Partner fidelity and asymmetric specialization in ecological networks

Supplementary material

Contents

All data and code to reproduce the analyses presented below are available on GitHub (https://github.com/mabarbour/partner_fidelity) and have been archived on Zenodo (https://zenodo.org/badge/latestdoi/107263795).

Dataset

Here's a summary of the full dataset we used in our analyses (table 1).

Table 1: Random sample of 10 rows from the full dataset.

connected	type	subtype	r_ND	c_ND	resource_sp	consumer_sp	id_pair	network_id
0	A	HostParasite	0.35	0.07	Cricetulus migratorius	Frontopsylla protera	3206	A_HP_029
0	A	HostParasite	0.47	0.25	Alticola argentatus	Frontopsylla elata	2710	A_HP_011
0	M	PlantPollinator	0.02	0.11	Hieracium pilosella	Formica fusca	839	M_PL_047
1	A	HostParasite	0.86	0.58	Microtus arvalis	Megabothris turbidus	3486	A_HP_048
1	A	PlantHerbivore	0.25	0.43	Xanthocephalum texanum	Melanoplus desultorius	2201	A_PH_005
1	A	PlantHerbivore	0.42	0.19	Croton pottsii	Melanoplus gladstoni	2159	A_PH_005
1	M	PlantPollinator	0.05	0.06	Ranunculus japonicus	Melanostoma scalare	1434	M_PL_053
1	M	PlantPollinator	0.16	0.05	Tanacetum vulgare	Sphaerophoria scripta	1824	M_PL_018
1	A	HostParasite	0.71	0.13	Clethrionomys glareolus	Rhadinopsylla integella	3008	A_HP_018
0	M	PlantPollinator	0.02	0.59	Cirsium arvense	Bombus pascuorum	331	M_PL_006

- **connected**: observed species interaction (0 = no interaction observed, 1 = interaction observed)
- **type**: type of interaction (A = antagonistic; M = mutualistic)
- **subtype**: specific type of interaction (PlantPollinator, PlantHerbivore, PlantSeedDisperser, HostParasite)
- **r_ND**: normalized degree of resource species (mean = 0.28, SD = 0.24)
- **c_ND**: normalized degree of consumer species (mean = 0.28, SD = 0.23)
- **resource_sp**: resource species ID (n = 444)
- **consumer_sp**: consumer species ID (n = 803)
- **id_pair**: consumer-resource interaction ID (n = 4075)
- **network_id**: ecological network ID (n = 133; labels match those on the Web of Life)

We also analyze a subset of these data that only consists of weighted networks (table 2), which we use to investigate the effects of sampling effort.

Table 2: Random sample of 10 rows from the subset of weighted networks.

connected	type	subtype	r_ND	c_ND	sum_shared	resource_sp	consumer_sp	id_pair	network_id
0	M	PlantPollinator	0.01	0.02	0	Reynoutria japonica	Eristalis tenax	1570	M_PL_044
0	A	HostParasite	0.16	0.40	0	Apodemus peninsulae	Ctenophthalmus congeneroides	2793	A_HP_049
1	A	HostParasite	0.47	0.69	3	Apodemus uralensis	Corrodopsylla birulai	2837	A_HP_020
0	M	PlantSeedDisperser	0.23	0.08	0	Cecropia schreberiana	Tyrannus dominicensis	2441	M_SD_005
0	A	HostParasite	0.54	0.15	0	Microtus arvalis	Neopsylla pleskei	3510	A_HP_044
0	M	PlantPollinator	0.06	0.09	0	Deutzia crenata	Episyrphus balteatus	561	M_PL_054
0	M	PlantSeedDisperser	0.15	0.44	0	Miconia affinis	Loxigilla portoricensis	2569	M_SD_004
1	A	HostParasite	0.65	0.56	57	Clethrionomys rutilus	Frontopsylla elata	3048	A_HP_020
1	A	HostParasite	0.12	1.00	7	Cricetus cricetus	Rhadinopsylla li	3358	A_HP_044
0	A	HostParasite	0.43	0.06	0	Cricetulus migratorius	Rhadinopsylla ucrainica	3249	A_HP_006

- **connected**: 0 = no interaction observed, 1 = interaction observed
- **type**: A = antagonistic, M = mutualistic
- **subtype**: HostParasite, PlantPollinator, PlantSeedDisperser
- **r_ND**: mean = 0.35, SD = 0.2
- **c_ND**: mean = 0.34, SD = 0.2
- **sum_shared**: mean = 4.5, SD = 2.2
- **resource_sp**: n = 167
- **consumer_sp**: n = 291
- **id_pair**: n = 1813
- **network_id**: n = 68

Note that the general structure of the subset of data is the same as the full dataset, except we have added one new variable. This variable corresponds to the number of observed interactions (sum of interaction frequency, **sum_shared**) for a consumer-resource pair in a network. This variable gives information on sampling effort. Note also that we only have three interaction **subtype**s now (no weighted networks for PlantHerbivore).

Prior to our analyses, we scaled normalized degree (mean = 0, SD = 1) for both consumers and resources. This allowed us to interpret both main effects and statistical interactions within the same model, and also allowed us to easily compare their effect sizes (Schielzeth, 2010). We also scaled the logarithm of observed interactions for both consumers and resources.

```
full.df <- full.df %>%
  mutate(sc.r_ND = scale(r_ND),
         sc.c_ND = scale(c_ND))


weighted_subset.df <- weighted_subset.df %>%
  mutate(sc.r_ND = scale(r_ND),
         sc.c_ND = scale(c_ND),
         sc.log.sum_r = scale(log.sum_r),
         sc.log.sum_c = scale(log.sum_c))
```

For **type**, we created a contrast so that the intercept term represents the average probability (Ave) of an interaction across mutualistic (M) and antagonistic (A) interactions, and this coefficient represents the effect of mutualistic (relative to antagonistic) interactions (table 3).

Table 3: Contrasts for **type**.

	A	M
Ave	0.5	0.5
_M.vs.A	-1.0	1.0

To test for the effect of network **subtype** within each **type**, we create two new variables:

```
full.df <- full.df %>%
  mutate(subtype_Herb.vs.Para = ifelse(type == "M", 0,
                          ifelse(subtype == "PlantHerbivore", 1/2, -1/2)),
         subtype_Poll.vs.Disp = ifelse(type == "A", 0,
```

```
                                    ifelse(subtype == "PlantPollinator", 1/2, -1/2)))
```

Now, **subtype_Herb.vs.Para** tests for an effect of herbivory (relative to parasitism), and **subtype_Poll.vs.Disp** tests for an effect of pollination (relative to seed dispersal).

Since we do not have multiple **subtype**s for antagonistic interactions in the data subset, we only fit a **subtype** contrast for mutualistic interactions.

```
weighted_subset.df <- weighted_subset.df %>%
  mutate(subtype_Poll.vs.Disp = ifelse(type == "A", 0,
                          ifelse(subtype == "PlantPollinator", 1/2, -1/2)))
```

Statistical Models

We fit the following statistical model to our full dataset:

```
interaction.formula <- brmsformula(
  connected ~ type + subtype_Herb.vs.Para + subtype_Poll.vs.Disp + sc.r_ND + sc.c_ND +
    type:sc.r_ND + type:sc.c_ND + sc.r_ND:sc.c_ND +
    type:sc.r_ND:sc.c_ND +
    (1 | resource_sp) + (1 | consumer_sp) + (1 | id_pair) + (1 | network_id),
  family = bernoulli(link = "logit")
)
```

and a similar model to the data subset:

```
interaction_subset.formula <- brmsformula(
  connected ~ type + subtype_Poll.vs.Disp + sc.r_ND + sc.c_ND +
    type:sc.r_ND + type:sc.c_ND + sc.r_ND:sc.c_ND +
```

```
    type:sc.r_ND:sc.c_ND +

    (1 | resource_sp) + (1 | consumer_sp) + (1 | id_pair) + (1 | network_id),

  family = bernoulli(link = "logit")

) # note that we do not include subtype_Herb.vs.Para, since we do not have

# PlantHerbivore interactions in the weighted subset.
```

These models analyze the probability of a species interaction as a function of all main effects, as well as two- and three-way interactions between the type of interaction (**type**) and scaled normalized degree of resources (**sc.r_ND**) and consumers (**sc.c_ND**)(fixed effects). Note that we only test for main effects of network subtypes within the type of interaction. This model also allows the probability of interactions to vary among resource and consumer species, the unique consumer-resource pair, as well as among unique ecological networks (random effects). Note that by including the unique consumer-resource pair as a random effect, we are testing how the different factors in our model influence partner fidelity (i.e., probability of two species to interact when they co-occur). Note also that specifying a Bernoulli distribution on the logit scale for the error distribution in our model makes it so that the fixed and random effects in our statistical model represent effects on the log odds of partner fidelity.

Choosing Priors

Given the number of random effects in our model, we used a Bayesian approach to estimate our model's parameters (as advised by Bolker et al. 2008). This required us to choose prior distributions for the fixed and random effects in our model.

We specified the following priors in our models:

```
interaction.priors <- c(

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A"),
```

```r
  set_prior("normal(0,2)", class = "b", coef = "subtype_Herb.vs.Para"),

  set_prior("normal(0,2)", class = "b", coef = "subtype_Poll.vs.Disp"),

  set_prior("normal(1,2)", class = "b", coef = "sc.r_ND"),

  set_prior("normal(1,2)", class = "b", coef = "sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "sc.r_ND:sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.r_ND"),

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.r_ND:sc.c_ND"),

  set_prior("normal(0,2)", class = "sd"))


interaction_subset.priors <- c(

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A"),

  set_prior("normal(0,2)", class = "b", coef = "subtype_Poll.vs.Disp"),

  set_prior("normal(1,2)", class = "b", coef = "sc.r_ND"),

  set_prior("normal(1,2)", class = "b", coef = "sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "sc.r_ND:sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.r_ND"),

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.r_ND:sc.c_ND"),

  set_prior("normal(0,2)", class = "sd"))


sampling_effect.priors <- c(

  set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A"),

  set_prior("normal(0,2)", class = "b", coef = "subtype_Poll.vs.Disp"),

  set_prior("normal(1,2)", class = "b", coef = "sc.log.sum_r"),

  set_prior("normal(1,2)", class = "b", coef = "sc.log.sum_c"),

  set_prior("normal(0,2)", class = "b", coef = "sc.log.sum_r:sc.log.sum_c"),
```

```
    set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.log.sum_r"),

    set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.log.sum_c"),

    set_prior("normal(0,2)", class = "b", coef = "type_M.vs.A:sc.log.sum_r:sc.log.sum_c"),

    set_prior("normal(0,2)", class = "sd"))
```

Choosing priors requires thinking on the scale of the model. Therefore, we first give a description of what each term quantifies in these models before justifying our choices. Note that all of these fixed effects (except for **Intercept**) can be interpreted as an effect on the log-odds of partner fidelity:

- **Intercept** = log-odds of partner fidelity across interaction types at the mean normalized degree of resources and consumers.
- **type_M.vs.A** = effect of a mutualistic interaction (relative to antagonistic).
- **subtype_Herb.vs.Para** = effect of herbivory relative to parasitism.
- **subtype_Poll.vs.Disp** = effect of pollination relative to seed disperser.
- **sc.r_ND** = effect of 1 SD increase in resource normalized degree across interaction types.
- **sc.c_ND** = effect of 1 SD increase in consumer normalized degree across interaction types.
- **type_M.vs.A:sc.r_ND** = effect of a mutualistic interaction (relative to antagonistic) on a 1 SD increase in resource normalized degree.
- **type_M.vs.A:sc.c_ND** = effect of a mutualistic interaction (relative to antagonistic) on a 1 SD increase in consumer normalized degree.
- **sc.r_ND:sc.c_ND** = nonadditive effect of 1 SD increase in resource and consumer normalized degree across interaction types. A positive value indicates that symmetry in partners normalized degree increases partner fidelity, whereas a negative value indicates that *asymmetry* in partners normalized degree increases partner fidelity (see justification for this in section **Asymmetry effect**).
- **type_M.vs.A:sc.r_ND:sc.c_ND** = nonadditive effect of a mutualistic interaction (relative to antagonistic) on a 1 SD increase in resource and consumer normalized degree. A positive value indicates that mutualistic interactions enhance the effects of symmetry on partner

fidelity, whereas a negative value indicates that mutualistic interactions enhance the effects of *asymmetry*.

For each of our random effects (**resource_sp**, **consumer_sp**, **id_pair**, and **network_id**), our model estimates the SD that describes the assumed normal distribution in their effect sizes.

Below, we give a justification for each of the prior distributions we chose for these parameters.

Type of interaction: type_M.vs.A

Let's take a hypothetical example, where the effect of **type_M.vs.A** on partner fidelity is really large, ranging from a probability of 0.25 to 0.75. The example below shows that this corresponds to a logistic regression coefficient of ~2.2.

```
# probability of a mutualistic interaction when two species co-occur

pM <- 0.75


# probability of an antagonistic interaction when two species co-occur

pA <- 0.25


# logistic regression coefficient, which is the difference in log-odds
# for 1 unit increase in the predictor

(mu_mutualist <- log(pM / (1-pM)) - log(pA / (1-pA)))

## [1] 2.197225
```

We would expect such a large effect to be unlikely though. Also, we have no strong prior expectation as to whether mutualistic or antagonistic interactions will have a positive or negative effect on partner fidelity. So let's explore what a normal distribution looks like when the coefficient is centered on zero, but the variance is large enough to allow for a large effect (**type_M.vs.A** = 2.2, denoted by dotted line below) if there is enough evidence to support it.
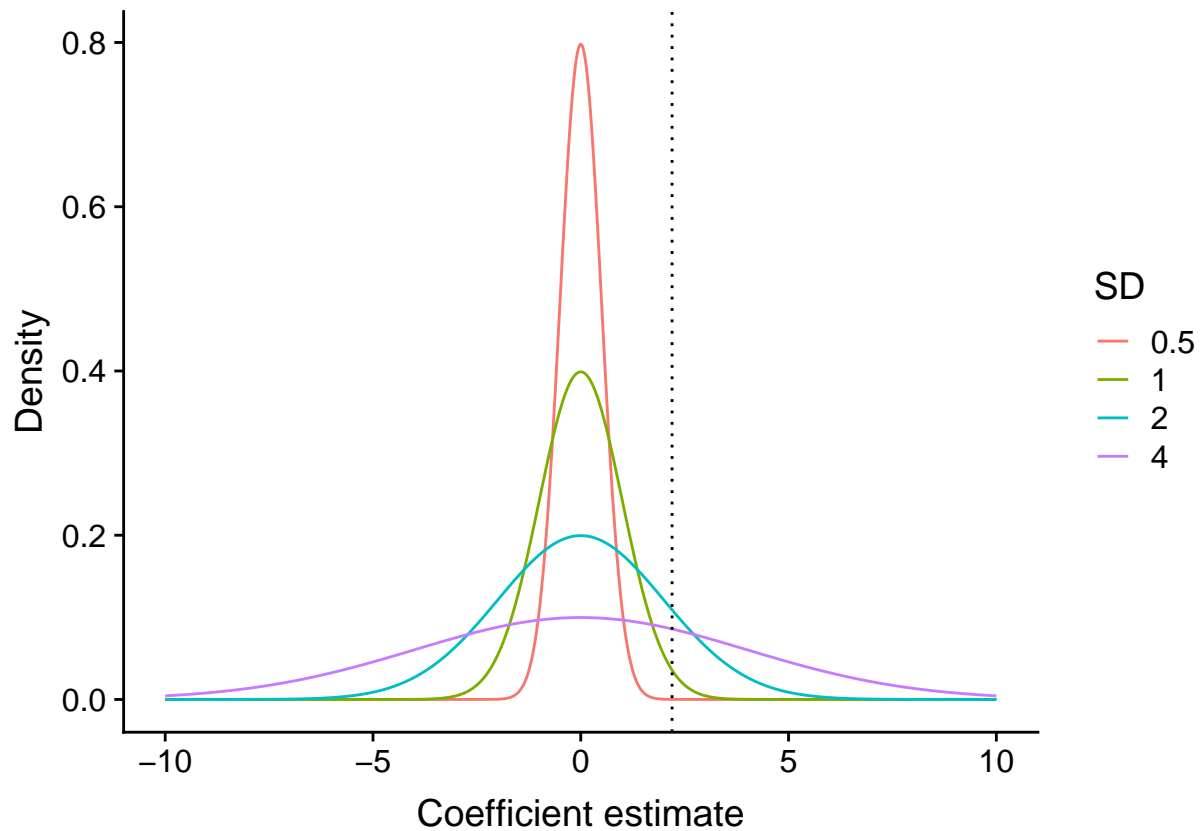
Figure 1: Possible prior distributions for the effect of interaction type.

Based on these distributions, we think a normal prior with mean=0 and SD=2 would be appropriate. This creates a regularizing prior where the mass of the distribution is centered on zero (i.e., no effect), but allows for the model to detect large effects if the data supports it.

Subtype of interaction: subtype_Herb.vs.Para and subtype_Poll.vs.Disp

We expect similar effects for different subtypes of interaction as we would for different interaction types. Therefore, we choose to use the same prior: normal(mean=0, SD=2).

Scaled normalized degree: sc.r_ND and sc.c_ND

Since the normalized degree of a species defines its probability of interacting with a co-occuring partner, regardless of its identity, our prior expectation is that there is a 1:1 relationship between the normalized degree of a species and its probability of interacting with another species. In other words, the probability of observing an interaction is the same as the normalized degree.

Let's get some intuition as to what this prior looks like when normalized degree is on a standardized scale (1 SD above the mean) and the response is in terms of log odds, which matches the assumptions of our model. Note that we chose to only look 1 SD above the mean because this reflects how the coefficient is estimated in the model (effect of 1 unit increase in predictor variable). We do this first for resources:

```
# probability of average species interacting
pMean_r <- mean(full.df$r_ND)


# probability of a relatively generalized species interacting
pGen_r <- mean(full.df$r_ND) + sd(full.df$r_ND)


# logistic regression coefficient, which is the difference in log-odds
# for a 1 SD unit increase in a species normalized degree.
(mu_sc.r_ND <- log(pGen_r / (1-pGen_r)) - log(pMean_r / (1-pMean_r)))

## [1] 1.040268
```

and then for consumers:

```
## Consumer species


# probability of average species interacting
pMean_c <- mean(full.df$c_ND)
```

```
# probability of a relatively generalized species interacting

pGen_c <- mean(full.df$c_ND) + sd(full.df$c_ND)


# logistic regression coefficient, which is the difference in log-odds

# for a 1 SD increase in a species normalized degree.

(mu_sc.c_ND <- log(pGen_c / (1-pGen_c)) - log(pMean_c / (1-pMean_c)))

## [1] 0.9944917
```

These examples indicate that we should have a prior expectation for the mean estimate of these coefficients to be ~1. How much variance around this coefficient might we expect though? Let's simulate a normal distribution with mean=1 (dotted line below), but different variances:
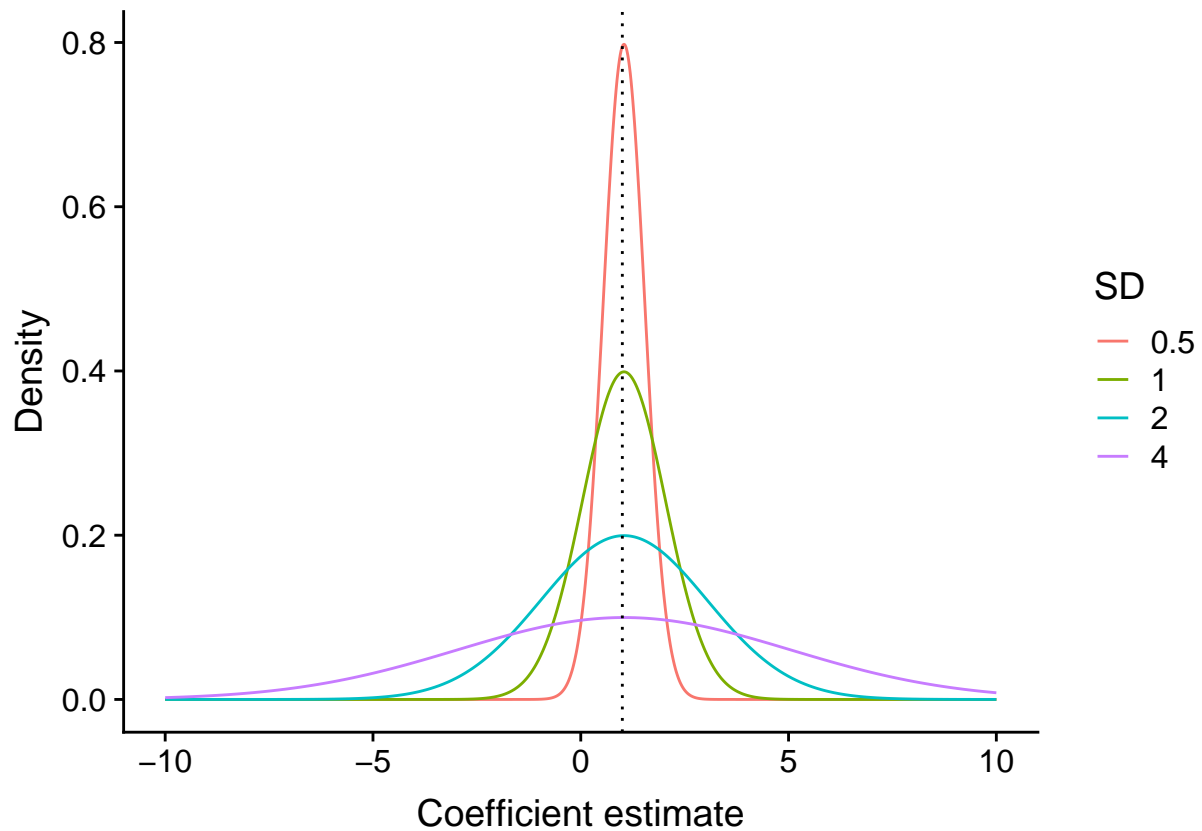
Figure 2: Potential prior distributions for the effect of scaled normalized degree.

Most standardized logistic regression coefficients are less than 5 (Gelman et al., 2008), so we feel that specifying a standard deviation of 2 is reasonable since it more than covers the range from 0 to 5. It will also make the data "work" for larger values, since the mass of the distribution is centered on 1.

Statistical interactions between interaction type and normalized degree: type_M.vs.A:sc.r_ND, type_M.vs.A:sc.c_ND

We specified the same regularizing prior as for **type_M.vs.A** (i.e., normal(mean=0, SD=2)), because we have no strong prior expectation for whether interaction type will have a positive or negative effect on these relationships, and we want to make the data "work" for any strong effects.

Partner (a)symmetry effect: sc.r_ND:sc.c_ND

Although it is not intuitive, the sign of the statistical interaction between consumer and resource normalized degree indicates whether partner symmetry or asymmetry increases partner fidelity. To illustrate this, let's first assume that the main effects of scaled normalized degree for both resources and consumers equals 1 (also our prior expectation). For simplicity, let's assume that the statistical interaction is either -1 or +1. With these coefficients, we can now calculate how a change in scaled normalized degree for both resources and consumers affects the log-odds of an interaction. Below, we explore these effects ± 1 SD for the scaled normalized degree of both resources and consumers.

```
sim.log.odds <- expand.grid(
  b_sc.r_ND = 1,
  b_sc.c_ND = 1,
  `b_sc.r_ND:sc.c_ND` = c(-1, 1),
  delta.sc.r_ND = seq(-1, 1, 0.01),
  delta.sc.c_ND = seq(-1, 1, 0.01)) %>%
  mutate(log.odds.connected =
           b_sc.r_ND * delta.sc.r_ND +                      # main effect of sc.r_ND
           b_sc.c_ND * delta.sc.c_ND +                      # main effect of sc.c_ND
           `b_sc.r_ND:sc.c_ND` * delta.sc.r_ND * delta.sc.c_ND, # statistical interaction
         main.log.odds = b_sc.r_ND * delta.sc.r_ND + b_sc.c_ND * delta.sc.c_ND,
         diff.log.odds = log.odds.connected - main.log.odds)
```
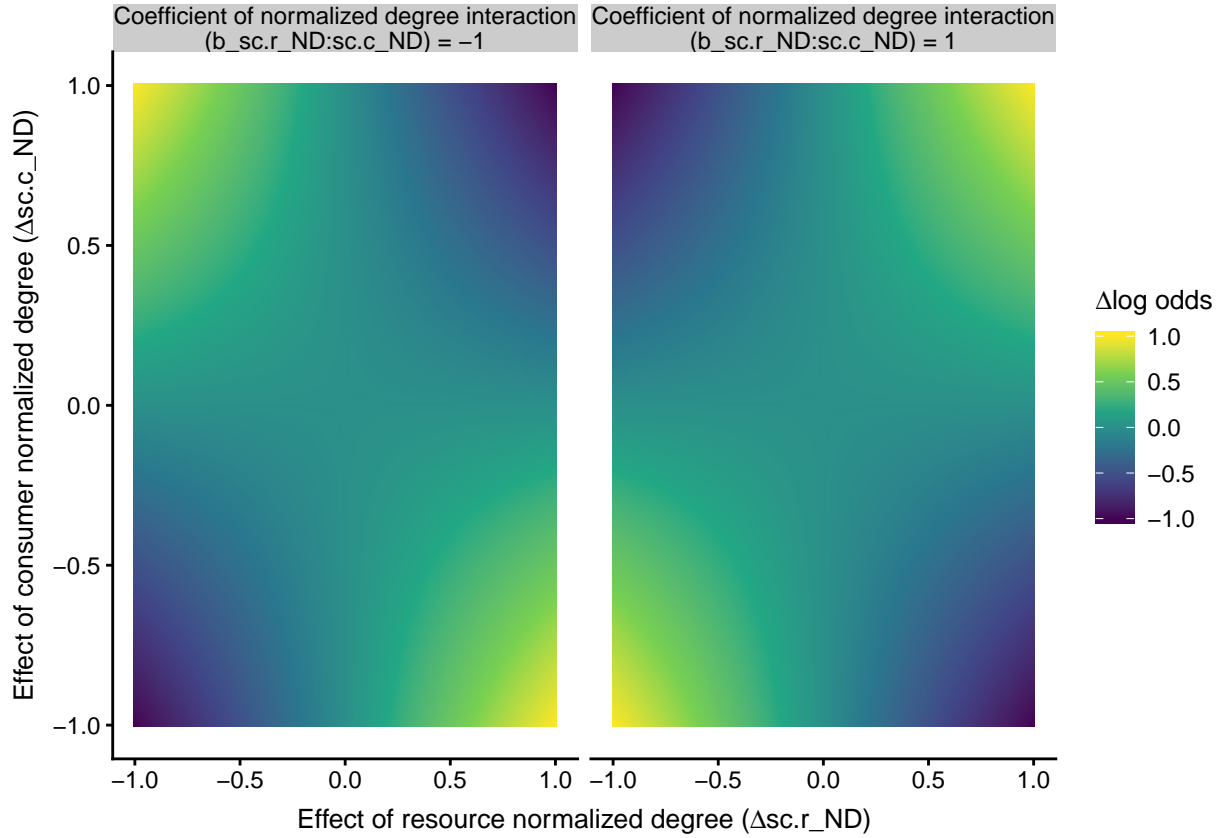
Figure 3: Plot of how the sign of the statistical interaction between resource and consumer normalized degrees (b_sc.r_ND:sc.c_ND) determines how symmetry (right panel) or asymmetry (left panel) in partners normalized degree affects partner fidelity.

By inspecting figure 3, one can see how the sign of the statistical interaction between resource and consumer normalized degree affects the log odds of an interaction. When the sign is positive (right panel), symmetric normalized degrees increase the probability of an interaction (relative to main effects). In contrast, when the sign is negative (left panel), asymmetric normalized degrees increase the probability of an interaction. For example, if a relatively specialized consumer (Δsc.c_ND = -1) interacts with a relatively generalist resource (Δsc.r_ND = +1), there is an increase in the log-odds of an interaction (yellow spot in lower right corner of left panel in fig. 3).

Since we had no prior expectation as to how symmetry or asymmetry would affect partner fidelity,

we set a normal prior with mean=0 and SD=2 to cover the range of most logistic regression coefficients (Gelman et al., 2008).

Effect of mutualism on partner (a)symmetry in normalized degrees: type_M.vs.A:sc.r_ND:sc.c_ND

We again set a normal prior with mean=0 and SD=2, because we had no strong prior expectation for how interaction type would modify the effect of (a)symmetry in normalized degree on partner fidelity.

Main effects and statistical interactions with observed interactions (sc.log.sum_)

As with normalized degree, we expect the log of observed interactions for a resource or consumer to increase the probability of observing an interaction between co-occuring species. Therefore, we specified the same priors as we did for normalized degree for both main effects (normal(mean=1, SD=2) for **sc.log.sum_r, sc.log.sum_c**) and statistical interactions (normal(mean=0, SD=2) for **sc.log.sum_r:sc.log.sum_c, type_M.vs.A:sc.log.sum_r, type_M.vs.A:sc.log.sum_c, type_M.vs.A:sc.log.sum_r:sc.log.sum_c**).

Random effects: resource_sp, consumer_sp, id_pair, network_id

We specified a half-normal prior with mean=0 and SD=2 for each of the random effects in our model. This prior assumes that the variance in these effect sizes is small, but with sufficient evidence, the model can still estimate larger effects. Note that we specify this as a normal distribution in the code, but the R package we use constrains this prior to only positive values since standard deviations cannot be less than zero.

Model Analyses

We used the *brms* package (Bürkner, 2017) and its default sampling behavior (four sampling chains for 2000 iterations each, discarding the first 1000 iterations as burn-in) to fit these statistical models. To mitigate bias in the posterior sampling distribution, we set **adapt_delta = 0.99** and **max_treedepth = 20**.

For the majority of our inferences below, we keep coefficients on the log odds scale. This is because effect sizes are invariant on this scale. For intercept terms, we make inferences on the probability scale, and note the specific values at which this effect is measured. To calculate probabilities, we applied the inverse logit, $\frac{\exp(\beta)}{\exp(\beta)+1}$, to estimates reported in each plot.

Full model

```
full.brm <- brm(

  formula = interaction.formula, data = full.df,

  prior = interaction.priors, algorithm = "sampling",

  chains = 4, iter = 2000, warmup = 1000,

  control = list(adapt_delta = 0.99, max_treedepth = 20))
```
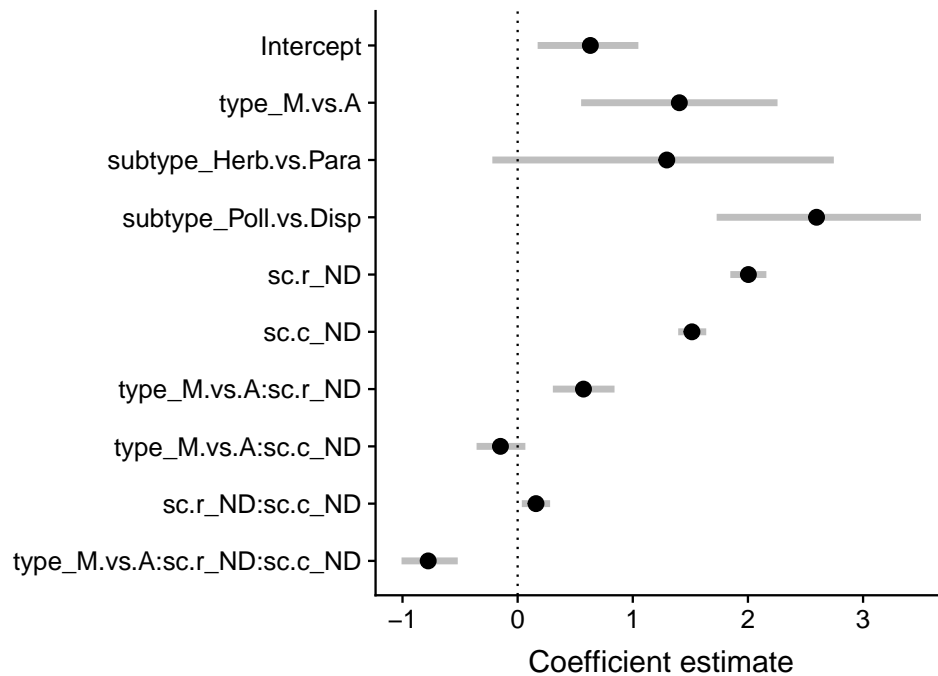
Figure 4: Mean and 95% credible intervals of fixed effects from our full model.

```
## Saving 6.5 x 4.5 in image
```

Our model provided a good fit to our data, explaining 40% of the variance.

```
bayes_R2(full.brm)
```

```
##      Estimate   Est.Error      Q2.5     Q97.5
## R2  0.4010955  0.006517277  0.3883389  0.4139209
```

Below, we give a biological interpretation of each term in this model (fig. 4):

- On the probability scale, the average level of partner fidelity across interaction types equals $0.65 (= \frac{\exp(\beta)}{\exp(\beta)+1}$, where $\beta = 0.63$) for the average level of normalized degree for a resource and consumer.

- Mutualistic interactions increase the log odds of partner fidelity by 1.4 relative to antagonistic interactions.

- There is no clear difference between herbivory and parasitism on partner fidelity (95% credible intervals overlap with zero).

- Pollination increases the log odds of partner fidelity by 2.6 relative to seed dispersers.

- A 1 SD increase in resource normalized degree increases the log odds of partner fidelity by 2 across interaction types.

- A 1 SD increase in consumer normalized degree increases the log odds of partner fidelity by 1.51 across interaction types.

- Mutualistic interactions increase the positive effect of resource normalized degree on the log odds of partner fidelity by 0.57 relative to antagonistic interactions.

- There is no clear evidence that mutualistic interactions (relative to antagonistic) modify the positive effect of consumer normalized degree on partner fidelity (95% credible intervals overlap with zero).

- Across interaction types, symmetry between partners in their normalized degree increases the log odds of partner fidelity by 0.16.

- Mutualistic interactions (relative to antagonistic) decrease the effects of symmetry on the log odds of partner fidelity by -0.78. Put another way, mutualistic interactions increase the effects of *asymmetry* on the log odds of partner fidelity by 0.78.

In addition to these fixed effects, there is considerable variation in partner fidelity explained by our random effects. In particular, **network_id** has a strong effect compared to the other sources of variation (fig. 5).
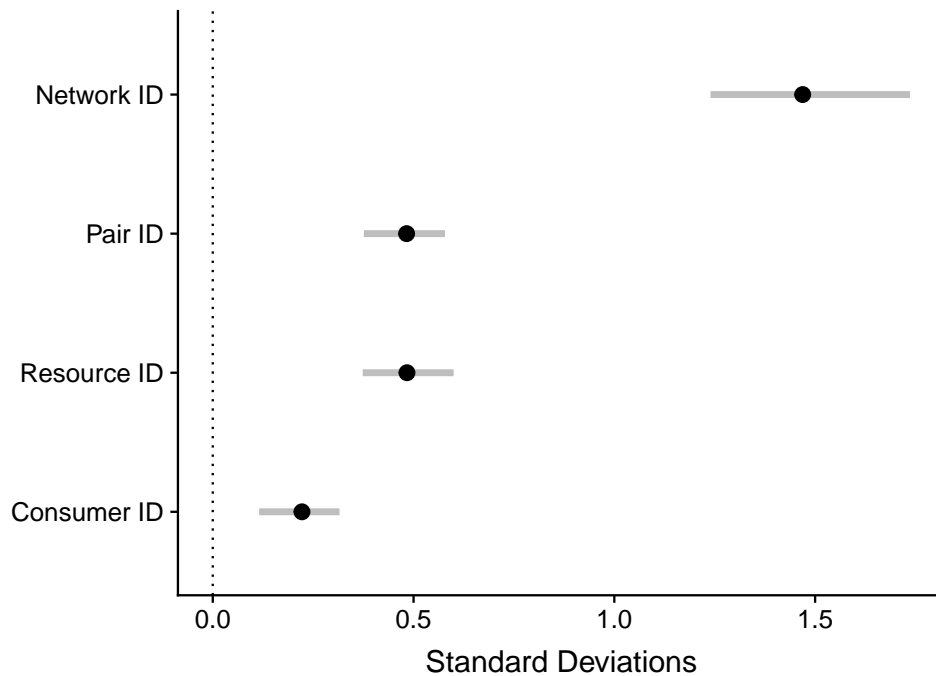
Figure 5: Mean and 95% credible intervals of random effects from our full model.

While the model above is useful for determining the effects of mutualistic relative to antagonistic interactions on partner fidelity, it is also useful to separately estimate relationships for mutualistic and antagonistic interactions. We can do this by removing the intercept term from the model, and estimating unique relationships for normalized degree for both mutualistic and antagonistic interactions.

```
no.intercept_formula <- brmsformula(
  connected ~ -1 + type + subtype_Herb.vs.Para + subtype_Poll.vs.Disp +
    type:sc.r_ND + type:sc.c_ND +
    type:sc.r_ND:sc.c_ND +
    (1 | resource_sp) + (1 | consumer_sp) + (1 | id_pair) + (1 | network_id),
  family = bernoulli(link = "logit"))
```

```r
no.intercept_priors <- c(

  set_prior("normal(0,2)", class = "b", coef = "typeA"), # corresponds to probability of 0.5

  set_prior("normal(0,2)", class = "b", coef = "typeM"), # corresponds to probability of 0.5

  set_prior("normal(0,2)", class = "b", coef = "subtype_Herb.vs.Para"),

  set_prior("normal(0,2)", class = "b", coef = "subtype_Poll.vs.Disp"),

  set_prior("normal(1,2)", class = "b", coef = "typeA:sc.r_ND"),

  set_prior("normal(1,2)", class = "b", coef = "typeM:sc.r_ND"),

  set_prior("normal(1,2)", class = "b", coef = "typeA:sc.c_ND"),

  set_prior("normal(1,2)", class = "b", coef = "typeM:sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "typeA:sc.r_ND:sc.c_ND"),

  set_prior("normal(0,2)", class = "b", coef = "typeM:sc.r_ND:sc.c_ND"),

  set_prior("normal(0,2)", class = "sd"))


no.intercept_brm <- brm(

  formula = no.intercept_formula, data = full.df,

  prior = no.intercept_priors, algorithm = "sampling",

  chains = 4, iter = 2000, warmup = 1000,

  control = list(adapt_delta = 0.99, max_treedepth = 20))
```
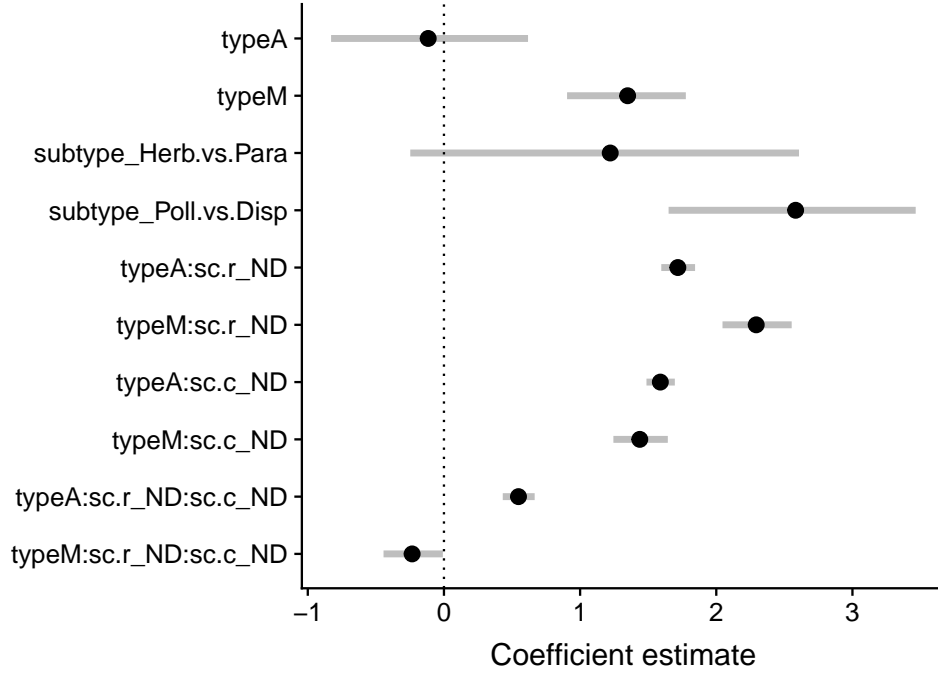
Figure 6: Mean and 95% credible intervals of fixed effects from model without intercepts.

The results from this model (fig. 6) can be interpreted as follows:

- The average level of partner fidelity for antagonistic interactions is 0.47 ($= \frac{\exp(\beta)}{\exp(\beta)+1}$, where β = -0.12) at the average level of normalized degree for a resource and consumer.

- The average probability of partner fidelity for mutualistic interactions is 0.79 ($= \frac{\exp(\beta)}{\exp(\beta)+1}$, where β = 1.35) at the average level of normalized degree for a resource and consumer.

- A 1 SD increase in resource normalized degree in antagonistic interactions increases the log odds of an interaction by 1.72.

- A 1 SD increase in resource normalized degree in mutualistic interactions increases the log odds of an interaction by 2.29.

- A 1 SD increase in consumer normalized degree in antagonistic interactions increases the log

odds of an interaction by 1.59.

- A 1 SD increase in consumer normalized degree in mutualistic interactions increases the log odds of an interaction by 1.44.

- Symmetry in partner normalized degrees increases the log odds of partner fidelity by 0.55 for antagonistic interactions.

- Asymmetry in partner normalized degrees increases the log odds of partner fidelity by 0.23 for mutualistic interactions.

Analysis of data subset

Before testing for potential biases due to sampling effort, we test whether we observe the same results for the data subset.

```
weighted_subset.brm <- brm(
  formula = interaction_subset.formula, data = weighted_subset.df,
  prior = interaction_subset.priors, algorithm = "sampling",
  chains = 4, iter = 2000, warmup = 1000,
  control = list(adapt_delta = 0.99, max_treedepth = 20))
```
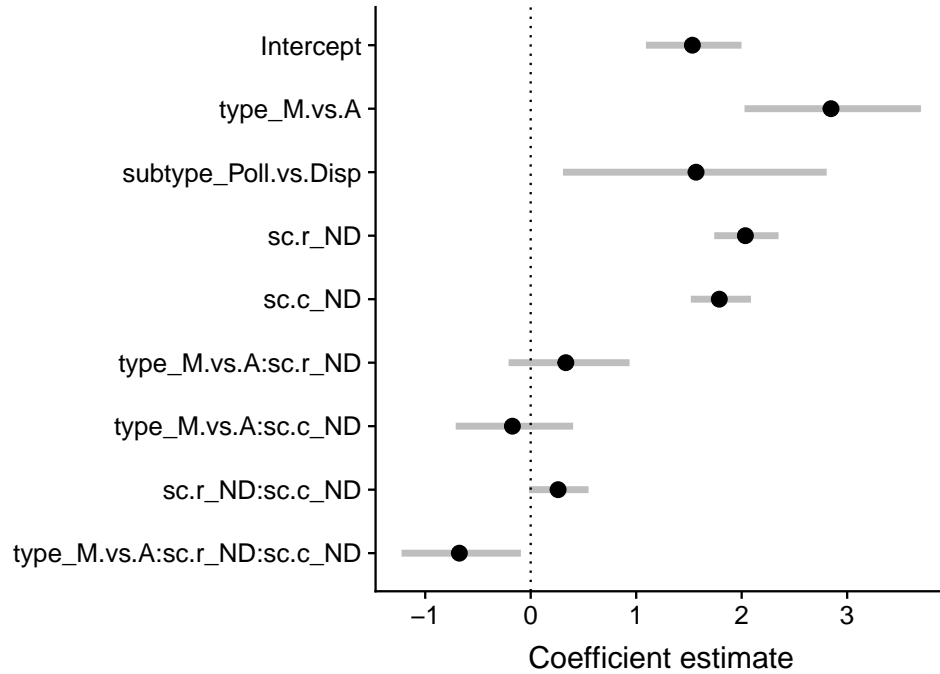
Figure 7: Mean and 95% credible intervals of fixed effects from our weighted subset model.

Note that the **Intercept** and effect of **type_M.vs.A** is higher in this subset of data (fig. 7). This is likely due to the fact that herbivory had a tendency to increase partner fidelity (**subtype_Herb.vs.Para** in fig. 4); therefore, its absence from the data subset enhances the average estimate of partner fidelity as well as the apparent effect of mutualistic interactions. Other terms are similar, except that there is less clear evidence of mutualistic interactions enhancing the effect of resource normalized degree (**type_M.vs.A:sc.r_ND** in fig. 7), and less clear evidence of symmetry in partner normalized degrees to positively affect partner fidelity (**sc.r_ND:sc.c_ND** in fig. 7). Importantly, there is still clear evidence that mutualistic interactions generally enhance partner fidelity (**type_M.vs.A** in fig. 7) and also enhance the effects of *asymmetry* in partner normalized degrees on partner fidelity (**type_M.vs.A:sc.r_ND:sc.c_ND** in fig. 7).

As with the full model, we observe a particularly strong effect of **network_id** compared to the other sources of variation (fig. 8).
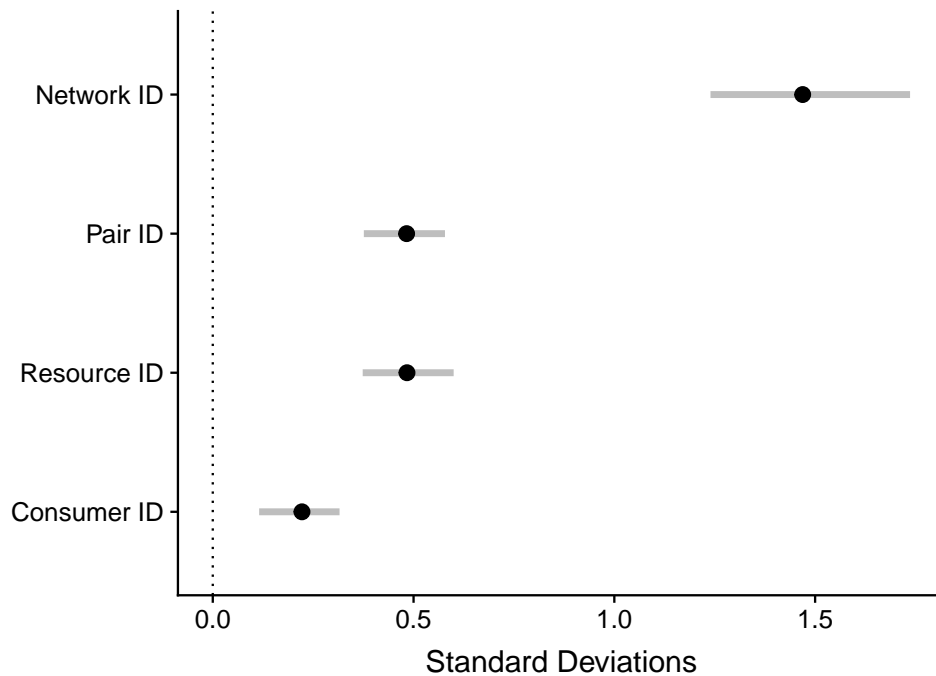
24

Figure 8: Mean and 95% credible intervals of random effects from our weighted subset model.

Testing for bias due to sampling effort

Our goal here is to test whether variation in sampling effort between mutualistic and antagonistic networks could explain the results we observed in the previous models, in particular, the three-way statistical interaction with resource and consumer normalized degree.

Using the subset of weighted data, we first create a long dataset where each row corresponds to an observed interaction.

```
# focus dataset
weighted_long <- weighted_subset.df %>%
  select(network_id, type, subtype, resource_sp, consumer_sp, connected, sum_shared)


# for each interaction, replicate it as many times as it was observed
weighted_long.list <- list()
```

```
for(i in 1:nrow(weighted_long)){

  if(weighted_long$sum_shared[i] > 0){

    weighted_long.list[[i]] <- slice(weighted_long[i, ],

                            rep(1:n(),

                              each = weighted_long$sum_shared[i]))

  } else {

    weighted_long.list[[i]] <- weighted_long[i, ]

  }

}


# tidy into a dataframe

weighted_long.df <- plyr::ldply(weighted_long.list) %>%

  select(-sum_shared)
```

To control for sampling effort, we conducted the following procedure:

1. Pair each mutualistic network with a random subset of the antagonistic networks;

2. Randomly subsample each network down to the interaction count of the paired network with the least number of interactions sampled;

3. Estimate the three-way interaction term for the subsampled data;

4. Repeat this procedure 1,000 times;

5. Compare the distribution of estimates to the reference estimated from the subset of networks with weighted data (i.e. point representing **type_M.vs.A:sc.r_ND:sc.c_ND** in fig. 7).

```
n_sims <- 1000

three_way.FE <- c() # vector of fixed-effect estimate for three-way interaction term

three_way.P <- c() # vector of P-values for the three-way term

for(i in 1:n_sims){
```

```r
# subsample Antagonistic networks to match the number of mutualistic ones
subsample_A_networks <- distinct(filter(weighted_long.df, type == "A"), network_id) %>%
  sample_n(size = 19, replace = F)


# no need to subsample because there are fewer
M_networks <- distinct(filter(weighted_long.df, type == "M"), network_id)


# randomly pair them together (note randomization was already done with subsample_A_networks)
random_pairs <- data.frame(network_pairs = LETTERS[1:19],
                           M = as.character(M_networks$network_id),
                           A = as.character(subsample_A_networks$network_id))


# create data frame to determine subsample size for each network
subsample_df <- left_join(random_pairs,
                          select(weighted_subset.df.network_level,
                                 M = network_id, M_sum = sum_shared)) %>%
  left_join(., select(weighted_subset.df.network_level,
                      A = network_id, A_sum = sum_shared)) %>%
  # subsample is based on smallest number of observed interactions in a network
  mutate(subsample_size = ifelse(M_sum < A_sum, M_sum, A_sum)) %>%
  select(network_pairs, M, A, subsample_size) %>%
  # organize for joining to other datasets
  gather(type, network_id, -subsample_size, -network_pairs)


# now I need to make the new data frame based on the random subsample
new_data <- weighted_long.df %>%
  # filter to randomly sampled networks
```

```r
    filter(network_id %in% c(as.character(M_networks$network_id),

                             as.character(subsample_A_networks$network_id))) %>%

    # following example from:

    # https://jennybc.github.io/purrr-tutorial/ls12_different-sized-samples.html

    # to get different sample sizes for each group

    group_by(network_id) %>%

    nest() %>%

    left_join(., subsample_df) %>%

    mutate(samp = map2(data, subsample_size, sample_n)) %>%

    select(-data) %>%

    unnest(samp) %>%

    # now that I've subsampled, I can reduce the dataset to the normal size for analysis

    # i.e. only 1 interaction per pair per network

    distinct %>%

    # add back in some data for the analysis

    # note that sc.r_ND and sc.c_ND are calculated from the original data and

    # not the subsampled interactions. this is because their normalized degree

    # is based on the entire interaction network rather than their partner fidelity

    # across networks

    left_join(., select(weighted_subset.df,

                        network_id, resource_sp, consumer_sp, id_pair, sc.r_ND, sc.c_ND))


# run test with glmer

# Note that we use a frequentist, rather than Bayesian approach, to calculate

# the three-way interaction term in order to speed up the simulation, but this should not

# matter since our results are not affected by our choice of priors

# (see **Robustness to Different Priors** section).
```

```r
new_glmer <- glmer(connected ~ subtype + type*sc.r_ND*sc.c_ND +

                     (1|consumer_sp) + (1|resource_sp) + (1|id_pair) + (1|network_id),

                   data = new_data, family = binomial(link = "logit"),

                   control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))


  # get model effects for 3-way interaction term

  new_glmer_effects <- broom::tidy(new_glmer, effects = "fixed")

  three_way.FE[i] <- filter(new_glmer_effects, term == "typeM:sc.r_ND:sc.c_ND")$estimate

  three_way.P[i] <- filter(new_glmer_effects, term == "typeM:sc.r_ND:sc.c_ND")$p.value

  # print(paste(i/n_sims*100,"% done!")) # track progress
}


# write data from simulation

write_csv(x = data.frame(FixedEffect = three_way.FE, P = three_way.P),

          path = "data/three_way_permutation_data.csv")
```
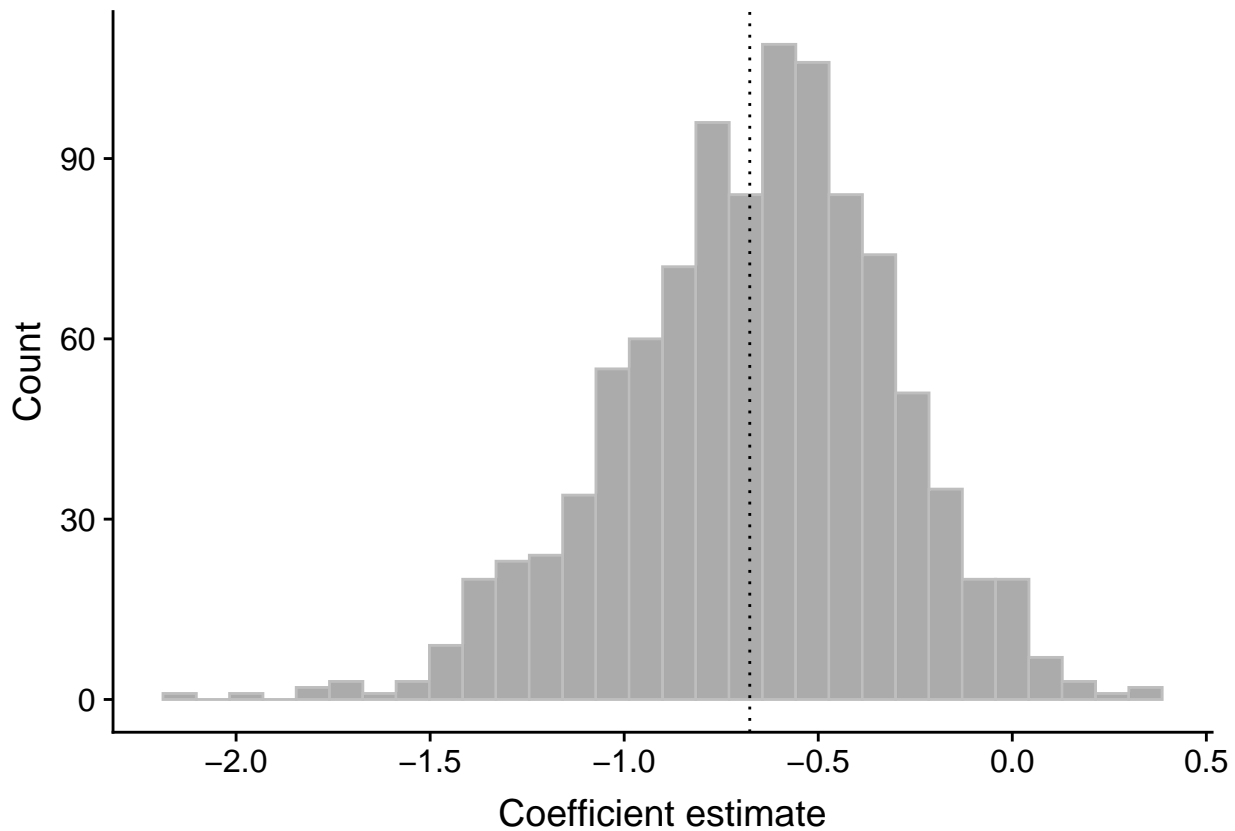
If variation in sampling effort between mutualistic and antagonistic networks were driving our results, then we should expect our reference estimate for the three-way interaction term to be lower than 90% or more of the subsampled values (i.e. a conservative one-tailed permutation test). In contrast, we see that the reference is lower than only 55% of the subsamples. This indicates that variation in sampling effort between mutualistic and antagonistic networks cannot explain our results.

Robustness to Different Priors

To test how robust our results were to a different choice of priors, we re-analyzed the full model with the default priors from the *brms* package, which are designed to be non or very weakly informative. Note that we had to increase **adapt_delta = 0.999** to avoid bias in the posterior sampling of this

model.

```
nopriors.brm <- brm(
  formula = interaction.formula, data = full.df,
  # prior = interaction.priors, # remove and use default priors
  algorithm = "sampling", chains = 4, iter = 2000, warmup = 1000,
  control = list(adapt_delta = 0.999, max_treedepth = 20))
```
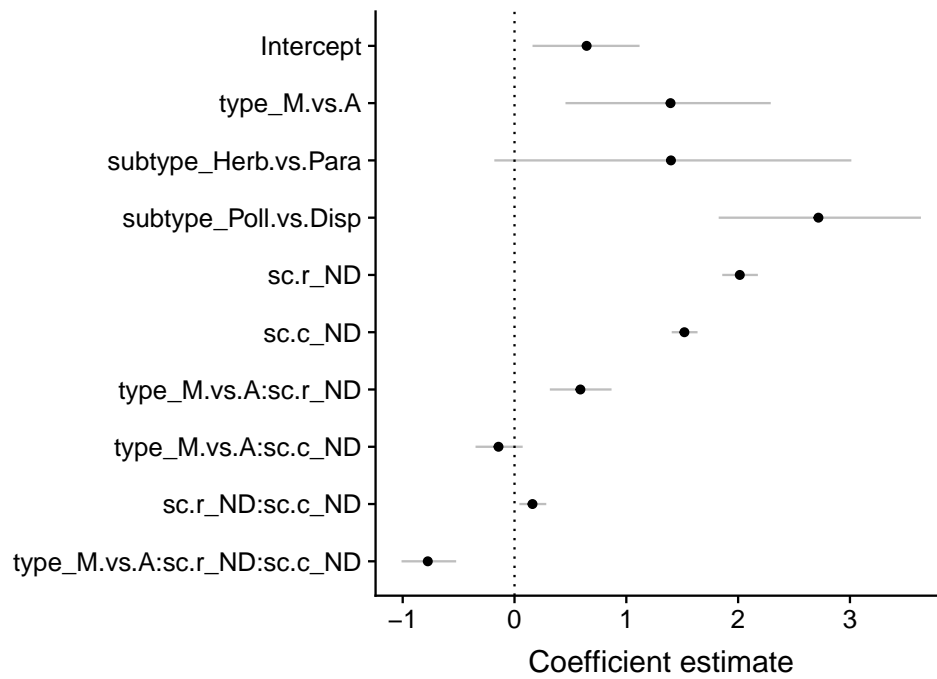
Figure 9: Mean and 95% credible intervals of fixed effects from our full model.
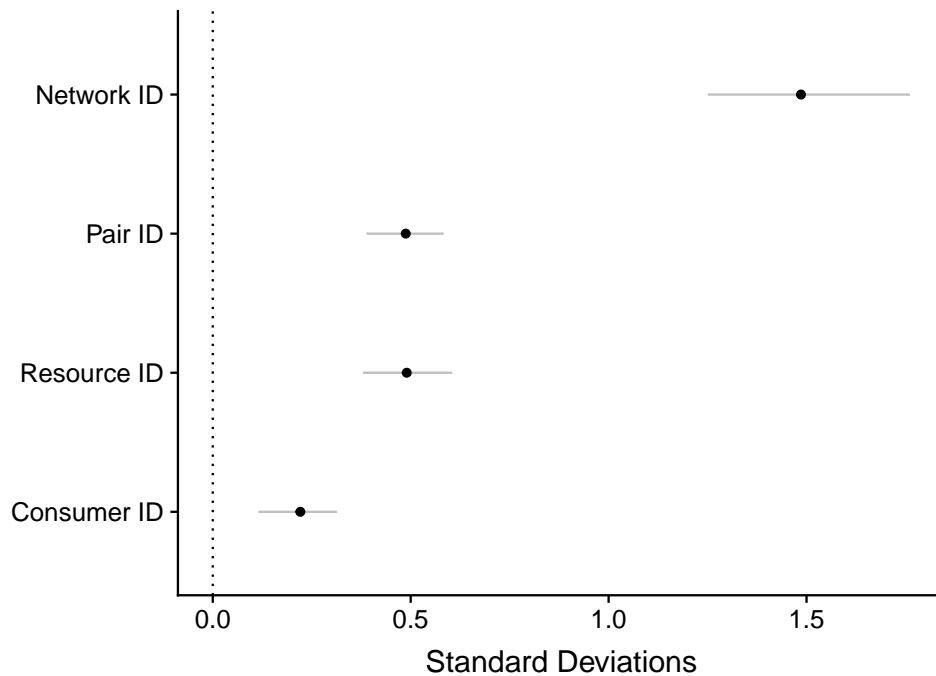
Figure 10: Mean and 95% credible intervals of random effects from the no priors model.

There is a close correspondence between these results (tables 9, 10) and the one where we specified the priors (tables 4, 5), indicating that our results are robust.

References

Bürkner, P.-C. 2017. brms: An R package for bayesian multilevel models using Stan. Journal of Statistical Software 80:1–28.

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Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.