

Human-Mediated Loss of Phylogenetic and Functional Diversity in Coral Reef Fishes

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Summary

Beyond the loss of species richness [1–3], human activities may also deplete the breadth of evolutionary history (phylogenetic diversity) and the diversity of roles (functional diversity) carried out by species within communities, two overlooked components of biodiversity. Both are, however, essential to sustain ecosystem functioning and the associated provision of ecosystem services, particularly under fluctuating environmental conditions [1–7]. We quantified the effect of human activities on the taxonomic, phylogenetic, and functional diversity of fish communities in coral reefs, while teasing apart the influence of biogeography and habitat along a gradient of human pressure across the Pacific Ocean. We detected nonlinear relationships with significant breaking points in the impact of human population density on phylogenetic and functional diversity of parrotfishes, at 25 and 15 inhabitants/km², respectively, while parrotfish species richness decreased linearly along the same population gradient. Over the whole range, species richness decreased by 11.7%, while phylogenetic and functional diversity dropped by 35.8% and 46.6%, respectively. Our results call for caution when using species richness as a benchmark for measuring the status of ecosystems since it appears to be less responsive to variation in human population densities than its phylogenetic and functional counterparts, potentially imperiling the functioning of coral reef ecosystems.

Results

While human activities undoubtedly shape the structure of ecological communities, biodiversity patterns also result

from historical, geographical, and environmental factors, all acting at different scales with complex interactions [8]. Although the multiple factors that drive species richness are relatively well understood, their effects on other aspects of biodiversity are still poorly described, especially at large scales [9]. Ultimately, disentangling the direct effects of human pressure from those of environment and biogeography on phylogenetic and functional diversity would contribute to our ability to identify tractable levers for conservation actions to counteract the ongoing biodiversity losses.

Here we assess the effect of human activities on the taxonomic, phylogenetic, and functional diversity of two major fish groups (parrotfish and butterflyfish) on coral reefs while teasing apart the influence of biogeography and habitat. We also seek to identify potential thresholds in these human-biodiversity relationships.

To address these aims, we used an extensive survey of coral reefs encompassing strong environmental and anthropogenic impact gradients across the west Pacific (Figure 1). Pacific coral reefs provide an ideal case study because of the high taxonomic, phylogenetic, and functional diversity within their fish communities [10]. These communities are important in maintaining the functioning of coral reef ecosystems since they support a large range of critical functional roles and services such as (1) the control of macroalgae that may outcompete hard corals, (2) the removal and transport of sediments to provide a hard and clean substratum for coral recruitment, and (3) the bioerosion of dead corals thus facilitating resilience to disturbances such as bleaching events [11, 12].

Socioeconomic surveys (questionnaires to households, fishers, key informants, and markets), human demographic data, and reef and island geographic data, provided 19 *human* (Table S5, part a, available online), 17 *biogeographic* (Table S5, part b), and 33 *habitat* variables (Table S5, part c) at each of the 63 sites.

Underwater visual census (UVC) of fish communities were conducted at these sites. Since these three categories of drivers (*human*, *biogeographic*, and *habitat*) have different numbers of variables with potential correlations, we performed a principal coordinates analysis (PCoA) on each category and retained the first five principal components (PCs) as independent explanatory factors in the model. To estimate the relative influence of *human* activities, *biogeography*, and *habitat* on the number of species (S), phylogenetic diversity (PD), and functional diversity (FD) of fish communities, we used boosted regression tree (BRT) models, a machine learning modeling method, which can cope with strongly interacting factors and nonlinear relationships (Supplemental Experimental Procedures).

The five PCoA axes explained between 48% and 81% of the total variance for each category (*human* activities, *biogeography*, and *habitat*). Using PCoA axes as explanatory factors (Supplemental Experimental Procedures), BRTs explained between 39% (FD of butterflyfish) and 62% (S of butterflyfish) of the variance (cross-validation procedure) for the different biodiversity components of fish communities (Table S1, parts a and b). Mean, SD, and range values of S, PD, and FD for both families are provided in Table S2.

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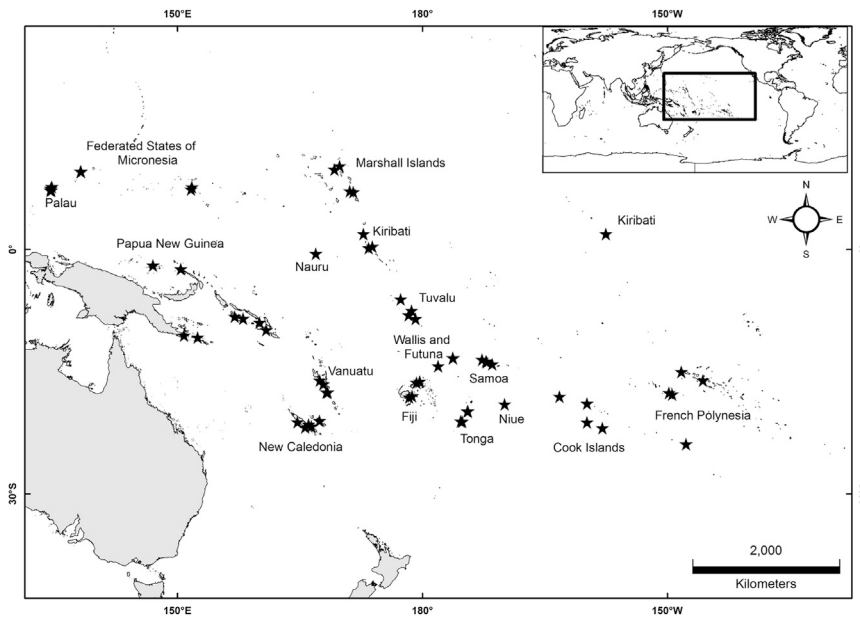


Figure 1. Countries Surveyed in the Pacific

Locations (stars) of the 63 sites surveyed from 2002 to 2009 for fish, *habitat*, *biogeography*, and *human activities* in 17 countries and territories across the southwestern Pacific.

The contributions of PCoA axes for each BRT model were extracted to assess the overall relative influence of each category on each fish biodiversity component (Figure 2). For parrotfishes, phylogenetic, and functional diversity patterns were primarily influenced by *human activities* (PD, 36.3%; FD, 39.2%), whereas species richness patterns were mostly shaped by *biogeography* (49.6%) and *habitat* (36.9%) (Figure 2). Specifically, parrotfish PD and FD were explained by the *human* PCoA axis 1 (PC1), 21.75% and 18.16%, respectively (Figure 2), which is related to population density and whether people derived their livelihoods from the formal-salaried employment sector (Table S3, part a). Human PC2 was the most influential factor of parrotfish FD (21.0%) (Figure 2) and was mainly related to ice being used in fishing activities, the proximity to human population densities of >50 inhabitants/km², and the degree to which people derived their livelihoods from fisheries, agriculture, and other sectors (Table S3, part a). Parrotfish species richness was mostly related to *biogeography* PC1 (24.6%), *habitat* PC1 (20.9%), and *habitat* PC2 (16.0%), while *human* PC1 only explained 13.0% of the variance (Figure 2).

In contrast, *biogeographic* and *habitat* categories were the main drivers of the butterflyfish biodiversity components. Biogeography accounted for 36.7% and 61.2% of S and PD variance, respectively, while *habitat* contribution ranged from 38.8% (PD) to 60.6% (FD) (Figure 2). Human activity, however, had no influence on butterflyfish PD and FD and contributed marginally to species richness (11.8%) (Figure 2). Biogeography PC1 contributed to 20.9% (S) and 26.7% (FD) (Figure 2) and was mainly related to the surface of reef in a 300 km buffer (Table S3, part b). Among the *habitat* factors influencing butterflyfish biodiversity components, *habitat* PC1 contributed from 19.3% (FD) to 22.8% (PD) of variation (Figure 2) and was related to mean depth, habitat complexity, strong relief, and outer barrier (Figure S3C). Habitat PC5 explained from 16.0% (PD) to 24.3% (FD) of variation (Figure 2) and was related to live coral cover and substrate heterogeneity (Table S3, part C).

To further explore how human pressure was related to biodiversity patterns on parrotfish, we extracted the “pure”

marginal effect of human density after teasing apart the other drivers (*habitat* and *biogeography*; Supplemental Experimental Procedures). To consider potential nonlinear relationships between the three fish biodiversity components and human population density, we tested the null hypothesis of no change of slope (Davies’s test) [13] to identify potential thresholds, and we performed breaking point regressions [14] when the null hypothesis was rejected (Statistical Analysis in the Supplemental Experimental Procedures).

The three biodiversity components decreased with increasing population density for parrotfish communities, but at different rates and with different shapes depending on the component (Figure 3). S decreased by 11.7% along the human density gradient, while phylogenetic and functional diversity dropped by 35.8% and 46.6%, respectively. Moreover, we detected nonlinear relationships with significant breaking points for the impact of human density on phylogenetic and functional diversity, while species richness decreased linearly with increasing human density. More precisely, phylogenetic diversity showed a steeper decrease at human population densities over 25 inhabitants/km² of coral reef, whereas functional diversity dropped more rapidly for a population density higher than 15 inhabitants/km² until it reached a second threshold at 420 inhabitants /km² of coral reef, after which functional diversity decreased at an even higher rate (Figure 3; Table 1). An alternative multiple linear regression model was fitted to the population density-functional diversity relationship and revealed only one threshold occurring at 381 inhabitants/km² of coral reef (Figure S1).

Discussion

Emerging experimental research in both terrestrial and marine ecosystems is demonstrating the importance of phylogenetic and functional diversity for ecosystem functioning [1, 2, 4–7], yet these aspects of biodiversity may be eroded by anthropogenic activities [15, 16]. Here, we use a large-scale assessment to show that human impacts have the same level of influence as biogeography and habitat on the phylogenetic and functional diversity of heavily targeted parrotfish communities. A key finding from our study is that human activities are inducing a loss of phylogenetic diversity that may alter the capacity for adaptive evolution [17–19] and even the breadth of ecological processes performed by a critically important family of fishes [4]. Indeed, after removing biogeographic and habitat influences, human activities were found to severely reduce parrotfish functional diversity, potentially leading to a loss of critical functional roles necessary for reef ecosystems to persist [20].

Human population density is a key driver of reef fish community structure that embraces many aspects of human

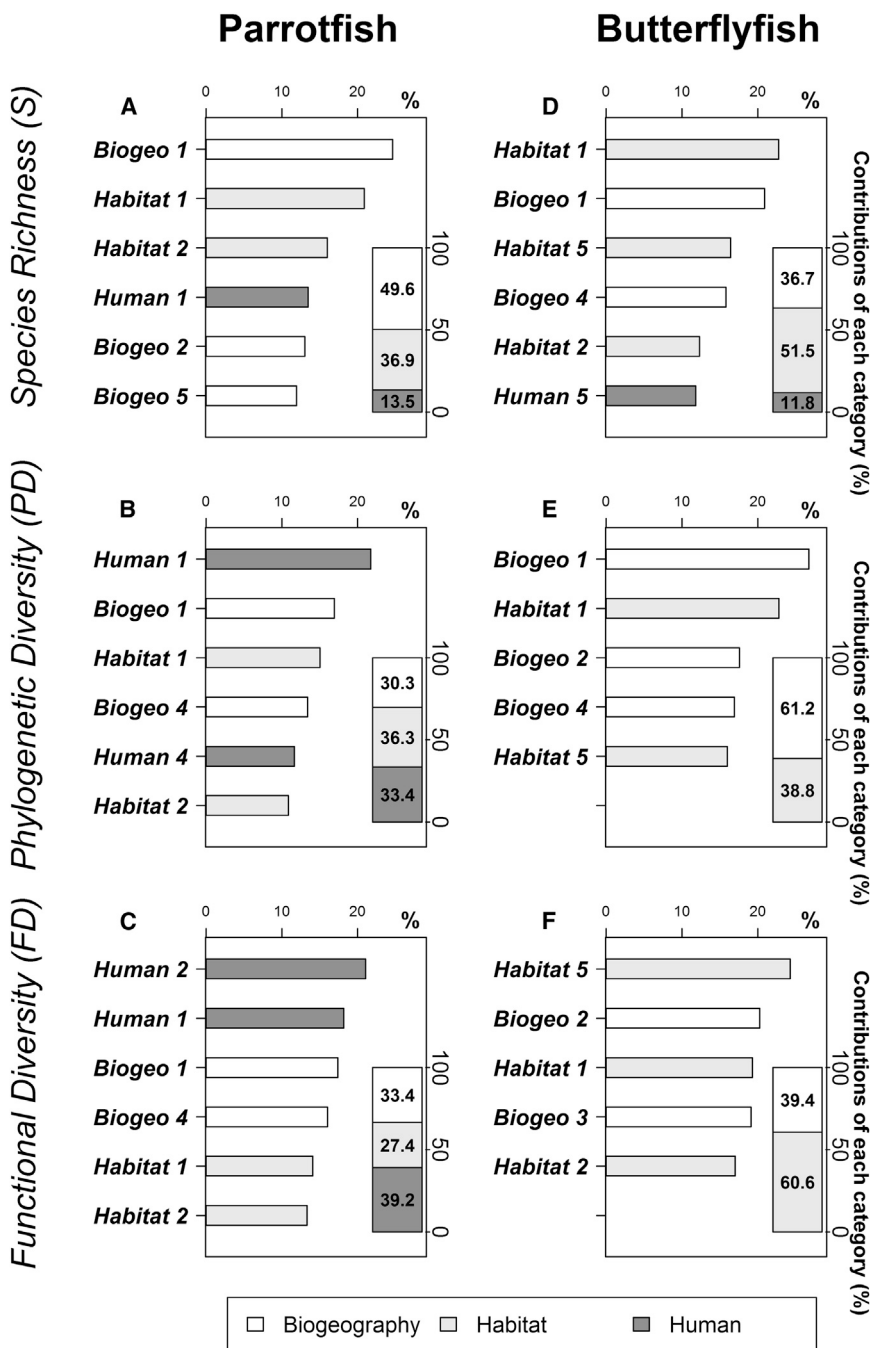


Figure 2. Contributions of Explanatory Factors for All Biodiversity Components

Horizontal bars show the decreasing contributions (in percentage) of PCoA axes (explanatory factors) for each driver category (*biogeography*: “biogeo” in white; *habitat*: “habitat” in light gray; *human activity*: “human” in dark gray) explaining variation in species richness (S), phylogenetic diversity (PD), and functional diversity (FD) for the communities of parrotfish (left) and butterflyfishes (right). Vertical bar plots sum up the contribution (in percentage) of each category of drivers to the variation of biodiversity components for fish communities. The contributions were calculated as the sum of the contributions (in percentage) of PCoA axes (factors) from simplified BRT models retaining only PCoA axes with a significant contribution (Supplemental Experimental Procedures). Values (in percentage) are indicated. See also Figures S2 and S3 and Tables S1, S2, S3, S4, and S5.

with the loss of a number of low-diversity long-branched lineages, many of which are associated to species of large body size. These species are typically the first impacted by humans, especially where gillnets and spear guns are used [24].

This is the case of the humphead parrotfish (*Bolbometopon muricatum*), one of the most phylogenetically unique and functionally distinct species. This is the world’s largest parrotfish and the largest coral predator on reefs, playing an important ecological role by removing an estimated five tons of carbonate annually (approximately half of which is living coral [25]). The humphead parrotfish ranges across the Indo-Pacific, where fishing pressure is low, and can be found in large schools [24, 25]. It has been one of the most heavily harvested species for decades, leading to local extinction in Guam and severe declines elsewhere [24]. In our study, the humphead parrotfish was one of the least common parrotfish, recorded in only 32 out of 1,553 transects.

The most responsive of all diversity components to human population

activities in coastal areas, including fishing and land use changes that may cause sedimentation and nutrient loading [21]. We find that the link between human density (the main component of the *human* PC1 axis) and phylogenetic and functional diversity of parrotfish is fundamentally nonlinear, with thresholds occurring along the human population gradient. Nonlinear relationships between human pressure and fish biodiversity have been documented previously with, for example, fish biomass [22, 23] and ecosystem functions of large parrotfishes [11]. Additionally, we reveal distinct lags in the response of biodiversity components along the human population gradient. Parrotfish PD exhibits a marked response to human population density above the threshold of approximately 25 inhabitants per km². This rapid decline is associated

density is parrotfish FD, with two distinct inflections. The first inflection, marking an onset of a steady decline, occurs at human densities of just 15 inhabitants per km². This inflection reflects the rapid shift observed in earlier studies of parrotfishes and marks the loss of large-bodied species [11]. Changes in functional capabilities thus offers an early warning of system decline, a pattern that is found herein with shifts in FD marking the first signs of diversity change in response to increasing human population densities.

The responses of PD and FD to human population are more acute than species richness for parrotfishes. Species richness, as a metric of biodiversity, is often used as a benchmark for measuring the status of ecosystems, with high levels being interpreted as a sign of an intact and resilient system [26].

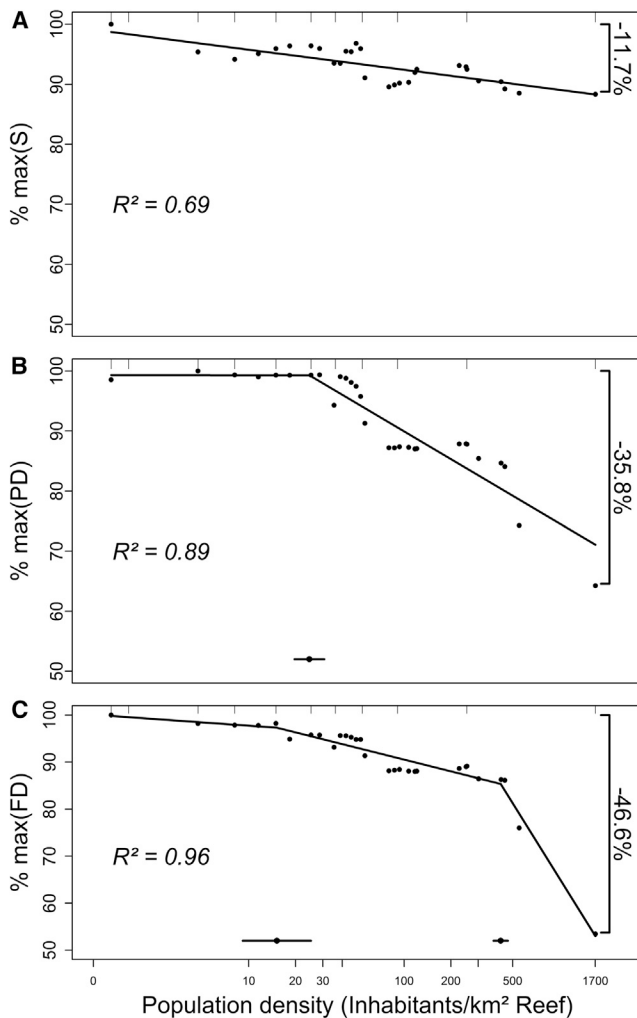


Figure 3. Partial Dependence Plots of Biodiversity Components
(A) Species richness (S), (B) phylogenetic diversity (PD), and (C) functional diversity (FD), for parrotfish communities along the human density gradient. Fitted variations were predicted using biogeography and habitat PCoA axes and population density as predictors in the BRT model. The y axis is the percentage of variation from the maximum value for each biodiversity component. The percentage of the maximum value is independent of the range and the unit of each biodiversity index. Consequently, indices and their declines are therefore comparable, in terms of percentage of loss, from the observed maximum values. Breaking-point estimates and 95% confidence intervals are plotted (see Table 1 for estimates and statistical significance). Rug plots at the top of the plots show the distribution of data, in deciles, of the original variable on the x axis. See also Figures S1, S2, and S3.

Although we need to be careful about generalizing from just two fish families, our results call for caution in this respect because species richness per se, in parrotfishes and butterflyfishes, appears to be less responsive to variation in human densities than its phylogenetic and functional counterparts. This may give a false sense of security, as species richness surveys may indicate stability while the phylogenetic and functional aspects of biodiversity are degrading [27]. This disjunction between species richness and other biodiversity components is particularly marked in the second inflection in FD, which is followed by a precipitous decline. In these circumstances, where human population exceeds 500 people per km², there is an extensive loss of functional diversity (over

Table 1. Estimated Break Points and 95% Confidence Intervals for Species Richness, Phylogenetic Diversity, and Functional Diversity

	Estimated Breaking Point	Confidence Interval (95%)	Estimated Breaking Point (Davies' Test)
S	–	–	25.2 (NS)
PD	24.6	19.7–30.7	24.5 (***)
FD1	15.2	9.3–24.9	21.0 (***)
FD2	422.8	373.5–478.7	380.9 (***)

Estimated breaking points and 95% confidence intervals for the relationship between each biodiversity components of parrotfish (species richness [S], phylogenetic diversity [PD], and functional diversity [FD]) and human density and test for significance using Davies' test for difference in slope. Note that there are two breaking points for FD, indicated by FD1 and FD2. NS, nonsignificant; ***, significant at $p < 0.001$.

46%), while species richness loss is just 11%. Parrotfishes thus represent a sensitive indicator of the impacts of human activity on ecosystem structure and function.

In comparison to parrotfishes, phylogenetic and functional diversity of lightly fished butterflyfishes were not related to any of the human activity factors. The contrasting responses between the parrotfishes and the butterflyfishes emphasize the selective nature of human influences on coral reefs and the differential sensitivity of the three biodiversity components. Butterflyfishes show a clear response in all three metrics to environmental features, biogeography, and habitat. In contrast, the three components for parrotfish reveal their differential sensitivities and the overwhelming response of phylogenetic and functional attributes to human population densities. Although probably mediated primarily through fishing activity, other aspects of human activity may be involved [21]. Our study emphasizes the need to consider not only the local and proximal factors such as fishing, but also land use in the watersheds upstream coral reefs [28, 29].

We provide the first empirical evidence, at a large scale, that human pressure has markedly reduced phylogenetic and functional diversity for a critically important fish family (up to 47% for parrotfishes), while it has only marginally impacted the level of species richness (12%). This finding calls for new approaches that will specifically address the influence of phylogenetic and functional diversity in ecosystem functioning with, for example, experiments manipulating species assemblages in controlled designs where species richness and relative abundances would be kept constant while the diversity of lineages and functions would vary according to realistic scenarios under increasing human pressure.

Experimental Procedures

We used a database encompassing 1,553 UVC of fish communities in 63 sites distributed across 17 Pacific island countries and territories (Figure 1). Highly impacted sites close to capitals, as well as small remote villages, have been sampled in each country (generally, four sites per country), providing a range of human density from 1.3 to 1,705 people per km² of coral reef.

We selected two contrasting taxa to assess the relative magnitude of drivers shaping fish biodiversity on coral reefs: the butterflyfish (Chaetodontidae), which are seldom exploited and have been used as indicators of coral health [30], and the parrotfish (a clade, Scarini, in the Labridae) [31], which are heavily exploited nearly everywhere in the Pacific. For those two taxa, we used a set of six functional traits (Table S4), a dated molecular phylogeny [31], and the entropy index [32] to estimate the phylogenetic and functional diversity of communities (Supplemental Experimental Procedures). The entropy index reflects not only the phylogenetic and functional composition of communities, but also their structure, by adding species biomass along

branches of phylogenetic trees and functional dendrograms, respectively. Where classical measures of phylogenetic and functional diversity are only sensitive to species gain or loss, the entropy index decreases when, for the same species composition, long branches (rare combinations of traits or unique evolutionary histories) have lower biomass.

To estimate the relative influence of *human activities, biogeography, and habitat* on the number of species, phylogenetic diversity, and functional diversity of fish communities, we used BRT models, a machine learning modeling method, which can cope with strongly interacting factors and nonlinear relationships (Results and Supplemental Experimental Procedures).

Once one of the most influencing human factor (*human PC1*) and its related human variable have been identified (Table S3, part a; Population Density in the Supplemental Experimental Procedures), we rerun a BRT model by replacing “*human PC1*” by “population density” while using the same set of *biogeographic* and *habitat* factors (Table S1, part c; Statistical Analysis in the Supplemental Experimental Procedures).

The pure effect of population density was then estimated after accounting for the average effects of all other variables in the model [33]. Since the relationship between all fish biodiversity components and human population density is nonlinear, we tested the null hypothesis of no change of slope (Davies’s test) [13] to identify potential thresholds and performed breaking point regressions [14] when the hypothesis was not verified (Supplemental Experimental Procedures).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, three figures, and five tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.01.049>.

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