Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance

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The mutualistic interactions between plants and their pollinators or seed dispersers have played a major role in the maintenance of Earth's biodiversity. To investigate how coevolutionary interactions are shaped within species-rich communities, we characterized the architecture of an array of quantitative, mutualistic networks spanning a broad geographic range. These coevolutionary networks are highly asymmetric, so that if a plant species depends strongly on an animal species, the animal depends weakly on the plant. By using a simple dynamical model, we showed that asymmetries inherent in coevolutionary networks may enhance long-term coexistence and facilitate biodiversity maintenance.

It is widely acknowledged that mutualistic interactions have molded biodiversity (1, 2). In the past decade, much has been learned about how communities shape coevolutionary interactions across time and space (3). However, although most studies on coevolution focus on pairs or small groups of species, recent work has highlighted the need to understand how broader networks of species coevolve (4–7). Such knowledge is critical to understanding the persistence and coevolution of highly diverse plant-animal assemblages.

Recent research on the architecture of plant-animal mutualistic networks has been based mostly on qualitative data, assuming that all realized interactions are equally important (Fig. 1A) (5–7). This has precluded a deeper assessment of network structure (8) and strongly limited our understanding of its dynamic implications. To understand how mutualistic networks are organized and how such an organization affects species coexistence, we compiled from published studies and our own work 19 plant-pollinator and 7 plant-frugivore quantitative networks (Fig. 1 and Database S1). These networks range from arctic to tropical ecosystems and illustrate diverse ecological and biogeographical settings. Each network displays information on the mutual dependence or strength between each plant and animal species, mainly measured as the relative frequency of visits (9). Thus, our networks describe ecological interactions, and evolutionary inferences should be made with caution. However, frequency of visits has been shown to be a surrogate for per capita reproductive performance (10). Our results could be more directly related to coevolution when the reproductive success of one species depends directly on visitation frequency. This seems to be the case when there is a high variation of dependences among species (10). Unlike previous studies on food webs

(11–16), for each plant-animal species pair, we have now two estimates of mutual dependence (defined in two adjacency matrices P and A): the dependence d_{ij}^P of plant species i on animal species j (i.e., the fraction of all animal visits coming from this particular animal species) and the dependence d_{ji}^A of animal species j on plant species i (i.e., the fraction of all visits by this animal species going to this particular plant species) (Fig. 1, B and C). Therefore, one can calculate an index of asymmetry for each pairwise interaction (17), depicting the relative dissimilarity between the two mutual dependences (Fig. 1, B and C).

Regardless of the type of mutualism, the frequency distribution of dependences is right-skewed, mostly with weak dependences and a few strong ones (Fig. 2). This is in agreement with previous work on ecological networks (9, 11–16). This heterogeneous distribution is highly significant and cannot be predicted on the basis of an independent association between plants and animals. On the contrary, the distribution of animal visits is highly dependent on plant species ($P < 0.00001$, G-test in all nine communities in which the test can be performed). To illustrate the effect of such weak dependences on community coexistence, we used a mutualistic model (18–21). For the simplest case, there is a positive community steady state (community coexistence) if the following inequality holds (21)

$$\alpha\beta < \frac{ST}{mn}$$

where α and β are the average per capita effects of the animals on the plants, and of the plants on the animals, respectively. Hereafter, such per capita effects are estimated by the mutual dependence values (21). S and T are the average intraspecific competition coefficients of plants and animals, and n and m are the number of plant and animal species, respectively.

As community size increases, the product of mutual dependences has to become smaller for the community to coexist (fig. S1). Two situations fulfill this requirement: (i) either both dependences are weak; or (ii) if one dependence

is strong, the accompanying dependence is very weak (so the product remains small). The dominance of weak dependences (Fig. 2) contributes to situation i. To assess the likelihood of scenario ii, we next look at the asymmetry of mutual dependences.

For each pair of plant species i and animal species j, we calculated the observed asymmetry of mutual dependences using (17). The frequency distribution of asymmetry values is also very skewed, with the bulk of pairwise interactions being highly asymmetric (Fig. 3). The question now is whether dependence pairs are more asymmetric than expected by chance. To answer this question, we calculated a null frequency distribution of asymmetry values to compare with the observed one by means of a χ^2 test. We achieved this by fixing the observed dependence d_{ij}^P of plant species i on animal species j and randomly choosing d_{ji}^A without replacement from the set of all dependences of the animals on the plants in this particular community. This procedure was repeated 10,000 times; the null asymmetry frequency distribution is the average of these replicates.

For pollination, only seven out of 19 communities (36.8%) showed a frequency distribution of asymmetry values that deviates significantly from the null frequency distribution (46.1% when considering only networks with at least 100 pairs). For seed dispersal, only one out of seven communities (14.3%) showed a frequency distribution of asymmetry values that deviates significantly from the null frequency distribution (20.0% when considering only networks with at least 100 pairs). These results show that in the bulk of the cases, the frequency distribution of asymmetry values originates exclusively from the skewed distribution of dependences. That is, most communities show mutual dependences that are asymmetric, but no more asymmetric than what we would expect by chance, given the distribution of dependence values.

Because strong interactions have the potential to destabilize ecological networks (16, 18, 22–24), we repeated the above calculations considering only dependence pairs in which at least one value is larger than or equal to 0.5 (other threshold values do not significantly affect our results). The fraction of large pollination networks (at least 100 pairs) with a frequency distribution of asymmetry significantly departing from expectation increased to 87.5% (seven out of eight communities). Similarly, for seed dispersal, the three largest communities ($n \geq 20$ pairs) also have frequency distributions of asymmetry values significantly departing from random (100%). Overall, these results suggest that there are constraints in the combination of strong mutual dependence values. Next, from the significant comparisons, we explored which intervals of asymmetry contribute to significance.

Asymmetry values range from 0 to 1 (Fig. 3). Within this range, some values may be over-

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represented and some underrepresented, relative to random expectation (again comparing the null frequency distribution with the observed frequency distribution by using a χ^2 probability distribution). We found that the first half of the range (low to moderate asymmetry) is significantly underrepresented ($P = 3.81 \times 10^{-6}$ for pollination and $P = 0.0156$ for seed dispersal; binomial test). This underrepresentation of low asymmetry values implies that a strong dependence value for one of the partners in the mutualistic interaction tends to be accompanied by a weak dependence value of the other partner. That is, two strong interactions tend to be avoided in a pair, which agrees with the analytic prediction (scenario ii).

Our above analysis of mutual dependences, however, is based on isolated analysis of pairwise interactions and thus provides only limited information on the complexity of the whole mutualistic network (25). For example, how does the pattern of skewed dependences and strong asymmetries scale up to account for properties at the community level? A more meaningful measure of network complexity is provided by the concept of species strength (25). The strength of an animal species, for example, is defined as the sum of dependences of the plants relying on this animal. It is a measure of the importance of this animal from the perspective of the plant set (Fig. 1, D and E). This measure is a quantitative extension of the species degree, which is the number of interactions per species in qualitative networks (5). Previous work showed that mutualistic networks are highly heterogeneous (i.e., the bulk of species have a few interactions, but a few species have many more interactions than expected by chance) (5). Next, we considered how this result stands when quantitative information is considered.

In all but one case, there is a significant positive relationship between species strength and species degree (Fig. 4). To explore deviations from linearity, we performed a quadratic regression and tested for the significance of the quadratic term. The quadratic term is significant in 35 out of the 52 cases (for each community, we looked at both plants and animals independently). This fraction increases to 24 out of 30 cases when considering only communities with at least 30 species. That is, species strength increases faster than species degree (Fig. 4), a pattern previously found for the worldwide airport network, but not for the scientific collaboration network (25). The strength of highly connected species is even higher than expected based on their degree, because specialists tend to interact exclusively with the most generalized species (6, 7) and so depend completely on them. Thus, specialists contribute disproportionately to increase the overall strength of the generalists they depend on.

Overall, previous results based on qualitative networks (i.e., their high heterogeneity in the number of links per species) (5) are confirmed

Fig. 1. A network approach to plant-animal mutualisms. (**A**) Example of a community of plants and their seed dispersers in Cazorla, SE Spain (see Database S1 for references and data sets). Green circles represent plant species and red squares represent animal species. A plant and an animal interact if there is a qualitative link between them. (**B** and **C**) Each of the above plant-animal interactions is described by two weighted links (arrows) depicting the relative dependence of the plant on the animal (green arrow) and the animal on the plant (red arrow). The asymmetry of the pairwise interaction is proportional to the difference between the thickness of both arrows. Here we show a symmetric (B) and an asymmetric (C) example. (**D** and **E**) A species degree is the number of interactions it has with the other set. Species strength is the quantitative extension of species degree, and can be defined as the sum of dependences of the animals on the plant (D) and the plants on the animal (E). Although the degree is four in both (D) and (E), the strength of the animal (E) is higher than that of the plant (D).
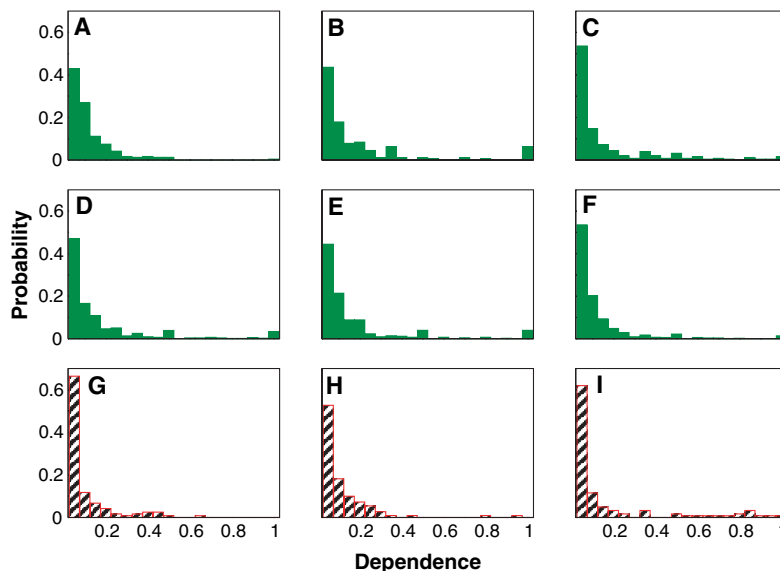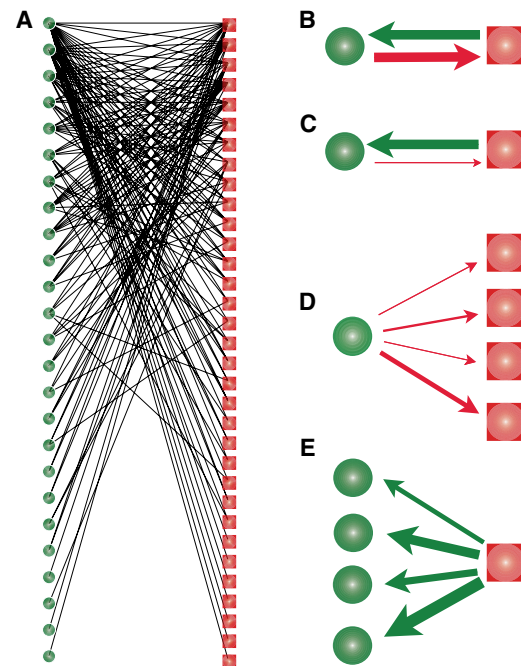

Fig. 2. Frequency distributions of dependence values within a mutualistic community. Green solid histograms (**A** to **F**) represent dependences of plants on pollinators, and red dashed histograms (**G** to **I**) represent dependences of seed dispersers on plants. See Database S1 for references and data sets.

by our analysis of quantitative networks. Second, previous work (i.e., asymmetry at the species level) (6, 7) provides a mechanistic explanation for some of the new results presented here as the higher-than-expected strength of generalist species. However, our results go a step further, because we show here that asymmetry is also a property at the link level based on species-specific mutual dependences.

Our results suggest that the architecture of quantitative mutualistic networks is characterized by the low number of strong dependences,

their asymmetry, and the high heterogeneity in species strength, all of which may promote community coexistence. Community coexistence, in turn, may favor the long-term persistence of reciprocal selective forces required for the coevolution of these species-rich assemblages (2, 3). By considering mutualistic networks as coevolved structures rather than as diffuse multispecific interactions, we can better understand how these networks develop (3). There are two forces that, acting in combination, may lead to networks with the reported architecture: coevolu-
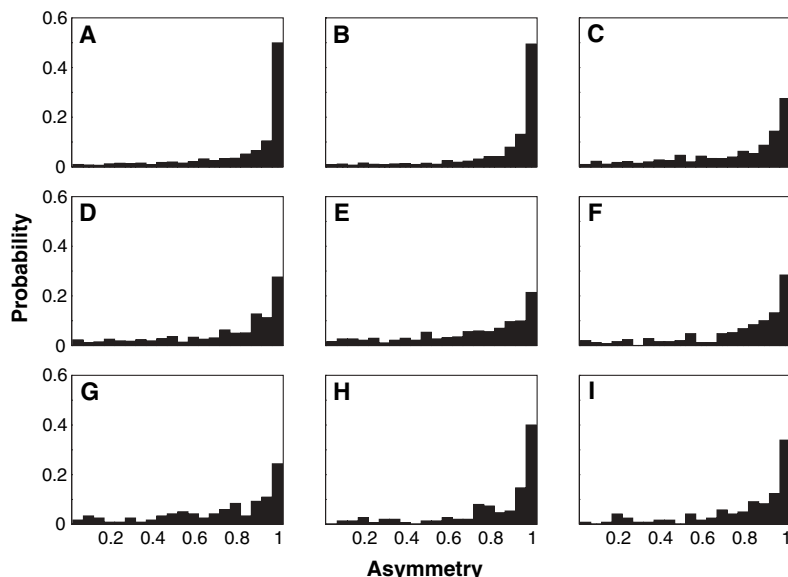
Fig. 3. Frequency distributions of asymmetry values of mutual dependences within a mutualistic community. (**A** to **F**) Plant-pollinator communities. (**G** to **I**) Plant seed–disperser communities. See Database S1 for references and data sets.
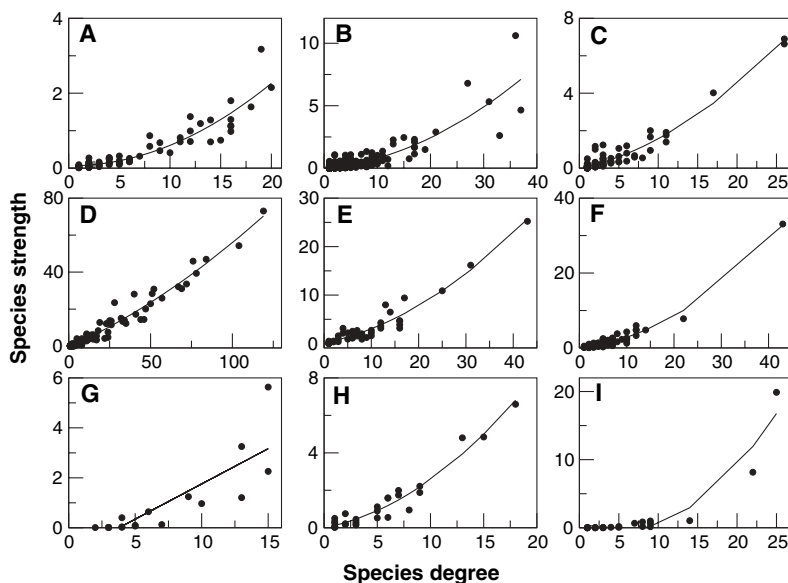

Fig. 4. Relationship between the number of interactions per species (degree) and its quantitative extension, species strength. (**A** to **C**) Pollinator species in plant-pollinator communities. (**D** to **F**) Plant species in plant-pollinator communities. (**G** and **H**) Animal species in plant seed–disperser communities. (**I**) Plants in a plant seed–disperser community. A quadratic regression is represented when the quadratic term is significant; otherwise a linear regression is plotted (G). As noted, in all cases but (G), species strength increases faster than species degree. See Database S1 for references and data sets.

tionary complementarity and coevolutionary convergence (*3*). Pairwise interactions build up on complementary traits of the plants and the animals (e.g., corolla and pollinator tongue lengths), whereas the convergence of traits allows other species to attach to the network as this evolves (e.g., convergence in fruit traits among plants dispersed by birds rather than mammals) (*3*). These forces differ from those shaping antagonistic interactions such as coevolutionary alter-

nation (i.e., selection favoring herbivores attacking less defended plants) (*2*, *3*). Thus, one could predict differences in the architecture of mutualistic and antagonistic networks. Other types of biological interactions also show high asymmetry values. For example, a large fraction of competitive interactions are asymmetric, especially in the marine intertidal (*26*, *27*). Our results highlight the importance of asymmetric interactions in mutualistic networks. Asym-

metry seems to be the key to both their diversity and coexistence. Whether asymmetry extends to other types of complex networks remains to be seen.

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Supporting Online Material for

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This PDF file includes:

Other Supporting Online Material for this manuscript includes the following:
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SUPPORTING ONLINE MATERIAL

The Database

A compressed Excel file is sent separately with the quantitative database (*Data-BA.zip*). It contains a description of each community, its reference, a list of plant and animal species, and the dependence and asymmetry values for each pairwise interaction.

Materials and Methods

The following model, an extension of the two-species mutualistic model by Robert May and others *(S1, S2)*, describes the dynamics of a set of n plant species and m animal species interacting mutualistically:

$$\frac{dP_i}{dt} = r_i P_i - S_i P_i^2 + \sum_{j=1}^{m} \alpha_{ij} P_i A_j, \tag{1}$$

$$\frac{dA_j}{dt} = q_j A_j - T_j A_j^2 + \sum_{i=1}^{n} \beta_{ji} P_i A_j, \tag{2}$$

where P_i and A_j represent the abundances of plant i and animal j, respectively; r_i and q_j are the growth rates of plant i and animal j, respectively; S_i and T_j are the intraspecific competition coefficients of plant i and animal j, respectively; α_{ij} is the per-capita effect of animal j on plant i; β_{ji} is the per-capita effect of plant i on animal j; n is the number of plant species, and m is the number of animal species.

Note that the above model can be generalized to describe the dynamics of other 2-mode networks describing, for example, the interactions between hosts and their parasitoids or plants and their herbivores.

For the sake of analytical simplification, let us assume that all plant species are equivalent ($r_i = r$, $S_i = S$, $\alpha_{ij} = \alpha$), and all animal species are equivalent ($q_j = q$, $T_j = T$, $\beta_{ji} = \beta$). Although a strong simplification, this strategy is commonly used in ecology to obtain analytic, general conclusions (see, e.g. ref. *S3*). In the steady state ($P_i = P^*$ $\forall i$, $A_j = A^*$ $\forall j$), the previous system can be rewritten as.

$$\frac{dP_i}{dt} = 0 = rP^* - SP^{*2} + m\alpha P^* A^*, \tag{3}$$

$$\frac{dA_j}{dt} = 0 = qA^* - TA^{*2} + n\beta P^* A^*. \tag{4}$$

There are four different solutions of the above system: $(0,0), (r/S, 0)$, $(0, q/T)$, and a non-trivial coexistence solution given by:

$$P^* = -\frac{rT + m\alpha q}{n\beta m\alpha - TS}, \tag{5}$$

$$A^* = -\frac{qS + n\beta r}{n\beta m\alpha - TS}. \tag{6}$$

The above non-trivial steady state will be positive if and only if:

$$\alpha\beta < \frac{ST}{mn}, \tag{7}$$

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provided that all parameters are positive. Positive growth rates can be assumed for facultative mutualisms.

Note that for the case of one plant and one animal, equation (7) becomes also the condition for the stability of the feasible steady state *(S2)*. Although equation (7) necessarily rests on the simplifying assumption of identical parameter values for each set, the results are robust with respect to departures from this symmetric case as shown by numerical simulations (fig. S1). The term $\alpha\beta$ can thus be generalized as the average product of per-capita effects across the plant-animal pairs.

While our empirical measure of dependence d_{ij}^P is a static index representing a relative frequency of visits, the parameter α_{ij} in the model represents a dynamic measure. Our approach, thus, assumes that per-capita effects can be estimated by dependences. A recent paper *(S4)* provides strong support for this assumption, as the frequency of interactions has been shown to be highly correlated with the total reproductive effect in plant populations. Also, one can theoretically show that the correlation between total per-capita reproductive effect and interaction frequency will be higher the greater the variation of dependences among species *(S4)*. This is fulfilled by the high heterogeneity in dependence values reported in here.

As with any theoretical exercise, our model makes strong assumptions to be able to provide simple, straightforward predictions. Our model assumes a fully connected, randomly interacting network, while we now know that plant-animal mutualistic networks are highly structured (i.e., non-random),

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and have a much lower density of links (see however inset in fig. S1). Models of mutualisms are also intrinsically destabilizing, so model (1-2) is only bounded if inequality (7) holds (left side of isocline in fig. S1). Previous work has looked at stabilizing factors such as temporal or spatial variability or third species such as predators or competitors *(S2)*. However, despite the simplifications of the model, it can be shown that close to equilibrium, it behaves qualitatively similarly to related models incorporating more realism, so conclusions derived from this model about coexistence are not significantly different from those derived from more realistic models *(S2, S5)*. Also, one has to look at this model not as a realistic representation of mutualistic networks, but as an exercise of the type *other things being equal, larger communities have to contain weak, asymmetric mutual dependences to coexist.* An important follow up of this paper will be to explore more realistic dynamic models accounting for the structure of real mutualistic networks. A recent paper *(S6)* has used such a model and compared its predictions with predictions from a random network of interactions. Although persistent quantitative differences were found, the overall results were qualitatively similar.
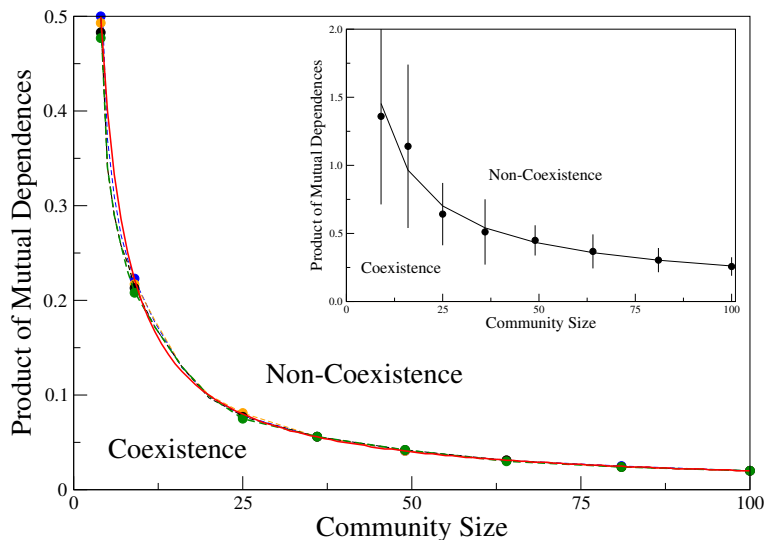
Figure S1. *Robustness of the analytical result (community coexistence criterion in main text) as we relax the assumption of symmetry in parameter values across species. The critical average product of mutual per-capita effects (dependences hereafter) separating the domain of coexistence of the feasible community steady state is plotted as a function of community size (animal species × plant species). Solid red line represents the isocline given by expression (7). Parameters are: $S = 1, T = 2$. Dots (interpolated by broken lines) correspond to numerical simulations of system (1-2). We assume communities with the same number of plants and animals and the following parameter values: r_i and q_j are randomly sampled from a uniform distribution with means 1 and 0.65, respectively, and variance 0.2 and 0.1, respectively; S_i and T_j are sampled from a uniform distribution with means 1 and 2 (as the analytic case) and variance 0, 10, 20, and 30%, respectively shown by different colors. To tune the average product of mutual dependences, all plants and animals in system (1-2) have the same dependence value; the square of such a value is the product of mutual dependences. Inset represents a similar analysis considering a connectivity equal to 0.2 instead of a fully connected matrix, and sampling each dependence value from a uniform distribution with the same mean as before and variance of 20%. Rest of parameters as before.*

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We represent the average and SD of 10 replicates. Solid line is the power regression of the means.

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