

LETTER

Interaction frequency as a surrogate for the total effect of animal mutualists on plants

Diego P. Vázquez,^{1,2*} William F. Morris³ and Pedro Jordano⁴

¹National Center for Ecological Analysis and Synthesis, University of California, 735 State St, Suite 300, Santa Barbara, CA 93101, USA

²Centre d'Ecologie Fonctionnelle et Evolutive, U.M.R. 5175, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France

³Department of Biology, Duke University, Box 90338, Durham, NC 27708-0338, USA

⁴Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080, Sevilla, Spain

*Correspondence: E-mail: dvazquez@lab.cricyt.edu.ar

Abstract

We evaluate whether species interaction frequency can be used as a surrogate for the total effect of a species on another. Because interaction frequency is easier to estimate than per-interaction effect, using interaction frequency as a surrogate of total effect could facilitate the large-scale analysis of quantitative patterns of species-rich interaction networks. We show mathematically that the correlation between interaction frequency (I) and total effect (T) becomes more strongly positive the greater the variation of I relative to the variation of per-interaction effect (P) and the greater the correlation between I and P . A meta-analysis using data on I , P and T for animal pollinators and seed dispersers visiting plants shows a generally strong, positive relationship between T and I , in spite of no general relationship between P and I . Thus, frequent animal mutualists usually contribute the most to plant reproduction, regardless of their effectiveness on a per-interaction basis.

Keywords

Abundance, effectiveness, interaction frequency, interaction networks, interaction strength, mutualism, plant–animal interactions, plant reproduction, pollination, seed dispersal.

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INTRODUCTION

Topological patterns of species interaction networks have been the focus of much research in recent decades. Although much of this research has focused on predator–prey (food-web) interactions (e.g. Cohen 1978; Pimm 1982; Pimm *et al.* 1991; Polis 1991; Williams & Martinez 2000; Dunne *et al.* 2002; Melián & Bascompte 2004), several studies have evaluated patterns in other interaction types, including those among plants and pollinators (Jordano 1987; Memmott 1999; Olesen & Jordano 2002; Bascompte *et al.* 2003; Jordano *et al.* 2003; Vázquez & Aizen 2004) and plants and seed dispersers (Jordano 1987; Bascompte *et al.* 2003; Jordano *et al.* 2003). These studies have identified a number of topological features of species interaction networks, as well as a variety of potential mechanisms accounting for such structure (Pimm *et al.* 1991; Williams & Martinez 2000; Bascompte *et al.* 2003; Cohen *et al.* 2003; Vázquez & Aizen 2005; Vázquez *et al.* 2005).

A major limitation of most past research on species interaction networks is that it has been based mostly on binary networks, which describe interspecific interactions as

either realized or not realized, assuming that all realized interactions are equally important. However, such equivalence of interactions is unlikely, considering that usually only few interspecific interactions are strong and most are weak (Schemske & Horvitz 1984; Jordano 1987; Paine 1992; Wootton 1997; McCann *et al.* 1998). This lack of equivalence has led many to suggest that patterns observed in binary networks may be misleading, and to call for a more quantitative approach that incorporates some measure of interaction strength (Paine 1988; Cohen *et al.* 1993; Memmott 1999; Bersier *et al.* 2002; Borer *et al.* 2002). In spite of some promising progress (e.g. Memmott 1999; Bersier *et al.* 2002; Emmerson & Raffaelli 2004; Bascompte *et al.* 2005), the development of such an approach has been slow, mainly because of the difficulties involved in quantifying interaction strength for large assemblages of species (Hurlbert 1997; Berlow *et al.* 2004). Conducting experiments to measure interaction strength among pairs of species may be feasible for small assemblages, but it is prohibitive for larger assemblages such as those normally considered in studies of interaction networks. Therefore, large-scale quantitative analyses of diverse interaction networks necessarily have to

rely on some surrogate of interaction strength that is easier to measure and yet captures the relative strength of interactions.

Recently, Morris (2003) used Monte Carlo simulations to evaluate the proportional pollination service lost to plants as different species of pollinators go extinct. His results indicate that in most cases the most abundant pollinator species provides a substantial proportion of total service, while rare pollinators are usually relatively unimportant in quantitative terms. In particular, frequency of interaction was more important than per-visit effect in predicting the total service provided by a pollinator species. These results suggest that frequency of interaction could be used as a surrogate of interaction strength in quantitative analyses of network structure.

In this paper, we evaluate how well interaction frequency serves as a surrogate for interaction strength, measured as the total effect of animal mutualists on the reproduction or seed dispersal of plants. We first explore the problem theoretically, asking under what conditions the total effect of a partner will be highly correlated with its frequency of interaction. We then use data from multiple sources to conduct a meta-analysis of effects of animal mutualists on plant reproduction and seed dispersal.

DEFINING INTERACTION EFFECTS

We are interested in the effect of animal mutualists on the reproduction and seed dispersal of plants. We define T as the total effect of an entire population of an animal mutualist on the per capita reproductive or seed dispersal performance of a plant species (hereafter referred to as 'total effect'). In turn, total effect is the product of two components, $T = IP$, where I is interaction frequency (the 'quantity' component; Herrera 1989; Schupp 1993; Jordano & Schupp 2000) and P is per-interaction effect (an estimator of the 'quality' component; Herrera 1987; Schupp 1993; Jordano & Schupp 2000).

Our per-interaction effect P is somewhat comparable with per capita measures of interaction strength used in the food web literature (see Berlow *et al.* 2004), with some important differences. First, in the prey interactions we are concerned with, individuals can interact multiple times (which is usually not possible for prey in predator-prey interactions). Thus, in the present context a 'per capita' effect would be the sum of multiple 'per interaction' effects. Second, this effect is not necessarily related to population-level processes for the plant population. Extrapolating these effects to the population level would require assuming strong dependence of plant density on seed production, which is not necessarily the case (Bierzychudek 1982; Ehrlén & Eriksson 1995; Parker 1997; Knight 2004). Notice also that this effect provides an estimate of the per-interaction reproductive effect of the animal mutualist on the plant, but

it does not give any information about the reciprocal effect (e.g. the nutritional effect of the plant on the animal).

WHEN WILL INTERACTION FREQUENCY BE A GOOD PREDICTOR OF TOTAL EFFECT?

We want to know under what conditions the total effect of an animal mutualist on a plant species is well described solely by the interaction frequency between the two species. Let P , I and $T = IP$ denote random variables defined as above. For mathematical convenience, we will work with the logarithms of I , P , and IP .

Let r_{it} be Pearson's correlation coefficient between log interaction frequency and log total effect. As we show in Appendix 1, r_{it} can be rewritten in terms of the variances of log I and log P and their correlation:

$$r_{it} = \frac{R + r_{ip}}{\sqrt{1 + R^2 + 2Rr_{ip}}} \quad (1)$$

where $R = \sqrt{\text{var}(\log I)}/\sqrt{\text{var}(\log P)}$ is the ratio of the standard deviations of log I and log P and r_{ip} is the correlation coefficient between log I and log P .

A minimal requirement for log I to be a good predictor of log IP is that the correlation between the two should be positive (i.e. $r_{it} > 0$), which requires that

$$R > -r_{ip} \quad (2)$$

If the most frequent interactors also tend to have the greatest effect per interaction, then r_{ip} will be positive, and condition (2) will be satisfied. Condition (2) will also be

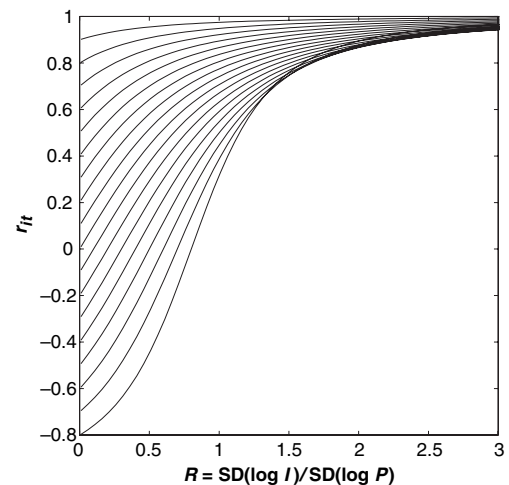


Figure 1 Pearson's correlation coefficient between log T and log I (r_{it}) as a function of R , the ratio of the standard deviations of log I and log P (see eqn 1 in main text). Lines correspond to different values of the correlation between log I and log P , as indicated by their y intercepts.

satisfied even if log interaction frequency and log per-interaction effect bear no relationship to one another ($r_{ip} = 0$), or if the most frequent interactors tend to be the least effective ($r_{ip} < 0$). In these cases, because $\log P$ will then be low for species with high $\log I$, the range of variation in $\log I$ among visitor species must be high enough to overwhelm the variability in $\log P$.

The correlation between log interaction frequency and log total effect as predicted by (1) is illustrated for different values of R and r_{ip} in Fig. 1. Interaction frequency will always be a good predictor of total effect if the correlation between interaction frequency and per-interaction effect is strongly positive, but if r_{ip} is zero or negative, interaction frequency will be highly correlated with total effect only if it varies sufficiently more than does per-interaction effect.

META-ANALYSIS

Data and measurement of interaction effects

We compiled a database with studies on animal pollination and seed dispersal available in the literature (Appendices 2 and 3). The studies we used included estimates of both interaction frequency and per-interaction effect. Because our analysis is based on published data, our definition of per-interaction effect of an animal mutualist on plants is to some extent limited by the definitions used in the original studies.

In the case of pollination, we considered studies that measured per-interaction effect P as the 'effectiveness' of different animal species as pollinators of particular plant species, usually measured in terms of the per visit contribution to the reproduction of the plant. Such contribution was quantified in terms of pollen deposition, pollinia removal (for some asclepiads), or fruit or seed set. Although this definition of effectiveness is undoubtedly a simplification (for example, it does not take into account the proportion of cross vs. self-pollen deposited on stigmas, or the viability of seeds produced by different pollinator species), it is useful as an approximation. In turn, frequency of interaction I was measured as the number of flowers visited by individuals of a pollinator species visiting a focal plant during a timed observation period. Finally, total effect was calculated by multiplying interaction frequency by per-interaction effect, i.e. $T = IP$.

In seed dispersal studies, we considered studies that measured per-interaction effect as the number of seeds or fruits removed per visit to the plant. Ideally, however, per-interaction effect should include not only the number of seeds and fruits removed but also the fate of seeds once the disperser leaves the mother plant, including the quality of the treatment the disperser gives to the seeds (e.g. whether seeds are destroyed when passing through the digestive tract

and whether such passage enhances germination) and the quality of deposition (related to the movement and deposition patterns of the disperser; Schupp 1993). This information was not available for most studies, and thus we were unable to include it in our analysis. Therefore, our measure of per-interaction effect for seed dispersal studies estimates only the number of seeds successfully dispersed away from the mother plants and is in this sense more restricted than the one used for pollination. Frequency of interaction was measured as the number of visits by individual frugivores recorded during observations at focal trees during timed observation periods. As before, total effect was calculated as the product of interaction frequency and per-interaction effect.

Statistical methods

We conducted a meta-analysis to evaluate the overall correlation between interaction frequency and per-interaction effect and between interaction frequency and total effect. Meta-analysis is a set of statistical methods that allow the quantitative integration of results from multiple individual studies (Rosenthal 1991; Arnqvist & Wooster 1995; Gurevitch *et al.* 2001). By defining a standardized measure of effect size, it is possible to gain insights about the generality of the outcome of studies. We used the normalized (ζ -transformed) Pearson's correlation coefficient (r) between $\log I$ and $\log P$ and between $\log I$ and $\log IP$ as measures of effect size. To this end, correlation coefficients were first normalized by applying Fisher's ζ transform, $\zeta = 0.5 \ln [(1 + r)/(1 - r)]$ (Zar 1999), and then weighted by multiplying them by the inverse of the sampling variance, $w = 1/\text{var}(r) = N - 3$ (Rosenthal 1991; Zar 1999; Gurevitch *et al.* 2001). The weighted mean of ζ (an estimator of true effect size) is thus defined as, $\bar{\zeta}_w = \sum w_i \zeta_i / \sum w_i$, thus giving individual ζ values with small variances greater weights than those with greater variances. We used a bootstrap resampling procedure written in Matlab (MathWorks 1999) to calculate the mean and 95% percentile confidence limits of $\bar{\zeta}_w$ (Manly 1997), with a bootstrap sample size of 10 000. When I or P contained zeros we added the smallest non-zero value to each element of the I or P vector before transforming into proportions and applying the natural logarithm. This situation occurred in a small number of data sets (seven pollination and two seed dispersal data sets for P ; one pollination and no seed dispersal data sets for I), and thus it is unlikely to affect our results significantly. We also conducted analyses using Spearman's rank correlation coefficient, for which zeros are not problematic; results were similar to those obtained with Pearson's coefficient. Therefore, we report results using Pearson's coefficient to facilitate comparing results of the meta-analysis with our mathematical framework, which was based on Pearson's coefficient.

RESULTS

Both for pollination and for seed dispersal there was no general relationship between per-interaction effect of animal mutualists on plants and their visitation frequency (see Fig. 2, for examples). Effect sizes showed a substantial spread, had both positive and negative values and their confidence interval overlapped zero [pollination: back-transformed $\bar{r}_{ip} = 0.17$, 95% confidence interval (-0.30, 0.48), range (-1.00, 0.98); seed dispersal: back-transformed $\bar{r}_{ip} = 0.16$, 95% confidence interval (-0.03, 0.39), range (-0.38, 1.00)]. This result confirms findings of previous studies suggesting that the most abundant animal mutualists are not necessarily the most effective ones on a per visit basis (e.g. Schemske & Horvitz 1984; Herrera 1987, 1989; Schupp 1993).

In contrast, there was a general positive correlation between total effect and interaction frequency (see Fig. 2 for examples). The estimated effect size (weighted average of the correlation coefficient) was substantially high, both for pollination [back-transformed $\bar{r}_{it} = 0.90$, 95% confidence interval (0.82, 0.95), range (0.35, 1.00)] and seed dispersal [back-transformed $\bar{r}_{it} = 0.89$, 95% confidence interval (0.81, 0.94), range (0.27, 1.00)]. Therefore, frequent animal mutualists tend to contribute the most to pollination or seed dispersal even if they are not very effective at the per-interaction level. Furthermore, the most abundant animal

mutualist tends to account for a disproportionately large fraction of the total benefit obtained by the plant. On average, the most frequent flower visitor accounted for 52% of the total pollination service [SD = 0.25, range = (0.09, 0.99)]. Similarly, the most frequent frugivore accounted on average for 42% of seed dispersal service [SD = 0.23, range = (0.02, 0.94)].

Plotting r_{it} as a function of both r_{ip} and $R = \text{SD}(\log I) / \text{SD}(\log P)$ makes clear why r_{it} is generally strong and positive: only a restricted combination of values of r_{ip} and R can result in correlations between I and IP that are either close to zero or negative, and most data sets fall outside this region of the parameter space (Fig. 3).

DISCUSSION

Our analysis suggests that the total effect of animal mutualists is strongly, positively related to their visitation frequency to plants. For both pollination and seed dispersal, studies conducted on a diverse set of plant species and using a variety of methodologies provide similar answers. This positive relationship between interaction frequency and total effect occurs in spite of no general relationship between interaction frequency and per-interaction effect. Differences in per-interaction effects among animal mutualists are generally overridden by differences in their interaction frequencies, and highly

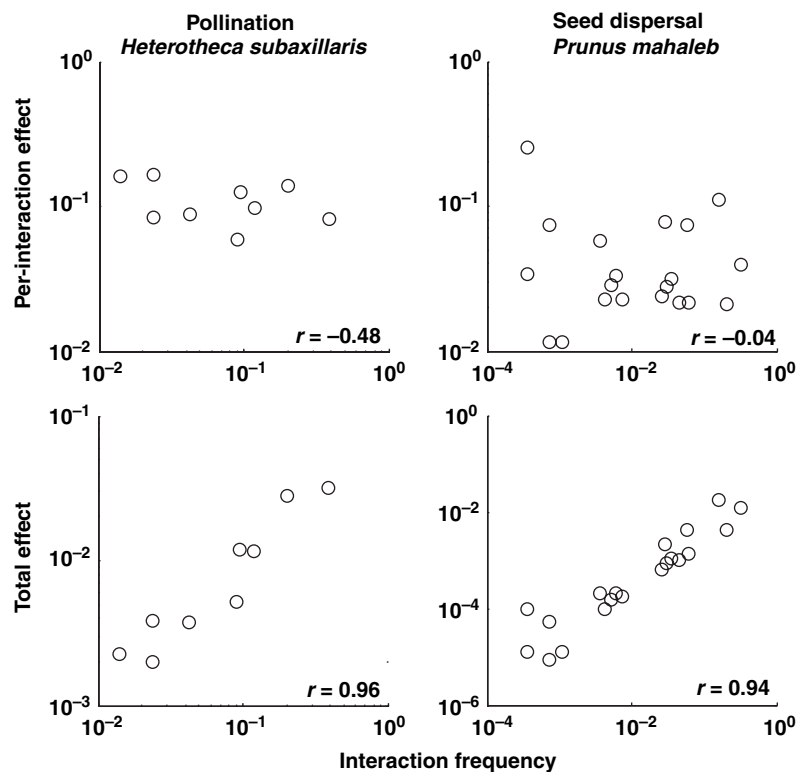


Figure 2 Examples of the relationships between interaction frequency and per-interaction effect (upper panels) and between interaction frequency and total effect (lower panels) among species of pollinators of *Heterotheca subaxillaris* (left column) and seed dispersers of *Prunus mahaleb* (right column). Both interaction frequency I and per-interaction effect P are given in relative terms (i.e. values for each species divided by the sum of I or P for all species). Pollination data from Olsen (1997); seed dispersal data from Jordano & Schupp (2000).

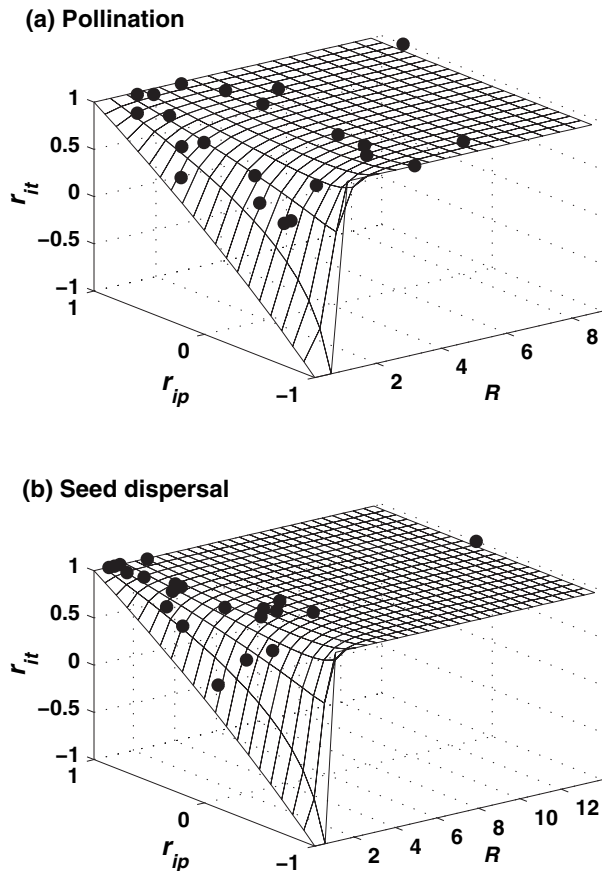


Figure 3 Pearson's correlation coefficient between the logarithms of interaction frequency and total effect, r_{it} , obtained in meta-analysis for (a) pollination; and (b) seed dispersal. Black circles are correlation coefficients calculated for data; plane represents parameter space of r_{it} as a function of r_{ip} and $R = SD(\log I)/SD(\log P)$.

frequent animal mutualists usually contribute disproportionately to the plant's reproductive success, even if their effectiveness is relatively low.

What causes interaction frequency to be a good predictor of total effect? As shown by eqn 1, interaction frequency I will be a good surrogate for total effect T if the ratio of the variation of I to the variation of per-interaction effect P is large, especially when the correlation between I and P is low. In the data sets included in our study, the ratio between the variation of I and P was always high enough to make the correlation between I and T substantially positive. This result makes sense in light of the biology of these mutualistic interactions, which we hypothesize may impose narrower bounds to P than to I . Interaction frequency is likely to be partly determined by species abundance, so that abundant animal species tend to interact more frequently than rare species (Jordano 1987; Dupont *et al.* 2003; Vázquez & Aizen

2005). The range of variation in species abundance, and hence interaction frequency, can indeed be extremely broad, from a handful of individuals to an upper limit imposed by the carrying capacity of the system. Conversely, per-interaction effect is jointly determined by the match between plant and animal phenotypic traits, including floral or fruit morphology and physiology (e.g. nectar production) and animal morphology and foraging behaviour. Therefore, variation in per-interaction effect should be limited not only by the independent phenotypic variation in animals and plants, but also by the possible combinations of phenotypes that make it possible for the interaction to actually occur. Thus, the animals that interact with the focal plant will be a subset of all potential animal mutualists, which will impose a constraint on the variation of per-interaction effect, but no constraint on the variation of interaction frequency.

Although we have focused on the effects of animal mutualists on plants, our conceptual elaboration can in principle apply to any kind of interaction. For example, the discussion could be extended to predator-prey interactions, in which the effect of prey populations on predators might be reflected in frequency of prey in the diet. Thus, we could ask whether frequency of consumption of each prey species is more important to the predator than energy per prey individual consumed. In spite of these parallels, there are important differences when the reciprocal effect of predators on prey is considered. In the context of predator-prey interactions, a successful attack by a predator leads to a mortality event (i.e. to a direct change in prey population size). Hence one can define the per capita effect of an individual predator on the density of a prey population. This extrapolation is not so straightforward in the context of plant-animal mutualisms, because each plant and animal individual can (and usually does) have multiple interactions. Furthermore, our 'total effect' is a measure of the effect of a population of an animal mutualist on the per capita reproductive or seed dispersal success of an individual plant (i.e. it is the total effect of a population on an individual). But, as pointed out above, to convert our 'total effect' to an effect on plant population density we would have to know to what extent seed production or dispersal influence population density, an influence that cannot be taken for granted.

Our results should be interpreted with caution, for several reasons. First, data used in our meta-analysis are mostly restricted to the immediate consequences of pollen deposited or seeds removed from trees per visit, but the per-interaction effect may have additional components (e.g. fraction of outcross pollen, germination rate of defecated seeds, etc.). Second, our analysis assumes that all visitors have non-negative effects. However, if visitors with negative effects exist (e.g. nectar robbers, pre-dispersal seed predators), their interaction frequency could be negatively

correlated with population-level effects. Third, our study is limited to the plant perspective, and we do not know if the same pattern will occur, for instance, in the case of plant nutritional effects on their animal mutualists (although, as we argued above, our reasoning applies to any kind of interaction). Fourth, the product of interaction frequency and per-interaction effect may not be a good measure of total effect if plant reproductive performance does not scale linearly with this product (as assumed in our analysis). For example, reproductive performance cannot increase indefinitely as mutualist visitation rate increases, due either to resource limitation of fruit and seed set (Ashman *et al.* 2004) or to saturation of stigmas with pollen grains and tubes (Cane & Schiffhauer 2003). Likewise, although we are assuming that per-interaction effect is invariant, it could in fact be a declining function of interaction frequency, which could result in a saturating or hump-shaped relationship between T and I (cf. Holland *et al.* 2002). This situation could occur, for instance, when an extremely frequent pollinator removes pollen previously deposited in stigmas by other pollinators without replacing it by new pollen, as has been observed for honeybees visiting grapefruit flowers in northwestern Argentina (V. Aschero and N.P. Chacoff, personal communication).

In spite of these caveats, our analysis provides a working alternative for obtaining quantitative estimates of the relative strength of interactions in studies of large assemblages of interacting species, for which experimentally measuring pairwise interaction strength for all pairs of interacting species may not be feasible. In these cases, our results suggest that interaction frequency may be a reasonable surrogate of interaction strength and the resulting estimate of dependence of a plant on its animal mutualists.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

Appendix S1 Derivation of correlation between interaction frequency and total effect in terms of interaction frequency and per-interaction effect.

Appendix S2 Pollination data sets used for the study.

Appendix S3 Seed dispersal data sets used for the study.

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