

## Supporting Information Text

**Derivation of the community average storage effect.** Here we present the theory for the storage effect given in the text. We derive formulae for the community average storage effect, which indicates how strongly the storage effect promotes coexistence in terms of how much it increases long-term low-density growth rates, on average(1). This approach is appropriate for quantifying coexistence because coexistence is a community-level property. In the next section (*Quantification of the magnitude of the storage effect*), these results are applied to the data from this system. Readers interested primarily in the application can go immediately to that section, which is self-contained.

The model we use is the seed bank model of Chesson et al.(2) applied in a temporal context, modified for lottery competition. Key quantities in that model are the fraction of seeds of species  $j$  germinating in year  $t$ ,  $G_j(t)$ , the survival and the growth of the germinating seedlings (vigor),  $V_j(t)$ , the yield of new seeds per unit plant biomass,  $Y_j$ , the competition,  $C'(t)$ , experienced by the growing plants, and finally, the survival,  $s_j$ , of seeds that remain dormant in the seed bank. The model can now be written

$$N_j(t+1) = s_j(1 - G_j(t))N_j(t) + \frac{Y_j V_j(t) G_j(t) N_j(t)}{C'(t)} \quad (1)$$

Thus, the density of the seeds of species  $j$  in the seed bank,  $N_j(t+1)$ , at the beginning of year  $t + 1$  is equal to the sum of the seeds that persist in the seed bank,  $s_j(1 - G_j(t))N_j(t)$ , plus production of new seed, which is the second term in equation (1). New seed production requires germination,  $G$ , survival and growth,  $V$ , but is of course limited by competition.

Competition,  $C'(t)$ , needs to be defined to represent how much growth is restricted by the demands placed on resources. Under lottery competition, each individual receives resources in proportion to its ability to extract them, which is assumed here to be proportional to the vigor of its growth. Assuming that the resources are limited, and are all used by these species, each individual is limited in its growth by the total ability (per unit area) of all seedlings of all species to extract those resources. This means that the resources received by an individual are proportional to  $V_j(t)/C'(t)$ , with  $C'(t)$  defined as the sum over species of the total density of seedlings weighted by the vigor of their growth:

$$C'(t) = \sum_{l=1}^n V_l(t)G_l(t)N_l(t).$$

The quantity  $V_j(t)G_j(t)N_j(t)/C'(t)$  is assumed to be the biomass of growing plants of species  $j$ . Multiplying by  $Y_j$  converts this biomass into the number of new seeds of species  $j$  produced per unit area.

Vigor,  $V_j(t)$ , deserves special mention. It is not the actual average mass of a plant, but the final mass of a plant at flowering when  $C'(t)$  is fixed at the minimal value of 1. It is intended as a measure of how strongly the physical environment in year  $t$  promotes survival and growth of the plants, and therefore how much demand they place on resources — hence their role in  $C'(t)$ . Vigor is not directly observable in nature. Only the actual average mass,  $V_j(t)/C'(t)$ , is observable. However, in equation (1) only the ratios of vigor for different species are needed, and these are observable. The particular observable related to vigor that is measured in this study is per germinant fecundity, here equal to  $Y_jV_j(t)/C'(t)$ . The time by species interaction of  $\ln$  per germinant fecundity, which features in our analysis, is exactly equal to the time by species interaction of  $\ln$  vigor, as discussed below.

To analyze the model, we focus on the growth rate,  $r_j(t)$ , which is defined as  $\ln[N_j(t+1)/N_j(t)]$ , i.e. the log of the finite rate of increase. For the model (1), this growth rate is

$$r_j(t) = \ln \left\{ s_j (1 - G_j(t)) + Y_j V_j(t) G_j(t) / C'(t) \right\}. \quad (2)$$

In other words, it is the natural log of the sum of per capita seed bank persistence, and per germinant fecundity. The theory of population dynamics in variable environments emphasizes that it is the sum of  $r_j(t)$  over time that determines population trajectories on the log scale (e.g. Chesson (3)), because population growth is multiplicative, and becomes additive on a log scale. Note also that key components of the model are multiplicative, under the assumption that nature works multiplicatively. In particular, per germinant fecundity equals  $Y_j V_j(t) G_j(t) / C'(t)$ , a product of four quantities. Transforming these quantities to the log scale (natural log,  $\ln$ ) converts this product into a sum. This transformation has two effects. First it greatly simplifies the formal mathematical analysis of the model following the procedures of Chesson(1, 3), and second it separates per germinant fecundity into additive terms amenable to statistical analysis by standard techniques.

To see how the storage effect coexistence mechanism arises from this model, we now formally define the environmental responses of the species. These are population parameters that vary with the physical environment in ways that differ between species, and thus separate their niches temporally. The correlations between species in their environmental responses thus need to be less than 1. There are two environmental responses in our development  $E_{G_j}(t) = \ln G_j(t)$  and  $E_{V_j}(t) = \ln V_j(t)$ , together with their combination  $E_j(t) = E_{G_j}(t) + E_{V_j}(t)$ . There is, however, but a single competitive response,  $C(t)$ , measuring the effect of competition on population growth, which is the natural log of competition,  $C'$ , defined above, i.e.

$$C(t) = \ln \left\{ \sum_i V_i(t) G_i(t) N_i(t) \right\}. \quad (3)$$

All of these responses use the log scale to facilitate the theoretical calculations and statistical analysis, as explained above.

The storage effect coexistence mechanism arises from the interactions between competitive response and the environmental responses in the way they determine  $r_j(t)$ . Fundamentally, persistence of dormant seeds in the seed bank provides a buffer against unfavorable conditions for seed production as defined by poor germination, low vigor, or high competition. This means that a species does not have to be successful every year to persist in the system. Success, however, involves the occurrence of favorable combinations of environmental and competitive conditions, which is especially important when a species has become depressed to low density and is to increase and recover from that low-density state. In the formal mathematical analysis, called invasibility analysis, such a species is called an *invader*. Other species not depressed to low density are called *residents*.

The concept of covariance between environment and competition helps us understand how an invader achieves a favorable combination of environmental and competitive conditions. Looking at the formula (3) for competition, it is quite clear that if a species does experience favorable environmental conditions, viz the combination of germination and vigor are high, then it contributes more to  $C(t)$ , which then places limitations on its own growth. However, because it is at low density, this effect is small. Of more concern is competition from other species, but if these species have environmental responses not strongly correlated with those of the invader, they will not always contribute strongly to  $C(t)$  when the invader is favoured by the environment. Mathematically, this means that the invader has low covariance between environment and

competition. In terms of population growth of an invader, it means that the invader will have times when it is favored both environmentally and competitively, and so can increase strongly.

It is important that these same opportunities are not as frequently available for the resident species, because then they would create levels of competition high enough to deprive the invader of an average population growth advantage. However, residents, being at higher density, do limit their own growth by competition when favored by the physical environment. The higher demands they place on resources do add up to important increases in competition. This means residents have strong positive covariance between environment and competition, leaving invaders at an average advantage. The storage effect thus depends on invader-resident differences in covariance between environment and competition (which provide opportunities for invader increase) and buffered population growth (which means that times of decrease cannot cancel out the long-term effects of strong periods of growth). The mathematical theory of the storage effect(1, 3) makes these ideas precise and quantitative. We show now how this theory is applied to the model in this paper.

Previous theory has considered just a single environmental response, and so needs to be extended to consider the interaction between competition and both environmental responses in the sense of how they jointly contribute to the growth rate  $r_j$ . These considerations lead to two distinct storage-effect contributions to coexistence. Although it has no effect on the final result, we analyze the model using the two environmental responses  $E_{Gj}(t)$  and  $E_j(t)$ . Any two of three above would give the same outcome. Some developments of the storage effect standardize the environmental responses before analysis, as described in Chesson(3). For simplicity, the development here is in terms of the original environmental and competitive responses, defined

above, rather than in terms of the more formal procedure standardizing these responses(3). These two approaches are equivalent, given appropriate care(4).

The development begins with a quadratic approximation of  $r_j$  in  $G_j$ ,  $V_j$ , and  $C^*$  about equilibrium values,  $G_j^*$ ,  $V_j^*$  and  $C^*$ , for which  $r_j = 0$ . We find below that we need to specify only one of these equilibrium values, viz  $G_j^*$ , which is set at the species and time average germination fraction. The others play no role in the final result. We need also the important quantity  $\beta_j = 1 - s_j(1 - G_j^*)$  which is the equilibrium probability that a seed leaves the seed bank (“the seed loss rate”). Note that  $\beta_j$  is equal to  $-\partial r_j / \partial C$  evaluated at the equilibrium parameter values. Next we need the interaction terms,

$$\gamma_j = \frac{\partial^2 r_j}{\partial E_j \partial C} = -\beta_j(1 - \beta_j), \quad (4)$$

and

$$\gamma_{G_j} = \frac{\partial^2 r_j}{\partial E_{G_j} \partial C} = -s_j G_j^* \beta_j, \quad (5)$$

both evaluated at the equilibrium values. These quantities define the extent to which population growth is buffered against unfavorable environmental conditions. Large negative values mean strong buffering.

We can now proceed to use these quantities to calculate the community average storage effect(1, 5). The community average storage effect indicates how strongly the storage effect promotes coexistence in terms of its average effect on increasing long-term low-density growth rates,  $\bar{r}_i$  (1). These are the average of  $r_i(t)$  over time for a species  $i$  in the invader state, and define

how strongly species  $i$  recovers from low density. A positive value of  $\bar{r}_i$  means that the species recovers in the long run, and remains in the community.

Here the community average storage effect has two components, one for each environmental response. We first calculate this component for the response  $E_j$ . From Chesson(5), the community average storage effect is

$$\bar{\Delta I} = \frac{1}{n} \sum_{j=1}^n \frac{\gamma_j}{\beta_j} \left( \chi_j^{\{-j\}} - \overline{\chi_j^{\{-i\}}^{i \neq j}} \right). \quad (6)$$

In this expression  $\chi_j = \text{cov}(E_j, C)$  (covariance between environment and competition), taken over time. The superscript  $\{-l\}$  indicates that this measurement is taken for species  $l$  (either  $i$  or  $j$  in (6)) in the invader state, as discussed in Chesson(1, 5). The bar with  $\{i \neq j\}$  indicates the average over all  $i$  except  $j$ .

These covariances are now approximated using the techniques in Chesson(3), which maintain accuracy so that errors are of a smaller order of magnitude than the storage effect terms being approximated, provided the variances of the environmental responses are not too large. See Chesson(3) for details. The competitive response is approximated linearly in the form

$$\tilde{C} = \sum_{u \neq i} A_u^{\{-i\}} \tilde{E}_u + b. \quad (7)$$

Here  $\sim$  indicates that the equilibrium value has been subtracted from the response. The quantities  $A_u^{\{-i\}}$  and  $b$  are random variables independent of the  $\tilde{E}_u$ . Defining  $a_u^{\{-i\}} = E[A_u^{\{-i\}}]$ , where  $E[\dots]$  means expected value taken according to the probability distribution over time (a time average), and  $\chi_{ij} = \text{cov}(E_i, E_j)$ , we see that

$$\chi_j^{\{-i\}} = \sum_{u \neq i} a_u^{\{-i\}} \chi_{ju} . \quad (8)$$

Now Chesson(3) appendix VI shows that  $a_u^{\{-i\}}$  is equal to the expected fraction of the seedling biomass attributed to species  $u$  when species  $i$  is in the invasion state. It follows that  $\chi_j^{\{-i\}}$  is a weighted average of the  $\chi_{ju}$  and can be approximated by the simple average

$$\chi_j^{\{-i\}} = \bar{\chi}_{ju}^{\{u \neq i\}} , \quad (9)$$

with error term equal to the covariance over resident species,

$$\varepsilon_j^{\{-i\}} = \text{cov}_{\{u \neq i\}} \left( (n-1)a_u^{\{-i\}} , \chi_{ju} \right) . \quad (10)$$

This error cannot be large except in the unlikely event of strong average dominance correlated with the environmental covariances.

Based on equation (9), the community average storage effect is approximated by

$$\frac{1}{n} \sum_{j=1}^n \frac{\gamma_j}{\beta_j} \left( \bar{\chi}_{ju}^{\{u \neq j\}} - \overline{\bar{\chi}_{ju}^{\{u \neq i\}}^{\{i \neq j\}}} \right) , \quad (11)$$

which simplifies to

$$\frac{1}{n} \sum_{j=1}^n \frac{\gamma_j}{\beta_j} \left( \frac{\bar{\chi}_{ji}^{\{i \neq j\}} - \chi_{jj}}{n-1} \right) . \quad (12)$$

This result leads to the approximation

$$\bar{\Delta I} \approx \frac{\overline{(\gamma / \beta)}}{n-1} \sum_{j=1}^n \left( \frac{\bar{\chi}_{ji}^{\{i \neq j\}} - \chi_{jj}}{n} \right) \quad (13)$$



with error term again a covariance over species and equal to

$$\delta = \text{cov}_j \left( \frac{\gamma_j}{\beta_j}, \frac{\bar{\chi}_{ji}^{(i \neq j)} - \chi_{ji}}{n-1} \right), \quad (14)$$

which is likely to be dominated by expression (13) in most circumstances. Moreover, the data on the species studied here do not show statistically differences in  $\gamma_j/\beta_j$ . Hence, it is expression (13) that we use for the community average storage effect.

The quantity  $\bar{\chi}_{ji}^{(i \neq j)} - \chi_{ji}$  can be written as

$$-\frac{n}{n-1} E \left[ (E_j - E[E_j]) (E_j - E[E_j] - \bar{E} + E[\bar{E}]) \right] \quad (15)$$

where  $\bar{E}$  is the average of  $E_j$  over  $j$ , and all expected values are taken over time (each  $E_j$  is a function of time). Because the sum over  $j$  of  $(E_j - E[E_j] - \bar{E} + E[\bar{E}])$  is zero, the average over  $j$  of (15) is equal to

$$\begin{aligned} & -\frac{1}{n-1} \sum_{j=1}^n E \left[ (E_j - E[E_j] - \bar{E} + E[\bar{E}]) (E_j - E[E_j] - \bar{E} + E[\bar{E}]) \right] \\ & = -\frac{1}{n-1} \sum_{j=1}^n E \left[ (E_j - E[E_j] - \bar{E} + E[\bar{E}])^2 \right], \end{aligned} \quad (16)$$

which is the negative of the theoretical time by species variance,  $\sigma_{txs}^2$ , combining germination and vigor. Thus, the community average storage effect for germination and vigor combined is approximated as

$$\bar{\Delta I} \approx \frac{(-\gamma/\beta)\sigma_{txs}^2}{n-1} = \frac{(1-\bar{\beta})\sigma_{txs}^2}{n-1} \quad (17)$$

The community average storage effect component for germination separately follows identically, but with  $\chi_{ij} = \text{cov}(E_{Gi}, E_j)$ . At the final stage, expression (16) is replaced by

$$-\frac{1}{n-1} \sum_{j=1}^n E \left[ \left( E_{Gj} - E[E_{Gj}] - \bar{E}_G + E[\bar{E}_G] \right) \left( E_j - E[E_j] - \bar{E} + E[\bar{E}] \right) \right]$$

which is the negative of the time by species covariance between germination and its combination with vigor on the log scale, designated  $\chi_{G,GV,txs}$ . Thus, this storage effect component is

$$\bar{\Delta I} \approx \frac{\overline{sG} \chi_{G,GV,txs}}{n-1}. \quad (18)$$

(Note that the subscripts  $G$ ,  $V$  and  $GV$  here are short hand for  $E_G$ ,  $E_V$  and  $E = E_G + E_V = \ln(GV)$ , here and below. This should cause no confusion as the analysis is on the log scale throughout.)

#### *Partitioning of the storage effect into functional components*

The time by species variance,  $\sigma_{txs}^2$ , splits into three components.

$$\sigma_{txs}^2 = \sigma_{G,txs}^2 + 2\chi_{G,V,txs} + \sigma_{V,txs}^2 \quad (19)$$

corresponding to the time by species variance in  $\ln$  germination fraction, twice the time by species covariance between  $\ln$  germination fraction and  $\ln$  vigor, plus the time by species variance in  $\ln$  vigor. Similarly, the covariance  $\chi_{G,GV,txs}$  splits into two components

$$\chi_{G,GV,txs} = \sigma_{G,txs}^2 + \chi_{G,V,txs}. \quad (20)$$

We can use these decompositions to rearrange the storage-effect contributions into

$$\overline{\Delta I}_G \approx \frac{s\sigma_{G,t \times s}^2}{n-1}, \quad (21)$$

due to variance in ln germination fraction alone,

$$\overline{\Delta I}_{G,V} \approx \frac{\bar{s}(2-\bar{G})\chi_{G,V,t \times s}}{n-1}, \quad (22)$$

due to the covariance between ln germination fraction and ln vigor (equivalently ln per germinant fecundity), and

$$\overline{\Delta I}_V \approx \frac{(1-\bar{\beta})\sigma_{V,t \times s}^2}{n-1} \quad (23)$$

due to the variance in ln vigor.

As mentioned above, the data *analysis* uses per germinant fecundity, not vigor. However  $\ln(\text{per germinant fecundity}) = \ln V_j(t) + \ln Y_j$ . The fact that  $Y_j$  does not depend on time means that it disappears from the time by species interaction for ln per germinant fecundity, leaving only ln vigor. Hence the per germinant fecundity can be substituted for vigor in the above expressions without changing the result.

Each of the quantities above represents an increase in the average over species (average over  $i$ ) of the long-term low-density growth rate,  $\bar{r}_i$ , of the species in the system due to that particular variance or covariance component, measured with time unit,  $1/\beta$ , which is the average time for the loss of a seed from the seed bank. This measurement is on the *natural timescale*(5) of seed generations, which is the most appropriate timescale for comparing organisms with

different life-histories. To convert these to contributions to per year rates, they are each multiplied by  $\bar{\beta}$ .

*Time by species interactions and correlation coefficients*

From the derivation of the community average storage effect, we know that the time by species interaction variance is equal to

$$\frac{1}{n} \sum_{j=1}^n (\chi_{jj} - \bar{\chi}_{ji}^{(i \neq j)}). \quad (24)$$

Now  $\chi_{jj} = \sigma_j^2$ , the variance of  $E_j(t)$  over time, and  $\chi_{ji} = \rho_{ji} \sigma_j \sigma_i$ , where  $\rho_{ji}$  is the temporal correlation between  $E_j(t)$  and  $E_i(t)$ . Therefore, equation (24) becomes

$$\overline{\sigma^2} - \bar{\rho} \left\{ \frac{1}{n(n-1)} \sum_{i \neq j} \sigma_i \sigma_j \right\}, \quad (25)$$

where  $\overline{\sigma^2}$  is the species average variance, and  $\bar{\rho}$  is the weighted average correlation,

$$\bar{\rho} = \sum_{i \neq j} \rho_{ij} \sigma_i \sigma_j / \sum_{i \neq j} \sigma_i \sigma_j. \quad (26)$$

A little algebra shows that

$$\frac{1}{n(n-1)} \sum_{i \neq j} \sigma_i \sigma_j = \overline{\sigma^2} - \frac{1}{n-1} \sum_j (\sigma_j - \bar{\sigma})^2, \quad (27)$$

so that the time by species covariance reduces to

$$\overline{\sigma^2} (1 - \bar{\rho}) + \frac{\bar{\rho}}{n-1} \sum_j (\sigma_j - \bar{\sigma})^2. \quad (28)$$

The key term here is,

$$\overline{\sigma^2} (1 - \bar{\rho}). \tag{29}$$

Added to this is the average correlation times the variance over species in the temporal standard deviation. If these standard deviations are similar, i.e. the species are about equally sensitive to environmental variation, on average, then expression (29) defines the time by species interaction. Expression (29) provides an intuitive understanding of the time by species interaction. It represents the time by species interaction as that part of the average variance that is independent between species, partitioning out the common fraction of variance,  $\bar{\rho}$ , leaving the fraction that is unique to a species,  $1 - \bar{\rho}$ . This partitioning is the essence of equation (24), but the precise form of the partitioning of variance is slightly different when different species have different variances, leading to the correction term that is added in equation (28). As the calculations here use the time by species interaction directly, they include this correction term. However, the approximation (29) provides the intuition behind this concept in the section on the workup of the empirical data.

**Quantification of the magnitude of the storage effect.** In the first scenario described in the main text, species coexistence is promoted if a set of species produce persistent seed banks with variable germination fractions that are not completely correlated(6). A second scenario involves temporal variation in the vegetative phase (i.e., post-germination growth and reproduction) of the life cycle. Here we partition the storage effect into these two mechanisms and their covariance. The formulae for magnitude of the storage effect, and its division into these three components,

are derived above (see *Derivation of the community average storage effect*) using the technique of quadratic approximation of Chesson 1994(3) and the community average approach of Chesson 2003(1). As mentioned above, the community average approach for quantifying coexistence is appropriate because coexistence is a community-level property. The component measures for the community average storage effect indicate how much the low density growth rates of the species are increased, on average, by the mechanism in question. These results are given on the per generation time scale, which is the reciprocal of the rate,  $\beta$ , at which seeds are lost from the seed bank. They are thus the amounts by which  $\bar{r} / \beta$  is increased on average. To convert these to per year rates, i.e. to  $\bar{r}$ , one just multiplies by  $\beta$ , which here has the average value of 0.77.

The storage effect component for germination is

$$\overline{\Delta I}_G \approx \frac{\bar{s} \sigma_{G,t \times s}^2}{n-1} \quad (30)$$

where  $\overline{\Delta I}_G$  is the symbol for this component of the community average storage effect,  $\bar{s}$  is the average survival rate of ungerminated seeds in the seed bank,  $\sigma_{G,t \times s}^2$  is the time by species interaction variance component for ln germination fraction, and  $n$  is the number of species. A more intuitive formula is given in terms of the average temporal correlation between species,  $\bar{\rho}_G$ , and average temporal variance,  $\overline{\sigma_G^2}$ , in ln germination fraction:

$$\overline{\Delta I}_G \approx \frac{\bar{s} \overline{\sigma_G^2} (1 - \bar{\rho}_G)}{n-1} \quad (31)$$

which is valid whenever the temporal variances do not vary too greatly between species, as derived above. **The quantity  $\overline{\sigma_G^2} (1 - \bar{\rho}_G)$  is an approximation to  $\sigma_{G,t \times s}^2$ , which shows that it and**

*the storage effect are driven by low correlations between species on average, and high variance over time.*

The contribution of per germinant fecundity to the storage effect is

$$\overline{\Delta I_V} \approx \frac{(1 - \bar{\beta}) \sigma_{V,t \times s}^2}{n - 1} \quad (32)$$

where  $\sigma_{V,t \times s}^2$  is the species by time interaction component of variance for ln per germinant fecundity,  $\ln(lb)$ , and  $1 - \bar{\beta}$  is the average probability that a seed in the seed bank neither germinates nor dies in a given year. Like ln germination fraction, this formula can be approximated by the more intuitive formula,

$$\overline{\Delta I_V} \approx \frac{(1 - \bar{\beta}) \overline{\sigma_V^2} (1 - \bar{\rho}_V)}{n - 1}. \quad (33)$$

A third contribution to the storage effect is due to the species by time interaction for the covariance of log germination fraction and log per germinant fecundity:

$$\overline{\Delta I_{G,V}} \approx \frac{\bar{s} (2 - \bar{G}) \chi_{G,V,t \times s}}{n - 1} \quad (34)$$

where  $\chi_{G,V,t \times s}$  is the time by species covariance component for ln germination and ln per germinant fecundity, and  $\bar{G}$  is the average germination fraction, taken over all species. A more interpretable approximation in terms of average covariances and correlations analogous to (31) and (32) above is available here too.

Sixteen years of long-term data on germination fraction(7) and the corresponding sixteen years of demographic data described in the **Materials and Methods** were used to calculate values of these parameters (Table S1). The species x time interaction was highly significant for ln-transformed germination, per germinant reproduction and their covariance ( $P < 2.8 \text{ E-}21$ ,  $P < 5 \text{ E-}06$ ,  $P < 2.7 \text{ E-}10$ ). The low-density population growth advantage due to germination variation is calculated to be  $\overline{\Delta I}_G = 0.067$ . This means that the storage effect contributed by this germination mechanism boosts the  $\bar{r} / \beta$  value by 6.7% per generation or boosts  $\bar{r}$  by 5.2%, in essence multiplying the finite rate of increase by 1.052. The low-density advantage due to reproductive variation is  $\overline{\Delta I}_V = 0.032$  (Table S2). The low-density advantage due to covariation of germination and reproduction is an additional  $\overline{\Delta I}_{G,V} = 0.035$ , making the total direct and indirect contribution of species by year interaction for reproduction equal to  $\overline{\Delta I} = 0.133$ , which means a substantial boost to growth equal to a 10.3% population growth rate advantage for species at low density.



## References

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