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1     **Comparative population genomics unveils congruent secondary suture**  
2                     **zone in Southwest Pacific Hydrothermal Vents**

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## Abstract

27           How the interplay of biotic and abiotic factors shapes current genetic diversity at the  
28 community level remains an open question, particularly in the deep sea. Comparative  
29 phylogeography of multiple species can reveal the influence of past climatic events,  
30 geographic barriers, and species life history traits on spatial patterns of genetic structure  
31 across lineages.

32           Here, we conducted a comparative population genomic study on seven hydrothermal  
33 vent species co-distributed in the Back-arc Basins of the Southwest Pacific region. Using  
34 ddRAD-seq, we compared distribution range-wide genomic diversity patterns across species  
35 and discovered a shared zone of phylogeographic break. Although species exhibit congruent  
36 patterns of spatial structure, they also show variation in the degree of divergence among  
37 lineages across the suture zone. Additionally, two species have a sympatric contact zone in  
38 the Woodlark Basin.

39           Demogenetic inference revealed shared histories of lineage divergence and secondary  
40 contact. Low levels of asymmetric gene flow probably occurred in most species between the  
41 Woodlark and North Fiji basins, but the exact location of contact zones varied from species to  
42 species. Results show that gene flow is heterogeneous across the genome, indicating possible  
43 partial reproductive isolation between lineages and early speciation.

44           Our comparative study sheds light on the factors that shape genetic variation at the  
45 community level, and our findings enrich our understanding of deep-sea biogeography  
46 patterns. Emphasizing the pivotal role of historical and contemporary factors, our research  
47 underscores the necessity for a holistic approach, and in particular filling in the gaps regarding  
48 life history traits of deep-sea species (generation time, development type, duration of the  
49 larval phase).

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## Introduction

53 Hydrothermal vents are one of the most emblematic chemosynthesis-based ecosystems that  
54 host a highly specialized fauna. This vent fauna depends on local hydrothermal activity and is  
55 likely to share historical patterns of colonization linked to the tectonic history of the ridge  
56 system (Plouviez et al., 2009, Matabos et al., 2011, Matabos & Jollivet., 2019). In contrast to  
57 other deep-sea ecosystems, vents represent a linear but highly fragmented and relatively  
58 unstable ecosystem based on chemosynthetic primary producers, which cannot thrive  
59 elsewhere. Hydrothermal activity is linked to specific geological features associated with the  
60 volcanic and tectonic activities of ocean ridges or submarine volcanoes (Hourdez and Jollivet,  
61 2020). Plate tectonics has previously been cited as a driver of most of the biogeographic  
62 distribution of the vent fauna (Tunnicliffe, 1991), that may lead to allopatric speciation with  
63 possible secondary contacts (Hurtado et al. 2004, Johnson et al. 2006, 2013, Faure et al. 2009,  
64 Plouviez et al., 2009, Matabos et al. 2011). On the East Pacific Rise, these previous studies  
65 pointed toward the emergence of a transition zone between biogeographic provinces initially  
66 separated.

67 Unlike other hydrothermal ecosystems, the fauna of the vents of the South-West  
68 Pacific is distributed across several geological Back-Arc-Basins (BABs) separated by abyssal  
69 plains, ridges and volcanic arcs, forming a fragmented and discontinuous complex. These BABs  
70 formations are estimated to be between 12 to 1 million years (My) old (Schellart et al., 2006).  
71 A Previous study highlighted contrasting phylogeographic patterns for few species, including  
72 some closely related species (Poitrimol et al., 2022). This suggested alternative dispersal  
73 strategies and evolutionary history to cope with fragmentation despite a common geological  
74 history of the vent habitat in this region. This geological dynamics provided a completely  
75 different and discontinuous situation of hydrothermal environments, in sharp contrast to the  
76 linear setting of mid-oceanic ridges such as the Mid-Atlantic Ridge (MAR) or the East Pacific  
77 Rise (EPR). These unique features raise questions about how abiotic and biotic factors shape  
78 the distribution of genetic diversity and the connectivity between populations of different  
79 lineages.

80 The vent fauna and communities inhabiting these Southwest Pacific BABs appear as a single  
81 biogeographic unit (Bachraty et al., 2009; Moalic et al., 2012; Tunnicliffe et al., 2024). In  
82 contrast to other hydrothermal communities, which are mainly composed of tubeworms,

83 mussels and shrimps, the BAB fauna is mainly composed of large symbiotic Provannidae  
84 gastropods, such as *Ifremeria nautilei* or *Alviniconcha* spp., and deep-sea *Bathymodiolus*  
85 mussels. These large engineer species create specific habitats for a wide assemblage of  
86 invertebrate species, including annelids from different families (e.g. Polynoidae, Alvinellidae,  
87 Siboglinidae), limpets (*Lepetodrilus* spp., *Shinkailepas* spp.), barnacles, holothurians, and  
88 crustaceans (copepods, amphipods, shrimps, and crabs) (Desbruyères et al., 2006).

89 While these vents form thriving oases of life, they also produce metallic sulfide deposits, which  
90 attract the interest of deep-sea mining companies. The upcoming management of the  
91 Southwest Pacific vent fauna will rely on understanding population delimitation and  
92 parameters, which are of crucial importance in conservation biology (Gena, 2013; Niner et al.,  
93 2018; Van Dover, 2011; Van Dover et al., 2017; Washburn et al., 2019). Anthropogenic  
94 exploitation of vent resources has already begun on a Japanese site in the Northwest Pacific  
95 and has been first planned in the Manus BAB (Solwara prospects) but recently abandoned,  
96 although the potential consequences of these activities are not yet known (Carver et al., 2020).

97 Connectivity and renewal of vent populations is mostly driven by larval dispersal due to the  
98 sedentary nature and the strict relationship with the vent fluid. While some vagile fauna, such  
99 as fish, crabs, or shrimp, may contribute to connectivity through adult migration in response  
100 to local environmental changes, but only to very limited spatial scale (vent fields) (Lutz et al.,  
101 1994; Shank et al., 1998). Direct connectivity assessment is not technically feasible for minute  
102 larvae numbering in millions and their life-traits characteristics (Levin, 1990, Vrijenhoek,  
103 2010). As consequence, demographic connectivity needs to be assessed by indirect methods  
104 such as population genetics, larval dispersal modeling or recent method of elemental  
105 fingerprints tracking (Mouchi et al. 2024).

106 Dispersal modeling in the region suggested possible but limited larval exchange between  
107 distant back-arc basins (Mitarai et al., 2016). However, in the context of the unstable and  
108 fragmented habitat of deep-sea hydrothermal vents, metapopulation theory predicts long-  
109 distance dispersal to mitigate risks of inbreeding and local extinction (Hamilton & May, 1977;  
110 McPeck & Holt, 1992). Initial genetic analyses of several vent species along mid-oceanic ridges  
111 however displayed conflicting evidence regarding dispersal capabilities, with some suggesting  
112 almost panmictic populations at the ridge scale while others hint at patterns of isolation by  
113 distance and stepwise (re)colonization (Teixeira et al., 2012; Audzijonyte & Vrijenhoek, 2011).

114 Present-day geographical distribution of genetic diversity reflects the complex interplay of  
115 connectivity patterns across space and time. Studying and disentangling the origin of these  
116 variations is the main objective of phylogeography (Avice, 2000, 2009; Avice et al., 1987).  
117 Expanding this approach, to a multispecies comparative framework within a given biome or  
118 ecosystems can highlight the effect of several factors shaping the genetic diversity (Hickerson  
119 et al., 2010; Papadopoulou & Knowles, 2016). Using new methods and approaches for large  
120 genomic dataset, we can start to disentangle past and present connectivity patterns and offer  
121 a unique opportunity to describe species distribution patterns at the community level and to  
122 improve scientific guidelines for conservation (De Jode et al., 2023, Gagnaire, 2020).

123 Our study aimed to elucidate genetic diversity and connectivity patterns across a  
124 biogeographic hydrothermal unit in the South West Pacific. We conducted a comparative  
125 population genomics analysis on seven vent species spanning various taxonomic groups  
126 inhabiting the same environment and geographic range, covering most basins of the South  
127 West Pacific region. Phylogeographic patterns exhibited by these species, each characterized  
128 by distinct life-history traits, were compared at a regional scale using a genome-wide analysis.  
129 This analysis revealed a clear phylogeographic break encompassing all seven species around  
130 the Solomon-Vanuatu archipelago islands, alongside a contact zone on the Woodlark ridge  
131 observed in two species. Based on inferred demogenetic histories, we propose a scenario of  
132 vicariance for all species. Furthermore, estimating genetic diversity and gene flow at the  
133 community scale underscores the importance of comprehending population connectivity  
134 across different geographic scales. This understanding is vital for informing potential  
135 management strategies, particularly in the context of future deep-sea mining activities, and  
136 for gaining more insights into biogeography of deep-sea species.

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## Material and methods

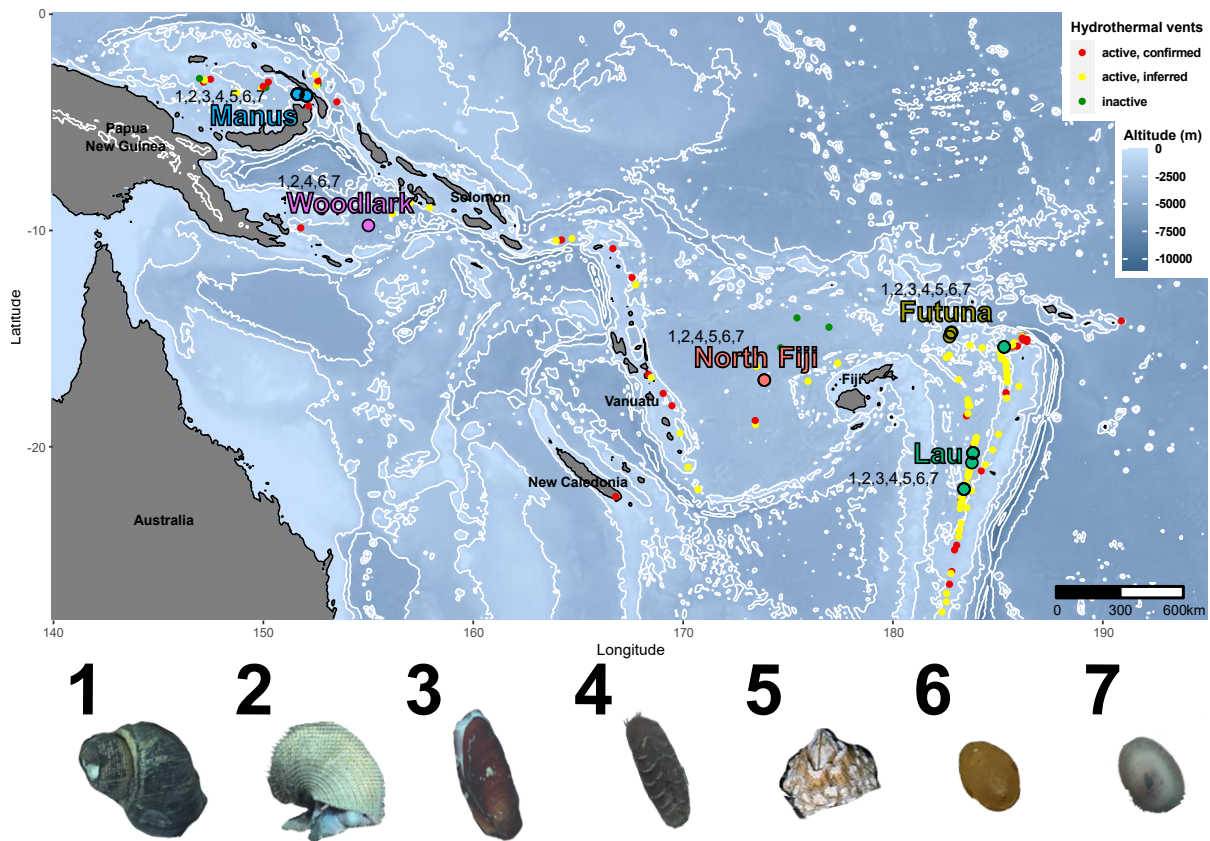
### 143 *Sampling*

144 Seven hydrothermal-vent species from four main vent habitats have been sampled over five  
145 Western Pacific regions (the Manus, Woodlark, North Fiji, Lau back-arc basins) and the Futuna  
146 volcanic arc (see SI Table 1 and Figure 1). These species include the emblematic symbiotic  
147 snails *Ifremeria nautilei* and *Alviniconcha kojimai*, the vent mussel *Bathymodiolus manusensis*,  
148 the limpets *Shinkailepas tollmanni*, *Lepetodrilus schrolli*, and *L. aff. schrolli* (recently described  
149 as *L. fijiensis* by Chen & Sigwart 2023 in North Fiji, Lau and Futuna BAB), which live on the  
150 shells of *I. nautilei*, *Bathymodiolus manusensis* and *B. septemdierum*, the cirriped  
151 *Eochionelasmus ohtai*, mostly found on the edge of diffuse venting areas, and, finally, the large  
152 scaleworm *Branchinotogluma segonzaci*, found on the walls of vent chimneys. Animal  
153 collections were made during the Chubacarc cruise in 2019 (chief scientists S. Hourdez & D.  
154 Jollivet) on board the RV *L'Atalante* with the ROV Victor 6000 (Hourdez & Jollivet 2019). All  
155 species, with the exception of *B. segonzaci*, were sampled from diffuse venting areas with the  
156 tele-manipulated arm of the ROV and brought back to the surface in thermally insulated  
157 boxes. The mobile chimney scaleworms *B. segonzaci* were collected using the slurp gun of the  
158 ROV and kept in 5 L bottles until the ROV recovery. On board, large animals (provannid  
159 gastropods, mussels, cirripedes and scaleworms) were dissected to separate tissues and  
160 individually preserved in 80% ethanol, and/or directly used for DNA extractions. A hierarchical  
161 sampling scheme was used for all species by sampling two replicate sites within each vent field  
162 (locality) and one to three vent fields per basin, for a total number of 21 sampling localities  
163 for each vent community (SI Table 1). A total number of 24 individuals were preserved for DNA  
164 extraction (or extracted directly) for each locality replicate and species.

165 This sampling scheme was however not possible for *B. manusensis*. It was only found at  
166 Manus, Futuna and one site of Lau (at the Mangatolo locality) in sympatry with *Bathymodiolus*  
167 *septemdierum* (previously known as *B. brevior*). It was not found at the site La Scala in the  
168 Woodlark Basin (no mussels), nor at the Southern localities of the Lau Basin and along the  
169 North Fiji Ridge, where *B. septemdierum* was only found. DNA extractions were directly  
170 performed on board for *I. nautilei* (foot tissue), *A. kojimai* (foot tissue), *B. manusensis* (mantle  
171 tissue), *S. tollmanni* and *L. schrolli* & *L. aff schrolli* (now *L. fijiensis*) (whole individual without  
172 the shell) and *E. ohtai* (whole individuals without the skeleton). For *B. segonzaci*, DNA



173 extractions were done later in the laboratory on ethanol-preserved tissues. DNA extractions  
174 were either performed with a modified CTAB 2%/PVPP 2% protocol (see Jolly et al. 2003) or  
175 the NucleoSpin®Tissue 96 kit (Macherey-Nagel, Karlsruhe, Germany).



176

177 *Figure 1: Sampling areas in the South-west Pacific Ocean. Colors represent the different areas (BABs and volcanic arc). Each*  
178 *square box contains species found and sampled for each sampling area. 1: *I. nautiliei*, 2: *A. kojimai*, 3: *B. manusensis* 4: *B.**  
179 *segonzaci*, 5: *E. ohtai*, 6: *S. tollmanni* and 7: *L. schrolli* (& *fijiensis*). Small points represent hydrothermal vents. Red, active and  
180 *confirmed. Yellow, Active and inferred. Green, Inactive. Vents activity data taken from InterRidge Vents Database V3.4.*

181

### 182 **Preparation of the ddRAD Libraries.**

183 The preparation of ddRAD genomic libraries was standardized by following the protocol  
184 described in Daguin-Thiébaud et al. (2021) and used for *I. nautiliei* in Tran Lu Y et al. (2022).  
185 These seven libraries comprise 294 individuals for *A. kojimai* (from Castel et al. (2022)), 469  
186 individuals for *S. tollmanni*, 282 individuals for *E. ohtai*, 195 individuals for *B. manusensis*, 262  
187 individuals for *B. segonzaci*, and 522 individuals for *L. schrolli* & *L. fijiensis*. All libraries were  
188 produced from gDNA digested with the enzymes *Pst1* and *Mse1*, except for *B. manusensis* that  
189 was digested with *Pst1* and *Msp1*.



190 These libraries also included 8 to 47 replicates (individuals replicated twice or three times as  
191 controls) used for quality control and parameter calibration. Single-end (only for *B.*  
192 *manusensis*) or paired-end 150 sequencing (all other taxa) was performed on HiSeq 4000 (*I.*  
193 *nautilei*) or Novaseq 6000 Illumina (all other taxa), by the Genoscope, France (*I. nautilei*), or  
194 Novogene Europe (Cambridge, UK; all other taxa). The Fastqc Software (V.0.1.19) was used to  
195 check the sequence quality of the raw reads prior to the *de novo* assembly for each species.

196 An independent assembly was performed from each species library with the “*de novo*” Stacks2  
197 module (Rochette et al., 2019) after demultiplexing individuals with the Process\_radtags  
198 module. Parameter calibration approach followed the recommendations of Mastretta-Yanes  
199 et al. (2015) and Paris et al. (2017), (see SI Calibration). For all species, the parameter  
200 calibration approach, data filtering, and the Stacks modules used were consistent with the  
201 methods described in Tran Lu Y et al. (2022). However, for *S. tollmanni* and *L. schrolli* & *L.*  
202 *fijiensis*, the data filtering was slightly modified to reduce the loss of SNPs and individuals while  
203 minimizing the proportion of missing data due to a greater allele divergence (SI Table 2).  
204 Additionally, for each species, the minor allele frequency filter was replaced by a masking of  
205 singletons in the demogenetic inference datasets (i.e. used with  $\partial a \partial i$ ). Finally, the “*de novo*”  
206 assembly of *B. manusensis* data was realized from single-end reads (R1, 150 bp).

### 207 ***Population structure and admixture across the southwest Pacific***

208 For each species, a series of independent population genomics analyses were performed to  
209 explore the population structure, phylogeographic and admixture patterns. Principal  
210 Component Analysis (PCA) was performed on individual genotypes with SNPRelate (V.1.21.7)  
211 to explore the spatial distribution of genetic diversity (Zheng et al., 2012). Further analyses to  
212 explore population differentiation and admixture proportions were performed with the  
213 software Admixture (V.1.3.0) (Alexander & Lange, 2011). Population trees including migration  
214 edges and  $F_3$  statistics were computed with the software Treemix (V.1.13) (Pickrell & Pritchard,  
215 2012) with ten replicates and migration events from 0 to 5.

216 The degree of genetic differentiation was estimated with pairwise  $F_{st}$  values between groups  
217 of individuals (genetic units or metapopulations, basins or localities) with Arlequin (V.3.5.2.2)  
218 (Excoffier & Lischer, 2010) and their statistical significance was assessed with 10,000  
219 permutations of genotypes between populations. All plots were produced with R (V.4.0.3) (R

220 Core Team, 2023) and ggplot2 (V.3.3.6) (Wickham, 2016). For *S. tollmanni*, Woodlark  
221 individuals were split into two groups according to their genetic assignment (See results).

222 In addition, the net divergence between two populations ( $D_a$ ) was calculated from the  
223 measure of absolute divergence ( $D_{xy}$ ) corrected by the average nucleotide diversity ( $\pi$ )  
224 estimated using Stacks2 (Rochette et al., 2019) by following the formula of Nei & Li (1979).  
225 The genetic diversity indices ( $H_e$ ,  $H_o$ ,  $\pi$ ) were also calculated for each species with the Stacks  
226 (V.2.52) population module on the final dataset. Indices were estimated for each genetic unit  
227 found by PCA and the Admixture analysis, which number depends on the species considered  
228 and on geography (five geographic regions/BABs listed in SI Table 1).

### 229 ***Evolutionary history of vent species and metapopulation connectivity***

#### 230 **Relative gene flow orientation.**

231 Gene flow orientation was assessed with the module Divmigrate (Sundqvist et al., 2016)  
232 contained in the R package diveRsity (V.1.9.90) (Keenan et al., 2013). This method uses allele  
233 frequencies and several estimators derived from the  $F_{st}$  statistics to calculate a migration  
234 matrix between populations, which is then normalized by the highest gene flow value found  
235 in the pairwise comparisons, setting gene flow value between 0 and 1 (where 1 represents  
236 100% gene flow and 0, no gene flow). Statistical significance of the difference between gene  
237 flow directions in a given pair of populations was estimated with 1000 bootstraps.

#### 238 **Demogenetic history of species metapopulations**

239 To understand the demographic history of populations and identify the best model of  
240 population divergence, we fitted joint allele frequency spectra to specific population models  
241 with the *dad*i software (V2.1.0) (Gutenkunst et al., 2009) for each taxon independently,  
242 considering the case of an ancestral population splitting into two daughter populations with  
243 or without migration. Our choice was dictated by the fact that populations of all vent species  
244 analyzed (with the exception of *L. schrolli* & *L. fijiensis*, see results) are only subdivided into  
245 two genetic units (Eastern vs. Western populations). Although, *L. schrolli* & *L. fijiensis* displays  
246 further minor subdivisions between basins, for the sake of the comparison with other species,  
247 we considered Eastern (NF/L) vs Western populations (M) (see discussion). One of the main  
248 advantages of the *dad*i approach is that it takes into consideration the effects of linked  
249 selection and heterogeneous migration across the genome. Ignoring these effects in

250 demographic inference may lead to erroneous reconstructions of the evolutionary history of  
251 populations (Ewing & Jensen, 2016; Ravinet et al., 2017). To discuss patterns of divergence  
252 and past and present genetic connectivity of all species, we re-used the models implemented  
253 in Tran Lu Y et al. (2022) with a similar population design for all taxa. These models considered  
254 a total of 28 possible scenarios extended from the 4 major divergence models (Strict Isolation  
255 (SI), Isolation with Migration (IM), Ancient Migration (AM) and Secondary Contact (SC)) that  
256 were initially developed and used in Rougeux et al. (2017) (also see Tran Lu Y et al., 2022 for  
257 further details). Briefly, different demographic and evolutionary processes have been  
258 considered within these models, such as the increase or the contraction in size of the two  
259 derived populations (G), the effect of barrier loci due to either hybrid counterselection or local  
260 adaptation by simulating heterogeneous migration along the genome (2m) and the effect of  
261 linked selection (2N).

262 The ancestral allele of each locus could not be identified because no external groups were  
263 available (or too divergent) for any of the taxa. Hence, we used folded joint allele frequency  
264 spectra (folded JAFS). All models were fitted 10 times independently for each species to check  
265 for model convergence. The Akaike Information Criterion (AIC) was used to compare models  
266 for each simulation. Given the gaps in the knowledge of the biology of these taxa, we  
267 estimated model parameters and divergence times (i.e.  $T_s$  since divergence,  $T_{sc}$  since  
268 secondary contact, and the absolute divergence time, which can be  $T_s$  or  $T_s+T_{sc}$ ) using an  
269 average mutation rate of  $10^{-8}$ . Parameter uncertainties were calculated using the Fisher  
270 Information Matrix (FIM) on the best fit model for each species. The uncertainties are  
271 calculated at the 95% confidence level.

272

## Results

### 273 ***Calibration parameters and filtering steps.***

274 The 150 bp paired-end sequencing yielded an average of 3.7, 3.3, 3.0 and 2.8 million of paired  
275 reads per individual for *S. tollmanni*, *E. ohtai*, *B. segonzaci* and *L. schrolli* & *L. fijiensis*,  
276 respectively. For *B. manusensis*, single read data were obtained with 2.9 million reads per  
277 individual. The raw reads used from *A. kojimai* and *I. nautilei* were obtained following the  
278 protocol described in Castel et al. (2022) and Tran Lu Y et al. (2022).

279 For each species, we identified the most appropriate set of assembly parameters with Stacks  
280 (V.2.52) by applying the same pipeline of the *de novo* assembly of bi-allelic loci used for *I.*  
281 *nautiliei* in Tran Lu Y et al (2022) following the procedure recommended by Mastretta-Yanes  
282 et al. (2015) and Paris et al. (2017). After running several sets of parameter combinations, we  
283 decided to use the assembly parameters that ranged between 4 and 6 for m, 4 and 11 for M  
284 and 5 and 11 for n, depending on the species under scrutiny (see SI Calibration & SI Table 3).  
285 In addition, we applied the same methodology, analyses, modules and filtering parameters  
286 that we used for *I. nautiliei* in Tran Lu Y et al. (2022) to better compare genetic patterns  
287 between species (see SI Calibration). The *de novo* assemblies and subsequent filtering steps  
288 resulted in a variable number of SNPs (2 904 to 47 547) obtained for 159 to 414 individuals  
289 retained for each of the 7 species (see SI Table 2 & 3).

290

### 291 **Population structure and admixture.**

292 Population structure analyses revealed similar patterns for the spatial distribution of genetic  
293 diversity for the seven species. The PCA showed a common genetic structure, separating the  
294 Manus individuals from those of the Eastern zones (i.e. North Fiji, Futuna and Lau, hereafter  
295 NF/F/L) on the first component (PC1), with 1.94% to 26.03% of the total variance explained  
296 (Figure 2). However, the site La Scala on the Woodlark Ridge (newly discovered, Boulart et al.,  
297 2021) showed contrasting results. First, *I. nautiliei*, *A. kojimai*, and *E. ohtai* are clearly  
298 subdivided into two genetic groups with individuals of Manus-Woodlark (M/W) on one hand,  
299 and individuals from NF/F/L on the other hand (Figure 2 A, B, D). However, the genetic  
300 relationships of individuals from Woodlark differ slightly for the other species. *S. tollmanni*  
301 was also subdivided into two genetic groups but individuals from Woodlark clustered with  
302 either the Manus or with the NF/F/L genetic groups, with one admixed individual positioned  
303 in between (Figure 2 E). For *L. schrolli* & *L. fijiensis*, all individuals from Woodlark are positioned  
304 as intermediates between Manus (*L. schrolli*) and NF/F/L (*L. fijiensis*). These intermediate  
305 individuals are genetically closer to the North Fiji individuals, which slightly differed from the  
306 Futuna/Lau (F/L) individuals on PC1 (Figure 2 G). A comparable situation also holds for the  
307 species *B. segonzaci* for which the Woodlark individuals are well separated from either  
308 individuals of Manus or those of the NF/F/L group but are a little bit closer to the latter (Figure  
309 2 F). For *B. manusensis*, which is absent from La Scala, a similar situation is observed (Figure 2  
310 C).

311 The second component (PC2) accounting for 0.62-0.76% of the total genetic variance, also  
312 showed slight differences at the regional scale for some species (Figure 2 B, F, G). Individuals  
313 from North Fiji exhibit a slight genetic differentiation from the group F/L on PC2 for both *A.*  
314 *kojimai* and *L. fijiensis*, and the same pattern is observed between Woodlark and Manus  
315 individuals for *B. segonzaci* and *L. schrolli*. According to the first two principal components of  
316 the PCA, the only species exhibiting a more basin-specific signature was the species complex  
317 *L. schrolli/L. fijiensis* (Figure 2 G and SI Figure 1).

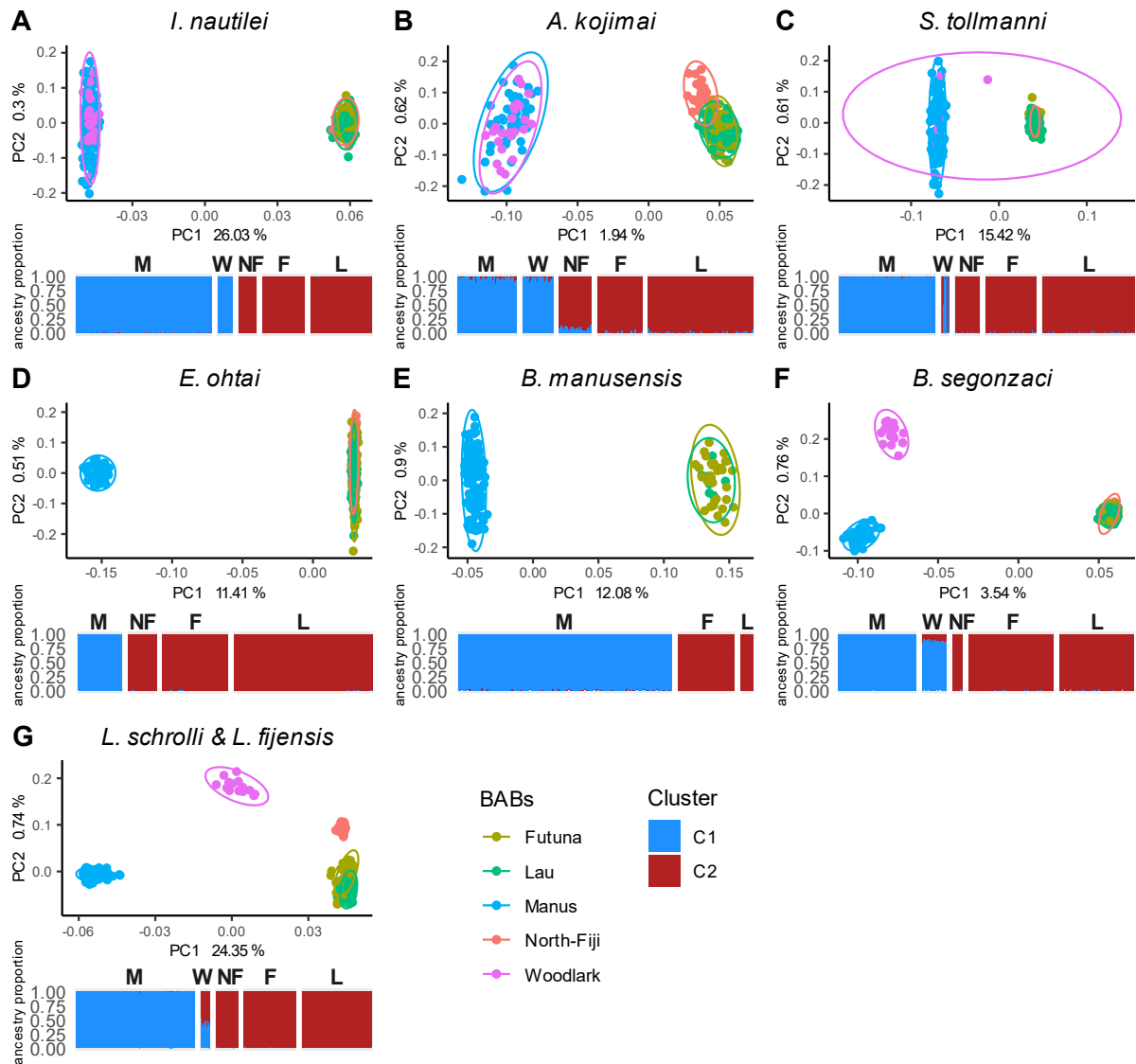
318 This shared distribution of the genetic variation was also captured by admixture analyses for  
319 all species. The optimal number of clusters identified was always  $k = 2$  (SI Figure 2). These two  
320 genetic units are composed, as previously found, of M/W individuals on one side, and NF/F/L  
321 on the other side. Except for some individuals from Woodlark and North Fiji BABs for which  
322 genome admixture ranged between 10 to 50% depending on the species under scrutiny, the  
323 proportion of shared ancestry between these two groups is very low for most individuals  
324 (Figure 2). Woodlark individuals for *L. schrolli/L. fijiensis*, *S. tollmanni* and *B. segonzaci* display  
325 shared ancestry from both genetic clusters. In *S. tollmanni*, the Woodlark population is  
326 composed of a mixture of parental types (both genetic backgrounds) and a putative F1 hybrid.  
327 In contrast, all Woodlark individuals displayed almost equal (~50%) shared ancestry from both  
328 *L. schrolli* (Manus group) and *L. fijiensis* (Eastern group) when  $k = 2$ . Admixture analyses also  
329 discriminate additional clusters for Woodlark and then North Fiji in the *L. schrolli/L.fijiensis*  
330 species complex with increasing values of  $k$  ( $K = 3$  to 5, SI Figure 3 & 4).

331 The  $F_3$  statistics showed significant negative values, indicating admixture in Woodlark, for two  
332 species only. The first species is *S. tollmanni*, with individuals from the Western (Woodlark2)  
333 population (Manus type) with source populations coming from both Manus (M) and the  
334 Eastern group (NF/F/L) and Woodlark1 (Lau type). The Woodlark *Lepetodrilus* individuals  
335 displayed a similar situation with source populations coming also from Manus (M) and the  
336 Eastern group (NF/F/L) (SI Figure 5).

337 Examining the overall genetic differentiation ( $F_{st}$ ) and the net divergences ( $D_a$ ) between the  
338 Western and Eastern groups provided three main patterns (Table 1). The first group of species  
339 (i.e. the limpets *Lepetodrilus* and *Shinkailepas*) is characterized by high values of  
340 differentiation (0.271-0.360) and divergence (0.013-0.019). The species of the second group  
341 (*I. nautiliei*, *E. ohtai* and *B. manusensis*) also have high values of genetic differentiation (0.203-

342 0.387) but low to moderate divergences (0.002-0.007). Finally, the last group comprising *B.*  
343 *segonzaci* and *A. kojimai* has low values of genetic differentiation (0.018-0.038) and moderate  
344 divergences (0.007).

345 Pairwise  $F_{st}$  also captured differentiation between localities, when the five regions were  
346 considered as separate populations, with  $F_{st}$  ranging from 0 to 0.364, depending on the species  
347 analyzed and the pair of populations compared (SI Table 4). Most cases of significant genetic  
348 differentiation between BABs were observed in pairwise comparisons between the Western  
349 and Eastern BABs (Manus or Woodlark against Lau, North Fiji and Futuna). Some  
350 differentiation was also observed at the basin scale within a group with some specific  
351 separation of the populations from North Fiji and Futuna/Lau for the species *A. kojimai* and *L.*  
352 *fijiensis*. No population differentiation between Lau and Futuna has been however observed  
353 except for *L. fijiensis*, where differentiation is extremely low but significant.



354  
 355 *Figure 2: All PCA (PC1 & PC2) and Admixture plots for the best number of genetic clusters (K = 2) for each species (A, B, C, D,*  
 356 *E, F, G). Colors in PCA plots represent regions (Manus, Woodlark, North Fiji and Lau Back-Arc-Basins, and the Futuna Volcanic*  
 357 *Arc). Open circles represent the multivariate normal distribution of each group of points (basins) at 95% in PCA plots. Colors*  
 358 *in Admixture plots represent each inferred genetic cluster. M: Manus, W: Woodlark, NF: North Fiji, F: Futuna, L: Lau.*

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366 Table 1: Fixation index ( $F_{st}$ ) and net nucleotide divergence ( $D_a$ ) measured between the two (Eastern and Western)  
367 metapopulations for each species.

Species	$F_{st}$ (M/W vs NF/F/L)	$D_a$ (M/W vs NF/F/L)
<i>Lepetodrilus schrolli</i> & <i>L. fijensis</i>	0.360	0.019
<i>Shinkailepas tollmanni</i>	0.271	0.013
<i>Ifremeria nautili</i>	0.387	0.008
<i>Eochionelasmus ohtai</i>	0.203	0.007
<i>Branchinotogluma segonzaci</i>	0.038	0.007
<i>Alviniconcha kojimai</i>	0.018	0.007
<i>Bathymodiolus manusensis</i>	0.206	0.002

368

369 Treemix analyses revealed a consistent two-group pattern of population differentiation across  
370 species, with varying optimal numbers of migration events (ranging from 0 to 2) between the  
371 two regions (SI Figure 6 and 7). These findings highlight the occurrence of a primary migration  
372 event between the Eastern and Western groups for all species, excluding *E. ohtai* and *B.*  
373 *manusensis*. Furthermore, a secondary migration event was exclusively observed for *I.*  
374 *nautili*, *A. kojimai*, and *S. tollmanni*, occurring between two different basins of the same  
375 genetic group (i.e., metapopulation). Notably, these interacting basins were not consistently  
376 the same across different species. *B. segonzaci* exhibited a distinctive pattern, featuring two  
377 migration events between the Eastern and Western groups: the first one from Futuna to  
378 Woodlark and the second from Lau to Manus.

### 379 **Genetic diversity of species**

380 Regardless of the statistics used ( $H_o$ ,  $H_e$  and  $\pi$ : SI figure 8 & 9), *S. tollmani* displayed a gene  
381 diversity twice higher than that of the other species. The level of genetic diversity of species  
382 slightly differed between the Eastern and Western groups, but not always in the same  
383 direction. *I. nautili*, *B. manusensis* and *L. schrolli/L.fijiensis* exhibit a slightly higher gene  
384 diversity in M/W compared with NF/F/L whereas it was the opposite for the other species (*A.*  
385 *kojimai*, *S. tollmani*, *E. ohtai* and *B. segonzaci*). These statistics displayed exactly the same  
386 pattern of distribution when calculated per basin (see SI Figure 9).

387 ***Evolutionary history of populations and connectivity at the multispecies scale***

388 **Relative migration rates**

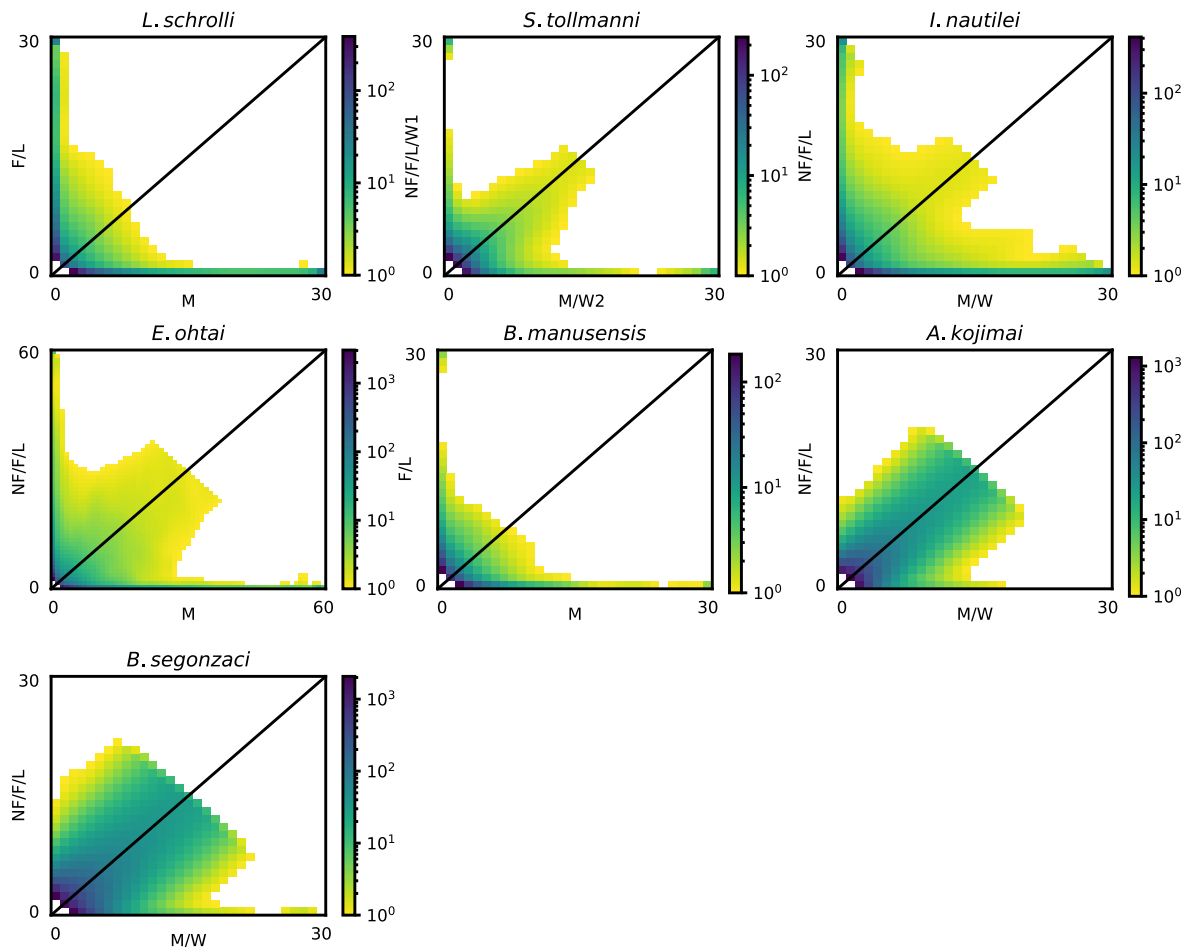
389 The Divmigrate analysis between the Eastern and Western groups revealed a robust and  
390 common pattern of bidirectional but asymmetrical gene flow in all species. The main direction  
391 of gene flow predicted by the analysis is westward from NF/F/L (1) to M/W (2), while gene  
392 flow in the opposite direction was about half to a two-third (SI Figure 10). The species complex  
393 *L. schrolli/L. fijjensis*, however, displayed a more complex bidirectional pattern with a much  
394 stronger gene flow between Futuna and Lau than between Futuna/Lau and North Fiji and  
395 virtually no gene flow between Woodlark, Manus and the others BABs.

396 **Demo-genetic inferences**

397 **Modes of divergence**

398 The folded JAFS (Figure 3) show the distribution of allelic variants between the Eastern and  
399 western metapopulations for each species. Of the 28 models tested for each species, the SC  
400 (Secondary Contact) model was almost always the best-fitting model selected by the  
401 Weighted AIC. The exceptions are *I. nautiliei* (Tran Lu Y et al., 2022) and *B. manusensis*, for  
402 which the SC model is slightly, but not significantly, better than the IM (Isolation with  
403 Migration) model. The Strict Isolation (SI) model was the worst model for all species. This  
404 indicated that all species are still able to maintain low levels of gene flow at the regional scale  
405 despite the large geographical distances and the abyssal plain separating the different regions.  
406 Increasing the complexity of the SC or IM population model by the addition of genomic  
407 heterogeneity (2N and/or 2m) or demographic change (G) parameters improved the model fit  
408 (see Figure 4 and SI Figure 11). Capturing linked selection (2N) improved the model fit more  
409 than the G or 2m parameters for most species except *E. ohtai*. Alternatively, adding  
410 heterogeneous gene flow (2m) to the SC model improved the model fit for *E. ohtai* (SC2mG),  
411 although the two metapopulations appeared to be well separated. This situation of semi-  
412 permeable barrier also holds for *S. tollmanni* and *L. schrolli/L. fijjensis*, for which genetic  
413 admixture is locally suspected. For these two latter species but also for *A. kojimai*, *B.*  
414 *segonzaci*, and *I. nautiliei*, the SC2N2mG was the best model after evaluating all possible  
415 parameter combinations. For *B. manusensis*, it was however not possible to discriminate

416 between the models IM2N, SC2N, and SC2N2m, and both SC2mG and SC2NG performed  
417 similarly as well as the SC2N2mG model for *B. segonzaci* (Figure 4 and SI Figure 11 & 12).



418  
419 *Figure 3: Folded Joint Allele Frequency Spectrum (JAFS) plots for all species. Each four plots represent, Observed Joint allele*  
420 *frequency spectrum (JAFS) between lineages East and West. NF: North Fiji, F: Futuna, L: Lau, M: Manus, W: Woodlark*

### 421 **Timing of divergence and gene flow**

422 Depending on the best model, we estimated divergent times  $T_s$  (time since the population split),  $T_{sc}$  (time  
423 since the secondary contact after the primary divergence), and  $T_{total}$  (which could be  $T_s$  or  $T_s+T_{sc}$ ), using  
424 a fixed mutation rate of  $10^{-8}$  (Table 2).  $T_s$  ranged by a factor of ten thousand generations to about one  
425 hundred thousand generations according to the species analyzed (40 000 for *A. kojimai* to 116 000 for *L.*  
426 *schrolli/L. fijensis*). Similarly, the time elapsed since secondary contact ( $T_{sc}$ ) changes also by a factor of 10  
427 from 6,386 generations for *S. tollmanni* to 69,371 generations for *I. nautilei* and *L. schrolli/L. fijensis*.  
428 However, the total time since the ancestral population split ( $T_s$  or  $T_s+T_{sc}$ ) varied less, with the lowest values  
429 being 40,892 and 42,117 generations for *A. kojimai* and *B. segonzaci* respectively, and the highest values  
430 being 94,071, 116,711 and 101,718 generations for *E. ohtai*, *L. schrolli/L. fijensis* and *B. manusensis*,  
431 respectively. For *B. manusensis*, the time of divergence however varied up to two-fold (43,644 to 101,718

432 generations) depending on the best models used. *I. nautiliei* and *S. tollmanni* produced intermediate values  
 433 of spitting times.

434 All species display heterogeneous gene flow (2m). Migration rate parameters estimated from *dad1* show  
 435 that present-day gene flow is stronger from NF/F/L to M/W (East to West) than the opposite, with the  
 436 exception of *L. schrolli/L. fijiensis* for both the two classes of gene flow ("neutral" migration  $m$  and  
 437 "reduced" (due to barrier loci) migration  $m_e$ , in relative genomic proportions  $P$  and  $1-P$ ; Table 3). For *B.*  
 438 *manusensis*, migration rates were similar in both directions. *I. nautiliei* and *E. ohtai* had about half of their  
 439 genome characterized by reduced gene flow ( $P \sim 1-P$ ). Only *A. kojimai* displayed high neutral gene flow  
 440 (with  $m > m_e$  and  $P \gg 1-P$ ) whereas *S. tollmanni*, *B. segonzaci*, *B. manusensis* and *L. schrolli/L. fijiensis*)  
 441 exhibited a larger proportion of barrier loci ( $1-P \gg P$ ) which strongly reduced gene flow ( $m_e \ll m$ ) between  
 442 the genome of the two genetic groups (Table 3).

443 *Table 2: Estimation of divergence times (Times are estimated with a fixed mutation rate per generation and site,  $10^{-8}$ ) and*  
 444 *estimation of mutation rate per site and generation for all species.  $T_s$ : time since the ancestral population subdivided into two*  
 445 *populations;  $T_{sc}$ : time since secondary contact.  $T_{total}$ :  $T_s$  and  $T_s + T_{sc}$ . For *I. nautiliei* using the AM2N2mG model,  $T_s$*   
 446 *corresponds to the time of the strict split after ancient migration ended ( $T_{sc}$ ).*

Species	Best model	$T_s$	$T_{sc}$	$T_{total}$
<i>I. nautiliei</i>	IM2N2mG		66 951	66 951
<i>I. nautiliei</i>	SC2N2mG	16 279	54 017	70 295
<i>I. nautiliei</i>	AM2N2MG	41	69 372	69 413
<i>A. kojimai</i>	SC2N2mG	29 157	11 735	40 892
<i>S. tollmanni</i>	SC2N2m	63 335	5 419	68 754
<i>S. tollmanni</i>	SC2N2mG	42 683	22 326	65 009
<i>E. ohtai</i>	SC2mG	37 278	56 793	94 071
<i>B. segonzaci</i>	SC2N2mG	18 194	15 375	33 569
<i>B. manusensis</i>	IM2N	101 718		101 718
<i>B. manusensis</i>	SC2N2m	40 752	2 892	43 644
<i>B. manusensis</i>	SC2N	56 394	37 940	94 335
<i>L. schrolli/L. fijiensis</i> )	SC2N2mG	48 381	68 331	116 712

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451 Table 3: Gene flow parameters estimated from  $\partial\text{adi}$  ( $m$  and  $m_e$  are the “neutral” and “reduced” migration rate parameters.  
 452  $P$  the proportion of the genome characterized by migration rate  $m$ , and  $1-P$  the proportion of the genome affected by reduced  
 453 migration  $m_e$ ). 1 : East population (NF/F/L); 2 : West population (M/W).

Species	Best model	$m_{1<-2}$	$m_{2<-1}$	P	$m_{e1<-2}$	$m_{e2<-1}$	1-P
<i>I. nautiliei</i>	IM2N2mG	0,444	0,825	0,483	0,038	0,283	0,517
<i>I. nautiliei</i>	SC2N2mG	0,422	0,810	0,439	0,038	0,270	0,561
<i>I. nautiliei</i>	AM2N2MG	0,461	0,825	0,471	0,039	0,300	0,529
<i>A. kojimai</i>	SC2N2mG	4,741	4,389	0,851	0,384	0,841	0,149
<i>S. tollmanni</i>	SC2N2m	0,321	3,314	0,014	4,334	13,866	0,986
<i>S. tollmanni</i>	SC2N2mG	0,268	1,048	0,205	1,048	2,800	0,795
<i>E. ohtai</i>	SC2mG	0,364	1,386	0,508	0,013	0,124	0,492
<i>B. segonzaci</i>	SC2N2mG	0,579	6,489	0,000	2,195	5,412	1,000
<i>B. manusensis</i>	IM2N	0,436	0,566				
<i>B. manusensis</i>	SC2N2m	3,988	4,891	0,323	0,227	0,646	0,677
<i>B. manusensis</i>	SC2N	0,520	0,537				
<i>L. schrolli/L. fijensis</i> )	SC2N2mG	0,878	0,308	0,180	0,009	0,007	0,820

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455

456 *Figure 4 : Weighted AIC value on the best runs for all models and parameters per species. Highest value represents the best*  
 457 *model fit (the lowest AIC value). Ifremeria nautiliei data are derived from Tran Lu Y et al. (2022).*

## 458 Discussion

459 Population genomics allowed us to gain a deeper understanding of factors that have shaped  
 460 genetic variation within and between populations in a context of a discontinuous ridge system  
 461 in a well-delimited biogeographic region. Our study was aiming to "put the geography (and  
 462 more) into comparative population genomics" (from Edwards et al., 2022) by applying such  
 463 an approach to seven very different taxa strictly associated with the hydrothermal habitat.  
 464 Using the same sampling scheme across all species, we show that these species share a  
 465 common biogeographic break and a similar demographic history despite their different life-  
 466 history traits. This pattern of differentiation was however slightly more complex for the limpet

467 *L. schrolli/L. fijiensis*, *S. tollmanni* and the scaleworm *B. segonzaci*, for which a further genetic  
468 subdivision between the Manus Basin and the Woodlark Ridge was also observed.

469 The multispecies transition zone between the Eastern and Western metapopulations is  
470 located on the Woodlark Ridge or between it and the western part of the North Fiji BAB,  
471 isolating the Manus Basin to the West and the North Fiji and Lau Basins, as well as the Futuna  
472 volcanic arc to the East. Based on demogenetic inferences, we found that after a primary  
473 allopatric divergence, these metapopulations were secondarily connected, resulting in weak,  
474 asymmetric, and predominantly westward ongoing gene flow. Levels of divergence and  
475 differentiation, however, varied between taxa, probably because of different generation times  
476 and life-history traits. Heterogeneous gene flow was also found in all species in various  
477 proportions, suggesting that primary divergence could have led to the generation of genomic  
478 incompatibilities, as commonly found in hybrid zones (Bierne et al., 2011; Matute et al., 2010).

479

#### 480 ***A suture zone around the Woodlark back-arc Basin.***

481 All seven species share a clear genetic break into two main metapopulations across their  
482 geographical range, with the Manus/Woodlark (M/W) BABs on one hand and the North Fiji,  
483 and Lau BABs and Futuna Volcanic Arc (NF/F/L) on the other hand. Despite this common  
484 phylogeographic pattern, the strength of differentiation between these Eastern and Western  
485 genetic pools estimated by  $F_{st}$  varied from very high (0.387) to very low (0.020), depending on  
486 the species. A transition zone, a region where previously isolated lineages come into contact  
487 and exchange genetic material, appears to be located somewhere between North Fiji and  
488 Woodlark BAB or even at Woodlark itself, where both lineages are found in sympatry for some  
489 species. This is clearly observed for the two limpet species complexes, *S. tollmanni* and *L.*  
490 *schrolli/L. fijiensis*, for which the Western and Eastern lineages co-occur in Woodlark and  
491 hybrid individuals, are detected. This signature is typical of the existence of a tension zone,  
492 where selection can operate against hybrid genotypes, probably due to the existence of  
493 underdominant genetic incompatibilities (Bierne et al., 2011) or other reproductive barriers.  
494 Variable levels of admixture detected between Western and Eastern lineages in all species  
495 present at Woodlark, and, to a lesser extent at North Fiji (Tran Lu Y et al. 2023), reinforced this  
496 view. The species variability in terms of population structuring can stem from diverse origins:  
497 differences in life history traits (generation time, dispersal capability, fecundity, ...) or in the  
498 genomic architecture of species (intensity of linked selection and number of barrier loci



499 (genetic incompatibilities) that whole genome information could help better visualize. These  
500 latter factors are noticeably linked with the depth of evolutionary history of divergence and  
501 the reproductive mode. Our study suggests two possible hypotheses. First, geophysical  
502 rearrangements at a given time may have limited (and are still currently limiting) effective  
503 dispersal for a number of species with different life history traits. Leading this common pattern  
504 of isolation, regardless of the timing of their origin in the Southwestern Pacific (isolation with  
505 migration, IM, one of the models supported by *∂∂i* for *Ifremeria nautilei* and *Bathymodiolus*  
506 *manusensis*). Alternatively, these species may have experienced one or more vicariance  
507 events, resulting in a period of primary divergence in allopatry followed by secondary contacts  
508 (SC) with a gene flow restart. The latter scenario is the most likely, supported by the *∂∂i*  
509 analyses for most species (Figures 3 & 4).

510 While evolutionary processes unfold independently in each species, our demogenetic  
511 reconstruction indeed indicates a scenario of secondary contact (SC) for five species. For two  
512 species, the model cannot decisively distinguish between secondary contact and isolation-  
513 with-migration (IM), possibly due to a prolonged period of secondary contact. These results  
514 nevertheless strongly suggest an allopatric initial divergence for all species. Modeling also  
515 underscored the detection of a genomic heterogeneity of differentiation in all species, with  
516 both heterogeneous gene flow across the genome (2m) and linked selection (2N). This finding  
517 suggests that the initial divergence was extensive enough to generate genomic  
518 incompatibilities between populations in a genome characterized by substantial background  
519 selection and low recombination. This pattern can be a feature of hydrothermal-vent species,  
520 which may undergo strong purifying selection in this challenging environment (Chevaldonné  
521 et al. 2002, Fontanillas et al. 2017, Thomas-Bulle et al. 2022).

522 The position of the contact zone between Western and Eastern lineages, today located at  
523 Woodlark or closeby, may have moved since the secondary contact took place, probably along  
524 the subduction arcs of Vanuatu or Solomon. Nevertheless, the Manus Basin appears more  
525 diversified in terms of species (Poitrimol et al., 2022) and could have served as a source of  
526 biodiversity for part of the Western Pacific hydrothermal fauna, suggesting a possible “out of  
527 Manus” hypothesis. In line with this idea, recent work on taxa network analysis redescribes  
528 the Western Pacific region for hydrothermal fauna not as a single biogeographic province, as  
529 suggested by Moalic et al. (2012), but as two distinct provinces, the North West Pacific and

530 the South West Pacific, with the Manus Basin as a possible hub connecting both (Tunnickliffe  
531 et al., 2024).

### 532 **Gene flow between BABs**

533 The connectivity and dispersal of hydrothermal vent species may be influenced by their life  
534 history traits, particularly the larval phase. Species with planktotrophic larvae, which can have  
535 an extended planktonic phase, should exhibit higher dispersal abilities and greater  
536 connectivity between populations. In contrast, species with lecithotrophic larvae, which rely  
537 on yolk reserves and usually have a shorter planktonic phase in coastal waters, are expected  
538 to show more limited dispersal and reduced connectivity (but see: Young 1994 for the deep-  
539 sea fauna). Our findings, with a consistent asymmetrical gene flow (lower eastward gene  
540 flow), unequivocally reject complete isolation between East and West  
541 metapopulation/lineages for all species, despite their contrasting dispersal life-traits. It  
542 partially also aligns with prior studies indicating very low gene flow between Manus and Lau  
543 BABs (Breusing et al., 2021; Plouviez et al., 2019; Thaler et al., 2011, 2014). However some  
544 other studies have reported a lack of genetic differentiation for *S. tollmanni* with some mito-  
545 nuclear incongruities (Yahagi etl., 2019, Poitrimol et al., 2022). Additionally, our demogenetic  
546 modeling indicates semi-permeability (2m) of gene flow for all species, probably from the  
547 accumulation of genomic incompatibilities and other barrier loci during primary divergence  
548 preceding secondary contact (Barton & Bengtsson, 1986).

549 The orientation of gene flow also partially aligns with previous simulations of larval dispersal  
550 at intermediate depth (Mitarai et al., 2016). However, the bi-directional nature of the gene  
551 flow suggests potential dispersal near the surface, where the main counter-current flows  
552 eastward, in addition to the deep-water westward dispersal. The current genetic data and the  
553 lack of information on the biology of the species are insufficient to assess the role of life-  
554 history traits, particularly the larval developmental mode of the species, in relation to the  
555 degrees of differentiation, divergence, or even the orientation of dispersal at this stage.  
556 Further analyses are required with a better understanding of the biology of these species.  
557 Depending on the life-history traits and potential presence of intermediate populations in the  
558 Vanuatu and Solomon archipelagos, the frequency and duration of secondary contacts may  
559 have varied between the Eastern and Western lineages. Nevertheless, present-day  
560 connectivity remains highly limited due to the existence of both genetic and physical barriers  
561 to dispersal. In this scenario, species with high dispersal abilities and/or long generation times

562 may have experienced less divergence (e.g., *A. kojimai*, *B. segonzaci*) compared to those with  
563 low dispersal abilities and short generation times (e.g., *L. schrolli*/*L. fijiensis*). This situation is  
564 well illustrated in vent copepods in the Lau Basin, which possess both of the latter attributes  
565 (Diaz-Recio Lorenzo et al., 2024).

#### 566 **Species specific variation**

567 While the West/East divergence is clear for all species, few species display some basin  
568 peculiarities.

569 *B. segonzaci* shows slight differentiation between Woodlark and Manus Basin populations,  
570 not solely due to allelic introgression from other Eastern regions. The North Fiji Basin  
571 population of *A. kojimai* differs slightly from the Lau/Futuna regions, despite the overall lack  
572 of genetic differentiation ( $F_{st} = 0.018$ ) at the regional scale. *B. manusensis* has been newly  
573 identified in the Eastern regions (north of Lau Basin and Futuna volcanic arc). This unusual  
574 presence in the East is notable, as it locally co-occurred with *B. septemdiarum*: the only mussel  
575 species typically found in that area. These Eastern scattered populations may represent a  
576 leading edge of range expansion but lack the expected reduced diversity (Dupoué et al., 2020).  
577 The slight basin differentiation for *B. segonzaci* and *A. kojimai* raises questions about limiting  
578 factors on connectivity, potentially influenced by larval dispersal depth, demographic turn-  
579 over, or putative depth selection in North Fiji Basin and Woodlark populations.

580 While most of our species exhibit a relatively low level of genetic divergence, the limpets *L.*  
581 *schrolli*/*L. fijiensis* and *S. tollmanni* show a high degree of divergence and differentiation, as  
582 well as a highly reduced gene flow between the Western and Eastern groups. *S. tollmanni*  
583 displays a clear admixture signal in Woodlark, where both lineages are in sympatry and one  
584 first generation hybrid was identified. Previous studies have shown a lack of genetic  
585 differentiation at the regional scale with the mitochondrial *Cox1* (Poitrimol et al., 2022; Yahagi  
586 et al., 2020). Based on genomic data, the two lineages West/East are strongly isolated and  
587 display very reduced and heterogeneous gene flow, where alleles can be exchanged at very  
588 few loci. This incongruity is consistent with our results. Indicating a strong reduction in gene  
589 flow, but where few loci can still be exchanged and captured, including mitochondrial  
590 genomes.

591 The species *L. schrolli* and *L. fijiensis* display a nearly identical divergence but with a clearly  
592 admixed population between the Manus and NF/F/L lineages at Woodlark. This result is in line  
593 with mtDNA *Cox1* results for Woodlark individuals, where half of them reflect Manus *Cox1*  
594 haplotype lineage and the other half, the NF/F/L haplotype one (Poitrimol et al., 2022). This  
595 is also consistent with previous results using 42 nuclear markers, which indicate very low and  
596 asymmetric gene flow between Manus and Lau BABs (Plouviez et al 2019). It indicates  
597 segregation for mtDNA markers in a sympatric population, consistent with the possible partial  
598 accumulation of genomic incompatibilities in which the mitochondrial genome is this time  
599 included. Our findings therefore reinforce the recent taxonomic revision of *L. schrolli* (M) and  
600 *L. aff schrolli*, now *L. fijiensis* (NF/F/L), as separate species (Chen & Sigwart 2023). This also  
601 suggests that the taxonomy of *S. tollmanni* may need some revision.

602 As previously mentioned, dispersal-related life history traits potentially influence connectivity.  
603 However, when we look at what we know about the life history traits of our seven species,  
604 there is no consistency with the type of larval development. *B. segonzaci* and *A. kojimai*, both  
605 colonizing the hottest parts of the West Pacific vent environment, display the lowest genetic  
606 differentiation and divergence between Eastern and Western populations, despite having  
607 different larval development modes. *B. segonzaci* is a free-living, mobile annelid with small  
608 local population sizes. Its large oocytes (ca. 150  $\mu\text{m}$ ) suggest lecithotrophic larval development  
609 that can remain for long times in cold oligotrophic waters. *A. kojimai*, on the other hand, has  
610 larger patchily distributed populations and produces much smaller oocytes, implying  
611 planktotrophic larval development in surface waters (Warèn & Bouchet, 1993, Sommer et al.  
612 2017, Kim et al., 2022). In these two species, the low level of regional differentiation therefore  
613 could be linked to the specific distribution of ‘hot’ vent emissions when compared to colder  
614 diffuse venting, provided that they are both able to widely disperse.

615 *B. manusensis* and *E. ohtai* also display a low level of divergence, but exhibit an intermediate  
616 level of differentiation between metapopulations. *E. ohtai* is a common sessile hydrothermal  
617 vent cirriped forming dense populations in diffuse areas. Its oocyte diameter (ca. 500  $\mu\text{m}$ )  
618 again suggests lecithotrophic development (~500  $\mu\text{m}$ ; SH unpublished data, Yamaguchi &  
619 Newman 1997, Tyler & Young 1999). In contrast, deep-sea bivalves such as *B. manusensis*  
620 typically have small oocytes and larvae are expected to be planktotrophic, as larvae of  
621 *Gigantidas childressi* (formerly known as "*Bathymodiolus*" *childressi*) have been detected in  
622 surface water and known to live up to 18 months (Arellano and Young, 2009).

623 Although the focus was on the Southwest Pacific BABs, the Kermadec Basin, hundreds of  
624 nautical miles south of the Lau Basin, has a very distinctive vent fauna. But, *B. segonzaci* and  
625 *L. fijiensis* are among the very few species shared with the most northerly location sampled  
626 here (SH unpublished data). It therefore appears that these species may have spread for a  
627 longer time and/or have greater habitat flexibility than other species. The addition of some  
628 individuals from Kermadec to the dataset showed no differentiation from the NF/F/L  
629 population for *B. segonzaci*, but did show some differentiation from NF/F/L for *L. fijiensis* (see  
630 details in SI Figures 13, 14, 15, data not shown).

### 631 ***Timing divergences and the hypothesis of vicariance***

632 The comparative study highlights common phylogeographic patterns across the Southwest  
633 Pacific Ocean for seven vent species. This pattern has probably been generated by a shared  
634 initial divergence event, due to either geological or climatic factors, generating two  
635 metapopulations, with the separation lying somewhere between Woodlark and North Fiji  
636 BABs, if we consider the populations have remained in place during the isolation process. This  
637 barrier is semi permeable to gene flow, allowing occasionally metapopulations to exchange  
638 genetic material through secondary contacts but not at the same rate and not over the same  
639 regions of their genomes. This reconnection may also be modulated by species-specific life-  
640 history traits, including type of larval development (planktotrophic vs. lecithotrophic), depth  
641 of larval dispersion, longevity, age of first reproduction and mean generation time or habitat  
642 fragmentation.

643 The estimation of net nucleotide divergence ( $D_a$ ), shows that species have undergone  
644 different periods of divergence. In particular, *L. schrolli/L. fijiensis*) and *S. tollmanni* both  
645 display particularly high net divergence values compared to the other species. This indirect  
646 approach suggests that these two species did undergo a longer period of isolation in allopatry  
647 or a much higher number of generations since a possible vicariant event. These results  
648 naturally pose the question of cryptic species and speciation processes. This level falls into the  
649 grey zone of speciation of Roux et al. (2017), where reproductive isolation between  
650 populations varies widely. Our demogenetic inferences shed some light not only on the  
651 intensity and genomic heterogeneity of gene flow (as previously discussed) but also on the  
652 timing of divergence.

653 The divergence time since the ancestral lineage split, in generations, indeed varies by a factor  
654 of three between species even if they all share the same population history. In this approach,  
655 time estimation strongly depends on the per generation nucleotide mutation rate and the  
656 mean generation time considered for each species. However, these biological parameters not  
657 yet known for the species studied here. This is a common limitation for many non-model  
658 organisms (and especially in the deep-sea), and has led us to make assumptions for both  
659 parameters that we have set to the same value for all species, although we acknowledge this  
660 is highly unlikely. Thus, a factor of three in the divergence time is not so great and can be  
661 largely due to the distinct species life history traits. Some studies on growth rates show that  
662 larger species have slower growth rates (Schöne & Giere, 2005), while small ones have higher  
663 rates (Poitrimol et al., 2024), suggesting discrepancy in the generation time and first age at  
664 maturity between species. In addition, bigger species often have smaller population sizes than  
665 smaller ones and we cannot exclude the possibility that they would have otherwise undergone  
666 relatively simultaneous demographic changes.

667 Resulting estimates of primary divergence may have begun between  $\sim 40,892$  to  $101,718$   
668 generations, while the secondary contact ranges from  $6,386$  to  $69,372$  generations, depending  
669 on the species. Considering an average mutation rate of  $10^{-8}$  and a quite short time of one  
670 generation per year, this primary divergence and secondary contact would take place in the  
671 Holocene between climatic oscillations. The initial split may be more specifically around the  
672 Last Glacial Maxima for the region ( $11,500$ - $20,300$  years ago (Tongo Glaciation),  $62,000$  years  
673 ago (Komia Glaciation) and  $130,600$ - $158,000$  years ago (Mengane Glaciation) (Barrows et al.,  
674 2011)).

675 At the other end of the range. If we consider a ten times lower mutation rates ( $10^{-9}$ ) that has  
676 been largely invoked in the molecular dating of the vent fauna as the result of strong purifying  
677 selection (Chevaldonné et al. 2002, Johnson et al. 2006, Matabos and Jollivet 2019). The  
678 magnitude of divergence would be in the order of  $400,000$  to  $1,000,000$  years and  $63,860$  -  
679  $693,720$  for the secondary contact. This primary divergence timeframe falls partly at the start  
680 of magmatic accretion in some actual active BAB ridges, such as Lau or Manus (Schellart et al.,  
681 2006). The geological structures that currently separate the two genetic entities are the  
682 Woodlark Basin, North-Fiji and the other geological structures between them (Vanuatu  
683 Trough (formerly New Hebrides), Vanuatu and Solomon Islands volcanic arc). These  
684 formations have a rather older geotectonic history with accretion times of several million

685 years (Woodlark: ~ 6 Ma, North Fiji: ~3Ma, Vanuatu Trough & volcanic arc: 12Ma, Solomon  
686 volcanic arc: Eocene, ~ 40 Ma) (Schellart et al., 2006). While this primary divergence period  
687 better fits these geodynamic features, the time frame for secondary contact still remains in  
688 the Holocene period and may be the consequences of climatic oscillations and possible  
689 changes in the overall Pacific water-mass circulation due to the ocean elevation.

690 Timeframe estimates remain very difficult to interpret due to many unknowns on the biology  
691 of the species, but all species were affected, suggesting a major climatic or geological  
692 reorganization of connectivity that probably initiated the primary divergence and the  
693 secondary contact. However, we cannot reject the hypothesis that some secondary contacts  
694 are much older than others since life-traits history varies between species.

#### 695 ***Limits of the method and other hydrothermal species***

696 The present study primarily focused on the most common and emblematic species in  
697 hydrothermal communities. Earlier studies on two of our target species and other  
698 hydrothermal vent inhabitants have yielded findings consistent with our results (Lee et al.,  
699 2019; Plouviez et al. 2019; Poitrimol et al., 2022; Thaler et al., 2014). Like all our species, they  
700 exhibit a 'common' pattern of genetic differentiation across the Western and Eastern parts of  
701 this region, implying a shared vicariant event. However, it is important to note that these  
702 results may primarily reflect the evolutionary history of the most highly abundant vent  
703 species. As mentioned earlier, these ecosystems are home to numerous other species. Many  
704 of them probably have lower population densities, are less dependent on vent fluids and have  
705 diversified much more rapidly towards endemism. Consequently, these less abundant and  
706 often smaller species may demonstrate more contrasted phylogeographic patterns. For  
707 example, based on *Cox1* data, some limpets, barnacles, and copepods have been shown to  
708 have a wide distribution, while others (sometimes closely related) have a basin-specific  
709 occurrence (Boulart et al., 2022; Poitrimol et al., 2022, Diaz-Recio Lorenzo et al. 2024).

710 Beyond the idea that we did not examine rare and occasional species, our comparative  
711 phylogeographic study also has some limitations. First, our sampling design, although quite  
712 extensive, focused on a fraction of the existing hydrothermal vents, lacking fine-grained  
713 representation within and across BABs. This limitation is common in deep-sea research, where  
714 potential habitats and populations are known or suspected but remain unsampled. In our  
715 case, the study area comprised a few unsampled - documented vents (e.g. Nifonea in



716 Vanuatu), and other 'ghost' undiscovered vent sites possibly located on seamounts along  
717 volcanic arcs. Additional data from these sites should not affect our main conclusions, but  
718 they would provide useful information to refine our patterns of population connectivity and  
719 the timing of contact zones. Second, we generated ddRAD datasets across a wide range of  
720 species with significant divergence between geographic lineages. These varying contexts of  
721 divergence may have influenced our results, as divergent lineages may share fewer ddRAD loci  
722 due to allele dropout and preferential bias towards less divergent loci to avoid missing data,  
723 although the number of remaining loci was still very high.

#### 724 ***Implications for conservation and future directions***

725 As previously shown, cases that correspond to geographically separated cryptic species need  
726 to be managed separately (e.g. *L. schrolli*/*L. fijiensis* or *S. tollmanni*). Other species depict much  
727 lower divergence but with some variation in population differentiation. Although sporadic and  
728 possibly rare, there is now clear evidence of present-day genetic connectivity between the  
729 Western and Eastern metapopulations with an apparent high genetic homogeneity within  
730 each of them. If larval exchange does not seem to be limited within each geographic group,  
731 the inter-metapopulation migration rate is probably too low to allow any regional rescue  
732 effect. Discussing effective migration and thus dispersal is however still quite challenging  
733 (Lowe & Allendorf, 2010; Waples & Gaggiotti, 2006). Recent studies based on simulations of  
734 particle dispersion at different depths (500 and 1000 meters) for *I. nautili* and *Alviniconcha*  
735 spp. suggested low but possible migration between BABs depending on the Pelagic Larval  
736 Duration (PLD) and depth (Breusing et al., 2021; Mitarai et al., 2016). However, based on our  
737 finding any rescue effect is likely to be basin-specific and highly sensitive to increasing local  
738 extinctions magnified by deep-sea mining.

739 Most of our knowledge on the stability of vent ecosystems through time is derived from times  
740 series established on the East Pacific Rise, a fast-spreading mid-oceanic ridge with a one-  
741 dimensional stepping-stone axis of colonization (Dupreez & Fisher 2018, Audzijonyte &  
742 Vrijenhoek 2011) and, some punctual physical barriers to dispersal (Plouviez et al. 2009, 2010,  
743 2013). There, the fast extinction and recolonization rates of active sites are likely to select for  
744 species, which can disperse far, and grow and reproduce fast. In back-arc basins, the ridge  
745 spreading rate is rather low but varies between basins (Dick 2019). Extinction and  
746 recolonization events are likely less common, which led to concerns about the ability of the  
747 populations to recover if the metal sulfide deposits formed by the hydrothermal vent activity

748 are mined (Dupreez & Fisher 2018). Within each of the two metapopulations, high genetic  
749 homogeneity of local populations can arise from either a substantial population size mitigating  
750 genetic drift or the presence of a sufficient number of migrants exchanged within BABs.  
751 Consequently, dispersal seems to be effective between nearby sites at the scale of either the  
752 Western or Eastern regions, but much more limited between them. Because BAB zones are  
753 spatially limited with a restricted number of active vent sites, mining the already known sites  
754 should compromise any local 'rescue' effect. The fact that introgressed alleles between  
755 metapopulations appear capable of reaching the Woodlark and North Fiji BABs only, suggests  
756 that the inter-basin dispersal will not compensate for population bottlenecks within each  
757 metapopulation. As shown by Bailleul et al. (2018), the apparent genetic homogeneity of  
758 demes within a metapopulation is often maintained by a limited genetic drift, even in the face  
759 of low inter-deme migration rates.

## 760 **Conclusion**

761 We have identified a strong phylogeographic break for several hydrothermal species of the  
762 Southwest Pacific back-arc basins, consistent with a common suture zone between the  
763 Woodlark and Lau basins. Although sharing a common pattern of population structuring,  
764 variability in the degree of population differentiation is observed among these species,  
765 potentially related to life history traits and species-specific demographic histories.

766 Our initial hypothesis that hydrothermal species of the Southwestern Pacific back-arc basins  
767 may have evolved toward long-distance dispersal strategies to cross over non-hydrothermal  
768 abyssal zones associated with a discontinuous system of oceanic ridges may only be valid for  
769 a few species. In fact, the western Pacific vent communities are composed of species with  
770 highly contrasted life-history traits and dispersal strategies, which are likely to promote the  
771 good replenishment of populations locally in spite of vent instability, fragmentation and  
772 geological discontinuities. Although some uncertainty remains about the timing of divergence  
773 and secondary contacts, connectivity patterns between the two geographic groups are similar  
774 among species, with asymmetric but bidirectional gene flow favoring the Western direction  
775 (with the exception of *L. schrolli*/*L. fijiensis* for which a Manus origin of colonization is  
776 suspected). This study clearly identified the existence of genetic barriers at some intermediate  
777 locations that are likely to slow down gene flow for some species. It also confirmed that most  
778 of the vent assemblages sustainability rather depends on the strength of the network of local

779 populations that makes up each regional metapopulation, rather than long distance dispersal.  
780 Ensuring the resilience of these communities requires sustainable management of their  
781 populations at the level of each biogeographic unit or back-arc basin, bearing in mind that the  
782 majority of current genetic exchange between the Eastern and Western basins are more  
783 specifically redirected towards the Manus Basin.

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794 perform preliminary ddRAD libraries over the different species to choose restriction enzymes  
795 and check the number of usable loci.

## 796 **Author contributions**

797 Stephane Hourdez and Didier Jollivet designed the CHUBACARC and CERBERUS projects,  
798 François Bonhomme supervised the genetic work. Adrien Tran Lu Y, Stéphanie Ruault, Claire  
799 Daguin-Thiébaud, Anne-Sophie le Port, Marion Ballenghein, Sophie Arnaud-Haond, Jade  
800 Castel, Camille Poitrimol, Eric Thiébaud, François Lallier, Thomas Broquet, François  
801 Bonhomme, Didier Jollivet and Stéphane Hourdez performed laboratory work. Adrien Tran Lu  
802 Y performed bioinformatic statistical analyses with the contribution of François Bonhomme,  
803 Didier Jollivet, Pierre-Alexandre Gagnaire, Nicolas Bierne and Thomas Broquet. Adrien Tran  
804 Lu Y, François Bonhomme, Thomas Broquet, Didier Jollivet and Stephane Hourdez wrote the  
805 manuscript with feedback and inputs from all authors. All authors approved the manuscript

## 806 **Conflict of interest**

807 The authors have no conflicts of interest.

## 808 **Data availability statement**

809 Raw sequence reads (Individual fastq files) are available at the European Nucleotide  
810 Archive (bioproject PRJEB47533; *I. nautilei*) and the NCBI sequence read archive  
811 (PRJNA768636 for *A. kojimai*; PRJNA779874 for *L. schrolli*; PRJNA772682 for *S.*  
812 *tollmanni*; PRJNA1044574 for *B. manusensis*; PRJNA1030156 for *E. ohtai*;  
813 PRJNA1044042 for *B. segonzaci*). Metadata relative to the samples are also available  
814 with Biosamples accessions and linked to the sequence reads accessions. Scripts used in  
815 this study (R, *daði*) are available on a public Github repository:  
816 (<https://github.com/Atranluy/Scripts-Ifremeria>). VCFs and associated metadata will be  
817 available on public repository upon peer-review and publication.

## 818 **Benefit-sharing statement**

819 In order to obtain the requested authorizations to work in national waters and in agreement  
820 with the Nagoya protocol, we contacted the authorities of the different countries (Papua-New  
821 Guinea, Fiji, and Tonga) and territories (Wallis and Futuna) for benefit sharing where sampling  
822 was performed. The data generated will be accessible on public databases (see above). The  
823 results obtained will also be communicated to these authorities which may have to make  
824 decisions regarding conservation of deep-sea hydrothermal vent communities in their EEZs.  
825 Observers for the different countries who took part in the on-board activities will be informed  
826 of our findings.

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