

NOTE

Partner Fidelity and Asymmetric Specialization in Ecological Networks

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ABSTRACT: Species are embedded in complex networks of interdependencies that may change across geographic locations. Yet most approaches to investigate the architecture of this entangled web of life have considered exclusively local communities. To quantify to what extent species interactions change at a biogeographic scale, we need to shed light on how among-community variation affects the occurrence of species interactions. Here we quantify the probability for two partners to interact wherever they co-occur (i.e., partner fidelity) by analyzing the most extensive database on species interaction networks worldwide. We found that mutualistic species show more fidelity in their interactions than antagonistic ones when there is asymmetric specialization (i.e., when specialist species interact with generalist partners). Moreover, resources (e.g., plants in plant-pollinator mutualisms or hosts in host-parasite interactions) show a higher partner fidelity in mutualistic interactions than in antagonistic interactions, which can be explained neither by sampling effort nor by phylogenetic constraints developed during their evolutionary histories. In spite of the general belief that mutualistic interactions among free-living species are labile, asymmetric specialization is very much conserved across large geographic areas.

Keywords: antagonistic interactions, mutualistic interactions, co-evolution ecological networks, geographic mosaic.

Introduction

Species are embedded in large networks of interdependencies that are constantly changing over time (e.g., Baird and Ulanowicz 1989; Schoenly and Cohen 1991; Alarcón et al. 2008; Olesen et al. 2008; Petanidou et al. 2008; Carnicer et al. 2009; Burkle et al. 2013; Pilosof et al. 2013; Saavedra et al. 2016) and across space (e.g., Krasnov et al. 2012; Dáttilo et al. 2013; Trøjelsgaard et al. 2015; Emer et al. 2016). In this context, quantifying to what extent interspecific interactions show partner fidelity (i.e., the tendency for two interacting species to interact wherever they co-occur) may be important in the face of global change to anticipate future community-wide scenarios. For example, low partner fidelity might buffer detrimental consequences of climate warming (e.g., Memmott et al. 2007; Bascompte et al. 2019), habitat loss and fragmentation (e.g., Tylianakis et al. 2007), and invasive species (e.g., Aizen et al. 2008).

Partner fidelity depends both on among-community variation and the nature of the interaction (terHorst et al. 2018). In plant-seed dispersal networks, the mutualistic interactions that have been repeatedly preserved across fragmented landscapes are those involving small-seeded, fast-growing plant species and generalist, small-bodied bird species (Emer et al. 2018). In plant-pollination networks, plants show higher partner fidelity to their mutualistic partners than pollinators (Trøjelsgaard et al. 2015). It is less clear, however, the extent to which partner fidelity prevails in antagonistic interactions (e.g., Price et al. 1980, 1986). Despite differences in the way interaction strength is measured in antagonistic and mutualistic networks, a meta-analysis (Morris et al. 2007) showed that mutualistic partners (pollinators and mycorrhizal fungi) have weaker effects on plants than antagonistic partners (herbivores and pathogens). Therefore, we would expect the strength or occurrence of interactions to vary more across communities for mutualistic than for antagonistic interactions. Shifting from interacting to not interacting (i.e., reducing the interaction

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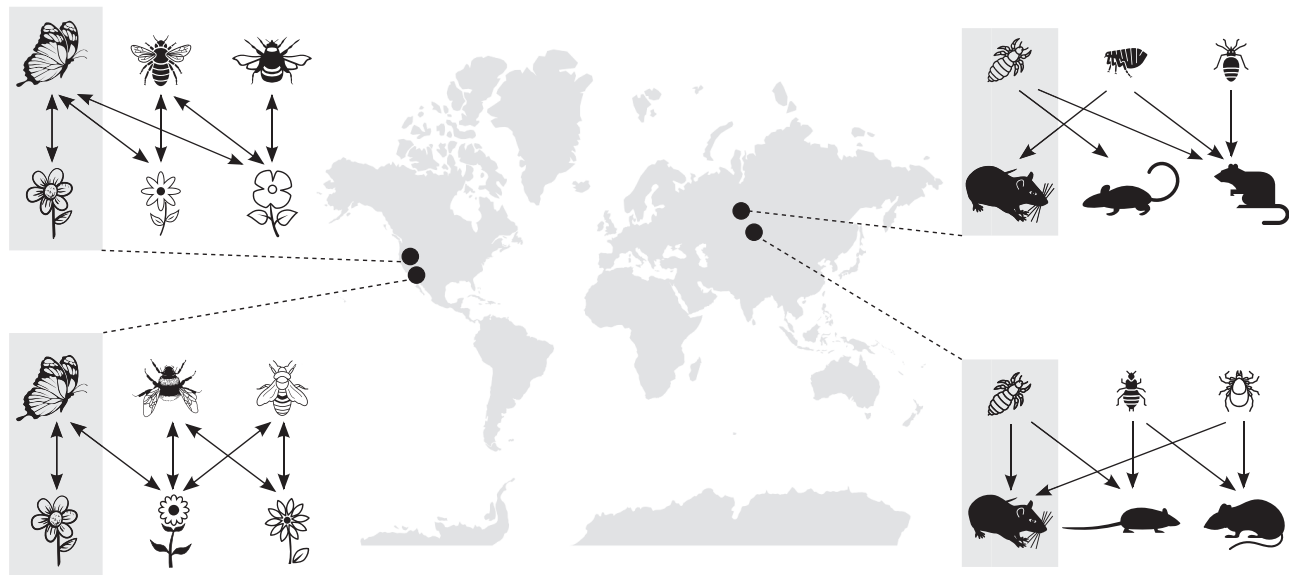


Figure 1: Image illustrating the concept of partner fidelity in a network context. Two small plant-pollinator mutualistic networks are shown on the left, and two small host-parasite antagonistic networks are shown on the right. Circles indicate geographic locations of the four hypothetical networks. Partner fidelity quantifies the tendency for two species to interact wherever they co-occur. For example, the two gray highlighted mutualistic species (i.e., butterfly and plant) interact in the two networks where they co-occur. However, the two gray highlighted antagonistic species (i.e., louse and rat) interact in only one of the two networks where they co-occur. Partner fidelity in this case is higher for the mutualistic partners than for the antagonistic partners.

strength to zero as an extreme case of change in magnitude) is what we use here to quantify partner fidelity.

In this study, we take a first step in quantifying to what extent species interactions are conserved across a broad geographic scale (see fig. 1). Our statistical framework complements previous studies based on a β -diversity approach aimed at quantifying the turnover of interactions, rather than the likelihood for two interacting species to interact whenever they co-occur (e.g., Trøjelsgaard et al. 2015). First, we focus on partner fidelity for mutualistic and antagonistic interactions. Second, we use the most extensive data set of species interaction networks worldwide, rather than a few geographically constrained networks (as in Trøjelsgaard et al. 2015). Third, we quantify the role of the number of interactions per species (i.e., level of generalism) on partner fidelity to explore the consequences of asymmetric specialization (i.e., specialist species interacting with generalist species; Bascompte et al. 2003; Vázquez and Aizen 2004).

Methods

Data Set

The Web of Life database (Fortuna et al. 2014) is the most extensive database on species interaction networks worldwide. Networks stored in the database are not col-

lections of isolated pairwise interactions reported from the literature, but rather come from studies designed explicitly to characterize the pattern of interactions within an ecological community. It is publicly available through a graphical user interface based on Google Maps and currently contains 50,238 pairwise interactions between 13,244 species embedded in 239 networks that were compiled from all over the world. When data were retrieved from the Web of Life (December 2, 2016), the database contained 102 mutualistic (68 plant-pollinator and 34 plant-seed disperser) networks and 58 antagonistic (51 host-parasite and seven plant-herbivore) networks.

To quantify the likelihood for two species to interact wherever they co-occur (i.e., partner fidelity), we focused only on interactions between partners—identified at the species level—that co-occur in more than one network and interact in at least one network. The total number of interactions after applying this filter (4,075 interactions involving 1,247 species embedded in 131 networks) was distributed as follows: 2,125 plant-pollinator interactions involving 275 plant and 516 insect species in 53 networks, 345 plant-seed disperser interactions involving 66 plant and 74 bird species in 23 networks, 1,403 host-parasite interactions involving 83 rodent (host) and 155 insect (ecto-parasite) species in 51 networks, and 202 plant-herbivore interactions involving 21 plant and 59 insect species in four networks. This subset of the interactions sampled from

each network still preserves the heterogeneity in the distribution of the number of interactions per species—a pervasive feature of species interaction networks (i.e., most species interact with a few partners and only a small number of species interact with a large number of partners).

Since the number of species embedded in a network and hence the number of potential partners varies greatly across communities, we normalized the number of partners of each species involved in the interactions considered in our data set to quantify the degree of generalization of a species. This normalized degree (ND) of species i in network j was computed as the number of realized interactions of species i in network j divided by the total number of potential partners in network j . We scaled the ND (mean = 0, SD = 1) to aid the interpretation of both main effects and statistical interactions in our analysis (Schielzeth 2010).

Statistical Analysis

We used a generalized linear mixed model to quantify the effect of the type of interaction (either mutualistic or antagonistic) on the probability for two species to interact wherever they co-occur (binomial distribution; link function = logit). We included the interaction subtype

as a fixed effect to test the effect of herbivory (relative to parasitism) and the effect of pollination (relative to seed dispersal). Since generalist species are expected to have higher partner fidelity than specialists just because they have more interactions, we explored to what extent the effect of the type of interaction is mediated by a species' ND. Therefore, we included a species' ND, and all two-way and three-way statistical interactions between a species' ND and interaction type, as fixed effects (see fig. 2). The two-way interaction between ND of consumers and resources represents the effects of symmetry in NDs on partner fidelity. Specifically, positive values indicate that symmetry in partner's degree enhances fidelity, whereas negative values indicate that asymmetry enhances fidelity (for a detailed explanation, see the supplemental PDF, available online). Therefore, the three-way statistical interaction measures differences between interaction types in the effects of (a)symmetry on fidelity. To account for different sources of nonindependence in species interactions, we included in the model the identity of the network, species identity of each partner, and identity of each unique pairwise interaction as random effects (see the supplemental PDF).

Given the complex structure of our random effects, we used a Bayesian approach to estimate our parameters

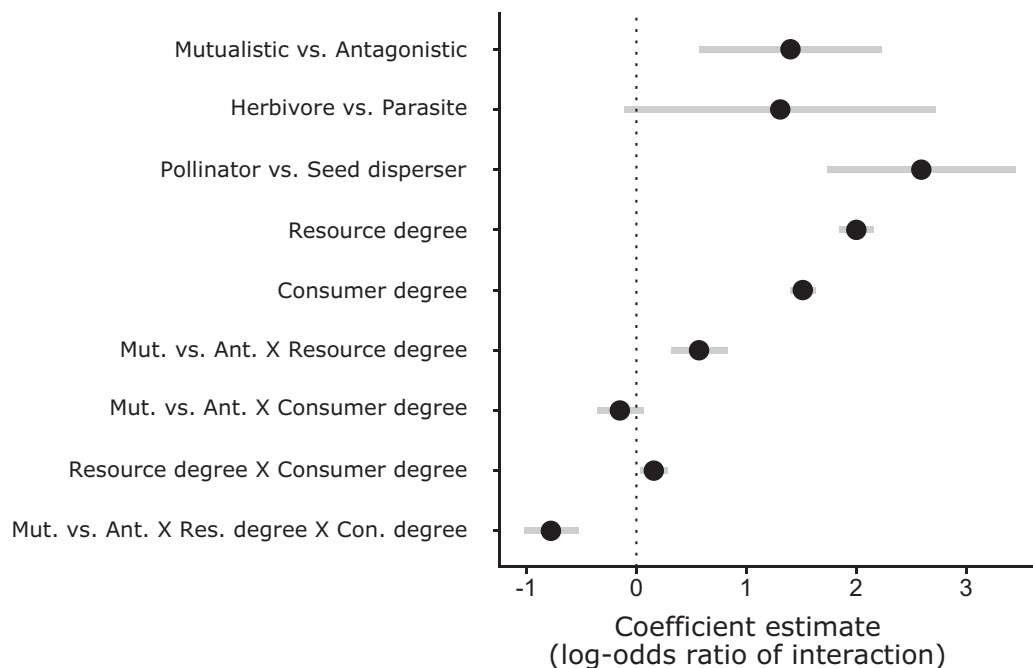


Figure 2: Mean and 95% credible intervals of fixed effects from the generalized linear mixed model. Type of interaction (mutualistic or antagonistic), subtype of interaction (herbivore vs. parasite and pollinator vs. seed disperser), and scaled normalized degree (ND) of both resource and consumer species were included as fixed effects, as were all two-way and three-way interactions between interaction type and partner NDs.

(Bolker et al. 2009). We simulated samples using Markov chain Monte Carlo (MCMC) sampling in the probabilistic programming language Stan (Gelman et al. 2015). We ran four chains with the No-U-Turn sampler for 3,000 iterations each, discarding the first 1,000 iterations as burn-in (Hoffman and Gelman 2014). We used regularizing prior distributions for the fixed effects in our statistical model. For interaction type, we specified a normal distribution with mean = 0 and SD = 2. Biologically, this means that the most likely effect of interaction type is zero and that a large positive or negative effect (absolute value of the coefficient >2) is unlikely but still possible. In other words, this prior distribution makes the data work to show evidence for an effect. For the effect of the ND of consumers and resources, we specified a normal distribution with mean = 1 and SD = 2. Since the ND of a species defines its probability of interacting with a co-occurring partner, regardless of its identity, our baseline expectation is that there should be a one-to-one relationship. For the statistical interaction between the ND of consumers and resources, we specified a normal distribution with mean = 0 and SD = 2, since we felt that both positive (symmetry) and negative (asymmetry) outcomes were plausible. For the two-way and three-way statistical interactions between interaction type and ND, we specified a normal distribution with mean = 0 and SD = 2 using the same rationale as we did for interaction type. For each random effect, we specified a half-normal distribution with mean = 0 and SD = 2 (variances must be >0). Note that even if we relax our assumptions about these prior distributions (e.g., flat priors for all possible values), we still reach the same qualitative (and virtually the same quantitative) conclusions (see the supplemental PDF). All coefficient estimates are on the log odds scale (e.g., fig. 2), but we explain our results on the probability scale, which is more intuitive to understand. To calculate these probabilities, we applied the inverse logit, $1/(1 + e^{-\beta})$, to estimates reported in figure 2 and tables included in the supplemental PDF. All statistical analyses were conducted using the brms package (Bürkner 2017) in R 3.5.0 (R Core Team 2018). All models converged with no warnings (for details, see the supplemental PDF), indicating that it is safe to make inferences about their parameter estimates. In the supplemental PDF, we provide a more detailed explanation of our statistical model, choice of priors, and the additional analyses that we conducted to account for variability in sampling effort across networks.

Sampling Effects

We have addressed the potential confounding effect of differences in sampling effort across networks (i.e., it is more likely to detect an interaction if sampling is more

intensive) by subsampling the more sampled networks from a subset of networks for which we have quantitative data (see the supplemental PDF).

Results

Our model provided a good fit to the data, explaining more than 40% of the variance. We found that partner fidelity (65% across interaction types) depends on the type of interaction (mutualistic or antagonistic) and the degree (i.e., generalism level) of both partners (fig. 2). Specifically, mutualistic interactions increased partner fidelity relative to antagonistic interactions (fig. 2). For example, partner fidelity was 79% for mutualistic interactions and only 47% for antagonistic interactions at the average level of consumer and resource degrees (see fig. S6; figs. S1–S11 are available online). As expected, increasing the degree of a species increased the probability for that species to interact with any of its partners wherever they co-occur. However, the strength of this relationship depends on the type of interaction and whether the species is a resource or a consumer (fig. 3). Specifically, increasing the generalism level of the species by 1 SD relative to the average degree increased partner fidelity from 63% to 93% when the species is a resource and to 89% when the species is a consumer. Moreover, mutualistic interactions increased the positive effect of resource degree on partner fidelity relative to antagonistic interactions (Mut. vs. Ant. \times Resource degree in fig. 2). For example, partner fidelity was larger when the generalist resource (1 SD above mean degree) was a mutualistic species (97%) than when it was an antagonistic species (83%; see fig. S6). However, we found no evidence that mutualistic interactions modify the positive effect of consumer degree on partner fidelity (Mut. vs. Ant. \times Consumer degree in fig. 2). Across interaction types, symmetry between partners in their degree increased partner fidelity (Resource degree \times Consumer degree in fig. 2); however, mutualistic interactions decreased the effects of symmetry on partner fidelity (Mut. vs. Ant. \times Res. degree \times Con. degree in fig. 2). For example, partner fidelity for a specialist consumer (1 SD below mean ND) and generalist resource (1 SD above mean ND) was 91% for a mutualistic interaction compared with 38% for an antagonistic interaction (left panel in fig. 3). Likewise, partner fidelity for a generalist consumer (1 SD above mean ND) and specialist resource (1 SD below mean ND) was 67% for a mutualistic interaction compared with 33% for an antagonistic interaction (right panel in fig. 3). This means that partner fidelity was higher for mutualistic than for antagonistic partners when the interaction takes place between one specialist and one generalist partner (i.e., when there is asymmetric specialization).

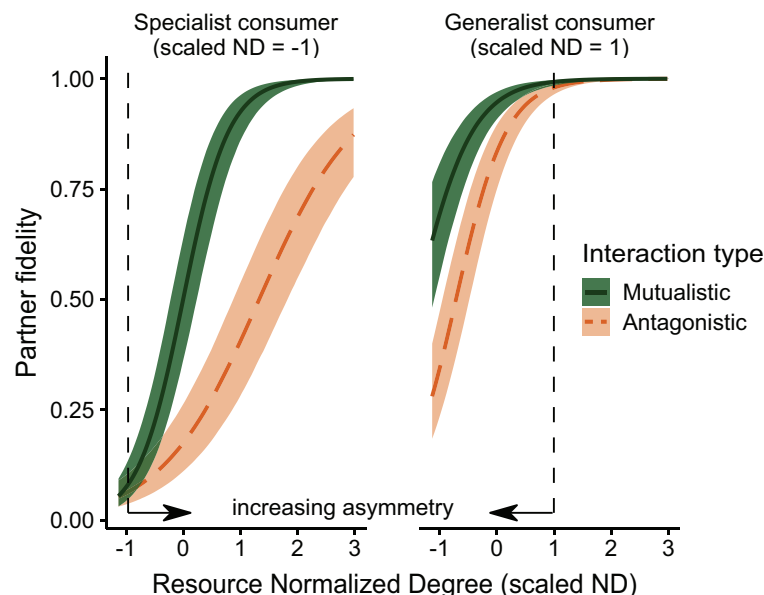


Figure 3: Asymmetric specialization enhances partner fidelity in mutualistic interactions. Lines and bands correspond to predicted means and 95% credible intervals from our model. Green and orange colors correspond to mutualistic and antagonistic interactions, respectively. As expected, increasing the normalized degree (ND) of resources enhances partner fidelity for both mutualistic and antagonistic interactions; however, mutualistic interactions have relatively higher partner fidelity when there is an asymmetry in partner NDs. For example, mutualistic interactions enhance partner fidelity for specialized consumers (left; scaled ND = -1) and generalist resources (scaled ND > 0) relative to antagonistic interactions. Likewise, mutualistic interactions enhance partner fidelity for generalized consumers (right; scaled ND = 1) and specialist resources (scaled ND < 0) relative to antagonistic interactions.

Our analysis on the potential confounding effect of differences in sampling effort across networks indicates that sampling effects do not explain the effect of mutualistic interactions on partner fidelity. That is, mutualistic interactions generally enhance partner fidelity and also enhance the effects of asymmetry on partner fidelity (see the supplemental PDF).

Discussion

There is enormous variation in the probability of observing an interaction between two potential partners whenever both species co-occur. The high partner fidelity found for mutualistic partners (79%) contrasts with the low partner fidelity found for antagonistic ones (47%; see fig. S6), which suggests that the traits involved in antagonistic interactions are more evolutionarily malleable (e.g., highly adaptive) and/or more sensitive to environmental effects. Note however that the vast majority of antagonistic interactions included in this study were among rodent species and their ectoparasites. Therefore, our conclusion holds for the interaction types that we sampled, but the addition of other interaction subtypes is worth exploring in future studies.

On the one hand, empirical evidence shows that the diversity of parasites found in the same host species is af-

ected by the availability of hosts (Fellis and Esch 2005; Goater et al. 2005; Krasnov et al. 2005) and that the diversity of the host range of the parasites varies geographically with environmental conditions (Krasnov et al. 2004; 2008; Korallo-Vinarskava et al. 2009). On the other hand, other studies have shown that species roles tend to be spatially and phylogenetically conserved across a wide range of antagonistic (Krasnov et al. 2012; Stouffer et al. 2012) and mutualistic networks (Rezende et al. 2007; Emer et al. 2016), which suggests some kind of stability in species interactions across space.

Resources in antagonistic interactions (mainly mammalian hosts) show a lower partner fidelity than resources in mutualistic interactions (mainly plants). It has been shown that when closely related host species are infected by many parasite species, such parasites exploit unrelated host species (Krasnov et al. 2012). That is, interactions are more phylogenetically constrained for hosts than for parasites. In contrast, in plant-animal mutualisms, plant phylogenies are less strongly associated with the pattern of interactions than animal phylogenies (Rezende et al. 2007). This weaker phylogenetic signal of plants suggests that consumers in mutualistic interactions constrain the pattern of interactions more than resources do. That is, plants involved in mutualistic interactions might exhibit more phenotypic plasticity than pollinators. Indeed, a

comparative study showed that resources are more strongly constrained than consumers in food webs (i.e., antagonistic networks), while animals show more constraints than plants (i.e., resources) in mutualistic networks (Rohr and Bascompte 2014). Therefore, the higher partner fidelity of resources in mutualistic interactions compared with that of resources in antagonistic interactions cannot be explained by their evolutionary histories but is most likely due to the environment acting weakly on pollinators and strongly on parasites.

Our last result is that partner fidelity is higher for mutualistic than for antagonistic species when there is asymmetric specialization. When searching for this network property across different types of interactions, asymmetric specialization is found less frequently in antagonistic than in mutualistic networks (Thébault and Fontaine 2008), a difference that seems to confer more stability to the community (Thébault and Fontaine 2010). The difference reported here in partner fidelity between mutualistic and antagonistic interactions agrees with those empirical and theoretical findings and supports the pervasiveness of asymmetric specialization in mutualistic networks. Therefore, our results show that asymmetric specialization in mutualistic interactions—widely documented at a local scale—leaves a signature at a large geographic scale.

Our approach has statistically controlled for many sources of variation by modeling them as random effects. Further studies will be needed to elucidate the mechanisms underlying these effects. For example, future directions could include quantifying the role of the local abiotic environment (Vázquez et al. 2007) in explaining variation in partner fidelity across networks due to the identity of the network (the stronger effect compared with the other sources of variation; see fig. S5).

In this study we do not focus on the mechanisms responsible for the spatial turnover of species co-occurrence (i.e., whether two species will co-occur, for example, because of environmental filtering), but rather on what happens when two potentially interacting species co-occur (i.e., whether they will interact). Recent methodological advances try to integrate the two components in a common mathematical framework (Graham and Weinstein 2018; Gravel et al. 2018). Further work should quantify the relative weight of observing two species co-occurring versus that of observing them interacting where they co-occur. This would allow us to better understand the mechanisms shaping the biogeography of species interactions.

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Statement of Authorship

M.A.F. conceived and designed the study; A.N. and M.A.F. performed the study; M.A.B. analyzed the data; and M.A.F., M.A.B., and J.B. wrote the manuscript.

Data and Code Availability

The data reported in this article and the code to analyze the data are available on GitHub (https://github.com/mabarbour/partner_fidelity) and have been archived on Zenodo (<https://zenodo.org/badge/latestdoi/107263795>).

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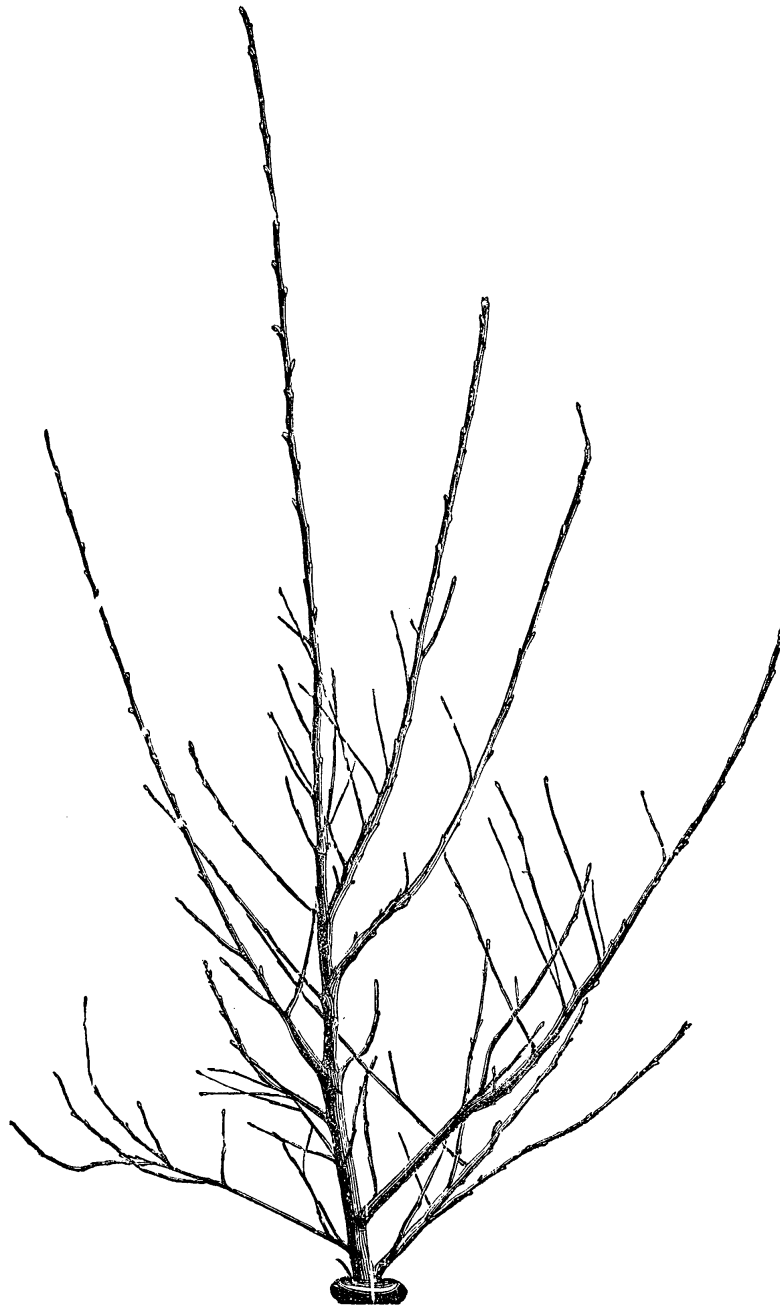
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