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Main ecological drivers of woody plant species richness recovery in secondary forests in China

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Identifying drivers behind biodiversity recovery is critical to promote efficient ecological restoration. Yet to date, for secondary forests in China there is a considerable uncertainty concerning the ecological drivers that affect plant diversity recovery. Following up on a previous published meta-analysis on the patterns of species recovery across the country, here we further incorporate data on the logging history, climate, forest landscape and forest attribute to conduct a nationwide analysis of the main drivers influencing the recovery of woody plant species richness in secondary forests. Results showed that regional species pool exerted a positive effect on the recovery ratio of species richness and this effect was stronger in selective cutting forests than that in clear cutting forests. We also found that temperature had a negative effect, and the shape complexity of forest patches as well as the percentage of forest cover in the landscape had positive effects on the recovery ratio of species richness. Our study provides basic information on recovery and resilience analyses of secondary forests in China.

The future of forests in the Anthropocene depends on balance between forest recovery and human-driven deforestation¹. Resilience, the capacity of an ecosystem to recover to pre-disturbance states from a disturbance, is key for forest restoration², biodiversity conservation³ and maintenance of ecosystem services⁴. Much effort has been conducted for understanding the recovery patterns of forest biomass⁵, species composition^{6,7}, species diversity and functional diversity⁸. Identifying ecological drivers that influence these patterns is of particular importance⁹, given the difficulties to anticipate the outcomes of forest recovery^{10,11}. A better understanding of these drivers could promote more cost-effective policies and management as well as more comprehensive ecological impact assessments^{12–14}.

China holds a large range of globally important forest ecosystems across a wide range of climates in both tropical and temperate regions¹⁵. Over the last 20 years, China has implemented numerous national policies for forest protection in order to slow down the forest degradation in association with the rapid economic growth¹⁶. The Natural Forest Protection Program promotes the conservation of natural forests through logging bans¹⁷ and the Nature Reserves Construction Program has been key in establishing nature reserve networks in the country¹⁶. Similar to other regions elsewhere¹⁸, the naturally regrowing forests which we call secondary forests in this paper, are becoming more and more important in China because they are potential reservoirs for primary forest biodiversity and sources of essential ecosystem functions^{9,19}. At present, secondary forests account for 57% of the total forest resources in China²⁰ and forest biodiversity has increased, which thanks to these progressive forest protection policies¹⁶.

Although China has a large area of secondary forests and the biodiversity is gradually recovering, the ecological drivers influencing the performance of natural forest recovery are poorly understood²¹. The recovery of secondary forests is affected by various drivers operating at multiple spatio-temporal scales⁹. Studies have shown that logging history, climatic conditions, land use and forest attributes can all affect forest recovery^{5,22–25}. A global meta-analysis showed that forest recovery was more successful when previous logging was less intensive and the

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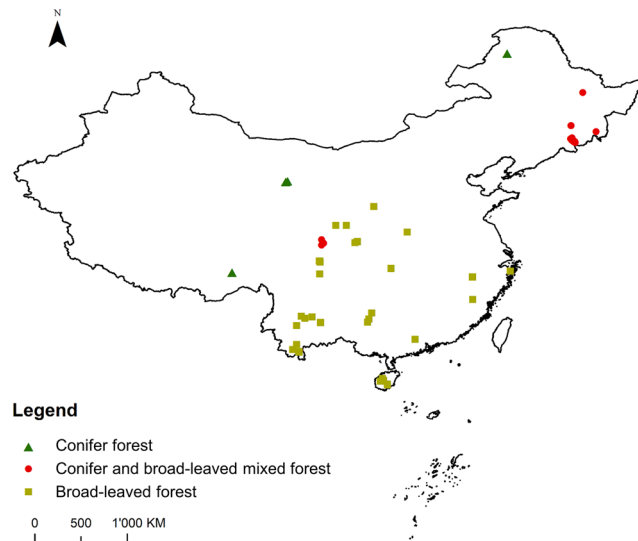


Figure 1. Study locations and forest types. This figure was created using ArcGIS by Esri (ArcMap10.5).

landscape was less fragmented²². In the Neotropics, the biomass recovery in secondary forests increased with the increase in rainfall⁵. During secondary succession, species availability (e.g. high efficient propagation of seeds) is crucial to whether the secondary forests can recover to primary forest states^{7,19}. Regional species pool is a set of species occurring in a particular region that can potentially inhabit a site because of suitable local ecological conditions²⁶. Larger regional species pool implies that there are more species that are able to grow in this specific ecological conditions, and therefore to have better recovery performance after disturbances¹¹. However the relative contribution of these ecological drivers that influence the recovery of secondary forests in China still need to be explored. Identifying these drivers is critical for resilience and secondary succession analyses as well as for advancing sustainable management of forests in future.

A previous published meta-analysis based on 125 pairs of secondary-primary forest data across China has revealed the recovery patterns of woody plant species richness in secondary forests²⁴. Here, following up on this previous meta-analysis, we further incorporate data on the logging history, climate, forest landscape and forest attribute to identify the main ecological drivers that influence the observed natural recovery of woody plant species richness in secondary forests in China. We hope this study could provide basic information on recovery and resilience analyses of secondary forests in China.

Results

We included the 125 pairs of secondary-primary forest data across China (Fig. 1), which were collected in the previous meta-analysis²⁴. The recovery was defined as the ratio of secondary forests woody plant species richness to the reference forests woody plant species richness, i.e. the primary forest woody plant species richness. Ecological drivers were indicated by the following variables: (i) logging type, (ii) recovery time after logging, (iii) annual temperature (°C), (iv) annual precipitation (mm/yr), (v) mean perimeter-area ratio of forest patches, (vi) proximity index, (vii) percentage of forest cover, (viii) regional species pool, and (ix) forest type.

In the regions where the secondary forests were collected, annual temperature ranged from -5 to 25 °C with a mean of 14.23 °C. Annual precipitation ranged from 250 to 2250 mm/yr with a mean of 1232.89 mm/yr. Since we only considered the secondary forests with presence of primary forests nearby (used as a reference for evaluating the recovery), the percentages of forest cover mainly varied between 60 to 100% . Regional species pools (woody plant species richness) ranged from 100 to 2200 . The recovery time of these secondary forests mostly ranged from 5 to 120 years. The frequency histograms of these collected independent variables were shown in Supplementary Fig. S1.

To identify variables impacting the recovery ratio, models of all possible combinations of the variables of the global models were fitted and ranked based on their Akaike Information Criterion corrected for small sample sizes (AICc). The model with the lowest AICc included 8 variables and 6 interactions, the model ranked second had two fewer parameters, while the next most parsimonious model with 4 Δ AICc included only 5 variables and 1 interaction (Table 1). Given the small Δ AICc and the large difference in the number of parameters, the two more complex models are poor competitors of the simpler models, thus only the coefficient estimates of the latter model are presented here. The model included exclusively logging type, temperature, perimeter-area ratio, percentage of forest cover, regional species pool and the interaction between logging type and regional species pool. The relative importance of those variables (≥ 0.78) was shown in Table 2, and pseudo- R^2 of this model was 0.42 . Further support for this model was the rank based on Bayesian Information Criteria (BIC). The BIC method more strongly penalizes for the number of parameters than the AIC. The model ranked first when using BIC, with a weight of 0.38 . It had the lowest AICc in 3% of instances over 1,000 bootstraps and was the most parsimonious amongst the top 10 models with the highest percentages in the bootstrapping analysis.

Model rank	Variables	LogLik	df	Δ AICc	w
1	Logging type + Forest cover + Perimeter-area ratio + Regional species pool + Temperature + Forest type + Proximity + Precipitation + Logging type: Regional species pool + Logging type: Perimeter-area ratio + Logging type: Proximity + Logging type: Precipitation + Forest type: Precipitation + Forest type: Temperature	-16.43	19	0	0.02
2	Logging type + Forest cover + Regional species pool + Temperature + Forest type + Proximity + Precipitation + Logging type: Regional species pool + Logging type: Proximity + Logging type: Precipitation + Forest type: Precipitation + Forest type: Temperature	-19.46	17	0.54	0.02
7	Logging type + Forest cover + Perimeter-area ratio + Regional species pool + Temperature + Logging type: Regional species pool	-31.44	8	2.03	0.01

Table 1. Candidate models for recovery ratios ranked according to Δ AICc, with their corresponding log likelihood (LogLik), degree of freedom (df) and Akaike weights (w). Only models with Δ AICc < 4 and fewer parameters were retained. The symbol “:” means interaction.

Independent variables and their interactions	Relative importance
Logging type	1.00
Temperature	1.00
Forest cover	1.00
Regional species pool	1.00
Logging type: Regional species pool	0.99
Forest type	0.92
Precipitation	0.85
Perimeter-area ratio	0.78
Proximity	0.74
Forest type: Precipitation	0.72
Logging type: Proximity	0.58
Logging type: Precipitation	0.52
Logging type: Perimeter-area ratio	0.43
Logging type: Temperature	0.42
Forest type: Temperature	0.42
Recovery time	0.32
Logging type: Forest cover	0.28
Forest type: Regional species pool	0.20
Forest type: Forest cover	0.14
Forest type: Proximity	0.12
Logging type: Recovery time	0.09
Forest type: Perimeter-area ratio	0.07
Forest type: Recovery time	0.05

Table 2. Relative importance of independent variables from AICc. The symbol “:” means interaction. The variables included in the most parsimonious model within 4 Δ AICc are in bold.

The regional species pool was positively related to the recovery ratio of species richness and the slope of selective cutting forests was steeper than that of clear cutting forests (Figs 2 and 3a). The temperature was negatively related to the recovery ratios (Figs 2 and 3b). The perimeter-area ratio of forest patches (Figs 2 and 3c) and the percentage of forest cover (Figs 2 and 3d) had positive effects on the recovery ratios of species richness. The result was robust after removing the outlier for which perimeter-area ratio was 0.005 (Fig. 3c and Supplementary Table S1).

Discussion

Impacts of the regional species pool and logging type on the recovery of woody plant species richness. In regional species pool, the disturbance-adapted and disturbance-sensitive species can directly influence the ecological profile of plant recovery⁹. The observed positive relationship between the regional species pool and recovery ratio might be because the region with larger species pool contains more information legacies namely adaptations to historical disturbance cycles, and more material legacies such as soil seed bank²⁷. Therefore it is more likely to have more disturbance-adapted species, which facilitate the seed availability¹⁹.

Additionally, there are multiple recovery trajectories of secondary forests^{9,28} because the recovery can be affected by various random factors and could reach different stable states other than the pre-disturbance state²⁹. If the secondary forests would be recovered to pre-disturbance state, not only the regional species pool contains

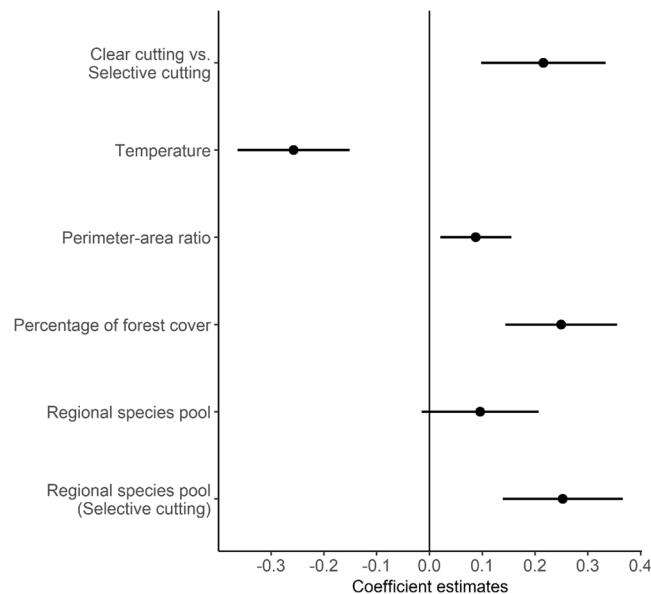


Figure 2. Variables and coefficient estimates for drivers of woody plant species richness recovery in secondary forests from the most parsimonious model within 4 Δ AICc. The coefficient estimates are for the natural log transformed recovery ratio and z-score rescaled continuous independent variables.

species that can unitedly play a leading role but also local dynamics are fast enough for early-arriving species to modify niches before other species arrive³⁰.

This is partially proved by our results on logging type. Our results indicate that the effect of regional species pool on recovery is more pronounced in selective cutting forests than in clear cutting forests. In general, the selective cutting forests could recover better than clear cutting forests since the disturbance is lighter²² and there are more remnant forests¹⁹. In selective cutting forests, the niches have been basically fixed because of the existence of pioneer species and local early-arriving species, so the role of regional species pool in forest recovery can be very strong. However in the forests after clear cutting, at least in the early succession, the recovery is affected by the competition between local species and alien species, as well as other diverse random factors, thus the effect of regional species pool is less strong. Our study does not include the dynamic changes of species composition and if we can integrate the data of species composition, we can better explain the impact of regional species pool on species recovery.

Admittedly, recovery time is an indispensable factor when evaluating the forest regeneration^{31–33}. However, our results did not show strong relationship between time and recovery ratio. This might be because our dataset include many different types of forest ecosystems. If the analysis is limited to a single forest ecosystem or in the same eco-region, we also expect that there would be a generalized linear correlation between recovery ratio and recovery time, as what has been found in other studies^{31,34}. Furthermore, before the ecosystem stabilizing, a unimodal relationship is also possible since species richness can increase with pioneer species and then decrease because of competition during coexistence³⁵. However, multiple ecosystems are included within the analysis, this pattern becomes less obvious. For example, the recovery pattern of broad-leaved forests in the south region is considerably different from that of conifer forests in the northeast region, where the regrowth rate of conifer forests in the northeast region is slower and the species richness of reference forests is lower.

Impacts of the temperature on the recovery of woody plant species richness. Many previous studies have shown that plant species richness is high in the places with high temperature along the latitudinal gradient³⁶. In contrast to this plant species richness distribution, we found that the recovery ratios of woody plant species richness would be high with low temperature. A study on Puerto Rico Island showed similar findings that relatively lower temperature and high precipitation facilitated forest recovery at high elevations^{37,38}. Temperature could influence plants through physiological processes (e.g. evapotranspiration of plants is higher in warmer conditions), grow processes (e.g. lower daily minimum temperatures are supposed to accelerate growth rates in tropical forest trees³⁹), soil nutrients (e.g. decreasing temperature is also associated with increasing soil C and N stocks⁴⁰), and ecosystem resilience (e.g. resilience of tropical forest might be reduced at the higher temperature⁴¹). However the specific mechanisms of how temperature impacts recovery of plant species richness and plant diversity need to be further explored.

Impacts of the landscape on the recovery of woody plant species richness. Our results suggest that higher forest cover could promote the species richness recovery. Indeed, surrounding forest are important sources for recolonization, especially for those forests with few soil seed banks¹¹. As such, the landscape with higher forest cover is likely to contain more native species and remnants of primary forests⁹, which helps secondary forests recover to pre-disturbance states⁷. In landscapes with lower surrounding forest cover, the secondary

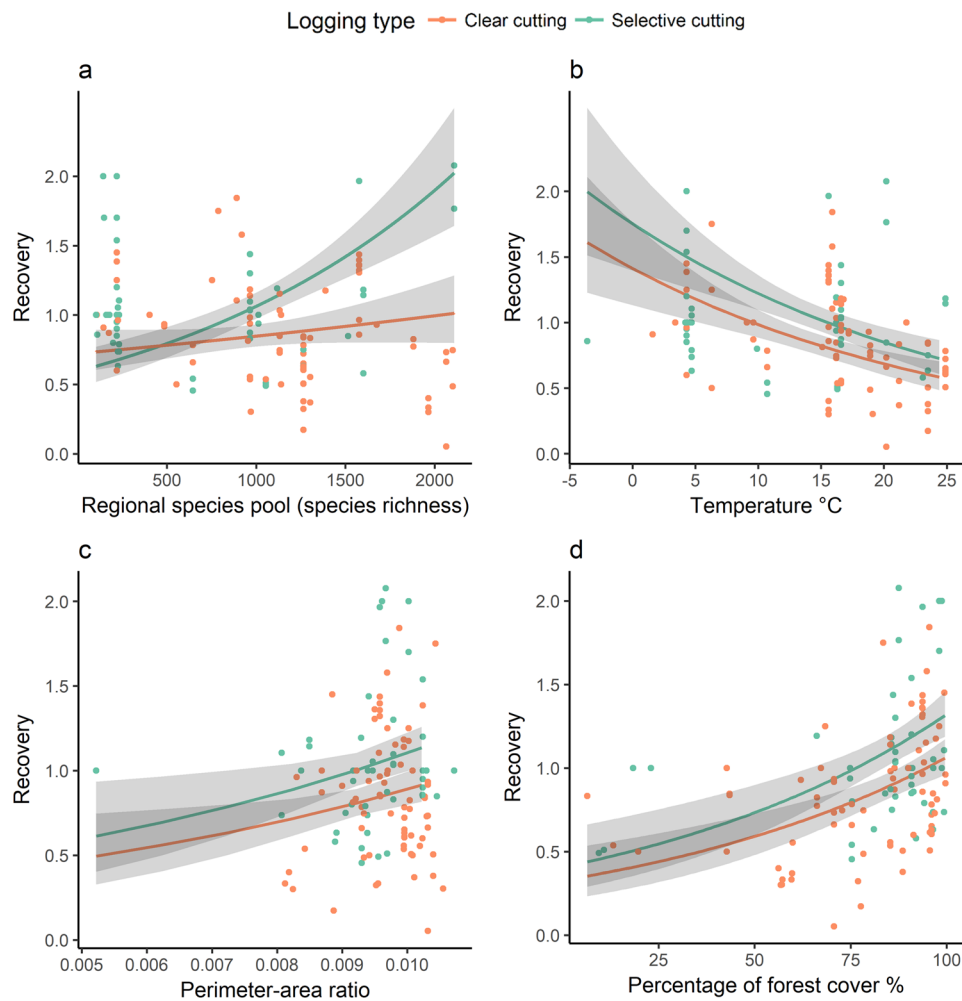


Figure 3. Relationships between the recovery of woody plant species richness and (a) regional species pool (b) temperature (c) perimeter-area ratio, and (d) percentage of forest cover (back-transformed). The pseudo- R^2 of the most parsimonious model with the lowest AICc within $4 \Delta AICc$ was 0.42. The dots are the observed data, the lines are the predictions from the model, and the shaded area is the 95% confidence interval.

forest may have a unique trajectory and is additionally influenced by its own biological and biotic factors^{28,42}, particularly those affecting the reproduction and dispersal⁹. Our results also suggest that higher shape complexity of forest patches would be conducive to species richness recovery. This effect may be explained by positive effects of landscape heterogeneity on species richness in fragmented landscape⁴³. Again, if we can further integrate data on species composition, in particular considering invasive species, it would help us to understand more deeply the impacts of landscape on plant species recovery.

Conclusion

Following up on a previous meta-analysis on the patterns of species recovery across China²⁴, we conducted a nationwide analysis of main drivers that influenced the recovery of woody plant species richness in secondary forests across the country. We collected the logging history, climate, forest landscape and forest attribute data and used an information-theory approach to identify the main drivers of species richness recovery in secondary forest. Results showed that forests with larger regional species pool had higher recovery ratios and the effect of regional species pool on recovery was stronger in selective cutting forests than that in clear cutting forests. We also found that the temperature was negatively related to the recovery. The shape complexity of forest patches and the percentage of forest cover in the landscape had positive effects on the recovery ratios of species richness. The results from our study provide more basic information on the natural recovery of secondary forests and deeper insight into resilience of secondary forests in China. We suggest future research to incorporate data on recovery of species composition, which can help to more accurately identify ecological drivers that affect recovery of plant diversity, as well as improve interpretation of these drivers on the forest recovery.

Methods

Ecological drivers and data collection. In this study, we considered four drivers of the recovery: logging history, climate, forest landscape and forest attribute. The logging history was indicated by (i) logging type (clear cutting or selective cutting) and (ii) recovery time after logging (in years, time since the last logging). The climate was indicated by (iii) annual temperature (°C) and (iv) annual precipitation (mm/yr). The forest landscape was indicated by (v) shape complexity of forest patches—measured as the mean perimeter-area ratio of forest patches, (vi) isolation—measured as the proximity index⁴⁴, and (vii) dominance of forest cover in the landscape—measured as the percentage of forest cover. The forest attribute was presented by (viii) regional species pool—using woody plant species richness, and (ix) the forest type (conifer forests, conifer and broad-leaved mixed forests, and broad-leaved forests).

Logging type and recovery time for each data point were obtained from the previous meta-analysis²⁴. Regional species pool of a forest site was defined as all the woody species occurring in the 50*50 km² grid cell where the secondary forest was located and was obtained from the *Database of China's Woody Plants*³⁶. Since the regional species pool in our study was defined within a 50*50 km² grid cell, we regarded it as one aspect of forest attribute. Annual temperature and precipitation were gathered from China Meteorological Data Service Center (<http://data.cma.cn/>). We used 300 m resolution land cover data for the year 2015 provided by the European Space Agency (<http://maps.elie.ucl.ac.be/CCI/viewer/>), which included eight forest cover classes. For the three landscape metrics, we used ArcGIS by Esri (ArcMap10.5) to generate 10 km radius buffers on the 300 m resolution land cover map, as a radius of 10 km buffer has been shown to be sufficient to conduct landscape analysis for plants communities²². To specify the location of secondary forest in each study, we tried to group sampling sites and extract the center location of sampling sites or the study area as the corresponding geographic coordinate, which means that the “landscape impact” was to reflect the unit of the analysis rather than single sampling site²². We contacted the authors to request this geographic information if the data were not available. Fragstats 4.2 was used to calculate the forest landscape metrics within each buffer area. The China administrative border map used in Fig. 1 was downloaded from <http://www.resdc.cn/>. The forest type (conifer forests, conifer and broad-leaved mixed forests, and broad-leaved forests) of each data point was judged according to both original literatures and eco-regions. We used the eco-region database defined by the WWF⁴⁵.

Data analysis. We fitted weighted generalized linear models (GLMs) and used an information-theory approach to identify the main drivers of species richness recovery in secondary forest⁴⁶. The unit of analysis was a pair of secondary forests woody plant species richness (SR) and reference primary forests woody plant species richness (PR). In this study, the recovery ratio (R_c) was calculated by Equation (1):

$$R_c = \frac{SR}{PR} \quad (1)$$

Recovery ratio was natural log transformed and the continuous independent variables were rescaled using z-score. The weight of each pair of secondary-primary forest data reflect the precision and amount of information of a particular study in the meta-analysis⁴⁷. We used the same weight as those used in the previous meta-analysis²⁴. We checked collinearity among drivers by assessing generalized variance inflation factor (GVIF) in each model and considered that a value of GVIF^{1/(2*df)}⁴⁸ above 10^{1/(2*df)}⁴⁹ indicated strong collinearity⁴⁹ (df, degree of freedom). We did not detect strong collinearity in our dataset (Supplementary Table S2). We initially fitted one global weighted generalized linear models with the response variable recovery ratio and the nine potential independent variables listed above, as well as the interactions between logging type and all the continuous variables, and the interactions between forest type and all the continuous variables. However, such a model could not converge due to the high number of parameters, so instead, we fitted multiple global models each including one of all the possible combinations of 10 interactions. We then fitted all possible models involving at least one variables and rank them according to Akaike Information Criterion corrected for small sample sizes (AICc), with the MuMIN package⁵⁰. We further used the Bayesian Information Criteria (BIC) method to obtain more support for our results. As all model sets were performed on the same dataset, they were directly comparable. We reported only the model with the lowest AICc and all models within 4 ΔAICc units but with fewer parameters.

As the data collection procedure implied resampling in the study landscape, we controlled for pseudo-replication. We calculated the percentage of times a model was ranked with the lowest AICc after 1,000 bootstraps^{22,51}. To speed up the computing process, bootstrapping was performed on a global model excluding all forest type interactions.

Finally, McFadden's R square⁵², as one type of pseudo-R² was calculated to show goodness of fit of the generalized linear models after model selection. Statistics analyses were conducted in R 3.4.1.

Data Availability Statement

Data are available in the Supplementary Dataset.

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Author Contributions

X.F.L., X.H.L. and C.G. designed the study. X.F.L., T.C. and J.G. performed analyses. X.F.L., J.G., T.C., X.H.L. Z.W. and C.G. wrote the manuscript. Z.W. provided the data of regional species pool.

Additional Information

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