Neutral competition among prey promotes chaos in two-level food webs

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Abstract

Neutral competition can be interpreted as a limit case between dominant intraspecific competition and dominant interspecific competition. Using a numerical model of an ecosystem with two trophic levels, we explore the surroundings of this limit case, that is, weak non-neutral competition interactions. It is shown that, the closer the competition is to neutrality, the higher are the chances of the system to develop chaotic behaviour. The competitive exclusion principle, based in equilibrium assumptions, is thus less likely to be applicable to neutral systems. As a result, these systems have more chances of developing supersaturated coexistence than non neutral ones.

Keywords: population dynamics, coexistence, competition, neutral competition, biodiversity paradox, chaos.

Contents

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TODOs

1 Background

Fascination for biodiversity is one of the main motivations for studying ecology. Even very young children feel the joy of learning about different species, so no prior knowledge of biology seems to be a requirement for being sensitive to the amazing variety of life. Scientific knowledge increases this sense of wonder even more as there is a big mystery: why are there so many species?

Robert: Why are there so many species is for me not the complete paradox. **Pablo**: I like this "poetical" introduction. Maybe I can properly define the paradox in next paragraph, after Gause's law?

The mystery comes into scene together with the competitive exclusion principle [1], sometimes referred to as Gause's law. This principle, which some authors trace back to Charles Darwin's *On the origin of the species* [2], is one of the classical keystones of ecology. The principle states that *"for each niche only one species will dominate in the long run, out-competing the rest"*. Most competition models satisfy this principle, and it has been observed experimentally under laboratory conditions. On the other hand, complete exclusion rarely occurs in nature [3], ~~being~~ the huge biodiversity in ~~Earth~~ its ~~most~~ noticeable counterexample. This contradiction is known as the biodiversity paradox. The paradox can be ~~carelessly (but poetically)~~ rephrased as *Why are there so many species if there ~~are~~ so few niches?*

There are several hypotheses to explain the paradox. For instance, Hutchinson [4] ~~reports his observations on two sympatric species of beetles competing for the same resource~~ but not simultaneously because of having different breeding seasons. In a later influential paper [5], Hutchinson proposes the possibility ~~of ecosystems to be driven by~~ external, time-dependent seasonal environmental changes. If the characteristic times of this environmental changes are fast enough, the ecosystem is prevented to reach an equilibrium. A pioneering quantitative discussion about ecosystems subject to periodically driven external perturbations can be found in [3].

After the discovery of chaos [6], it has been shown that non-equilibrium ecosystems can arise as well under constant environmental conditions [7, 8]. More specifically, those ecosystems develop cyclic or chaotic dynamics instead of fixed points. Of course, chaotic dynamics can arise as well in seasonally changing environments in a food web (as, for instance the model with multiple predators studied in [9]).

All the previous hypotheses refer to the time domain. Regarding the spatial dimension, the inhomogeneity of ecosystems, and the possibility of migration

between them has been pointed out as another possible explanation of the paradox [10] .

~~Another hypothesis deserving attention is that of neutral competition, whose better known exponent is~~ *Hubbell's neutral competition theory* [11]. In neutral models, similar species inside an ecological community are assumed to have identical *per capita* rates of birth, death, reproduction, etc. In those models, the long term differences between species are a result of ~~random events~~. Despite its counter-intuitive and controversial foundations, neutral models have been successfully applied to populations of rainforest trees [11]. Some evidence about the counter-intuitive fact that similarity can give rise to coexistence can be found in [12].

Most of the previously mentioned theories involve competition only, whereas ~~our model includes predation~~. It is known that the inclusion of a multi-species predation trophic level increases the probability of chaos [9], and may thus contribute to increase the number of coexisting species. In the present paper we explore the links between the heterogeneity at the competition level of a two trophic levels model ~~(see figure 1)~~ and the type of long term dynamics exhibited ~~(see figure 2). Our simulations show that the likelihood of chaotic dynamics increases when heterogeneity at the competitors' trophic level is minimal. That is, that neutrality in combination with multiple predators may promote chaos. The competitive exclusion principle, based in equilibrium assumptions, is thus less likely to be applicable to neutral ecosystems. As a result, these systems have more chances of holding a higher amount of coexisting species than non neutral ones.~~

2 Methods

2.1 Model description

We focused our attention on food webs with two trophic levels, one of consumers and another of prey (see figure 1). The consumers predate on the prey, and the prey populations compete among each other for a common source of resources.

The dynamics were modelled as a system of ordinary differential equations. We used the Rosenzweig-MacArthur predator-prey model [13] generalized to a higher number of species [14]. Our model is composed of n_P prey species and n_C consumer species. $P_i(t)$ was used for accounting the size of the population of prey i at time t, and $C_j(t)$ for the population of consumer j. When it is not explicitly stated, i runs from 1 to n_P, and j from 1 to n_C. The prey compete directly among themselves, while the consumers compete indirectly by sharing the same food. The consumers eat all kind of prey, but find some of them more preferable than others. All these interactions are summarized in figure 1. The overall structure looks like:
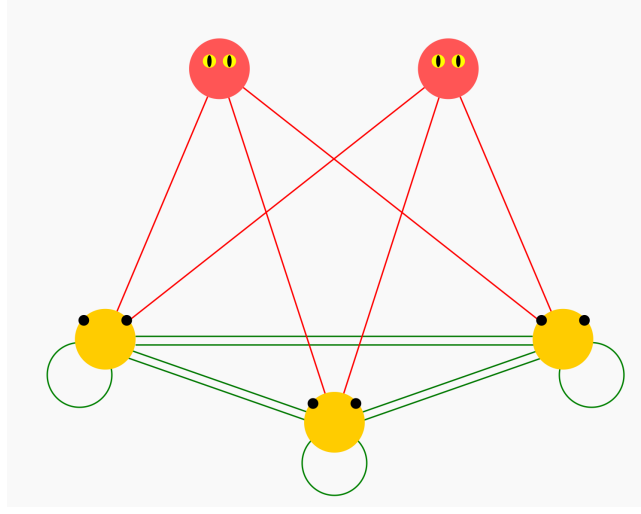
Figure 1: Example with 2 consumers and 3 prey. Each one of the red links represents a predation interaction (coded in the matrix of predator preference coefficients, S). Each green link represents a competition interaction (coded in the matrix of competition coefficients, A). The closed green loops are related with carrying capacity (diagonal elements of A) interpreted here as intra-species competition.

$$\begin{cases} \frac{d}{dt}\left(Prey\right) = Growth - Predation + Immigration \\ \frac{d}{dt}\left(Cons\right) = Feeding - Death \end{cases}$$

The growth term is modelled as a multispecies logistic growth. The strength of the competition between species i and k is given by the community matrix element A_{ik}. So, for prey i, we have:

$$Growth_i = rP_i\left(1 - \frac{1}{K}\sum_{k=1}^{n_P} A_{ik} \cdot P_k\right) \tag{1}$$

A secondary source for prey's growth in our model will be a constant immigration term f, representing immigration from neighboring areas. We ~~introduce~~ this term ~~in order~~ to avoid complete extinctions.

The predator preference for each prey species is given by S_{ij}. That is, the matrix element S_{ij} represents the relative proportion of prey i in consumer's j *menu*. ~~Being a multispecies model,~~ we ~~can~~ define an auxiliary ~~variable~~ V_j as a sum of the prey's populations weighted by the predator preference coefficients. Biologically, this represents the composition ~~of the~~ ~~*menu*~~ ~~of~~ consumer j:

$$V_j(P) \equiv \sum_{k=1}^{n_P} S_{jk} \cdot P_k \tag{2}$$

We hypothesized that the feeding term will be linear in C_j. The dependency on V_j happens through a Holling type II functional response with half saturation constant H in order to account for consumer satiation [15].

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$$Feeding = egC_j \frac{V_j}{V_j + H} \qquad (3)$$

e represents the assimilation efficiency of the predation. Thus, the effect of consumer j on all prey's populations is given by $Feeding_j/e$. Knowing this, we can sum the effect of all consumers in the prey species i as follows:

$$Predation_i = g \sum_{k=1}^{n_C} \left(\frac{S_{ki} P_i}{V_k} \right) C_k F_2(V_j; H) \qquad (4)$$

Where the term inside the parentheses represents the relative proportion of prey species i inside "the menu" of predator k, and F_2 is a shorthand for the Holling type II functional form introduced before. It is interesting to note that the way the predation and feeding terms are defined satisfies the following property:

$$\sum_{j=1}^{n_C} Feeding_j = e \sum_{i=1}^{n_P} Predation_i \qquad (5)$$

that is, all the deaths at the prey level are invested in the growth of consumers. For future clarity, it is a good idea to define the auxiliary function R_i as a summary of the effect of all consumers on prey i:

$$R_i(P, C) \equiv \sum_{k=1}^{n_C} \left(\frac{S_{ki} P_i}{V_k(P)} \right) C_k F_2(V_k(P); H) \qquad (6)$$

Putting all together, the dynamical system reads:

$$\begin{cases} \dot{P}_i = rP_i \left(1 - \frac{1}{K} \sum_{k=1}^{n_P} A_{ik} \cdot P_k \right) - gR_i(P, C) + f \\ \dot{C}_j = egC_j F_2(V_j(P); H) - lC_j \end{cases} \qquad (7)$$

Depending on the parameters and the initial conditions, this system can give rise to three types of asymptotic behavior, each of them roughly corresponding to a different type of attractor. The easier one, corresponding to a stable point attractor, generates a constant species composition. Cyclic attractors give rise to periodically changing species composition. Beyond fixed points and cycle attractors, there is a wide variety of more complex possible behaviors. As a simplification, we'll refer to all them as chaotic. Chaotic behavior makes the species composition keep changing without reaching a fixed point nor giving rise to periodicity (see figure 2).

2.2   Parameterization

For the parameterization of our model we used [9] as a reference. Dakos' model, focusing on plankton communities, uses as well a Rosenzweig-McArthur dynamic with two trophic levels (that of zooplankton and phytoplankton). Unlike Dakos, who uses seasonally changing parameters, our parameters will be constant.

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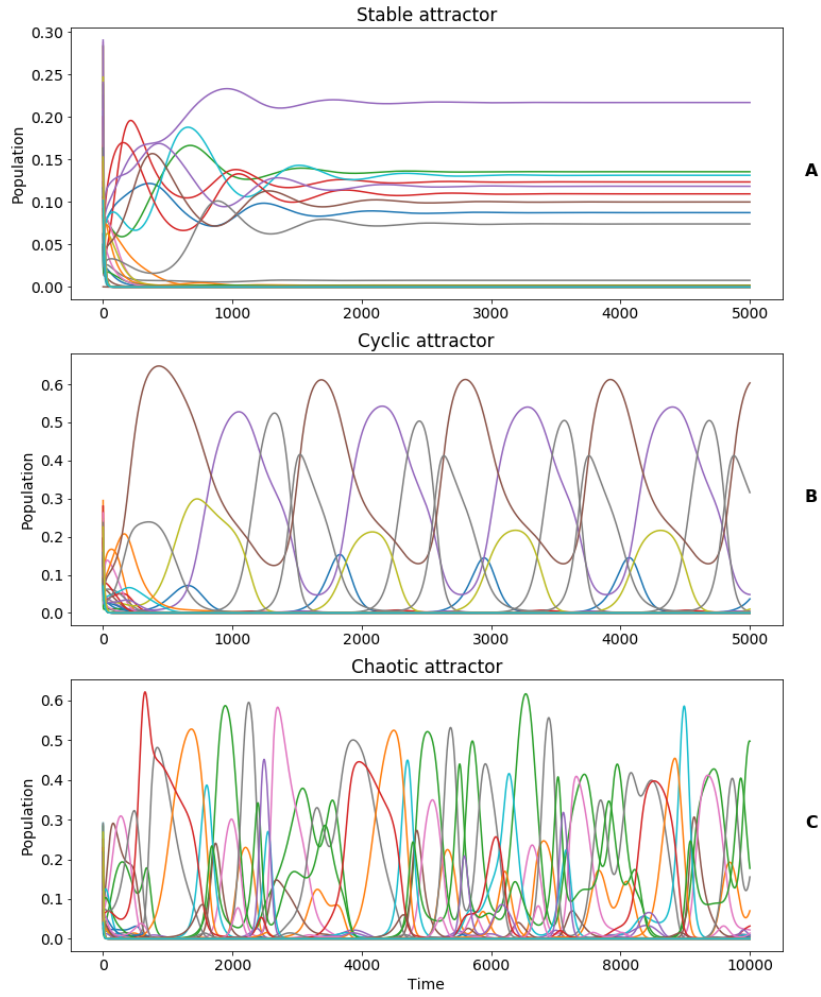
Figure 2: Our model generates time series of the population of each species. The time series can be classified in 3 types depending on their asymptotic behavior: *stable*, *periodic* and *chaotic*. In **figure A**, the system reaches a stable attractor after a transient time. In **figure B**, a periodic attractor, with an approximate period of 1000 days, is reached after the transient time. The system in **figure C** never reaches a stable nor a cyclic attractor, but a chaotic one.

Symbol	Interpretation	Value	Units
r	Maximum growth rate	0.50	d^{-1}
K	Carrying capacity	1.00	$mg\ l^{-1}$
g	Predation rate	0.40	d^{-1}
f	Immigration rate	10^{-5}	$mg\ l^{-1}\ d^{-1}$
e	Assimilation efficiency	0.60	1
H	Half-saturation constant	2.00	$mg\ l^{-1}$
l	Loss rate	0.15	d^{-1}
S	$n_C \times n_P$ predator preference matrix	$S_{ij} \sim (0,1)$	1
A	$n_P \times n_P$ competition matrix	See section 2.2.1	1

Figure 3: Values and meanings of the parameters used in our numerical experiment

2.2.1 Competition parameter

~~Our aim is to analyze the dynamics of the system described in equation 7 for competition interactions differing in heterogeneity.~~ In order to ~~quantify heterogeneity and~~ controlling how far from neutral the competition is, we introduce the competition parameter ϵ. This dimensionless parameter allows us to vary continuously from interactions where intraspecific competition is stronger than interspecific (for $\epsilon < 0$) to the opposite case (for $\epsilon > 0$). The border between both cases (i.e. $\epsilon = 0$), where neither the intra nor the interspecific competition is dominant, represents neutral competition (see figure 4).

The numerical implementation of these ideas can be easily achieved by building a competition matrix whose diagonal terms are identically 1, and whose non-diagonal terms are drawn from a uniform probability distribution centered at $1 + \epsilon$ and with a given width (here we chose $w = 0.2$).

This parameterization allows us to travel continuously from strong dominant intraspecific ($\epsilon < 0$) to strong interspecific competition ($\epsilon > 0$), meeting neutral competition at the border in between (i.e., at $\epsilon = 0$).
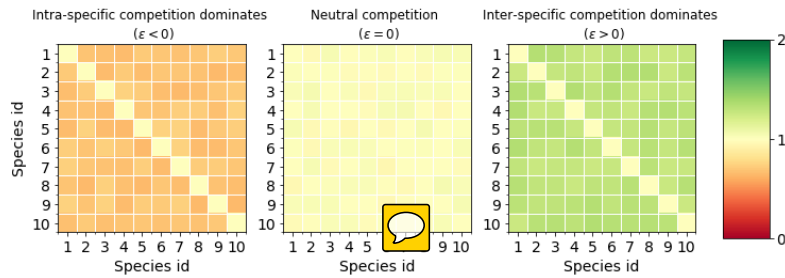
Figure 4: The competition matrix on the left is a clear case of dominant intraspecific competition. The central one represents a case of neutral competition. The matrix in the right panel shows a case of dominant interspecific competition. The difference between them is the relative size of the non-diagonal elements respective of the diagonal ones. This qualitative property of the competition matrices is controlled by the parameter ϵ.

2.3 Numerical experiment

Our target is to estimate the probability of reaching a chaotic attractor under different ~~degrees of heterogeneity.~~ In order to achieve this, we'll simulate several ecosystems with different initial conditions and relative predation intensities, but sharing the same competition parameter. ~~We consider thus that those ecosystems share a qualitative property: the same degree of heterogeneity.~~

Numerical methods are used to integrate the equation 7. A first stabilizing run of 2000 days is generated in order to get closer to the attractor. Simulating for 5000 more days, we obtain time series as the ones in figure 2. Using the Gottwald-Melbourne test [16], we classify each individual simulation as *chaotic* or *non-chaotic*. Our numerical experiment was repeated 200 times for each competition parameter. The ratio of attractors found to be chaotic can be used to estimate the probability of ecosystems of a given degree of heterogeneity developing chaotic asymptotic behavior.

Additionally, the experiment was repeated for food webs of different sizes. In our simulations, we kept a ratio of 2:3 for the number of species at the consumer and the prey level.

For the sake of reproducibility, we provide a *GitHub* link to the analysis scripts used[1]. For further information, please refer to the *read me* file.

3 Results

Plotting the probability of chaos against the competition parameter (see figures 5 and 6), we observe a clear maximum around $\epsilon = 0$. That is, for neutral competition at the prey's trophic level, the likelihood of chaotic behaviour is higher than for dominant inter or intraspecific competition.

There's another local maximum for $\epsilon = -1$. This means that ecosystems with weak competition coupling also promote chaos. ~~We consider this a reasonable result, as predation is the driver of chaos.~~

~~The probability of chaos has a local minimum between $\epsilon = -1$ and $\epsilon = 0$, whose exact position differs between experiments. We interpret this result as a consequence of the two previous effects: assuming continuity, there should be necessarily at least one local minimum between two local maxima. This is a direct consequence of applying Bolzano's theorem to the first derivative. Intuitively: there should be at least one valley between two mountains.~~

The overall likelihood of chaos, which can be interpreted as the area under the curve, increases with the size of the food web (see figure 5). This effect should not be surprising: the more dimensions the phase space has, the easier is to fulfill the requirements of the complex geometry of a chaotic attractor [17]. We can understand this intuitively as increasing the available room for the trajectories to pack closer and closer without ever crossing each other nor collapsing to a point. Even in those higher dimensional cases, there is still a maximum at neutral competition.
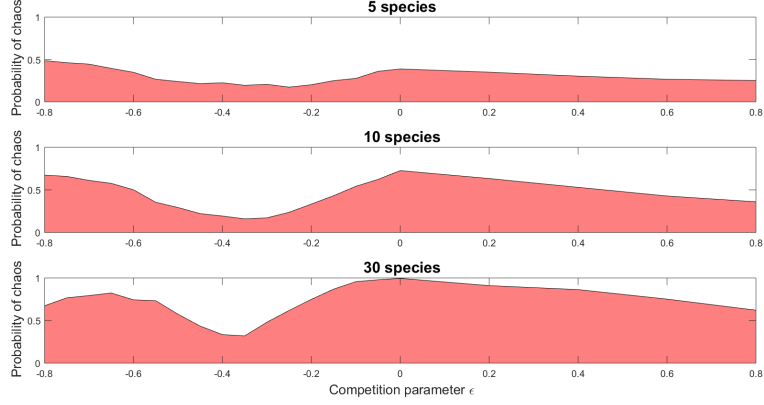
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[1] https://github.com/PabRod/Chaos-and-neutrality

Figure 5: Results for a low, medium and high dimensional system. Notice how the probability of chaos has a local maximum around $\epsilon = 0$. The overall probability of chaos, understood as the area under the curve, grows with the system size. The local maximum stays at $\epsilon = 0$ even for systems with a big amount of species.
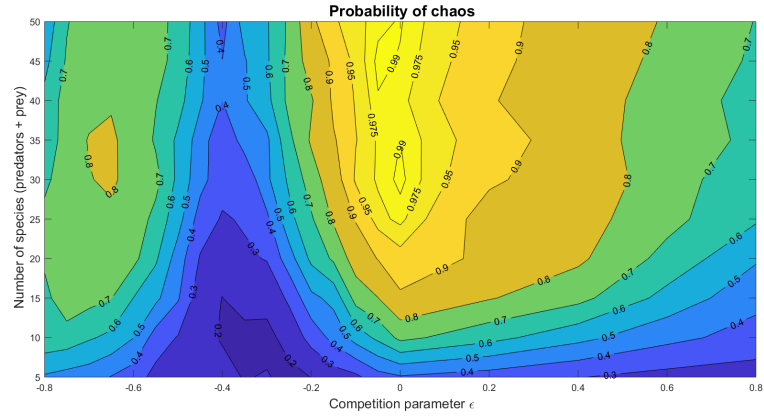
Figure 6: Contour map showing the probability of chaos for various competition parameters (horizontal axis) and ~~prey populations~~ (vertical axis). The consumers' population is fixed as 2/3 of the prey's population, ~~in order to control the overall size of the system with a single parameter~~. Notice that chaotic attractors appear more easily (i.e., for smaller systems) the closer is the competition to neutral (i.e., $\epsilon = 0$).

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4 Discussion

The asymptotic dynamics of our model are affected by ~~the degree of heterogeneity of the competition~~. Particularly, the closer to neutrality our food web is, the higher are the chances of developing chaotic behaviour. This suggests that in a system with predation, near-neutrality may increase the probability of ~~non-equilibrium~~ dynamics. Provided the competitive exclusion principle rests on the assumption of equilibrium, near-neutrality reduces the chances of the principle to be applicable, improving the chances for a high number of coexisting species. Additionaly, this observation suggests that the hypothesis of non-equilibrium and Hubbell's hypothesis of neutrality are not completely independent.

In the spirit of mathematical modelling, we chose the simplest realization required for the effects to be observed. We didn't use Allee effect, nor noise, and the functional form of each term has been chosen to account for satiation and saturation in the simplest possible ways. The choice of a two-level model may seem in contradiction with the pursue of simplicity, but actually it is a fundamental requirement for the effect under research to take place. In the absence of predation, chaos will never develop in a model with neutral competition. The reason for this is that if all interactions become equally strong, the differences among species at the same trophic level fade out. This makes labeling each species meaningless, and thus the prey-only system can be reduced just to one differential equation, that of the total population. Using the Poincaré-Bendixson theorem, it can be proven that chaos cannot be developed in autonomous systems with less than 3 dimensions [17].

We used the simplest predation network, that is, one with random prey preference for the predators. A possible continuation of this paper could be studying the effect of different types of predation (generalist, specialist, neutral) on the asymptotic dynamics.

The competition parameters were also drawn randomly. It is known that the asymptotic behaviour of this kind of systems can be very sensitive to the parameters choice. In particular, introducing correlations between parameters can greatly modify the probabilities of chaotic attractors to be reached (see for instance [18], in response to the letter [19]). In the present paper we didn't introduce any correlation, i.e., all our random parameters were drawn independently from the others. Studying the effect of different physiological scenarios (in the sense of [18], that is, constrains between the parameters) on the probabilities of chaos could be a straightforward continuation to this paper.

It may be worth noting that the position of both the maxima we've found (i.e.: $\epsilon = -1$ and $\epsilon = 0$) have something in common: the community matrix A at those values of the parameter is very symmetric in both cases. It will be interesting to develop a similar method that, instead of varying neutrality, varies the less restrictive property of symmetry.

Interestingly enough, a relatively small number of replicates suffices to generate a remarkably clear maximum in the probability of chaos for neutral competition. The position of this maximum is independent of the number of interacting species. This suggests that the parameter ϵ, originally motivated by numerical convenience, may have a biological interpretation by itself. ~~It will be interesting to reverse-engineer this parameter given a set of community matrices validated by experimental or field observations.~~

Numerical detection of chaos has fundamental limitations, that can be boiled

down to the fact that, in general, numerical methods cannot distinguish robustly between long transients and genuine chaos. In the present paper three parallel approaches were followed: Lyapunov exponents estimation, Gottwald-Melbourne *0-1* test and visual inspection. Despite differences in the exact probabilities, the three of them led us to the same qualitative conclusions. We found the results of the Gottwald-Melbourne test most consistent with visual inspection. We called chaotic all those time series complicated enough to trigger both the 0-1 test and the visual inspection tests. We think that this approach to chaos detection, despite being open to improvement, suffices to hold the biological conclusions.

The paradox of biodiversity is a tremendously complex scientific problem. With this experiment we definitely do not claim to have solved it, but just to have addressed an interesting effect observed in our particular model. We hope at least to have contributed a bit to shed some light into this fascinating question.

5   Acknowledgements

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