Relationship between Diversity and Productivity at Ratargul Fresh Water Swamp Forest in Bangladesh

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Abstract
One of the most concerned topics in ecology is the relationship between biodiversity and ecosystem functioning. However, there are few field studies, carried out in forests, although many studies have been done in controlled experiments in grasslands. In this paper, we describe the relationship pattern between three facets of diversity and productivity at Ratargul Fresh Water Swamp Forest (RFWSF) in Bangladesh, which is the only remaining fresh water swamp forest of the country. Sixty sample plots were selected from RFWSF and included six functional traits including leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), tree height, bark thickness and wood density. In analyzing TD, we used Shannon diversity and richness indices, functional diversity was measured by Rao’s quadratic entropy (Rao 1982) and Faith’s (1992) index was used for phylogenetic diversity (PD). It was found that, TD, FD and PD were positively related with productivity (basal area) due to resource use complementarity but surprisingly the best predictor of tree productivity was FD. The results contribute to the understanding the effects of biodiversity loss and it is essential for conservation decision-making and policy-making of Ratargul Fresh Water Swamp Forest.

Key Words: taxonomic diversity, functional diversity, phylogenetic diversity, traits, productivity

Introduction
A number of studies have been exploring the effect of plant diversity in ecosystem functioning during the last two decades (Tilman et al. 1997; Stevens and Carson 2001; Petchey et al. 2004; Cadotte et al. 2008; Paquette and Messier 2011; Roscher et al. 2012; Genung et al. 2014). Scientists concern on this because of global loss of biological diversity, which comprise the natural and managed plant communities, is related to global environmental change (Chapin et al. 1998; Hooper et al. 2005). Now, studying on biological diversity has become interesting as the vital role of diversity in ecosystem functioning is recognized (Naeem et al. 2009).

Here we study on three facets of biodiversity named taxonomic diversity (TD), which has two components such as richness and evenness (Biswas and Mallik 2011), functional diversity (FD), a biodiversity component deals with the diversity of functional trait of species in a community (Petchey and Gaston 2006) where morphological, physiological and phenological characteristics of organisms are indicated by functional trait (Violle et al. 2007) and phylogenetic diversity (PD), based on evolutionary history which disentangles distance between species. PD can be defined also as the minimum total length of all the phylogenetic branches which is required spanning a certain set of species.
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on the phylogenetic tree (Faith 1992).

Many experiments measured species richness or species diversity explaining diversity-ecosystem functioning relationship (Tilman et al. 2001; Hedlund et al. 2003; Ruijven and Berendse 2005; Zuo et al. 2012). But species diversity cannot explain similarities or variation of functional traits among species (Hooper et al. 2002) which has made FD a better predictor than TD in explaining productivity (Petchey et al. 2004; Roscher et al. 2012). Again, PD disentangles better than FD and TD too (Maherali and Klironomos 2007; Cadotte et al. 2009; Cadotte 2013). This occurs because results vary with different functional traits and usually it is difficult to collect essential functional traits those are needed for measuring FD. On the other hand, phylogenies can develop through online databases like the GenBank, the genetic sequence repository or TreeBASE where phylogenetic data are stored from publications or Phylomatic (Cadotte et al. 2009).

There have found different patterns of relationship between diversity and productivity in ecology (Xiao et al. 2010). Several studies have got five patterns in diversity-productivity relationship such as positive, negative, U-shaped, hump-shaped and no relationship (Hector et al. 2010; Ma et al. 2010). Although there are strongest evidence of positive relationship in diversity-productivity study (Cadotte et al. 2008; Zuo et al. 2012; Genung et al. 2014).

Here we examine the relationship pattern between three facets of diversity and productivity at Ratargul Fresh Water Swamp Forest (RFWSF) in Bangladesh which is the only remaining fresh water swamp forest of the country. This forest is categorized as wet evergreen forest. In stabilizing the wetland ecosystem, the plant species has an important contribution though RFWSF possess low species diversity (Choudhury et al. 2004). Here we test the hypothesis that TD, FD and PD will show positive relationship pattern with productivity in this forest and PD will be the best predictor representing such pattern.

Numerous studies explained diversity-productivity relationship in grassland communities (e.g. Tilman et al. 2001; Roscher et al. 2012; Zuo et al. 2012) where few recent studies have examined on forests and tree-dominated ecosystems (Nadrowski et al. 2010). Because, study on large, long-lived trees has benefits but poses undeniable challenges (Töchner et al. 2013). To our knowledge, we did not find any study related to this work in Ratargul Fresh Water Swamp Forest. In this study we took 60 sample plots where seven tree species exist. This study will be helpful to manage and assess the tree-dominated ecosystems to face global changes (Töchner et al. 2013).

Materials and Methods

The study site

The research was done in the Ratargul fresh water swamp

Fig. 1. Map of the Study Area (Banglapedia 2013).
forest under the Ratargul forest beat (latitude 25°00.025’N
and longitude 91°58.180’E) under Sylhet Forest Division,
Bangladesh (Fig. 1).

The forest (118.55 ha) was declared as Reserved Forest
under the Assam Forest Act in 1932 (Choudhury et al.
2004). The soil texture is mostly clayey loam to clayey
under the vegetation. The soils of this region are gray
and heavy (Hossain 2011). The mean maximum temperature
is about 32°C. This area receives 1250 mm of rain on average
and the relative humidity is approximately 74% during
December while on July-August, it is over 90% (Choudhury
et al. 2004). This forest is subject to regular flooding. The
banks are flooded by the adjoining Goyain river. Inundation
level changes with the intensity of rain. The water regime
thus fluctuates but the entire forest remains highly wet all
through the monsoon period (May to October) (Hossain
2011).

This forest possesses around 80% of canopy coverage
and height of the canopy is about 15m. The RFWSF looks
like a two stored forest where Koroch consists the top store
and the under story consists of the Patipata, with the combi-
nation of some other natural species. Patipata represents a
very dense cover (Choudhury et al. 2004).

Research methods

At Ratargul, total 60 sample plots were selected randomly
for sampling. The size of each sample plot was 20 m×20 m
(0.04 ha) which were subdivided into 2 m×2 m sub-plots.
Within each plot the number was counted and species name
of all the trees were counted and recorded. All trees (d.b.
h > 10 cm) were identified for each 60 plots. Diameter at
breast height (DBH; at 1.3 m height from ground level)
was measured using a surveyor’s tape. Trees, which pos-
sessed more than a single stem, the main trunk were meas-
ured at the narrowest point below the branches. High but-
tressed trees were measured at about 30 cm above of the
convergence of the protrusions of the buttresses on the bole.

We collected leaf area, specific leaf area, leaf dry matter
content, tree height, bark thickness and wood density as
functional trait data from the study area to measure func-
tional diversity. We gathered bark thickness data for each
individual present in each study plots. At least three fully
expanded leaves (small, medium, large) and wood were also
collected for each individual from all plots to calculate leaf
area (LA), Specific leaf area (SLA), Leaf dry matter con-
tent (LDMC) and Wood density using the protocols of
Cornelissen et al. (2003).

In calculation of leaf area, we used a scanner and a soft-
ware Pixel. We measured SLA as leaf area of a fresh leaf
divided by its oven-dry mass (mg/kg⁻²). After determining
leaf area, leaves were oven-dried at a temperature of 65°C
for 72 hours in a laboratory before weighing. Average
oven-dry weight of leaf was divided by its average green
weight (mg g⁻¹) deriving LDMC. SLA and LDMC were
calculated by measuring the green weight of leaves in the
field with a help of electronic balance meter. Tree height was
measured with Sunto clinometers by taking top reading,
bottom reading and angle for each and every tree. We col-
cected wood from the individuals to measure wood density.
In laboratory we measured the length of wood and dried the
woods at 65°C for three days and then weighed.

Data analysis

Our analysis focused on Shannon diversity and richness
indices getting a clear picture of diversity of tree species in
the study area. Species richness(S) means the total number
of species found in the sample. It is considered as the sim-
plest description of community structure. It was calculated
according to the following equation:

\[ H = - \sum P_i \ln P_i \]

where

H=Shannon diversity index, p_i=ratio of the
number of individuals of one species and total number of
individuals in the samples (Maguran and McGill 2011).

The above analysis was done using BiodiversityR pack-
page in R 3.0.1.

We used Rao’s quadratic entropy (Rao 1982) as a func-
tional diversity index that addresses the mean functional
distance between two randomly chosen individuals. Distance
matrix is a base of this index which includes species abun-
dance (Maguran and McGill 2011). We used the software
FD package in R 3.0.1. for data analysis. In measuring
Rao’s quadratic entropy, two matrixes: functional traits data
and abundance data were used. The formula is given below:

\[ Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i p_j \]
where $S=$ number of species in the community, $p_i$ and $p_j=$ relative abundances of species $i$ and $j$ respectively and $d_{ij}=$ trait distance between species $i$ and $j$ in the community.

Phylogenetic diversity (PD) was computed as Faith’s (1992) index for each sample in the phylo.

Faith’s PD index (sum of all branch length among all taxa in sample, including the root node of the tree) is reported, as the total branch length in the phylogeny, and the proportion of the total branch length in the phylogeny associated with the taxa in each sample. At first we developed a species list based on the APG III (2009) to analyze phylogenetic diversity. Then I used phylomatic resolved super tree of angiosperms (R20091110; available online at www.phylodiversity.net) to assemble a species list in to a phylogeny. The analysis was done using software Phylocom 4.2. The PD value, for any subset of taxa of size $N$, reduces to a simple function of the number of different nodes on the cladogram that lie along the corresponding minimum spanning path:

$$PD=(N-1)+\text{no. of internal nodes (branching points) on the minimum spanning path}$$

Thus, the best subset of $N$ taxa is the one that spans the greatest number of nodes on the cladogram, and the best addition to a subset is the taxon adding the greatest number of nodes to the minimum spanning path.

Garnier et al. (2004) proposed to calculate the mean of trait values weighted by the relative abundances of every species which is known as the community-weighted mean trait value and analyzed by the software FD package in R 3.0.1. It is computed by the following formula:

$$\text{CWM} = \sum_{i=1}^{S} p_i x_i$$

where $S=$ number of species in the community, $p_i=$ species biomass proportions and $x_i=$ species-specific trait values for species $i$.

**Results**

A small number of tree species were found in the study area. A total of 607 individuals of trees belong to 7 species of 7 genera and 7 families were counted in the study area (Table 1). Among seven species about 479 Koroch individuals were found. Koroch is the dominant species of the study area.

**Species diversity of ratargul fresh water swamp forest**

Species accumulation curve assesses the adequacy of sampling in diversity study. Fig. 2a shows that the number of new species increases up to 30 plots. But there were found no more new species by additional sampling plots after taking 30 plots. For the accuracy of diversity measurement, we took 60 plots as we measured taxonomic, functional and phylogenetic diversity in this paper.

**Statistical description of diversity indices**

In RFWSF maximum species richness was 4 whereas minimum was 1. Taxonomic diversity was differed from 0.26 to 1.12. Functional diversity was higher than taxonomic diversity and maximum number of this diversity was 1.56 whereas minimum number was 0.32. Highest phylogenetic diversity was found 1120, lowest 400 and mean value 700 (Table 2).

| Family            | Scientific name                           | Genus          |
|-------------------|-------------------------------------------|----------------|
| Anacardiaceae     | Lannea coromandelica. Houtt                | Lannea         |
| Euphorbiaceae     | Treizia nudiflora. L                       | Trewia         |
| Fabaceae          | Pongamia pinata. L. Pierre                 | Pongamia       |
| Lecythidaceae     | Barringtonia acutangula (L.) Gaertn       | Barringtonia   |
| Moraceae          | Ficus benghalensis. L.                     | Ficus          |
| Myrtaceae         | Syzygium formosum. Wall                    | Syzygium       |
| Rubiaceae         | Anthocephalus chinensis (Lam.) A. Rich. ex Walp | Anthocephalus |
Table 2. Descriptive Statistics of Different Diversity Indices

| Diversity                  | Minimum | Maximum | Mean     | Standard deviation |
|----------------------------|---------|---------|----------|--------------------|
| Species richness           | 1       | 4       | 2.2      | ±0.88              |
| Taxonomic diversity        | 0.26    | 1.12    | 0.50     | ±0.35              |
| Functional diversity       | 0.32    | 1.56    | 1.65     | ±6.25              |
| Phylogenetic diversity     | 400     | 1120    | 700      | ±203.89            |

Table 3. Summary of Regression results between diversity and productivity

| Model No. | Relation   | a          | b          | $R^2$ | F     | p value |
|-----------|------------|------------|------------|-------|-------|---------|
| 1         | BA-TD      | 1243.5***  | 2803.3***  | 0.4491| 47.29 | 4.719e-09|
| 2         | BA-FD      | 1690.07*** | 615.29***  | 0.4906| 55.87 | 4.672e-10|
| 3         | BA-PD      | -80.909    | 3.903***   | 0.301 | 24.98 | 5.668e-06|

a, intercept; b, slope; BA, Basal area; TD, Taxonomic diversity; FD, Functional diversity; PD, Phylogenetic diversity.
***Significance level.

Fig. 2. (a) Species accumulation curve and (b) Species abundance curve.

Fig. 3. Relationship between productivity and diversity, (a) productivity and taxonomic diversity, (b) productivity and functional diversity, (c) productivity and phylogenetic diversity.
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Table 4. CCA Ordination Results

|                      | CCA axes |
|----------------------|----------|
|                      | Axes 1   | Axes 2   | Axes 3   | Axes 4   |
| Eigenvalue           | 0.496    | 0.392    | 0.197    | 0.081    |
| Production trait correlations | 0.911    | 0.956    | 0.913    | 0.724    |
| Cumulative percentage variance of productivity data | 25.6     | 45.9     | 56.0     | 60.2     |
| Cumulative percentage variance of productivity trait relation | 40.4     | 72.3     | 88.3     | 94.9     |
| Sum of all eigenvalue | 1.938    |          |          |          |
| Sum of all canonical eigenvalue | 1.230    |          |          |          |

Fig. 4. Tri-plot CCA Ordination.

Relationship between plant diversity and productivity

Overall, we found a significant positive linear relationship between plant diversity and productivity (basal area) in RFWSF as we expected. The biomass production was increased with increasing TD ($R^2=0.4491$, $p=4.719e^{-9}$), FD ($R^2=0.4906$, $p=4.672e^{-10}$) as well as PD ($R^2=0.301$, $p=5.668e^{-6}$) (Table 3, Fig. 3).

Interestingly, the best predictor of tree productivity was FD ($R^2=0.4906$) in our dataset than either TD or PD (Table 3, Fig. 3) which was against our hypothesis. So, functional diversity model is the best fitted diversity model for present study area.

Canonical Correspondence Analysis

The first CCA axis was significant ($p<0.01$, 499 permutations under reduced model). All constrained CCA axes were also significant. The eigenvalue of first axis is 0.496 (Table 4) and productivity trait correlations for the first axis is 91.1%. Gradual decrease of eigenvalue of first four axes indicates a well-structured dataset. These indicated that the CCA analysis performed well in describing relationships between productivity and trait variables presented in the tri-plots (Fig. 4). The cumulative percentage variance of productivity data implied that the first axis explained about 25.6% of the total variation (inertia) 1.938. Cumulatively first four axes together explained about 60.2% of variance in productivity data (Table 4). For the first four axes cumulative productivity - trait value is about 94.9%; it indicated that productivity data are strongly related with trait variables.

Table 5 shows the correlation between trait variables and CCA axis. Leaf dry matter content showed significant correlation with first two axes. The dominant trait variables correlated with CCA first axis were leaf area, specific leaf area and leaf dry matter content. Bark thickness, height and wood density were significantly correlated with CCA axis 2.

Table 6 shows the correlation among the trait values. Bark thickness showed the significant positive relation with height, leaf dry matter content and wood density. Leaf dry matter content is positively correlated with bark thickness and negatively related with height and leaf area.

Table 7 shows the marginal and conditional effect of the trait variables. In marginal effect, all variables show their independent effects. Results from the marginal effects, bark thickness is the most important trait which is correlated with production. Then wood densities, height, LDMC are respectively correlated with production. In conditional effects, all trait variables show the significant contribution in production except height. Height did not show significant
**Table 5.** Correlation between Trait Variables and CCA Axes

| Trait variables       | CCA 1  | CCA 2  | CCA 3  |
|-----------------------|--------|--------|--------|
| Height                | 0.239  | -0.685 | -0.27  |
| Bark thickness        | 0.015  | -0.937 | -0.23  |
| Leaf area             | -0.343 | 0.109  | 0.46   |
| Specific leaf area    | -0.322 | -0.022 | 0.51   |
| Leaf dry matter content| 0.320  | -0.545 | -0.32  |
| Wood density          | 0.191  | -0.802 | -0.31  |

**Table 6.** Correlation between Trait Variables

| Trait      | H   | B   | LA  | SLA | LDMC |
|------------|-----|-----|-----|-----|------|
| B          | 0.85162 | -0.24239 | -0.100 | 0.985 | |
| LA         | -0.24239 | -0.100 | 0.985 | | |
| SLA        | -0.109  | 0.029 | 0.985 | | |
| LDMC       | -0.25797 | 0.729 | -0.380 | -0.258 | |
| W          | -0.16933 | 0.926 | -0.304 | -0.169 | 0.925 |

B, Bark thickness; LA, Leaf area; SLA, Specific leaf area; LDMC, Leaf dry matter content; W, Wood density; H, Height.

**Table 7.** Marginal and Conditional Effects

| Variable | Var.N | Lambda1 | Variable | Var.N | LambdaA | P     | F     |
|----------|-------|---------|----------|-------|---------|-------|-------|
| B        | 2     | 0.37    | B        | 2     | 0.37    | 0.002 | 13.66 |
| W        | 6     | 0.32    | W        | 6     | 0.19    | 0.002 | 8.03  |
| H        | 1     | 0.28    | SLA      | 4     | 0.1     | 0.024 | 4.31  |
| LDMC     | 5     | 0.24    | LA       | 3     | 0.16    | 0.018 | 8.02  |
| SLA      | 4     | 0.17    | H        | 1     | 0.02    | 0.3   | 0.6   |
| LA       | 3     | 0.15    | LDMC     | 5     | 0.39    | 0.002 | 29.48 |

B, Bark thickness; LA, Leaf area; SLA, Specific leaf area; LDMC, Leaf dry matter content; W, Wood density; H, Height.

The Bi-plot CCA Ordination (Fig. 5) revealed that production was highly influenced by the trait variables. Bottom side of the diagram indicates that the productivity of Koroch and Hijol are strongly affected with all of trait variables but bark thickness, wood density, height and leaf dry matter content are highly influenced the productivity. Top right side of the diagram indicates that, productivity of the Pitali and Kadam are highly influenced by the leaf area. This diagram also reveals that three species viz. Jiyol, Panijam and Bot have no contribution in the productivity. The Tri-plot CCA Ordination (Fig. 4) shows the production within plot.

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Fig. 5. Bi-plot CCA Ordination.
Relationship between Diversity and Productivity

Discussion

Relationship between diversity and productivity

In our study, taxonomic diversity (TD), functional diversity (FD) and phylogenetic diversity (PD) were positively related with productivity. It has been demonstrated in other plant related studies that productivity increases with increasing TD, FD and PD (Tilman et al. 1997; Petchey et al. 2004; Ruijven and Berendse 2005; Paquette and Messier 2011; Zuo et al. 2012; Genung et al. 2014). The mechanism behind such result is resource use complementarity (Tilman et al. 1997; Petchey 2003; Cadotte 2013). In case of complementarity, species diminish interspecific competition by niche partitioning. Community can use the total available resources if species utilize several resources or they use same resources at different times or different space (Ewel 1986). Complementarity increases if there are great differences in functional traits (Chesson et al. 2002).

Tilman et al. (2001) showed that, aboveground biomass was increased with species number in higher biodiversity sites than monoculture due to niche complementarity. In an experimental grassland ecosystems, PD explained biomass more significantly than the number of species and functional groups (Cadotte et al. 2008). A significant increase was found in biomass with species richness in the drought plots of bryophyte communities in New Zealand (Mulder et al. 2001). In contrast of our study, phenological complementarity was not the mechanism in the relationship between species diversity and ecosystem function in an early successional plant community (Stevens and Carson 2001). Negative relationship was the evidence between above-ground biomass and species richness, functional group richness and functional diversity in a plant community of UK (Thompson et al. 2005). Vilà et al. (2003) also found this type of relationship in Spain in tree assemblages.

Best predictor of productivity

From regression analysis, this study demonstrates that functional diversity is the best predictor to understand the community productivity pattern in present study area. This result is surprising because our hypothesis was that, phylogenetic diversity will be the best predictor of productivity. We found such result because functional traits may disentangle considerable phenotypic plasticity (Cadotte et al. 2009).

How an organism extracts resources from its environment, is determined by functional traits (McGill et al. 2006). In our study, Canonical Correspondence Analysis showed that the functional traits we used highly influenced the productivity. We measured six functional traits where LA can estimate physiological processes in forest ecosystems like photosynthetic efficiency, evapotranspiration, carbon assimilation (Hietz et al. 2010). It has influence on light interception by which LA can regulate plant growth and productivity (Waring and Schlesinger 1985). SLA can evaluate growth rate, photosynthetic rate (Cornelissen 2003) and has an impact on primary productivity (Cornelissen et al. 1999). Species which have high SLA tend to contain high nutrient concentrations and also have high photosynthesis and respiration rates (Wright et al. 2004). LDMC is an important functional trait because it is important for aboveground biomass (Bu et al. 2014). High LDMC tends to be easily resistant against physical hazards like wind, hail etc. (Cornelissen 2003) and provide a good performance under low resources and drought (Wilson et al. 1999; Markesteijn et al. 2011). Reproductive strategy and growth rate are related to wood density (Paquette and Messier 2011). According to Poorter et al. (2010), wood density plays a vital role in species performance and life history strategies of tropical tree species. Height is considered as a fundamental role to get access of light (Westoby 1998). It is related to competitive vigour, whole plant fecundity. This functional trait tends to be correlated with aboveground biomass, rooting depth, lateral spread and leaf size (Cornelissen et al. 2003). Bark thickness has fire protecting property (Hoffmann et al. 2009) and it is considered as the best predictor of the probability of tree stem survival after fire (Ryan et al. 1988). Besides, bark can store a high amount of carbon (Jenkins et al. 2003).

Phylogenetic diversity explained productivity best than functional diversity in Minnesota, USA, which may occurred because that study did not measure root types, rooting depth as functional traits, which were representing by phylogeny (Cadotte et al. 2009). Cadotte et al. (2008) showed PD as a best predictor of biomass production but there were much variation in the explanatory value of PD.
where $R^2$ ranged from 0.01 to 0.69 in a meta-analysis across 29 experiments throughout the world. In a study of Canada, beyond PD, FD interpreted tree productivity better based on three traits such as seed mass, wood density and maximum height related to reproduction, growth and successional status (Paquette and Messier 2011).

From CCA Ordination Diagram, it is clear that bot, jiyol and panijam had no contribution in production with the trait variability because these species may have low survival capacity in this forest.

**Conclusion**

Our results identified here that functional diversity is the best explanator for predicting productivity beyond taxonomic diversity and evolutionary diversity at Ratargul Fresh Water Swamp Forest in Bangladesh, though three facets of diversity were positively increased with productivity. We dealt with aboveground biomass which is related to carbon storage and can interpret the sensitivity of ecosystem processes with changing species richness (Cardinale et al. 2011). Different species possess certain functional traits as all species are not identical, due to which the loss or addition of some species may have a great impact while others have little impact on a certain ecosystem processes (Tilman et al. 1997). Therefore, it is important to identify the key functional traits which may have contribution to understand the drivers of different ecosystem processes (Roscher et al. 2012). In our study, we used the functional traits which have great contribution in productivity and may bring functional diversity as a best predictor in diversity-productivity relationship in RFWSF. This study will be helpful to manage and assess the functioning of tree-dominated ecosystems meeting global changes (Törnner et al. 2013). In conservation decision-making and policy-making our research will keep a great contribution. In addition, it is necessary to manage ecosystem sustaining human well-being (Elmqvist et al. 2010). This study can be better defined if some other vital components of environment such as soil macro and micro element, climatic parameters, topographical features were included in this study. Thus further detailed research including some more influential gradients is suggested.

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