

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/267507194>

Endemic and widespread coral reef fishes have similar mitochondrial genetic diversity

Article in *Proceedings of the Royal Society B* · December 2014

DOI: 10.1098/rspb.2014.1068

CITATIONS

23

READS

249

3 authors, including:



[Erwan Delrieu-Trottin](#)

Ecole Pratique des Hautes Etudes

45 PUBLICATIONS 641 CITATIONS

[SEE PROFILE](#)



[Serge Planes](#)

French National Centre for Scientific Research

779 PUBLICATIONS 20,845 CITATIONS

[SEE PROFILE](#)

Endemic and widespread coral reef fishes have similar mitochondrial genetic diversity

Erwan Delrieu-Trottin, Jeffrey Maynard and Serge Planes

Proc. R. Soc. B 2014 **281**, 20141068, published 29 October 2014

References

[This article cites 38 articles, 8 of which can be accessed free](#)

<http://rsob.royalsocietypublishing.org/content/281/1797/20141068.full.html#ref-list-1>

Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (1796 articles)

[molecular biology](#) (150 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Research



Cite this article: Delrieu-Trottin E, Maynard J, Planes S. 2014 Endemic and widespread coral reef fishes have similar mitochondrial genetic diversity. *Proc. R. Soc. B* **281**: 20141068.
<http://dx.doi.org/10.1098/rspb.2014.1068>

Received: 2 May 2014

Accepted: 25 September 2014

Subject Areas:

ecology, molecular biology

Keywords:

endemism, coral reef fish, mitochondrial genetic diversity, range size, vulnerability

Author for correspondence:

Erwan Delrieu-Trottin

e-mail: erwan.delrieu.trottin@gmail.com

Endemic and widespread coral reef fishes have similar mitochondrial genetic diversity

Erwan Delrieu-Trottin^{1,2}, Jeffrey Maynard^{1,2,3} and Serge Planes^{1,2}

¹CRIOBE-USR 3278, CNRS-EPHE-UPVD, 58 Avenue Paul Alduy, 66860 Perpignan cedex, France

²Laboratoire d'Excellence 'CORAIL', 58 Avenue Paul Alduy, 66860 Perpignan cedex, France

³Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA

ED-T, 0000-0002-4120-9316; JM, 0000-0002-6444-6373

Endemic species are frequently assumed to have lower genetic diversity than species with large distributions, even if closely related. This assumption is based on research from the terrestrial environment and theoretical evolutionary modelling. We test this assumption in the marine environment by analysing the mitochondrial genetic diversity of 33 coral reef fish species from five families sampled from Pacific Ocean archipelagos. Surprisingly, haplotype and nucleotide diversity did not differ significantly between endemic and widespread species. The probable explanation is that the effective population size of some widespread fishes locally is similar to that of many of the endemics. Connectivity across parts of the distribution of the widespread species is probably low, so widespread species can operate like endemics at the extreme or isolated parts of their range. Mitochondrial genetic diversity of many endemic reef fish species may not either limit range size or be a source of vulnerability.

1. Introduction

Endemic species have been a popular focus of evolutionary science for those wishing to understand the causes and consequences of the geographical distribution of life on the Earth [1]. Genetic diversity can be both a cause and a consequence of species biogeography, and it can be difficult to determine the extent to which each applies [2,3]. The general view is that genetic diversity can drive whether a species range size can increase and that diversity increases with range size [4]. There are two premises for this view. First, effective population sizes often increase as the range size increases; second, species adapt as they extend into new environments. Both factors can increase genetic diversity [4]. The result is that endemic species are widely viewed as having lower genetic diversity than species with greater distributions [5]. However, the popularity of this viewpoint is based nearly entirely on research from the terrestrial environment [2,6–11].

Relationships between genetic diversity and range size were first explored in plants [8,9]. In these and other studies [2,11,12], genetic diversity was found to relate positively to range size. In other related studies, researchers have accounted for the effect of differences in phylogenetic history by comparing the genetic diversity of species from the same genus [5,10]. These studies also find rare plant species to have significantly lower genetic diversity than widespread plants. The same relationship has been found when comparing endemic mammal and bird species from islands with related mainland species [12]; genetic diversity was positively related with range size. For insects, Leffler *et al.* [3] showed that in the genus *Drosophila* widespread species were more genetically diverse than large range endemics, which were more diverse than small-range endemics.

There are high levels of endemism in the marine environment especially among the diverse coral reef fishes of remote islands. Endemic coral reef fish

species tend to be concentrated in the periphery of the Indo-Australian hotspot [13] and the remote islands in the Pacific Ocean have especially high rates of endemism for coral reef fishes. As examples, approximately 25, 22 and 11% of the reef fish species of the Hawai'ian, Easter and Marquesas Islands, respectively, are endemic [14–16]. Yet few studies have tested whether the relationships between genetic diversity and range size seen for terrestrial species apply in the marine environment. At the time of publication, there are only two published studies with a specific focus on comparing the mitochondrial genetic diversity of endemic versus widespread marine species. Eble *et al.* [17] studied three Hawai'ian surgeonfish (Acanthuridae) species and found the mitochondrial genetic diversity of the two endemic species to be lower than the diversity of the widespread species. In contrast, Hobbs *et al.* [18] found that the mitochondrial genetic diversity of an endemic angelfish (Pomacanthidae) species of Christmas Island and Cocos (Keeling) Islands is similar to two closely related widespread species. Both Eble *et al.* [17] and Hobbs *et al.* [18] sampled only one location each (Hawai'ian archipelago and Christmas–Cocos (Keeling) Islands, respectively) and three species, and have contrasting results. These studies have thus not clarified whether there is a relationship between genetic diversity and range-size distribution in the marine environment, and assessing that for coral reef fishes is the objective here.

This study presents the largest-scale comparison of the mitochondrial genetic diversity of endemic versus widespread species conducted to date in the marine realm. We analyse the mitochondrial genetic diversity of 33 reef fish species from remote archipelagos of the Pacific Ocean (figure 1a). The species included are a mix of widespread species and small- and large-range endemics. Five families and several different reproductive strategies are represented. We describe the evolutionary processes probably responsible for our results, and discuss the scientific and management implications of our findings.

2. Material and methods

(a) Sampling

A total of 1049 reef fishes (25 different species) were collected using polespears or anaesthetic in the Gambier archipelago in October 2010 and the Marquesas archipelago in November 2011. Mitochondrial genetic diversity indices and demographic history tests for reef fish species sampled across the Hawai'ian archipelago (eight species) come from the following published works: Eble *et al.* [17] for *Ctenochaetus strigosus*, *Zebrasoma flavescens* and *Acanthurus nigrofasciatus*; DiBattista *et al.* [19] for the endemic *Acanthurus nigroris* (see Randall *et al.* [20]); DiBattista *et al.* [21] for *Chaetodon ornatissimus*; and Craig *et al.* [22] for *Chaetodon multicinctus*, *C. militaris* and *C. fremblii*. Five different families are represented: Acanthuridae, Apogonidae, Chaetodontidae, Pomacentridae and Serranidae. Several reproductive strategies are represented (table 1). Some of the families included in this study are sequential hermaphrodites (e.g. Pomacentrids) while others (e.g. Acanthurids) are gonochoristic. These traits can have an impact on the calculation of effective population sizes, which we do not compute or use in this study. Species were classified as widespread (range size > 12 000 km, 13 species), large-range endemic (1000–8000 km, 13 species) and small-range endemic (less than 500 km, seven species),

depending on their maximum range extent (figure 1a). Range extent is used here instead of range surface area as extent can be easily calculated from guidebooks (e.g. [23]) and is less subjective (i.e. polygons encompassing range area can be drawn many ways). Using a maximum range extent of 8000 km for endemics is consistent with Hodge *et al.* [24], whose largest range area for endemics equates to a range extent of 9000 km (*Anampses femininus*).

(b) Laboratory procedures and genetic analyses

Whole genomic DNA was extracted from fin tissue preserved in 96% EtOH kept at ambient temperature. DNA extraction was performed using QIAxtractor (Qiagen, Crawley) according to manufacturer's protocols. Cytochrome *b* fragments (approx. 800 bp, mitochondrial DNA) were amplified using PCR protocols and sequencing as described by Williams *et al.* [25]. All unique sequences have been deposited in GenBank. Sequences were aligned with CLUSTAL W [26] and edited using GENEIOUS v. 5.4 [27]. The indices of genetic diversity used are haplotype diversity (*h*) and nucleotide diversity (π). Both indices were estimated for the 12 widespread species and 14 endemic species using DNASP v. 5.1 [28], which implements diversity indices algorithms described by Nei [29]. We used the summary statistics Tajima's *D* [30], *F_s* [31] and *R₂* [32] to detect departures from a neutral Wright–Fisher model. Significant negative values of Tajima's *D* and *F_s*, and significant small positive values of *R₂*, indicate population growth (or a selective sweep). Significant positive values of Tajima's *D* are a signature of genetic subdivision, population contraction or diversifying selection. All three summary statistics were produced using DNASP v. 5.1 [28] and tests for significance were carried out following 1000 coalescent simulations.

(c) Data analyses

Sample sizes varied widely among species, so we tested first whether the genetic diversity indices were correlated with the number of individuals collected. Pearson's and Spearman's tests were used for haplotype and nucleotide diversity, respectively, as *h* followed normality assumptions and π did not. No correlation was found between either of the indices and sample size (Pearson's correlation for *h*: $t_{df=30} = -1.21$, $p = 0.24$; Spearman's correlation for π : $S = 7363.15$, $P = 0.19$, $\rho = -0.23$). We investigated differences in the genetic diversity of endemic and widespread species and the potential drivers of any differences using five approaches. (i) Student test for haplotype diversity and Wilcoxon–Mann–Whitney test for nucleotide diversity were used to compare genetic diversity *between* endemic and widespread species. (ii) ANOVA and Kruskal–Wallis were used to test for significant differences in haplotype and nucleotide diversity, respectively, *among* the three range-size classifications. We used the (iii) Wilcoxon signed-rank test analysis to compare the genetic diversity indices for endemic species that had a widespread congener caught in the same archipelago, following Karron [10] and Gitzendanner & Soltis [5]. (iv) Permutational multivariate ANOVA [33] was used to determine the amount of variation in normalized haplotype and nucleotide diversity explained by the following five predictor variables: family, demographic history, archipelago, range-size classification and reproductive strategy (see table 1 for this information for all species). We then used (v) a multivariate regression tree (MRT) [34] to hierarchize the significant predictor variables from the PERMANOVA. Prediction error was used to assess model fit and determine the appropriate tree size, and the tree was pruned by cross-validation using the minimum rule presented by Breiman *et al.* [35]. All statistical analyses were performed on R v. 3.0.2 [36], using the vegan package [37], mvpart package for MRT [38] and ggplot2 for graphics [39].

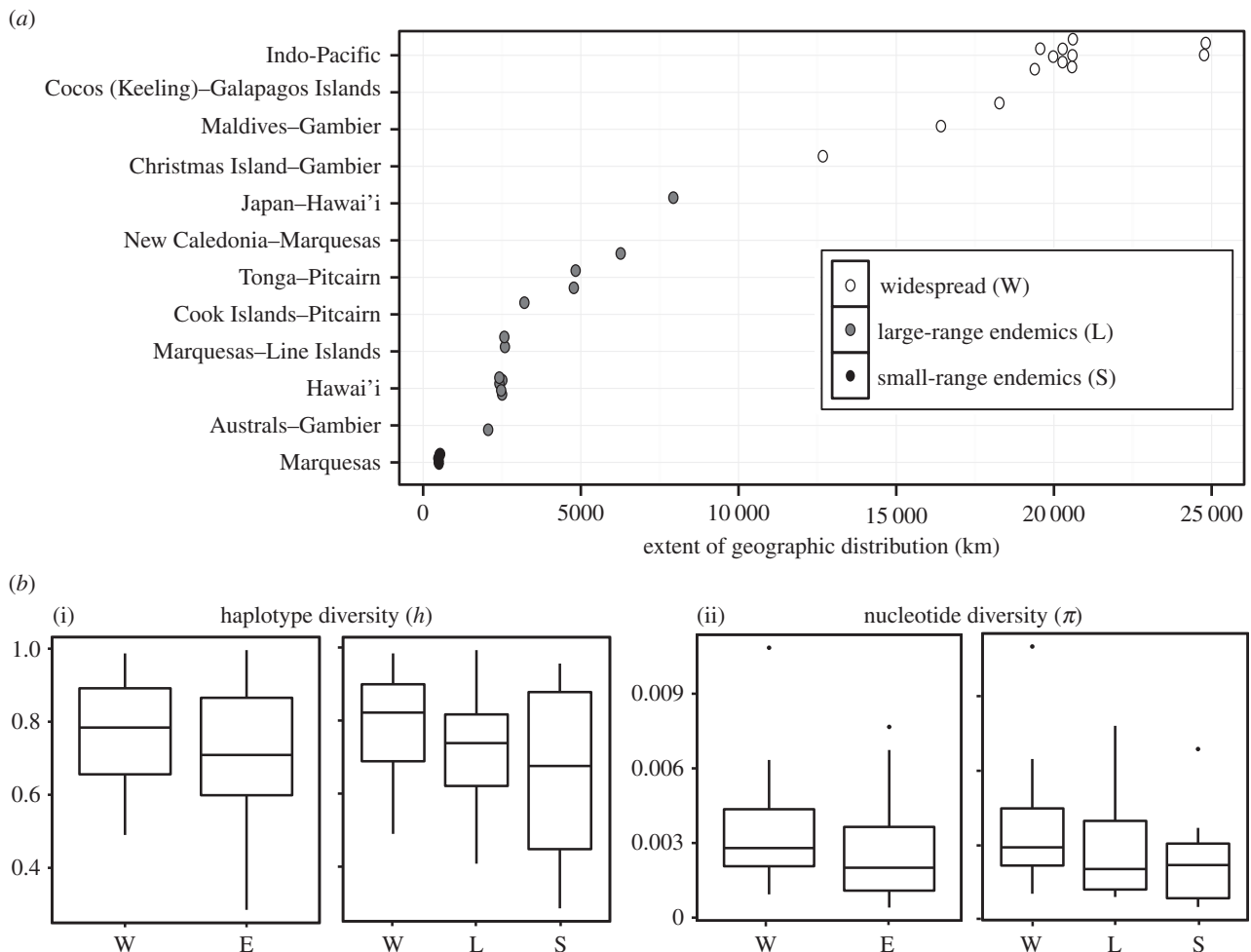


Figure 1. Geographical distribution and mitochondrial genetic diversity for all range-size classifications. (a) Extent of geographical distribution for each studied species. (b) Box and whisker plots of (i) haplotype and (ii) nucleotide diversity for all species when classified as widespread (W) or endemic (E), and widespread, large-range endemic (L) or small-range endemic (S). Midlines are medians, boxes and whiskers are first/second and third quartiles, respectively, and points are outliers.

3. Results and discussion

There is no consistent pattern or relationship between mitochondrial genetic diversity and range size for the 33 species and three archipelagos included here. In contrast to the general pattern seen for terrestrial species, endemic and widespread coral reef fish species have similar mitochondrial genetic diversity. Three main lines of evidence supporting this statement are presented.

- (1) Haplotype (h) and nucleotide diversity (π) varied widely among widespread and endemic species. Mitochondrial genetic diversity (both indices) is shown as box and whisker plots in figure 1b for the grouping of large- and small-range endemic species and for each range-size classification. When the endemics are grouped and when separated, the boxes forming the first and third quartiles for mitochondrial genetic diversity overlap with the boxes for widespread species, and this is the case for both diversity indices. The statistical tests support the visual interpretation of the figure 1b plots. The haplotype and nucleotide diversity of endemic and widespread species are not significantly different when small- and large-range endemics are grouped (h : $t_{29.5} = -1.4055$, $p = 0.17$; π : $W = 99.5$, $p = 0.27$) or when the endemics are separated into small and large range (h : $F_{2,30} = 0.909$, $p = 0.33$; π : $H_2 = 1.539$, $p = 0.46$). There are small- and

large-range endemic species as well as widespread species that have low (less than 0.5) haplotype diversity, and for each there are species with high (greater than 0.9) haplotype diversity (*, ** in table 1).

- (2) Haplotype and nucleotide diversity are also not significantly different when analysing congener pairs made up of an endemic and widespread species (h : $V = 52$, $p = 0.68$; π : $V = 35$, $p = 0.50$). For five of the pairs (1, 2, 3, 7 and 13; figure 2), the endemic species have a higher mitochondrial genetic diversity than their widespread congeners. These pairs of species are from the families Pomacentridae and Chaetodontidae. For four other pairs (5, 6, 10 and 11), the endemic species have a lower mitochondrial genetic diversity than their widespread congener. Among these four pairs all families are represented except Serranidae. There are four pairs in which the comparisons of haplotype and nucleotide diversity are not concordant (4, 8, 9 and 12); for these pairs and for each diversity index there is an endemic with greater mitochondrial genetic diversity than a widespread, and vice versa. For all three types of results— $E > W$, $W > E$ and ‘not concordant’—all three of the archipelagos and both small- and large-range endemics are represented. None of the endemic–widespread sister-species pairs of this study shared mtDNA haplotypes.
- (3) Lastly, of the five factors (family, demography, archipelago, range-size classification and reproductive strategy)

Table 1. Molecular diversity indices and demographic history results for all species. Species names, sampling locations (G, Gambier archipelago; H, Hawai‘ian Islands; M, Marquesas Islands) and associated diversity indices and demographic test results structured by range-size classification. Significant test results are in bold and indicate a population expansion. Superscripts after species names denote the 13 congener pairs tested for differences in mitochondrial genetic diversity in figure 2. For reproductive strategy codes: [p] eggs released in pelagic environment, [b] eggs laid on the bottom and [m] mouthbrooding. *h*-values < 0.5 are considered low and are highlighted with a single asterisk, *h*-values > 0.9 are high and are highlighted with a double asterisk. For demography, E signifies an expansion, which is indicated by at least 1 of Tajima’s *D* or Fu’s *F*s for Hawai‘ian species or at least 2 of Tajima’s *D*, Fu’s *F*s and R2 for Marquesas and Gambier.

range size	family	species	<i>n</i>	locality	<i>h</i>	π	Tajima’s <i>D</i>	Fu’s <i>F</i> s	R2	demography	source
W	Acanthuridae [p]	<i>Acanthurus nigriscans</i> ⁵	35	M	0.881	0.002	−2.43	−19.30	0.0354	E	this study
W	Acanthuridae [p]	<i>Acanthurus nigrofasciatus</i> ¹²	305	H	0.740	0.002	—	−19.93	—	E	17
W	Apogonidae [m]	<i>Ostorhinchus apogonoides</i> ⁹	44	M	0.982**	0.006	−1.70	−31.03	0.0504	E	this study
W	Apogonidae [m]	<i>Pristipogon kallopterus</i> ¹⁰	36	M	0.965**	0.006	−1.92	−18.53	0.0469	E	this study
W	Chaetodontidae [p]	<i>Chaetodon citrinellus</i> ⁴	45	M	0.784	0.002	−1.25	−3.14	0.0659	—	this study
W	Chaetodontidae [p]	<i>Chaetodon ornatissimus</i> ^{13,14,15}	61	H	0.590	0.0030	—	0.90	—	—	21
W	Pomacentridae [b]	<i>Abudefduf sordidus</i> ⁶	48	M	0.824	0.002	−2.30	−21.74	0.0315	E	this study
W	Pomacentridae [b]	<i>Chromis agilis</i> ³	47	G	0.902**	0.003	−2.18	−16.12	0.0329	E	this study
W	Pomacentridae [b]	<i>Chrysiptera glauca</i> ²	50	G	0.690	0.001	−1.93	−21.00	0.0416	E	this study
W	Pomacentridae [b]	<i>Plectroglyphidodon lacrymatus</i> ⁸	43	M	0.854	0.003	−0.60	−1.92	0.0903	—	this study
W	Pomacentridae [b]	<i>Plectroglyphidodon leucozonus</i> ⁷	46	M	0.554	0.004	0.45	2.24	0.1259	—	this study
W	Pomacentridae [b]	<i>Stegastes fasciatus</i> ¹	27	G	0.490*	0.001	−2.26	−5.97	0.0694	E	this study
W	Serranidae [b]	<i>Pseudogramma polycanthum</i> ¹¹	44	G	0.987**	0.011	−1.81	−25.33	0.0462	E	this study
L	Acanthuridae [p]	<i>Acanthurus nigris</i> ¹²	441	H	0.52	0.0008	−2.38	−3.4 × 10 ³⁸	—	E	19,20
L	Acanthuridae [p]	<i>Ctenochaetus strigosus</i>	531	H	0.610	0.001	—	−29.80	—	E	17
L	Acanthuridae [p]	<i>Zebrasoma flavescens</i>	560	H	0.740	0.003	—	−5.93	—	—	17
L	Apogonidae [m]	<i>Apogon lativittatus</i> ^{9,10}	48	M	0.819	0.004	−1.55	−9.72	0.0562	E	this study
L	Chaetodontidae [p]	<i>Chaetodon declivis</i> ⁴	45	M	0.771	0.004	−0.17	−0.21	0.1042	—	this study
L	Chaetodontidae [p]	<i>Chaetodon multicinctus</i> ¹³	280	H	0.408*	0.002	−2.30	−29.14	—	E	22
L	Chaetodontidae [p]	<i>Chaetodon miliaris</i> ¹⁴	408	H	0.652	0.001	−2.45	−28.82	—	E	22
L	Chaetodontidae [p]	<i>Chaetodon fremblii</i> ¹⁵	358	H	0.878	0.005	−2.07	−29.14	—	E	22
L	Pomacentridae [b]	<i>Chromis bairdii</i> ³	42	G	0.931**	0.004	−1.65	−5.83	0.0528	E	this study
L	Pomacentridae [b]	<i>Chrysiptera galba</i> ²	44	G	0.741	0.002	−2.25	−20.09	0.0336	E	this study
L	Pomacentridae [b]	<i>Stegastes aureus</i>	41	M	0.622	0.0011	−2.09	−8.26	0.0472	E	this study
L	Pomacentridae [b]	<i>Stegastes emeryi</i> ¹	48	G	0.659	0.001	−1.27	−5.21	0.0615	—	this study
L	Serranidae [b]	<i>Pseudogramma xanthurus</i> ¹¹	22	G	0.996**	0.008	−1.77	−15.86	0.0588	E	this study

(Continued.)

Table 1. (Continued.)

range size	family	species	<i>n</i>	locality	<i>h</i>	π	Tajima's <i>D</i>	Fu's <i>F_s</i>	<i>R₂</i>	demography	source
S	Acanthuridae [p]	<i>Acanthurus reversus</i> ⁵	48	M	0.828	0.002	−1.76	−11.30	0.0470	E	this study
S	Pomacentridae [b]	<i>Abudefduf conformis</i> ⁶	35	M	0.301*	0.0004	−0.71	−0.76	0.1045		this study
S	Pomacentridae [b]	<i>Chromis abrupta</i>	49	M	0.677	0.002	−2.37	−17.88	0.0329	E	this study
S	Pomacentridae [b]	<i>Chromis fatiuhivae</i>	30	M	0.959**	0.007	−1.61	−12.70	0.0600	E	this study
S	Pomacentridae [b]	<i>Chromis flavipicis</i>	44	M	0.285*	0.0004	−1.21	−2.13	0.0775		this study
S	Pomacentridae [b]	<i>Dasyllus strasburgi</i>	45	M	0.595	0.001	−1.24	−3.80	0.0634		this study
S	Pomacentridae [b]	<i>Plectroglyphidodon sagmarius</i> ^{7,8}	44	M	0.933**	0.004	−1.44	−10.12	0.0605	E	this study

tested with the PERMANOVA and their interactions, only family ($p = 0.01$), demography ($p = 0.001$) and range-size classification \times demography ($p = 0.007$) are significant; range-size classification as an independent predictor is not significant ($p > 0.05$). Using the significant predictor variables, a six-leaf MRT for normalized haplotype and nucleotide diversity had the smallest estimated predictive error and explained 64.2% of the variance (figure 3). Family is the most important factor, explaining 44% of the variance in mitochondrial genetic diversity. The next node separates species based on whether the diversity indices suggest a population expansion occurred (7.5% of variance). Both of the following nodes are based on range-size classification (5.2 and 7.5% for presence/absence of an expansion, respectively). As above, range-size classification as an independent predictor is not significant and explains only 12.7% of the variance in mitochondrial genetic diversity observed, and only when combined with demographic history.

An order of magnitude more species (33) are included here than in the two previous published studies (3) that compared the mitochondrial genetic diversity of endemic and widespread coral reef fishes. Here, all the possible results are seen in that the endemic species have greater, less and similar mitochondrial genetic diversity compared with the widespread species. This explains why the results of the two previously published studies—by Eble *et al.* [17] and Hobbs *et al.* [18]—contrast with one another. If the mitochondrial genetic diversity of only a few reef fish species are sampled and compared our results show that finding the mitochondrial genetic diversity of endemic species to be greater than widespread species is as likely as finding the opposite result. We make the case that the explanations for our finding mainly relate to effective population size and connectivity, along with differences among species in demographic history and speciation/divergence.

Genetic diversity and effective population size are inextricably linked and positively related [40,41]. As above, for the congener pairs the mitochondrial genetic diversity of some endemic species is greater than the diversity of the widespread congener (case 1; 5 of 11 pairs) and vice versa (case 2; 4 of 11 pairs), and there is a plausible explanation related to effective population size for each of these cases. The plausible scenario for case 1 ($E > W$) is that the effective population size of the endemic species in its range is greater than the effective population size of the widespread species where we sampled. The widespread species may have a far greater effective population size than the endemic species throughout its entire range, but the sampling location and other locations where the species occurs may have low connectivity, so mixing is low. Mixing may only be sufficient to maintain the integrity of widespread species and may only occur during rare migration events. Studies have shown that populations of widespread species are sometimes depauperate at the geographical extremes of their distribution [42,43]. We posit that among our sampled widespread species the remoteness of some islands limits gene flow so much that some of the species are essentially operating like endemics, and that some others have higher degrees of connectivity to the broader population. For the former, isolation is having the same effect as being at the

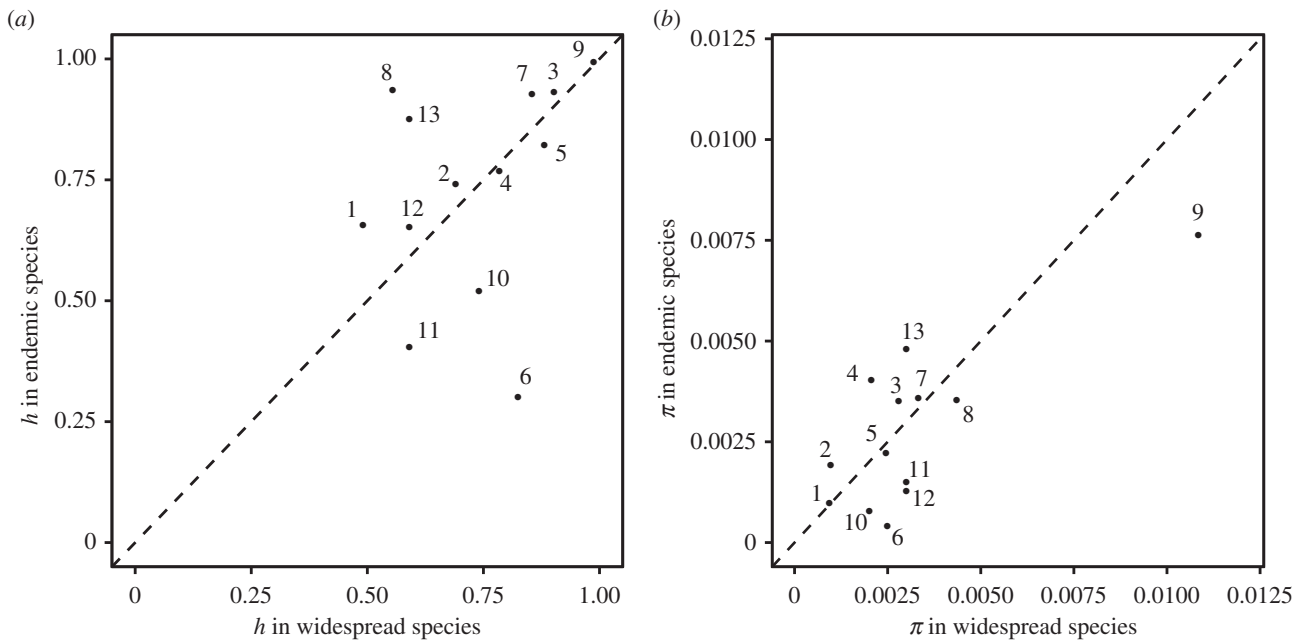


Figure 2. Comparisons of haplotype and nucleotide diversity for congener pairs. Scatterplots of (a) haplotype (h) and (b) nucleotide (π) diversity for each of 13 congener pairs; diversity for the pairs is equal on the dashed line. Species names for the congener pairs are shown in table 1.

geographical extreme of the distribution. Many of our widespread species (69%) display a signature of population expansion, which has potentially been the consequence of local bottlenecks, increasing the likelihood that the genetic diversity will not be significantly greater than found for the endemic congeners. In support of this, several studies have shown that isolated archipelagos can host genetically differentiated populations of some widespread reef fishes (*Acanthurus triostegus* [44], *Scarus psittacus* [42], *Lutjanus kasmira* [45], *Centropyge flavissima* [46]). Furthermore, Messmer *et al.* [43] show a decline in genetic diversity among widespread species from west to east in the Pacific region where we sampled, indicating that some of our widespread species may be both isolated and at the extreme ends of the range. When the mitochondrial genetic diversity of the widespread species is greater than the endemic congener (4 of the 11 cases), the plausible scenario is that the effective population size of the widespread species is either greater or far greater than that of the endemic. In these cases, the degree of connectivity to the regional/global population may be greater than for the cases where the endemic species has greater diversity than the widespread congener.

Hobbs *et al.* [47] showed that local abundance and geographical range size are not correlated in marine fishes. Many marine endemic reef fish are abundant [48] and local population size of small-range endemics can be an order of magnitude greater than the population size of widespread species at the same location [49]. Endemic species studied here were abundant, and only *Pseudogramma xantha*, *Chromis fatuhivae* and *Chromis flavapicis* were found to be especially rare. These species exhibit contrasting mitochondrial genetic diversity; *P. xantha* and *C. fatuhivae* have high mitochondrial genetic diversity (0.996 and 0.959 respectively), and *C. flavapicis* has low mitochondrial genetic diversity (0.285).

The wide range in mitochondrial genetic diversity seen for widespread species, as well as small- and large-range endemics, also suggests that each group may include species with both different demographic histories as well as old and recent divergence. Stebbins & Major [50] distinguish two

types of endemism based on the age of species. Neoendemic species are young species that may expand their geographical range as they evolve; they fit the 'age and area' hypothesis first proposed by Willis [51]. Palaeoendemic species once had far larger distributions, but their biogeographical range has greatly decreased. Whether the endemics included here are neo- or palaeoendemics is unknown; it is likely though that there is a mix of each type among the 18 endemics included. Having a mix of the two types of endemics increases the likelihood that a wide range of mitochondrial genetic diversity will be seen among sampled endemics, especially given the range of environmental conditions and habitats sampled here. We describe above that the widespread species sampled probably include a range in levels of connectivity with the broader population. As with the endemics, the widespread species sampled probably include a range of demographic histories (i.e. species have varying degrees of isolation that could relate to time since settlement, and some have expanded while others have faced bottlenecks). We show that all sampling locations are represented among the endemics with greater mitochondrial genetic diversity than their widespread congener, and for the opposite case. This result lends strong support to our suggestion that for all locations, there are species—widespread and endemic—with very different demographic histories.

In summary, the results presented clearly show that the mitochondrial genetic diversity of endemic reef fish species (Osteichthyes) is not different than that of closely related widespread species; at least not consistently so in the Indo-Pacific. Here, mitochondrial genetic diversity of the endemic species in our congener pairs is greater than the diversity of widespread species nearly as often as the opposite is the case. The key message is that range-size distribution is not either a strong driver or a good predictor of the mitochondrial genetic diversity of coral reef fish in the Indo-Pacific. There are three critically important implications of this result for the way the scientific and management community view both endemic and widespread marine species. First, we cannot assume that low (or lower) mitochondrial genetic diversity is limiting the ability of endemic marine species

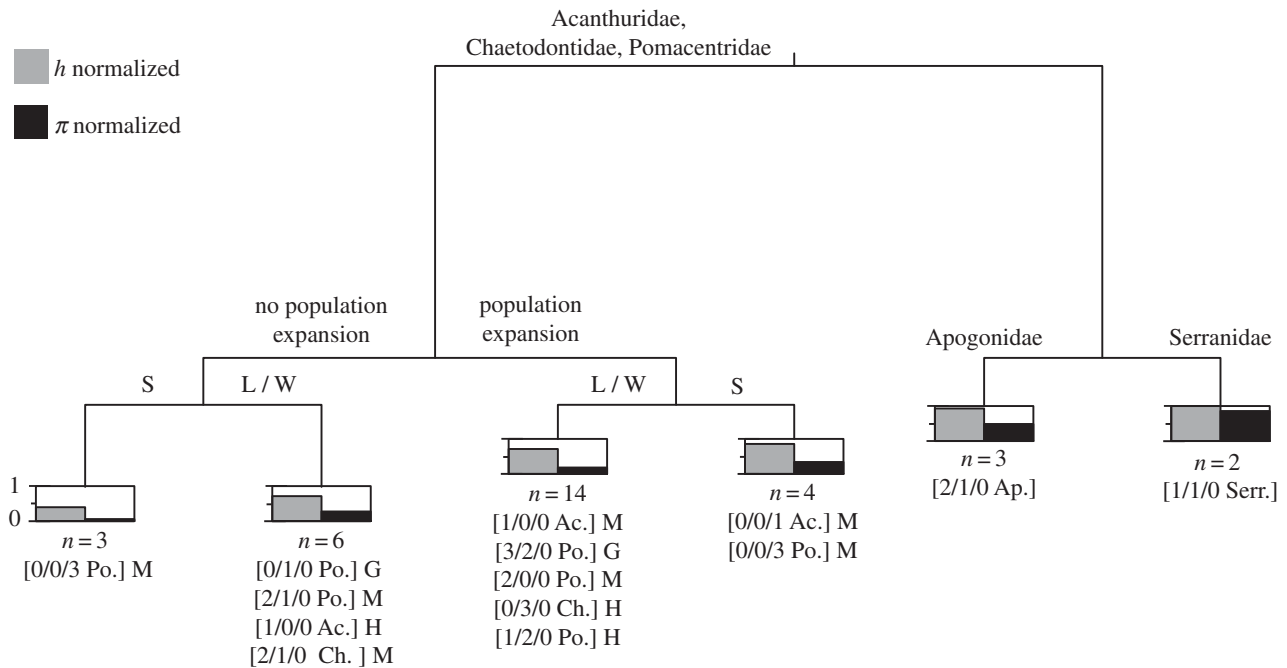


Figure 3. Multivariate regression tree (MRT) of normalized haplotype diversity (h normalized) and nucleotide diversity (π normalized) using the predictor variables from PERMANOVA that are significant: family (Ac., Acanthuridae; Ap., Apogonidae; C., Chaetodontidae; Po., Pomacentridae; Serr., Serranidae), range-size classification (W, widespread; L, large-range endemic; S, small-range endemic) and demographic history. Location codes: G, Gambier archipelago; H, Hawai'ian Islands; M, Marquesas Islands. A total of 64.2% of variance is explained; length of branches is proportionate to the variance explained.

to expand their distribution. There are certainly cases where this will be true, but our results suggest that for many of the endemic species included here other drivers of the ability to expand, like connectivity and competition, have greater influence than mitochondrial genetic diversity. Second, there will be cases where genetic diversity can be a source of vulnerability for endemic species, but we cannot assume this will always be the case. Low connectivity due to isolation is probably a far greater source of vulnerability than genetic diversity for many of the endemic coral reef fish species included here. Lastly, if viewing biodiversity from the perspective of genetic diversity, extinction of some local populations of widespread species may result in a net loss of biodiversity similar to that for total extinction of an endemic species.

Data accessibility. GenBank accession numbers: KM455125–KM455538.

Acknowledgements. We thank Jeffrey T. Williams, Pierre Sasal, Johann Mourier, Thomas Cribb, Michel Veuille, René Galzin and Michel Kulbicki, who assisted with the sampling, along with numerous other colleagues and the crew of the *Braveheart*. For comments on the statistical analyses, we thank Gareth Williams. We thank John B. Horne and an anonymous reviewer for providing constructive reviews of versions of the manuscript.

Funding statement. This work was supported by grants from the French National Agency for Marine Protected Area, which funded sampling expeditions, together with the Contrat de Projet Etat-Territoire in French Polynesia through the project 'CORALSPOT'. Additional funding was provided by the IFRECOR in French Polynesia. E.D.-T. was funded through a PhD fellowship from the French Ministry for Research and High Education, and J.M. was supported by funding from the French Ministry for Ecology and Sustainable Development and by a Marie Curie Actions fellowship.

References

- Gaston KJ. 2003 *The structure and dynamics of geographic ranges*. Oxford, UK: Oxford University Press.
- Hamrick JL, Godt MJW. 1989 Allozyme diversity in plant species. In *Plant population genetics, breeding, and genetic resources* (eds AHD Brown, MT Clegg, AL Kahler, BS Weir), pp. 43–63. Sunderland, MA: Sinauer Associates.
- Leffler EM, Bullaughey K, Matute DR, Meyer WK, Laure S, Venkat A, Andolfatto P, Przeworski M. 2012 Revisiting an old riddle: what determines genetic diversity levels within species? *PLoS Biol.* **10**, e1001388. (doi:10.1371/journal.pbio.1001388)
- Charlesworth D, Willis JH. 2009 The genetics of inbreeding depression. *Nat. Rev. Genet.* **10**, 783–796. (doi:10.1038/nrg2664)
- Gitzendanner MA, Soltis PS. 2000 Patterns of genetic variation in rare and widespread plant congeners. *Am. J. Bot.* **87**, 783–792. (doi:10.2307/2656886)
- Barrett SCH, Kohn JR. 1991 Genetic and evolutionary consequences of small population size in plants: implications for conservation. In *Genetics and conservation of rare plants* (eds DA Falk, KE Holsinger), pp. 3–30. New York, NY: Oxford University Press.
- Ellstrand NC, Elam DR. 1993 Population genetic consequences of small population size: Implications for plant conservation. *Annu. Rev. Ecol. Syst.* **24**, 217–242. (doi:10.1146/annurev.es.24.110193.001245)
- Stebbins GL. 1942 The genetic approach to problems of rare and endemic species. *Madroño* **6**, 241–258.
- Kruckeberg AR, Rabinovitz D. 1985 Biological aspects of endemism in higher plants. *Annu. Rev. Ecol. Syst.* **16**, 447–479. (doi:10.1146/annurev.es.16.110185.002311)
- Karron J. 1987 A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evol. Ecol.* **1**, 47–58. (doi:10.1007/BF02067268)
- Hamrick JL, Godt MJW. 1996 Effects of life history traits on genetic diversity in plant species. *Phil. Trans. R. Soc. Lond. B* **35**, 1291–1298. (doi:10.1098/rstb.1996.0112)
- Frankham R. 1997 Do island populations have less genetic variation than mainland populations? *Heredity* **78**, 311–327. (doi:10.1038/hdy.1997.46)

13. Bowen BW, Rocha LA, Karl SA, Craig MT, DiBattista JD, Eble JA, Gaither MR, Skillings D, Bird CJ. 2013 The origins of tropical marine biodiversity. *Trends Ecol. Evol.* **1666**, 1–8. (doi:10.1016/j.tree.2013.01.018)
14. Randall JE. 1998 Zoogeography of shore fishes of the Indo-Pacific region. *Zool. Stud.* **37**, 227–268.
15. Randall JE. 2001 Four new cardinal fishes (Perciformes: Apogonidae) from the Marquesas Islands. *Pac. Sci.* **55**, 47–64. (doi:10.1353/psc.2001.0006)
16. Randall JE. 2007 *Reef and shore fishes of the Hawaiian Islands*. Honolulu, HI: UH Sea Grant.
17. Eble JA, Toonen RJ, Bowen BW. 2009 Endemism and dispersal: comparative phylogeography of three surgeonfishes across the Hawaiian Archipelago. *Mar. Biol.* **156**, 689–698. (doi:10.1007/s00227-008-1119-4)
18. Hobbs J-PA, van Herwerden L, Jerry DR, Jones GP, Munday PL. 2013 High genetic diversity in geographically remote populations of endemic and widespread coral reef angelfishes (genus: *Centropyge*). *Diversity* **5**, 39–50. (doi:10.3390/d5010039)
19. DiBattista JD, Wilcox C, Craig MT, Rocha LA, Bowen BW. 2011 Phylogeography of the Pacific Blueline Surgeonfish *Acanthurus nigroris* reveals a cryptic species in the Hawaiian Archipelago. *J. Mar. Biol.* **2011**, 1–17. (doi:10.1155/2011/839134)
20. Randall JE, DiBattista JD, Wilcox C. 2011 *Acanthurus nigroris* Günther, a valid species of surgeonfish, distinct from the Hawaiian *A. nigroris* Valenciennes. *Pac. Sci.* **65**, 265–275. (doi:10.2984/65.2.265)
21. DiBattista JD, Rocha LA, Craig MT, Feldheim KA, Bowen BW. 2012 Phylogeography of two closely related Indo-Pacific butterflyfishes reveals divergent evolutionary histories and discordant results from mtDNA and microsatellites. *J. Hered.* **103**, 617–629. (doi:10.1093/jhered/ess056)
22. Craig MT, Eble JA, Bowen BW. 2010 Origins, ages and population histories: comparative phylogeography of endemic Hawaiian butterflyfishes (genus *Chaetodon*). *J. Biogeogr.* **37**, 2125–2136. (doi:10.1111/j.1365-2699.2010.02358.x2125)
23. Randall JE. 2005 *Reef and shore fishes of the South Pacific: New Caledonia to Tahiti and the Pitcairn Islands*. Honolulu, HI: University of Hawaii Press.
24. Hodge JR, Read CI, van Herwerden L, Bellwood DR. 2012 The role of peripheral endemism in species diversification: evidence from the coral reef fish genus *Anampses* (Family: Labridae). *Mol. Phyl. Evol.* **62**, 653–663. (doi:10.1016/j.ympev.2011.11.007)
25. Williams JT, Delrieu-Trottin E, Planes S. 2012 A new species of Indo-Pacific fish, *Canthigaster criobe*, with comments on other *Canthigaster* (Tetraodontiformes: Tetraodontidae) at the Gambier Archipelago. *Zootaxa* **3523**, 80–88.
26. Thompson JD, Higgins DG, Gibson TJ. 1994 CLUSTAL W: improving the sensitivity of progressive multiple alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. *Nucleic Acids Res.* **22**, 4673–4680. (doi:10.1093/nar/22.22.4673)
27. Biomatters. 2009 Geneious v. 4.6. See <http://www.geneious.com/>.
28. Librado P, Rozas J. 2009 DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25**, 1451–1452. (doi:10.1093/bioinformatics/btp187)
29. Nei M. 1987 *Molecular evolutionary genetics*. New York, NY: Columbia University Press.
30. Tajima F. 1989 Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **123**, 585–595.
31. Fu YX. 1997 Statistical tests of neutrality of mutations against population growth, hitchhiking, and background selection. *Genetics* **147**, 915–925.
32. Ramos-Onsins SE, Rozas J. 2002 Statistical properties of new neutrality tests against population growth. *Mol. Biol. Evol.* **19**, 2092–2100. (doi:10.1093/oxfordjournals.molbev.a004034)
33. Anderson MJ. 2001 A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.* **26**, 32–46. (doi:10.1111/j.1442-9993.2001.01070.pp.x)
34. De'ath G. 2002 Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* **83**, 1105–1117.
35. Breiman L, Friedman JH, Olshen RA, Stone CG. 1984 *Classification and regression trees*. Belmont, CA: Wadsworth International Group.
36. R Core Development Team. 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
37. Oksanen J, Kindt R, Legendre P, O'Hara RB. 2011 *Vegan: community ecology package*. R package version 2.0–2. See <http://cran.rproject.org/web/packages/vegan/index.html>.
38. Therneau TM, Atkinson B, Ripley B, Oksanen J, De'ath G. 2004 The mvpart: multivariate partitioning. R package version 1.6-1. See <http://cran.rproject.org/web/packages/mvpart/index.html>.
39. Wickham H. 2009 *ggplot2: elegant graphics for data analysis*. New York, NY: Springer.
40. Wright S. 1931 Evolution in Mendelian populations. *Genetics* **16**, 97–159.
41. Wright S. 1938 Size of population and breeding structure in relation to evolution. *Science* **87**, 430–431.
42. Winters KL, van Herwerden L, Choat JH, Robertson DR. 2010 Phylogeography of the Indo-Pacific parrotfish *Scarus psittacus*: isolation generates distinctive peripheral populations in two oceans. *Mar. Biol.* **157**, 1679–1691. (doi:10.1007/s00227-010-1442-4)
43. Messmer V, Jones G, Munday P, Planes S. 2012 Concordance between genetic and species diversity in coral reef fishes across the Pacific Ocean biodiversity gradient. *Evolution* **66**, 3902–3917. (doi:10.1111/j.1558-5646.2012.01725.x)
44. Planes S, Fauvelot C. 2002 Isolation by distance and vicariance drive genetic structure of a coral reef fish in the Pacific Ocean. *Evolution* **56**, 378–399. (doi:10.1554/0014-3820(2002)056[0378:IBDAVD]2.0.CO;2)
45. Gaither MR, Toonen RJ, Robertson DR, Planes S, Bowen BW. 2010 Genetic evaluation of marine biogeographical barriers: perspectives from two widespread Indo-Pacific snappers (*Lutjanus kasmira* and *Lutjanus fulvus*). *J. Biogeogr.* **37**, 133–147. (doi:10.1111/j.1365-2699.2009.02188.x)
46. DiBattista JD, Waldrop E, Bowen BW, Schultz JK, Gaither MR, Pyle RL, Rocha LA. 2012 Twisted sister species of pygmy angelfishes: discordance between taxonomy, coloration, and phylogenetics. *Coral Reefs* **31**, 839–851. (doi:10.1007/s00338-012-0907-y)
47. Hobbs J-PA, Jones GP, Munday PL. 2011 Extinction risk in endemic marine fishes. *Conserv. Biol.* **25**, 1053–1055. (doi:10.1111/j.1523-1739.2011.01698.x)
48. Hobbs J-PA, Jones GP, Munday PL, Connolly SR, Srinivasan M. 2012 Biogeography and the structure of coral reef fish communities on isolated islands. *J. Biogeogr.* **39**, 130–139. (doi:10.1111/j.1365-2699.2011.02576.x)
49. Hobbs J-PA, Jones GP, Munday PL. 2010 Rarity and extinction risk in coral reef angelfishes on isolated islands: interrelationships among abundance, geographic range size and specialisation. *Coral Reefs* **29**, 1–11. (doi:10.1007/s00338-009-0580-y)
50. Stebbins GL, Major J. 1965 Endemism and speciation in the California flora. *Ecol. Monogr.* **35**, 1–35. (doi:10.2307/1942216)
51. Willis JC. 1922 *Age and area: a study in geographical distribution and origin of species*. Cambridge, UK: Cambridge University Press.