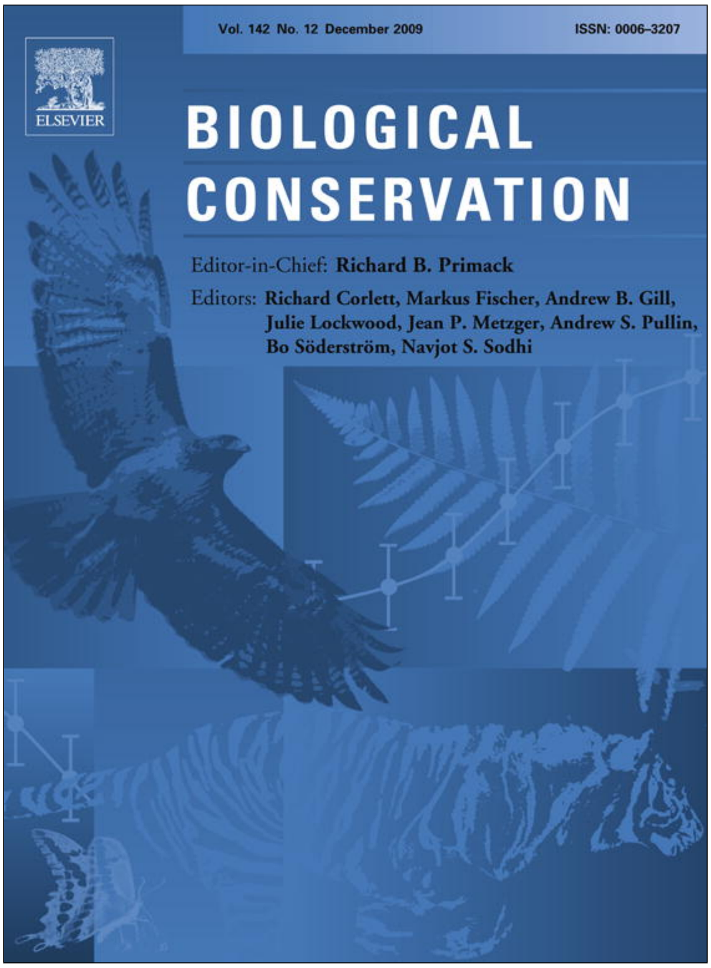
Vol. 142 No. 12 December 2009
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Richard B. Primack
Editors: Richard Corlett, Markus Fischer, Andrew B. Gill,
Julie Lockwood, Jean P. Metzger, Andrew S. Pullin,
Bo Söderström, Navjot S. Sodhi

Biological Conservation 142 (2009) 2881–2885

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Recent decline and potential distribution in the last remnant area of the microendemic Mexican axolotl (*Ambystoma mexicanum*)

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A R T I C L E   I N F O

Article history:
Received 19 January 2009
Received in revised form 8 July 2009
Accepted 16 July 2009
Available online 18 August 2009

Keywords:
Amphibian decline
Salamander
Conservation
Xochimilco
Mexico
Ecological niche modeling
GARP

A B S T R A C T

Native populations of the axolotl (*Ambystoma mexicanum*), a microendemic salamander from Central Mexico, have seen alarming decline in the last decades owing to habitat loss caused by urban growth. The last remnant of its distribution is in a highly heterogeneous urban–rural water system in the Xochimilco region, at the southern edge of Mexico City. We developed a model of the species local distribution based on its ecological niche, using occurrence data and *ad hoc* limnetic variables via the Genetic Algorithm for Rule-set Production (GARP), to identify suitable areas for the species and prioritize conservation efforts. Results indicated that potential distribution of the axolotl in Xochimilco is limited to 11 sites in six reduced, isolated, and scattered areas, located mostly in zones where traditional agriculture (*chinampas*) is the primary land use. Recent surveys found only a single organism in the whole study region, in one of the predicted sites, suggesting a critical situation for the long-term survival of the axolotl in the wild, and demanding urgent actions toward habitat and population restoration. This study also illustrates the utility of niche modeling approaches for aquatic systems at a fine scale.

1. Introduction

In recent years, amphibian populations and species have suffered dramatic declines caused directly and indirectly by human activities (Beebee and Griffiths, 2005; Pounds, 2001). Amphibians are particularly sensitive to environmental change, so habitat alteration is likely to be a major direct cause for their decline (i.e., pollution and eutrophication of waterbodies; Collins and Storfer, 2003). Climate change has also been identified as an important indirect threat for amphibian populations in recent decades (Blaustein and Kiesecker, 2002; Pounds et al., 2006).

The axolotl (*Ambystoma mexicanum*), a neotenic salamander microendemic to the Mexican Central Valley (MCV), is among the species that have seen a dramatic population reduction due to habitat transformation (Zambrano et al., 2007). Originally, the whole MCV was occupied by a series of lakes and wetlands holding populations of this species. As Mexico City expanded throughout the valley, the axolotl distribution contracted down to its current last remnant in the Xochimilco area, in the southeastern portion of the MCV.

Xochimilco is a complex water system of ≈40 km^2 of artificial channels, small lakes and temporary wetlands between rural and urban areas (Zambrano et al., 2009). This system plays a key role in the hydrological dynamics (water provision and sewage) of Mexico City – *a* > 18 million people megalopolis. Most of the water of Xochimilco comes from treated water, whereas a much smaller amount comes from rainfall and springs. This area supports a diversity of activities and processes that directly impact water quality, such as traditional agriculture (*chinampas*), greenhouses, tourism, and urban development. This highly complex and dynamic water network produces a heterogeneous landscape, which directly impacts the habitat availability for the axolotl.

The current distribution of axolotls within Xochimilco is barely known, but direct and indirect evidence indicates that populations have been declining alarmingly in recent decades (Graue, 1998; Zambrano et al., 2007). Due to its low population numbers, *A. mexicanum* is in the IUCN Red List categorized as critically endangered, and is declared under special protection by the Mexican law (NOM-059-SEMARNAT-2001). It becomes urgent, thus, to identify those areas where axolotl populations still exist in order to carry out *in situ* conservation and restoration actions. As such, we present a spatial analysis for this salamander based on an ecological niche model to produce a predictive map, aiming to identify specific areas for searches for as-yet unknown populations (García, 2006; Guisan et al., 2006; Pawar et al., 2007; Raxworthy et al., 2003) and prioritize conservation efforts.

2. Methods

The ecological niche model for the axolotl was built with the Genetic Algorithm for Rule-set Production (GARP) system

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0006-3207/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2009.07.008

(Stockwell and Noble, 1992), using the desktop version 1.1.6 (http://www.nhm.ku.edu/desktopgarp/). In general, this algorithm detects non-random relationships between two sets of data: (a) georeferenced occurrence records of the species, and (b) a set of digital raster data layers representing environmental variables potentially relevant to determining the species' geographic distribution at that particular scale of analysis (Pearson and Dawson, 2003).

Traditionally, niche modeling in freshwater systems has been limited because raster data layers directly relevant to this realm are very scarce or non-existent for most regions in the world (Chen et al., 2007; McNyset, 2005; Wiley et al., 2003). Previous studies have had to rely on variables derived from terrestrial measurements as surrogates for aquatic dimensions (e.g., surface temperature and precipitation, Domínguez-Domínguez et al., 2006; Iguchi et al., 2004; Zambrano et al., 2006). In this study, such limitations were overcome by generating the environmental variables directly from field sampling.

2.1. Sources of data

2.1.1. Occurrence data

Axolotls were sampled with a cast net or "atarraya" (5.8 m diameter and 1/2-in. mesh size) from September 2002 to November 2003. Within this period of time, we performed 27 field trips, having at least one field trip per month. The survey was performed on seven channels, by casting at least 40 nets along each of the channels. In total, 1821 cast net throws were carried out. Each axolotl captured was weighed, measured, and released. Each site where the amphibian was captured was georeferenced.

2.1.2. Environmental layers

From June to September of 2004, eleven water physicochemical variables were measured, including: depth, temperature, pH, conductivity, salinity, turbidity, dissolved oxygen, percentage of oxygen saturation, nitrate, ammonium, and phosphate. The environmental variables chosen to build this GARP model are normally considered relevant for a good number of aquatic species (Wetzel, 1983) and particularly for amphibians. Some of these variables such as temperature, pH, oxygen, nitrates and ammonium are relevant in axolotls living in colonies (Kiesecker, 1996; Schrode, 1972).

Sampling site selection for environmental variables was based on finding those places suitable to generate an interpolation map. Therefore, sampled channels were selected using the following criteria: (1) channels with lengths over 500 m, (2) these channels were interconnected, and (3) channels with any length but in which axolotls were detected in the 2003 survey. With these criteria, a total of 59 points were selected across 40 channels and eight lakes. Sampling points were georeferenced with a portable GPS (Garmin III plus). The total length surveyed was 31,521 m, with an average channel size of 900 m (s.d. = 623).

A raster map was built for each environmental variable using the Inverse Distance Weighted (IDW) interpolation technique using the ArcMap 8.0 geographic information system (GIS; ESRI, 1999–2001), masking the analysis only to waterbodies. Final resolution (pixel size) of all raster layers was 1 m^2 (Zambrano et al., 2009).

2.2. Ecological niche modeling

The general procedure using GARP algorithm to build the niche model and projected map follows the next series of steps. First, input presence records are re-sampled to reach 1250 observations, and an equal number of points are selected randomly from pixels not holding presence records (pseudo-absences). These 2500 points are randomly divided in two equal groups, one for model training and the other one for model testing. Next, training data are used to generate a series of seed models via four different methods: a logistic regression and three environmental envelope rules. Seed models take the form of if-then statements ('environmental rules'), which are then evaluated using the testing dataset. After that, seed rules are perturbed mimicking chromosomal evolution (i.e., mutations, insertions, deletions) and evaluated again, if a daughter rule performs better than the seed rule, the former is retained in a population of rules. This process is repeated until a fixed number of iterations (1000 in this case) or until convergence (i.e., when model does not improve for more than 1% from one iteration to the next). Finally, the niche model is projected onto a geographic scenario to produce a binary map representing suitable (1) or unsuitable (0) environmental conditions for the species. A detailed description of GARP can be found elsewhere (Stockwell and Peters, 1999; Stockwell and Noble, 1992). In previous studies, GARP has proven reliable for predicting the geographic distribution of aquatic species (Domínguez-Domínguez et al., 2006; Iguchi et al., 2004; McNyset, 2005; Wiley et al., 2003; Zambrano et al., 2006).

Because GARP produces somehow different results from one run to the next using the same input dataset due to all the randomization involved in the process, we developed 100 independent prediction models for our analysis, from which we selected a subset of 10 best models based on two criteria: (1) A first set of 20 models with <10% omission error was selected. (2) From them, we selected the 10 models closest to the median in the area where the species was predicted as present (Anderson et al., 2003). These 10 models were then summed in a GIS, generating a consensus map with pixel values ranging from 0 to 10, where 0 represents areas in which all models predicted absence of the species and 10 represents areas where all models agree on predicting the species' presence. Finally, the consensus map was reclassified to build a presence/absence map, using as a threshold the minimum value in which all training occurrences were predicted (Lowest Presence Threshold or LPT).

Our final model was statistically validated using a jackknife method especially designed for low occurrence numbers (Pearson et al., 2007). In this procedure, each locality is removed once from the totality of occurrences and a model is built; predictive ability is then tested with the excluded locality. The same steps are repeated for each one of the localities of the whole set, which in our case were five. The number of predictive successes and failures are used to calculate a test criterion (D) and a p-value, which reflects the probability that observed success is better than random expectations. This test requires a threshold value for deciding the area predicted as present in each independent model, which in this case was established as the LPT, being the most conservative criterion (Pearson et al., 2007).

Once the predictive distribution map was built, verification surveys were carried out through 37 field trips from October 2005 to January 2006. Channel selection was based on 11 sites where the species was predicted to be present (five of them with prediction values above three in the GARP outputs) and 13 channels where axolotl was predicted as absent. All channels were distributed across the complete study area. Axolotl sampling methods were identical as in the previous survey, but with a total of 668 nets casted and at least 17 throws per channel.

3. Results

In the 2002–2003 surveys, 23 axolotls were found in only four sites, with a sampling effort of 0.013 organisms per throw. Channels and lakes where axolotls were found were scattered and separated by 1.5–4.0 km (Fig. 1).

Model predictions identified 11 potential occurrence areas (Fig. 1) that occupy 6% of the 0.7 km^2, covering the sampled channels area. During the 2005–2006 sampling, only one axolotl was found at La Virgen lake, one of the sites where the model predicted potential presence, and that was not sampled before. Remarkably, no axolotls were detected at any of the four sites at which they were previously found (Fig. 1). Predictive success was relatively low in the jackknife test ($q = 0.4$) since only two of the five independent models were able to predict the excluded localities. However, this result was significantly better than random expectations ($p < 0.002$) due to the very small proportional area predicted as present in each run.

Interestingly, most areas predicted as suitable for the species are associated with local traditional agricultural land use (*chinampas*) (Table 1). However, this landscape is highly heterogeneous, and different land cover types are interspersed in small areas. For

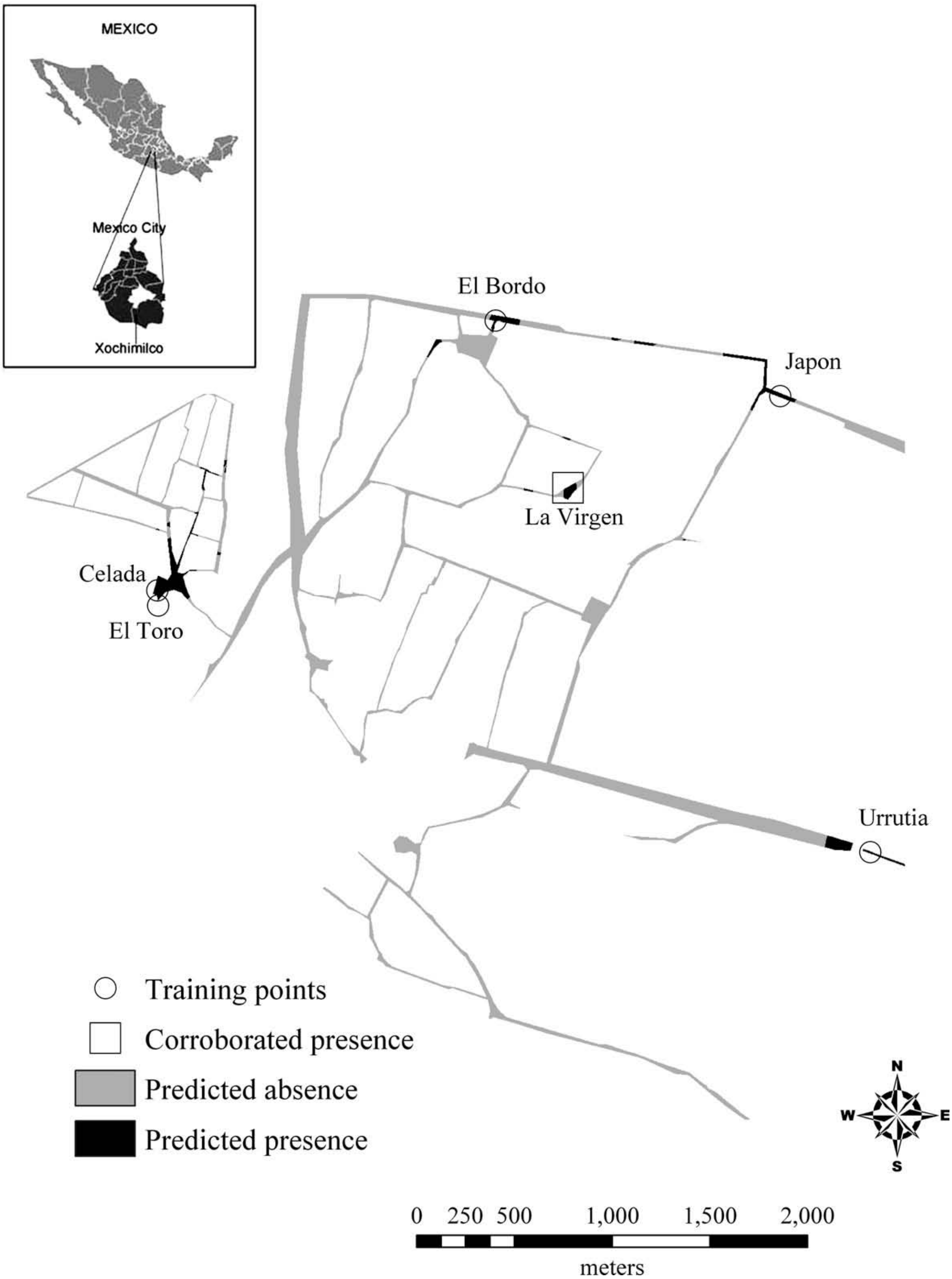

Fig. 1. Channel system of the Xochimilco area in Mexico City indicating (in black) the sites where the axolotl was predicted present by the ecological niche model.

Table 1
Average values of limnetic variables and abundances of axolotls in occurrence sites. The first value in the abundance column represents the number of organisms collected in 2002–2003 and were used to build the model; the second value represents the number of organisms found during the validation sampling in 2006. DO = dissolved oxygen, *T* = temperature, Cond = conductivity, Tur = turbidity.

Channel	Land use	Depth (m)	*T* (°C)	Cond (μS cm^{-1})	pH	Tur (NTU)	DO (mg l^{-1})	NH_4–N (mg l^{-1})	PO_4–P (mg l^{-1})	NO_3–N (mg l^{-1})	Axolotl abundance (02–03/06)
Japon	Chinampa	0.90	22.69	0.71	7.94	63.80	5.89	0.87	6.70	4.93	1/0
Bordo	Chinampa	0.70	22.13	0.57	9.19	76.00	6.74	0.25	1.13	2.85	2/0
Urrutia	Chinampa/urban	1.00	16.17	0.94	6.97	6.10	0.07	1.56	9.20	8.93	26/0
Toro	Chinampa	0.60	20.95	0.99	8.10	30.80	3.25	0.79	11.90	0.57	1/0
Celada	Chinampa	0.60	20.95	0.99	8.10	30.80	3.25	0.79	11.90	0.57	1/0
Virgen	Chinampa	0.50	20.80	0.70	8.30	89.50	9.05	0.71	8.40	0.00	0/1

instance, one of the predicted sites, Puente de Urrutia, is next to a greenhouse complex, while Laguna del Toro and Celada are surrounded by urban areas, and Japon is next to a dairy production area. Consequently, water quality varies across short distances (Table 1) despite the fact that all of the lakes and channels are interconnected.

4. Discussion

This study is one of few ecological niche modeling applications to aquatic organisms (Chen et al., 2007; Domínguez-Domínguez et al., 2006; Drake and Bossenbroek, 2004; Iguchi et al., 2004; McNyset, 2005; Olden and Jackson, 2001; Ron, 2005; Wiley et al., 2003; Zambrano et al., 2006). However, in previous studies, environmental predictors have generally been at global or regional scales, making difficult to generate conclusions at local scales. In our study, existing variables for the Xochimilco area were not sufficiently fine-grained to represent the actual heterogeneity of the system, so, it was necessary first to generate microclimatic and water quality layers at high resolution (1 m^2) to use as predictors (Zambrano et al., 2009) on which to develop the niche model. In this sense, this study represents a novel effort to predict a species' distribution at such a fine spatial scale.

Heterogeneity and spatial complexity in Xochimilco channels are high, and are related to limnological variables affected by different levels of urbanization, land and water uses. Such environmental variability in a relatively small area is reflected in the patchiness and fragmentation of axolotl distribution. Our predictions indicated a highly scattered and disjunct local distribution for the species, identifying only seven potentially suitable areas beyond the other four already-known sites. Although our results are perhaps influenced by the low number of occurrences used for building the model (Wisz et al., 2007), the sole confirmed presence of a single axolotl at one of the predicted sites during validation sampling across 24 sites supports to some degree the reliability of our model.

Our findings suggest that land use influences axolotl distribution as all records are located in *chinampas* areas. Furthermore, axolotls have been detected in association with some of the few natural springs that still remain in Xochimilco. Spring water is clear, cold, and with lower ammonium and nitrates concentrations than the rest of the channels, which seem important features for axolotl survival. This amphibian needs clear water to detect prey (Abrahams and Kattenfeld, 1997); high temperatures makes them more vulnerable to parasites; and high concentrations of nitrates and ammonium are toxic, reducing their performance in sub-lethal concentrations (Camargo et al., 2004; Cheng and Chen, 2002; Harte and Hoffman, 1989; Jensen, 1996; Robles-Mendoza et al., 2009; Scott and Crunkilton, 2000). Further analyses and fieldwork are necessary to identify limiting factors for axolotl, and to understand how the different land uses influence them.

Although axolotls are able to survive under unsuitable conditions for short periods of time, which could be thought as an advantage for dispersal, an isotopic trophic web analysis suggests high fidelity to home ranges, resulting in reduced mobility (Zambrano unpub. data). Therefore, the patchy distribution observed in the present analysis may have multiple implications for the long-term persistence of the species. First, isolation may alter population dynamics and consequently viability, owing to negative effects of density dependence, such as intraspecific competition (Zambrano et al., 2007). Also, isolation makes mate finding difficult (Allee effects) and reduces genetic flow. In the end, all these consequences reduce effective population sizes, making the species more prone to extinction by stochastic events.

In conclusion, the general picture appears critical for the axolotl, compromising its survival in the near future, as also suggested by a recent population viability analysis (Zambrano et al., 2007). Previous population density estimates for this species have been reported low, but alarming declines were observed recently: from 6000 ind/km^2 estimated in 1998 to 1000 in 2004 (Zambrano et al., 2007) to 100 in 2008 (unpublished data), a 10-fold reduction in 4 years and 60-fold in 10 years. Local fishermen have also reported very few individuals in 2008. It is necessary to take immediate conservation and restoration actions if viable axolotl populations are to be maintained in the wild. It is our hope that this study can help to identify specific sites where such efforts should be oriented in tight coordination among local people, authorities, and academia.

Acknowledgments

Thanks to Richard Griffiths for his invaluable comments during development of this study. Beatriz Contreras, Town Peterson and two anonymous reviewers made important improvements to the manuscript. Roberto Altamirano helped in the field work, and Umbral Axochiatl NGO provided logistics support. The project was partially funded by the Instituto Nacional de Ecologia, The Darwin Initiative, the Consejo Nacional de Ciencia y Tecnologia (which provided a scholarship for VC), and the Posgrado de Ciencias Biologicas, UNAM. Sampling permits: SAGARPA 230402-613-03-0266 and SEMARNAT FAUT 0112.

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