Research paper

Development and Evaluation of Seed Dispersal Functions in the Kenting Forest Dynamics Plot

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【Summary】

Developing appropriate seed dispersal functions to quantify seed dispersal is one of the important themes in plant ecology, because the post-dispersal distributions of seeds translate spatial patterns of parent plants to offspring and result in significant ecological consequences. In this study, the best-fitting seed dispersal functions were identified for 4 tree species in the Kenting forest dynamics plot in Taiwan. Dispersal functions between animal- and wind-dispersed species were also compared. Seed rain data were collected weekly from 72 seed traps (0.5 m^2) along 4 transects within a 10-ha permanent plot (400×250 m) in Kenting from August 2006 to April 2009. We chose 2 animal-dispersed species, and 2 wind-dispersed counterparts for this study. Applying the inverse-modeling approach, we developed seed dispersal functions via maximum likelihood methods. Weibull, lognormal, and 2-dimensional t (2Dt) models with negative binomial errors were used. Akaike's Information Criterion was used to determine the best-fitting model. The results indicated that the lognormal and 2Dt models were the best-fitting models for the studied species. The best-fitting models did not differ between the 2 dispersal modes since they were equally represented for animal- and wind-dispersed species. However, the level of goodness-of-fit was higher for wind-dispersed than animal-dispersed species. In the future, mechanistic models should incorporate the behavior of seed dispersers to improve model fitting.
Key words: dispersal agents, forest dynamics plot, inverse modeling, seed dispersal.
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研究報告

墾丁森林動態樣區種子傳播模式之發展與評估

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摘　要

　　發展合適的種子傳播模式，量化種子傳播特性，是植物生態學研究上的重要課題，因為，種子經傳播後的空間分布，代表植物族群之啟始分布，將顯著影響許多後續的生態過程。本研究的目標在於使用逆向模式法，發展墾丁高位珊瑚礁森林動態樣區內，4種樹種的種子傳播模式，將種子傳播之特性量化。此外，我們並比較風力與動物傳播物種於種子散布模式上的差異。自2006年8月至2009年4月，每週於墾丁高位珊瑚礁10公頃森林動態樣區中，4條穿越線上所設置的72個種子網內，收集種子，所得種子予以分類與計算數量。本研究利用逆向模式分析法(inverse modeling analysis)，分析2種藉動物傳播、2種藉風力傳播之樹種。種子散布模式採用韋伯(Weibull)、對數常態分布(lognormal)與二維t分布(2-dimensional t model, 2Dt)3種模式進行模擬，以最大概似度法(maximum likelihood methods)估算參數，並利用AIC準則(Akaike's Information Criterion)決定最適模式。結果顯示，對數常態分布與二維t分布為較好模式，最適模式並未因種子傳播媒介不同而有差異，但模式適合度以風力傳播的樹種較動物傳播的樹種高。未來，我們計劃發展混合或機制模式，將種子傳播者之行為加入種子傳播模式，以改善模式的適合度。

關鍵詞：傳播媒介、森林動態樣區、逆向模式分析法、種子傳播。

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INTRODUCTION

Seed dispersal is recognized as one of the most critical ecological processes during a plant's life cycle, because seed dispersal represents an important mobile stage of plants and results in significant ecological and evolutionary consequences (Howe and Smallwood 1982, Nathan and Muller-Landau 2000, Levin et al. 2003). For example, the post-dispersal distributions of seeds in relation to the parent plant, defined as the "seed shadow", determine the initial spatial template for plant populations and affect the local neighboring relationships of individual plants. Empirical studies showed that such neighboring relationships have a long-lasting impact on subsequent dynamics of plant populations

(Miriti et al. 2001, Lin and Augspurger 2008) and communities (Levin et al. 2003). Furthermore, seed dispersal is a key process by which plants expand their current distribution ranges, and it determines the probability of plants colonizing a new habitat (Howe and Smallwood 1982). The distance and properties of seed dispersal directly influence rates and patterns of plant migration. Quantifying seed dispersal, therefore, has become an important theme in plant ecology in the past few decades.

Seed dispersal patterns are quantified by seed dispersal functions (Clark et al. 1999, Nathan and Muller-Landau 2000). Seed dispersal functions are mathematical models that

describe how seed density changes with the distance from a parent tree (Nathan and Muller-Landau 2000). Previous research indicated that a higher proportion of seed deposition occurs in areas closer to the parent plant than areas that are far way (Wilson 1993). In other words, seed density declines as the distance from the parent tree increases. Mathematical models with a skewed property have been applied to illustrate this density-distance relationship. Commonly used seed dispersal functions include negative exponential, Weibull, and lognormal distributions (Nathan and Muller-Landau 2000). The shape and scale of different seed dispersal functions, however, greatly vary. It is important to select appropriate seed dispersal functions that are representative of plant populations so that proper conclusions about ecological consequences of seed dispersal can be reached.

Traditionally, seed dispersal functions were obtained via regressing seed density against distance (Wilson 1993). A series of seed traps placed at varying distances around an isolated parent plant were used to carry out the estimation (Wilson 1993). This approach, however, can result in inappropriate seed dispersal functions of plant populations. Clark et al. (1999) pointed out 2 problems with the traditional approach. First, isolated parent trees are often located in an open area and yield more seeds than an average reproductive tree in a closed forest. Second, the sampling of parent trees usually seems biased toward large trees when isolated parent trees are selected. Such sampling may lead to overestimations of plant fecundity and dispersal distance of a tree population.

Therefore, seeking an alternative approach to estimate seed dispersal functions representative of a tree population is an urgent task for studying seed dispersal. A new approach, inverse modeling, was developed

in recent years (Ribbens et al. 1994). This approach inversely estimates parameters from field observations. Seeds collected from each seed trap are assumed to be a summation of seeds dispersed from all possible parent trees within a given area. The probability of a seed arriving in a trap is determined by the distance to the parent tree and the size of the parent tree (Ribbens et al. 1994). This approach estimates seed dispersal functions from the overall population and makes it possible to obtain reasonable seed dispersal functions that are representative of the tree population.

The inverse modeling approach has been widely applied to estimate seed dispersal functions in many tropical and temperate forests (Clark et al. 1999, Nathan and Muller-Landau 2000). The functions estimated from those studies, however, show high levels of variability. A portion of the variation might be attributed to differences in dispersal modes. Clark et al. (2005) discovered that the mean dispersal distance of animal-dispersed species was larger than that of wind-dispersed species. Seed shadows of animal-dispersed species may be affected by the behavior and movements of seed dispersers (Cousens et al. 2008). Furthermore, many studies indicated that dispersal functions are context-dependent (Cousens et al. 2008), i.e., they depend on the composition of local dispersal vectors and site characteristics. Before any generalizations can be drawn, case studies of a wide range of species, dispersal agents, and sites are necessary.

In this study, we sought to quantify seed dispersal of tree species via inverse modeling in a tropical forest in Kenting, Taiwan. Three objectives were identified. First, we developed and selected the best-fitting seed dispersal functions representative of various tree populations in the forest. Second, seed dispersal functions of species with different dispersal modes were compared. Third, we

characterized the seed dispersal of tree species from the best-fitting models.

MATERIALS AND METHODS

Study site

We conducted this study in a tropical seasonal forest in the Kenting Uplifted Coral Reef Nature Reserve on the Hengchun Peninsula (21°58'N, 120°48'E), southern Taiwan. The forest features widely distributed uplifted coral reefs (Wang et al. 2004). The average mean temperature is 25.1℃ with an annual precipitation of 1963.8 mm (1977~2006). The climate in the area is characterized by a distinct annual monsoon season which lasts from October to March (Wang et al. 2004). A forest dynamics plot (FDP) was established in 1997, and it is 10 ha in size (Wang et al. 2004). Dominant species in the plot include *Diospyros maritime*, *Ficus benjamina*, *Melanolepis multiglandulosa*, *Bischofia javanica*, *Palaquium formosanum*, *Aglaia formosana*, and *Pouteria obovata*.

Field sampling

Seed rain was collected weekly by 72 seed traps from August 2006 to April 2009. These 72 traps were placed along 4 east-west transects at 20-m intervals (Fig. 1). Each transect was 340 m long, starting at a point 30 m from the western edge and ending 30 m from the eastern edge of the plot. Areas within 30 m from the plot edges were excluded to avoid edge effects. Seed traps were comprised of 1-mm wire-mesh screens 0.5 m^2 in area which were supported by PVC frames and were 1 m above the ground.

Reproductive parts of woody plants, including flowers, fruits, and seeds, were col-
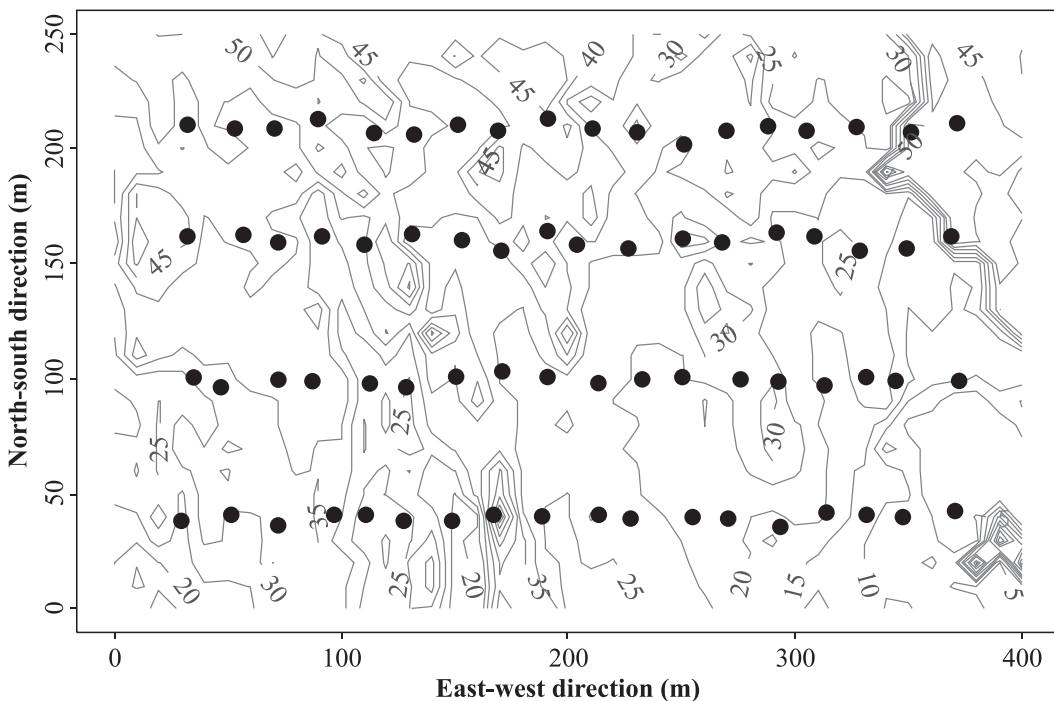

Fig. 1. Contour map and locations of seed traps in the Kenting forest dynamics plot. The black dots are seed traps overlain with 10-m contour lines.

lected weekly. Samples from each trap were quantified and identified by species. Only mature seeds, either contained within mature fruits or presenting as an independent unit, were included in the analysis. Locations of parent trees were obtained from a census during 1997~2002 by a research team led by Wang and Sun (Wang et al. 2004). The parent trees were assumed to be trees with a diameter at breast height (DBH) ≥ 10 cm.

Data analysis

We developed seed dispersal functions for 4 target species. The target species were *B. javanica* (Euphorbiaceae), *Dendrocnide meyeniana* (Urticaceae), *Lagerstroemia subcostata* (Lythraceae), and *Fraxinus griffithii* (Oleaceae). The target species were chosen based upon the number of seeds collected from the seed traps and their distributions within the plot. These 4 species had sufficient sample sizes for model development. In addition, seeds of the study species reached more than 20% of the traps. Among the 4 species, the first 2 species are recognized as animal-dispersed species, while the other 2 species were identified as wind-dispersed species. The dispersal mode of the species was determined by fruit and seed morphology. Species with fleshy and succulent fruits were classified as animal-dispersed species, and species containing winged seeds were treated as wind-dispersed species (Huang 1994). The timing of fruiting was similar among the study species. Mature seeds of the majority of the species were mostly collected from September to December. Among the species, *Den. meyeniana* has an extended fruiting period. Mature seeds of *Den. meyeniana* were collected in 11 mo in 2007 and 2008.

Seed dispersal functions were developed via inverse modeling. There were 3 steps in the inverse modeling approach: 1) model

specification, 2) parameter estimation, and 3) model selection.

1. Model specification

There were 2 components of a seed dispersal function, fecundity (Q) and a dispersal kernel $f(r, \Phi)$. A dispersal kernel is a probability density function (PDF) which expresses the relative density of seeds at different distances from the parent plant. A mathematical formula of a seed dispersal function is as follows:

$$S(r, \Phi) = Q f(r, \Phi);$$

where $S(r, \Phi)$ refers to the seed density at a given distance, r, and angle, Φ; Q is the annual fecundity; and $f(r, \Phi)$ is a 2-dimensional seed dispersal kernel. With a given angle (θ) and distance ranges (r), the number of accumulated seeds can be expressed as:

$$\int_r^{r+dr} \oint_\theta f(r, \Phi)\, d\Phi dr = \theta \int_r^{r+dr} r f_\theta(r)\, dr.$$

Isotropic seed dispersal functions are the product of 2πr and a 1-dimensional seed dispersal function ($f_\theta(r)$). Annual fecundity (Q) was expressed as a function of the size of the parent tree (B). Annual fecundity can be described as:

$$Q = kB^2;$$

where k is an empirical coefficient and B is the DBH of the parent tree.

Three alternative seed dispersal functions, Weibull, lognormal, and the Clark 2-dimensional *t* model (2Dt), were used in this study (Table 1). These 3 models are widely used and were shown to well fit empirical data in the literature (Nathan and Muller-Landau 2000, Greene et al. 2004). Among these 3 models, the Clark 2Dt model is an extension of an exponential model with a normally distributed variable for the scale parameter (Clark et al. 1999). Two parameters were included in the 3 models. These 2 parameters were expressed as scale (*s*) and shape (*a*) parameters (Table 1). To simplify the estimation, shape

Table 1. The 3 seed dispersal functions used in this study. Distance from the parent plant is expressed as *x*. The shape and scale parameters in the models are expressed by *a* and *s*, respectively. N is a normalizer to standardize the function. Formulas were from the 1-dimensional model. 2-dimensional seed distribution kernel was obtained by multiplying the 1-dimensional model by 2πx (Greene et al. 2004)

Dispersal function	Formula	Parameters
Weibull	$(1/N) (\exp(-ax^s))$	a, s
Lognormal	$[1/((2\pi)^{1.5} sx^2)] \exp(-[ln(x/a)]^2/(2s^2))$	a, s
2-dimensional *t* (2Dt)	$s/(\pi a [1 + (x^2/a)]^{s+1})$	a, s

parameters were set to 2 in the 2Dt model (Clark et al. 2005) and 3 in the Weibull model (Ribbens et al. 1994).

2. Parameter estimation

Parameters within each of the 3 dispersal functions were estimated by maximum likelihood methods (Greene et al. 2004). Errors were assumed to be a negative binomial distribution. Our preliminary analysis indicated that dispersal functions with negative binomial errors performed better than models with Poisson errors. Therefore, we only applied negative binomial errors to the final analysis. A bootstrapping procedure was used, and medians of 1000 bootstrap samples for all parameters were taken as estimates of the parameters (Efron and Tibshirani 1993).

3. Model selection

We used Akaike's Information Criterion (AIC) to compare alternative models and to select the best-fitting model (Burnham and Anderson 1998). The AIC was defined as:
AIC = -2L + 2*p*;
where L is the log likelihood and *p* is the number of parameters in the model. The best-fitting model has the smallest AIC value among all alternative models (Burnham and Anderson 1998). The goodness-of-fit of the model was evaluated by Pearson's correlation coefficients between the observed number of seeds per trap and predicted number derived

from the best-fitting models (Dalling et al. 2002). The number of seeds per trap was log-transformed. After the best-fitting models were selected, the mean dispersal distance was estimated for each of the studied species. The mean dispersal distance was estimated via the moment-generating function (Cousens et al. 2008). All modeling and statistical analyses were performed in R language (R Development Core Team 2008).

RESULTS

Parameter estimates varied greatly among species (Table 2). The estimates derived from the 3 alternative functions had similar magnitudes and yielded comparable seed distributions for the same species (Table 2, Fig. 2). The lognormal and 2Dt models were the best-fitting models for the studied species. The AIC values of the lognormal function were lowest for *B. javanica* and *L. subcostata* (Table 3). The 2Dt models performed the best for *Den. meyeniana* and *F. griffithii* (Table 3). Differences in the AIC values, however, were small for the lognormal and 2Dt functions.

The lognormal and 2Dt functions were equally represented within each of the 2 dispersal modes (Table 3). One lognormal and 1 2Dt model were selected for animal- and wind-dispersed species, respectively (Table 3). Pearson correlation coefficients be-

Table 2. Parameter estimates of 3 alternative seed dispersal functions in the Kenting forest dynamics plot in Taiwan. The 3 seed dispersal functions included the Weibull, lognormal, and 2-dimensional *t* (2Dt) models

Species	Weibull	Lognormal	2Dt
Animal-dispersed species			
Bischofia javanica			
Fecundity (seeds/cm^2)	4232.79	5140.34	5298.19
Shape parameter (*a*)	3.00	0.61	2.00
Scale parameter (*s*)	14.96	6.39	83.91
Dendrocnide meyeniana			
Fecundity (seeds/cm^2)	10,947.31	9534.57	8299.32
Shape parameter (*a*)	3.00	0.45	2.00
Scale parameter (*s*)	12.66	8.10	130.30
Wind-dispersed species			
Lagerstroemia subcostata			
Fecundity (seeds/cm^2)	1775.98	990.58	1119.42
Shape parameter (*a*)	3.00	1.21	2.00
Scale parameter (*s*)	95.87	9.10	477.39
Fraxinus griffithii			
Fecundity (seeds/cm^2)	673.73	973.11	960.61
Shape parameter (*a*)	3.00	0.64	2.00
Scale parameter (*s*)	60.72	27.25	1608.09
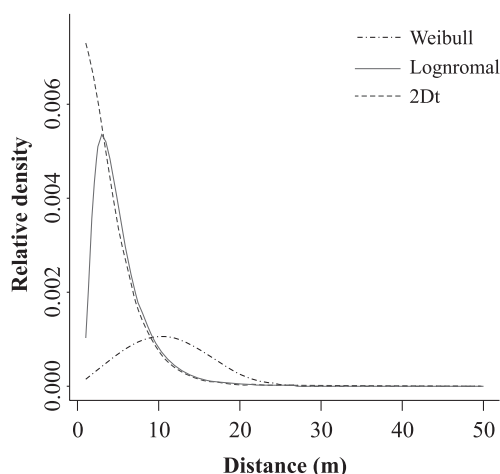
Fig. 2. Seed dispersal curves derived from the 3 alternative seed dispersal functions of *Bischofia javanica* in the Kenting forest dynamics plot. The above curves were derived from 1-dimensional functions. 2Dt, 2-dimensional *t* model.

tween observed and predicted values ranged 0.07~0.71 (Table 3). Correlation coefficients were larger for wind-dispersed species than for animal-dispersed species, suggesting a higher level of goodness-of-fit for wind-dispersed species (Table 3).

The mean dispersal distance obtained from the best-fitting model ranged 7.70~31.49 m (Table 3). Seeds of wind-dispersed species dispersed farther than those from animal-dispersed species (Table 3).

DISCUSSION

The lognormal and 2Dt functions were the best-fitting seed dispersal functions for the 4 species studied in this report. Minor differences in AIC values between the lognormal and 2Dt models indicated that these models

Table 3. Akaike's Information Criterion (AIC), mean dispersal distances derived from the best-fitting functions, and Pearson correlation coefficients between observed and predicted log (seed density + 1) of the 4 study species in the Kenting forest dynamics plot in Taiwan. The best models were the models with the smallest AIC values

Species	Weibull	Lognormal	2Dt	Best-fitting model	Mean dispersal distance (m)	Pearson correlation coefficient
Animal-dispersed species						
Bischofia javanica	782.82	770.22	771.09	Lognormal	7.70	0.23
Dendrocnide meyeniana	677.18	671.50	671.12	2Dt	8.97	0.07
Wind-dispersed species						
Lagerstroemia subcostata	294.52	256.73	265.43	Lognormal	18.90	0.60
Fraxinus griffithii	179.27	175.36	172.96	2Dt	31.49	0.71

2Dt, 2-dimensional *t* model.

performed almost equally well in fitting the empirical data. In contrast, the Weibull model did not perform as well as the other 2 models, because the Weibull model was not selected as the best-fitting model for any of the studied species and yielded relatively larger AIC values. Our results were similar to other studies. Greene et al. (2004) showed that the lognormal model was the best-fitting function for tree species of a temperate forest in southern Quebec, and the 2Dt model preformed well for many tropical and temperate species (Clark et al. 1999, Muller-Landau et al. 2008). This good fit was attributed to their flexible curve shapes (Clark et al. 1999, Greene et al. 2004). Compared to some of the other commonly used models such as the Gaussian model, the lognormal and 2Dt models predict a higher relative density near the seed source and generate a fatter tail at the end of the curves (Cousens et al. 2008). Thus, the functions can fit empirical data relatively well at both the near and far ends of the dispersal curves (Clark et al. 1999, Greene et al. 2004).

Furthermore, the best-fitting models did not differ between the 2 dispersal modes, although the Pearson correlation coefficients were higher for wind-dispersed species than

for animal-dispersed species. The results suggested a higher level of goodness-of-fit for wind-dispersed species. The process of seed dispersal by wind is much simpler than that by animals. Simulations generated by mechanistic models suggested that seed dispersal by wind can be represented by unimodal and leptokurtic curves which are similar to dispersal curves produced by seed dispersal functions via an inverse modeling approach (Cousens et al. 2008). In contrast, seed dispersal by animals is a rather complicated process and can be influenced by more than 1 dispersal vector (Nathan and Muller-Landau 2000). As a result, animal dispersal can result in multimodal dispersal curves (Cousens et al. 2008). Unimodal curves generated by the seed dispersal functions used in this study were insufficient to describe seed density in relation to the parent tree. Two approaches were suggested to improve seed dispersal models for animal-dispersed species. First, mixed models that combine multiple seed dispersal functions can be applied to quantify seed dispersal by animals (Cousens et al. 2008). Mixed models are a linear combination of various seed dispersal functions and, therefore, simultaneously retain the characteristics of multiple seed dispersal

functions. These models are suitable for describing seed dispersal by multiple dispersal vectors. Second, mechanistic models which include patterns of animal foraging and movements can be developed (Morales and Carlo 2006, Russo et al. 2006). These models incorporate the behaviors of seed dispersers and model the subsequent fate of individual seeds. Such models can provide the most detailed and accurate patterns of seed dispersal (Cousens et al. 2008). These improved approaches may provide better models than the original approach and allow us to incorporate more species into the analysis. In this study, we focused only on 4 species due to unreasonable parameter estimates. Species with unreasonable parameter estimates are often highly aggregated in space and have small sample sizes.

The estimated mean dispersal distances ranged 7.70~31.49 m in this study. Such distances are relatively short compared to estimates from other studies (Dalling et al. 2002, Clark et al. 2005). These short dispersal distances might have arisen from environmental heterogeneity at this study site. The topography of the Kenting forest is highly heterogeneous (Wang et al. 2004). Limestone from uplifted coral reefs is widely distributed across the landscape and results in sharp topographic changes within a short horizontal distance. These uplifted coral reefs can serve as barriers to seed dispersal and result in short dispersal distances. To evaluate the effects of spatial heterogeneity on seed dispersal, Schurr et al. (2008) modified the inverse modeling approach and incorporated spatial heterogeneity into the seed dispersal functions. Linking functions were added to seed dispersal models to characterize the alteration of seed dispersal by habitat heterogeneity (Schurr et al. 2008). Such models would be appropriate in a highly heterogeneous habitat like the Kenting Uplifted Coral Reef Forest.

CONCLUSIONS

This study indicated that the lognormal and 2Dt models were the best-fitting models for the studied species. The best-fitting models did not differ between the 2 dispersal modes, but the model fitting of animal-dispersed species was not as good as that of wind-dispersed species. Therefore, we proposed to develop mixed or mechanistic models to include foraging behavior of various dispersal vectors in the models.

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