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Demographic history of a remote ichthyofauna assemblage reveals common processes driving colonization and persistence in endemic coral reef fishes

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Elucidating demographic history during the settlement of ecological communities is crucial to properly inferring the mechanisms that shape species diversity and their persistence through time. We used genomic data to elucidate for the first time the demographic dynamics associated with the settlement by endemic reef fish fauna of one of the most isolated islands of the Pacific Ocean, Rapa Nui (Easter Island). We compared the demographic history of nine endemic species including seven small-range (restricted to Rapa Nui and Motu Motiro Hiva) and two large-range (present in Rapa Nui and other southern subtropical islands of the Pacific) endemic species in order to explore the onset of community settlement and associated demographic history. We found that most Rapa Nui endemic species share a common demographic history, with a demographic expansion initiated during the last interglacial period and related to the last sea level high-stand. The commonality of this pattern suggests that eustatic fluctuations associated with Milankovitch cycles have played a central role in species demographic history and the final stage of contemporary community assembly of Rapa Nui reef fishes. We discuss the potential role of seamounts in the colonization / extinction / recolonization dynamics of populations of the Rapa Nui Archipelago.

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1. Introduction

Local and regional processes jointly drive community assembly, *i.e.* the dynamics of species aggregations in ecological communities and the number of coexisting species at a given place. The importance and nature of local (e.g. environmental filtering, species interactions inside a community) and regional (e.g. dispersal, immigration of new species from outside of a community) processes in the origin and maintenance of biodiversity in communities is one of the oldest question in ecology [1,2]. Phylogenetic analysis of community assembly can give a better understanding of the relative importance of local and regional dynamics in shaping community assembly [3] as they provide a temporal framework [4]. However, the difficulty of reconstructing accurate divergence times between species due to the incompleteness of available phylogenies limit the power of such analyses. In the meantime, community assembly, especially in island systems, is known to be dynamic, with regular colonization / extinction / and recolonization of populations occurring through time [2,5,6], processes which cannot be assessed using species level approaches. Investigate shallower time scale, population genetics can provide insights into both assembly time and species demographic history during community assembly, hence helping understanding the mechanisms by which species persist through time. Thus by comparing the demographic histories of multiple species in a community and estimating the timing of the early stages of community assembly, it is possible to disentangle not only the relative contribution of historical (*e.g.* tectonic, eustatic changes) and ecological (*e.g.* competitive exclusion, habitat filtering) dynamics but also the scale of the processes (local vs. regional) in shaping the final stage of contemporary community assembly.

Rapa Nui (Easter Island, Chile, 166 km^2) is one of the most remote islands on Earth and hosts an exceptional reef fish community. The mechanisms at the origin of

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this diversity and its persistence through time remain enigmatic. Rapa Nui (RN) is the second hotspot of endemism of the Indo-Pacific Ocean, with 21.7% of fishes endemic to these islands [7,8]. This reef fish community is known for being extremely species poor (only 169 fish species; 139 shore fishes) compared to the species-rich islands of the Indo-Australian Archipelago for instance. RN and the islet Motu Motiro Hiva (MMH) (Salas y Gómez, 0.15 km^2), located 400 km further east, which shares the same reef fish fauna as RN [9], constitute the only two emerged islands of the Easter Chain. RN and MMH are relatively young; 2.5 and 1.7 My, respectively [10], but they are embedded in a network of numerous seamounts. This seamount chain extends 2,232 km east to the Nazca seamount (23°360 S et 83°300 W) [10,11] and these mounts have emerged to various degrees during periods of low sea level. In this context, an "Ancient Archipelago" hypothesis has been formulated to account for the high level of endemism observed in RN and MMH, young islands, hypothesizing that "most if not all endemic species were acquired from elsewhere in the region" [12]. Seamounts, which were once likely islands, could have provided potentially suitable habitat for at least the past 29 My for endemics of the region to evolve and persist up to present times [12]. However, a recent analysis of the divergence times of endemic species from their closest relatives has shown that small-range endemics are not older that the emergence of RN and MMH; they are thus neoendemics [13], thereby questioning the ancient origin of RN endemics. Yet, the seamounts nearby RN could have played a major role in long-term species persistence through time, especially during the Pleistocene. This era is characterized by notable Milankovitch cycles, historical processes resulting in the alternation of glacial and inter-glacial time that resulted in sea levels 150 m below present level. Such paleo-environmental perturbations might be expected to have left a footprint of bottlenecks and expansions in the demographic history of populations of many marine species [14–17]. These major sea level changes altered shallow water habitats; exposing continental shelves during low sea levels but

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also giving access to habitat otherwise too deep to colonize such as relatively shallow seamounts. Thus, these features of the Pleistocene could have temporally expanded the range distribution of endemic species and their population sizes[18].

Reef fish community assembly in remote islands is dependent on colonization / extinctions / recolonization processes. The RN reef ichtyofauna is very dynamic; several species that were reported as being abundant in 1969 in RN waters were then reported as rare or even absent 16 years later. Along the same line, numerous species are reported as present in RN waters but are actually vagrants, i.e. species that colonize RN from time to time without being able to establish a population locally [7]. The endemic RN reef ichtyofauna is composed of two types of endemics, small-range and large-range endemic species. It is possible to hypothesize that *local* processes, at the scale of the RN and MMH community, influence the demographic history of small-range endemics as these fishes are restricted to these two islands. On the contrary, large-range endemics are present both in RN and in other southern subtropical islands of the Pacific. As such, populations of these fishes are embedded in metapopulations of larger geographic ranges than those of small-range endemics. Thus the population dynamics of large-range endemics are likely to also be affected by *regional* processes such as fragmentation and dispersal outside of the RN and MMH community.

Through genome-wide sequencing (ddRAD), we explore the demographic history of nine endemic species of RN. The species studied here represent the two types of endemics (small-range and large-range), seven major reef fish families, and three different reproductive strategies endemics. We examine whether demographic histories vary (1) according to the current range distribution of the species; (2) with life history traits; doing so, we investigate the consequence of historical processes such as

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sea level changes or ecological dynamics driven by reproductive strategy on the genetic diversity. If historical processes are more important than ecological processes in the maintenance of endemic species in RN, we expect to find similar population dynamic for the two types of endemic species. In the same way, if local processes are more important than regional processes in the maintenance of endemic species in RN, we expect to find similar assembly time for the two types of endemic species. Implications for the biogeography of the area are discussed.

2. Material and methods

(a) Sampling

A total of 143 reef fishes (nine species) were collected using polespears or an anesthetic (clove oil) in Rapa Nui in October 2016 (Table 1). Species were classified as either small-range or large-range endemics. Small-range endemics only present around RN and MMH and have a maximum range of <500 km in linear distance, see Delrieu-Trottin et al. [19]. Southern subtropical endemics have large-ranges (1,000–8,000 km in linear distance, see Delrieu-Trottin et al. [19], hereafter large-range endemic species) and are distributed from Southern Polynesia to RN (regional endemics in Friedlander et al. [9]). The species analyzed here also possess different reproductive strategies, with five species producing pelagic eggs, three species producing demersal eggs, and one species brooding eggs in their mouths (Table 1).

(b) Library preparation and sequencing

Whole genomic DNA was extracted from fin or gill tissue preserved in 96% ethanol using the GeneJet Genomic DNA purification kit according to the manufacturer's protocols (Thermo Fisher Scientific). Double-digest restriction-associated DNA (ddRAD) libraries were prepared following Peterson et al.' protocol [20]. The genomic

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libraries obtained were sequenced in 3 lanes of a HiSeq 2500 Illumina sequencer (single end, 125 pb). Illumina reads are available from the Sequence Read Archive (SRA) at NCBI under the Accession nos. XXXXXX–XXXXXXX.

(c) De novo assembly

We used the 'process_radtags.pl' pipeline in STACKS version 2.0 [21,22] to demultiplex and quality filter the sequences obtained. In the absence of reference genomes for the species under study, RADSeq loci were assembled de novo using the 'denovo_map.pl' pipeline in STACKS. We used the parameter combination recommended by Mastretta-Yanes et al. [23]; this included minimum read depth to create a stack (m) = 3, number of mismatches allowed between loci within individuals (M) = 3, number of mismatches allowed between loci within catalogue (n) = 3 and required a locus to be present in all individuals of each species (r = 1). Following de novo mapping, an initial data-filtering step was performed using the population component of STACKS removing all loci with maximum observed heterozygosity higher than 0.8. We first kept all single-nucleotide polymorphisms (SNP) per stack (*i.e.* locus) and did not use any threshold regarding the minor allele frequencies as we obtained a high coverage for each individual. We then removed all loci displaying more than three SNPs to avoid potential paralogs. Summary statistics based on the resulting vcf file (Supplementary material) such as nucleotide diversity (π on variable loci), heterozygosity (*H*) and F_{IS}, were calculated for every SNP using the *populations* program in STACKS. The folded Site (Allele) Frequency Spectrum (SFS) was computed in R [24] with the package *pegas* [25].

(d) Demographic analyses

Variation in the effective population size (*Ne*) through time was investigated using the composite likelihood approach implemented in the software *stairwayplot* [26]. The

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stairwayplot is a non-parametric model where *Ne* is free to vary at each coalescent interval. The composite likelihood is evaluated as the difference between the observed SFS and its expectation under a specific demographic history. To confirm the results obtained by the *stairwayplot*, we ran an additional approximate Bayesian computation algorithm based on coalescent simulations following Maisano Delser et al [27]. Briefly, we performed 1,000,000 coalescent simulations of a demographic model with three instantaneous changes of *Ne*. The model is therefore defined by seven parameters: four values of *Ne* and three instantaneous time changes (hereafter, *T*). We set the same uniform distribution for the four *Ne* values and incremental uniform distribution for the three *T* parameters, similarly to Maisano Delser et al [27]. Coalescent simulations and SFS computation were performed with *fastsimcoal* [28]. We used the SFS and the mean pairwise differences (computed with a custom R script) as summary statistics. We retained the best 5,000 simulations to perform a local linear regression [29] and reconstructed the abc skyline at user specified time points starting from the posterior distribution as in Maisano Delser et al [27]. We used a mutation rate (μ) of 1.0×10^{-8} / site / generation following [30–34] and generation times found in the literature (Table 1) or inferred using maximum standard length.

As data did not meet assumptions of normality, we computed the Wilcoxon-Mann-Whitney and Kruskal-Wallis non parametric tests to examine differences in demography (TMRCA) considering four factors: range size, familiy, generation time, and reproductive strategies. All statistical analyses were performed in R, using the package *vegan* [35] and *ggplot2* was used for graphical representations [36].

3. Results

Raw sequence filtering, assembly, and SNP calling. A total of 31 543 967 reads of 121 bp each were obtained for the 143 individual samples from the nine species endemic to

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RN. An average of 3 504 885 reads were found per species (min: 2 983 062, max: 4 430 571). The different filtering steps resulted in the building of an average of 41 470 loci (min: 25 331; max: 63 590) per species out of which an average of 23 693 (min: 19 246; max: 28 855) were variable (Table 2). The variable loci harbored an average of 37 107 SNPs (min: 28 239; max: 46 718). The depth of coverage per SNP ranged from 31x to 50x (43x averaged across species).

*Genetic diversity statistics***.** Different levels of genetic diversity were found for the nine species (Table 2). *Cantherhines rapanui* displayed the highest values of heterozygosity (max: 0.262) and nucleotide diversity (32.73×10^{-4}). *Chrysiptera rapanui* showed the lowest values of heterozygosity (0.136) while *Ostorhinchus chalcius* displayed the lowest values of nucleotide diversity (0.063).

Community assembly time. The mean TMRCA retrieved with the stairway plots for the nine species was very recent 253,871 YBP (+/- 119,482 YBP) and ranged from 105,232 YBP (*Ostorhinchus chalcius*) to 398,058 YBP (*Sargocentron wilhelmi*) (Figure 1). The TMRCAs retrieved did not differ significantly among types of endemics (W = 5, $p = 0.6667$), families ($H_6 = 7.4667$, $p = 0.2798$), or reproductive strategy ($H_2 = 2.56$, $p = 0.278$). The only significant factor was generation time ($H_2 = 6.1111$, $p = 0.0471$).

Changes in historical effective population size. We recovered very similar demographic patterns with the two methods (stairway plots and the abc skylines; Figure 1, S1). Patterns of population expansions were recovered for seven out of nine endemic species studied, constant population size through time was found for one species (*Sargocentron wilhelmi*) and a decrease in population size was recovered for one species (*Cantherhines rapanui*). Expansion times retrieved were highly similar between the two methods for four out of the seven species, while abc skylines estimated older

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expansion times than those inferred with the stairway plots for the three other cases. In the same way, the bottleneck found for *Cantherhines rapanui* was dated slightly older with the abc skyline than with the stairway plot analysis.

4. Discussion

Rapa Nui endemic species share a common history, with population expansions dominating the demographic histories dated during the last interglacial period for both small-range and large-range endemics. These expansions, shaped by historical processes, indicate that their current effective population size established in RN during the last glacial maxima (25 000 - 115 000 YBP), a period characterized by climatic cooling and decreased sea levels [37]. These results agree with those found for expansions and bottlenecks of other marine organisms suggesting that sea level oscillations during the last 800 000 years level [38,39] has greatly influenced reef fish populations [40–49]. Rapa Nui endemics, however, differ in their ecology compared to organisms of other reefs in the Pacific region, as they are far less restricted in terms of depth range. Many of the RN endemic species have the particularity to be found from shallow waters to the mesophotic zone (100 - 150 m) in RN water and in seamounts nearby RN (Table 1). Considering the network of seamounts surrounding RN, low sea levels during glacial maxima would have produced periods of maximum reef habitat extension (Figure 2). As such, population expansions during glacial maxima could reflect the colonization / recolonization history of RN from MMH or other seamounts of the RN archipelago. While the Ancient Archipelago hypothesis of Newman & Foster [12] has been invalidated at the species level for this island system [13], this hypothesis could explain what is observed at the population level for RN endemic species. Overall, historical metapopulation dynamics within the RN Archipelago combined with sea level

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fluctuations during glacial maxima could have driven the population dynamics and hence community assembly of RN endemics.

The common demographic and temporal patterns found for large-range and small-range endemics provide insights into the mechanisms that shaped the RN ichthyofauna. Community assembly in remote islands is expected to rely on colonization / extinction / recolonization processes. The concordant expansions detected for all species except *Cantherines rapanui* and *Sargocentron wilhelmi* suggest a concomitant establishment of current population sizes during the last glacial cycle. This pattern does not seem to be influenced by the size of the species range distribution as both small-range and large-range endemics display similar patterns. Actually, populations of large-range endemics sampled around RN could potentially operate at a regional scale, being also present in several other islands of the South Pacific, but the similar expansion times observed here for both types of endemism argue in favor of population demography driven by historical processes.

Local processes rather than regional processes seem to have driven the final stage of community assembly among endemic species around RN, as indicated by the similar TMRCAs retrieved here for both types of endemism. This result is also suggested by the lower species richness observed there compared to in other Pacific islands. The low species diversity in RN reefs might not only be due to the difficulty for larvae to colonize such remote islands, but also due to the difficulty to establish a viable population / metapopulation that functions at such local scales. This hypothesis is reinforced by the fact that the two large range endemics studied here are among the most abundant species of RN [9], yet they are rare throughout the rest of their distribution [50]. Assessing the amount of gene flow between RN populations with

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those of Pitcairn or Austral Island for these large range endemics could help to test this hypothesis.

The relatively small range of TMRCAs retrieved here could also reflect the success of speciation for small-range endemic species. This has been hypothesized for French Polynesian small-range endemics which display similarly population expansions older than the Last Glacial Maximum [17]. Speciation is not an instantaneous process, and could takes at least 2 My to complete in various vertebrate clades [51]. Divergence times, upper bound of the speciation time, are known to be quite recent for several small-range species of this study (*Cantherhines rapanui* 0.54 Ma (0.07 - 1.3 95% HPD), *Chrysiptera rapanui* 1.39 Ma (0.50 - 2.83 95% HPD), *Chromis randalli* 2.02 (0.58 - 4.3 95 % HPD), *Coris debueni*: 2.31 (0.72 - 4.11 95% HPD); see [13]). Only a study in a genomic framework based on pairs of sister species could provide a better estimate of the timing of speciation (**e.g** [33]).

Coalescence time does vary across loci and across sets of individuals. By screening thousands of loci, the inferences made on the demographic history of the populations should not be biased by the loci observed. However, uncertainty in both mutation rates and generation times can potentially bias molecular dating. Mutation rates for SNP data of fish range from 2.5 x 10^{-8} [52] to 3.5 10^{-9} [53] and their selection for estimating demographic histories is not often justified. As such, we chose the fish SNP mutation rate most often used in the litterature. Finally, estimations of generation times in the wild for fishes are scarce. Most of the generation times we used (six out of nine) were selected from the literature from species that are phylogenetically close-related to the species studied here (same genus). Additionally, we used maximal length to infer generation times for three species as maximum standard length and generation time are positively correlated [54]. If TMRCAs were found to be correlated to

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generation time, it seems that this parameter did not influence the expansion time estimates here as we retrieved a common temporal pattern for most species.

Conclusion

We elucidate for the first time the community assembly time of the RN endemic reef fish community using genomic data and demographic inferences. We show that the RN reef fish endemic community shares a common history, with expansion occurring during the last glacial cycle for the two different types of endemic species. Local processes based on the seamounts system around RN should have played a major role in the foundation and persistence of this endemic reef fish community through dynamic of colonization / extinction / recolonization throughout the RN Archipelago.

Ethics. All applicable institutional guidelines for the care and use of animals were followed. Specimens were collected under permit No. 724, 8 March 2016 obtained from the Chilean Subsecretary of Fishing. The Universidad Austral de Chile Ethical Care Committee and Biosecurity Protocol approved our use and handling of animals.

Data accessibility. All Fastq sequence files are available from the GenBank at the National Center for Biotechnology Information short-read archive database (accession number: *forthcoming*).

Authors' contributions.

E.D.-T. and P.S.-A. conceived the study; E.D.-T., P.S.-A. and S.M. acquired the funding; E.D.-T., E.C.G., V.N, C.R.E. and P.S.-A., collected the field data; EDT, P.C.-B. and A.S. produced the data; E.D.-T.; E.D.-T., N.H., S.M, and P.S.-A. analyzed the

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data; E.D.-T., N.H., E.C.G., S.M, and P.S.-A wrote the manuscript. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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Figure captions

Figure 1. Stairway plots for large-range (red) and small-range endemics (black) representing the variation of effective population size through time and sea level fluctuations for the past 400 000 years using data from [37]. Dark tones indicate glacial era characterized by rises of the sea level while greys tones indicate inter-glacial era with lower sea level.

Figure 2. Surface of potential habitat for Rapa Nui endemic reef fish species computed using the package marmap [55] in R [24]. Present conditions (red) and past conditions during the glacial maximums (orange).

Supplementary Material.

Figure S1. Median of effective population sizes (Ne) based on stairway plots and abc skylines analyses.

Table 1 Ecological data on the species of interest of this study. Range size (S: small-range size; L: large-range size), Family, Maximum Depth where the species have been observed (Max. depth) and reference associated ([1]: specimens photographed at those depths by Luiz A. Rocha; [2]: personal observation from Cristian Rapu-Edmunds freediving); generation time used for this study and references associated, maximum size of the species. Codes for reproductive strategy are: [p] pelagic eggs, [b] demersal eggs and [m] mouth brooding.

Range Size	Family	Species	Max. depth (m)	Generation time (years)	Max. size (TL, cm)
S	Monacanthidae [b]	*Cantherhines rapanui*	20 [7]	3	20
S	Apogonidae [m]	*Ostorhinchus chalcius*	25 [7]	2	16
L	Pomacanthidae [p]	*Centropyge hotumatua*	50 [7]	1 [56]	9
S	Pomacentridae [b]	*Chrysiptera rapanui*	72[1]	1 [57]	7.8
S	Labridae [p]	*Coris debueni*	70[1]	3	27
L	Holocentridae [p]	*Myripristis tiki*	80[2]	3 [41]	26.5
S	Pomacentridae [b]	*Chromis randalli*	105[1]	2 [57]	15
S	Chaetodontidae [p]	*Chaetodon litus*	105	2 [42]	15.5
S	Holocentridae [p]	*Sargocentron wilhlmi*	157 [58]	3 [41]	19.5

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Table 2. Summary of genetic data for each species. Sample size and molecular metrics for each species of the study. Observed (Ho) and expected (He) heterozygosity computed on variable loci; F_{IS}, inbreeding coefficient. [1]Nucleotide diversity across all loci (π accross all loci = π on variable loci x No. SNP / No. of variable RADSeq loci x length of RAD loci). Maximum (in bold) and minimum (italics) values are highlighted for all columns.

Species	No. of ind	No. of Sites TOTAL	No. of RADSeq loci	No. of variable RADSeq loci	No. SNP	π accross variable sites	Ho	He	F_{IS}	π accross all sites [1] (10^{-4})
Cantherhines rapanui	15	5 373 281	44 233	20 052	*28 239*	**0.271**	**0.262**	**0.260**	0.023	**32.73**
Centropyge hotumatua	15	3 563 265	29 195	21 684	38 816	*0.163*	0.156	0.158	0.032	25.21
Chaetodon litus	15	5 024 341	41 439	21 905	33 421	0.227	0.220	0.219	0.022	29.86
Chromis randalli	13	4 247 760	34 893	24 673	43 844	0.172	0.161	0.165	**0.043**	26.34
Chrysiptera rapanui	18	*3 104 187*	*25 331*	*19 246*	35 735	0.145	*0.137*	*0.141*	0.039	23.25
Coris debueni	14	5 817 876	47 949	28 594	45 870	0.216	0.208	0.209	0.029	29.94
Myripristis tiki	18	5 522 762	45 432	**28 855**	**46 718**	0.165	0.159	0.160	0.025	23.00
Ostorhinchus chalcius	19	**7 702 975**	**63 590**	24 019	32 224	0.166	0.165	0.162	*0.008*	*19.19*

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Sargocentron wilhlmi	16	5 009 870	41 234	24 207	37 860	0.224	0.217	0.217	0.026	30.98

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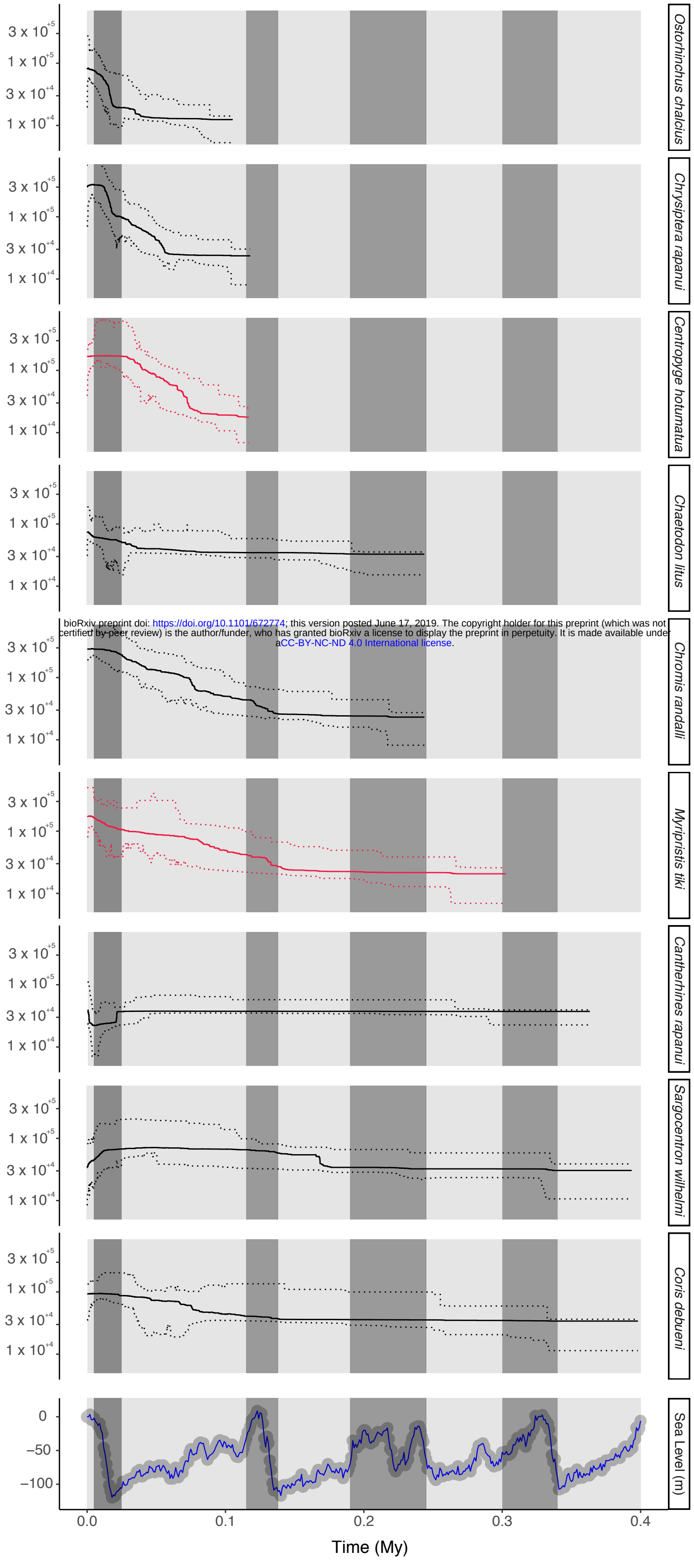

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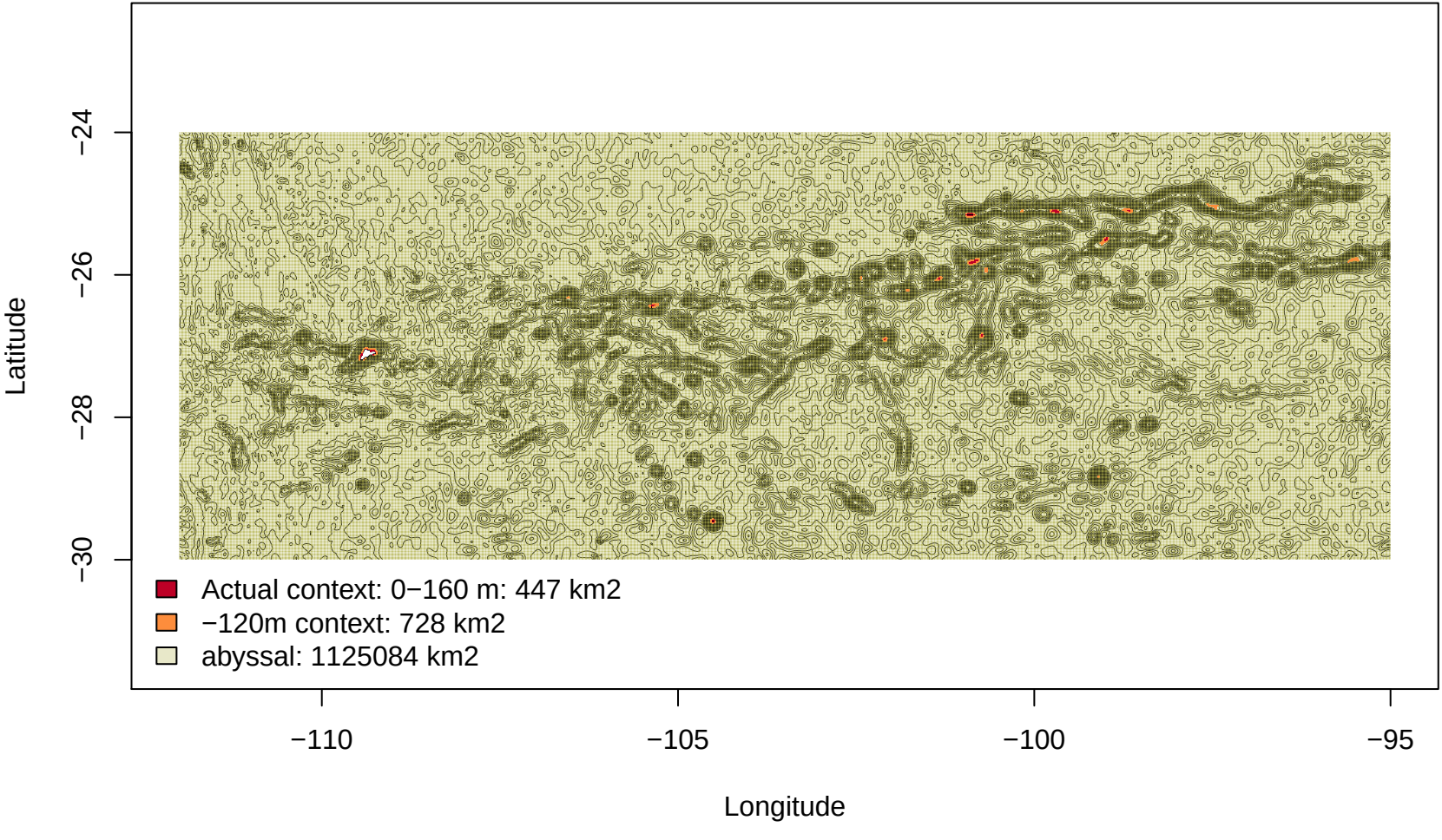
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−28
−30
Actual context: 0−160 m: 447 km2
−120m context: 728 km2
abyssal: 1125084 km2
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−105
−100
−95
Longitude