Bee foraging distances are dependent on body mass and level of eusociality

Kendall, L.K.[1], Mola, J. [2], Portman, Z.[3], Cariveau, D. [3], Smith, H. [1], Bartomeus, I.[4] (TBC)

31 March, 2021

Affiliations:

[1] Centre for Environmental and Climate Science, Lunds Universitet, Lund, Sweden
[2] U.S.D.A. Geological Survey?
[3] University of Minnesota
[4] Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio 26, Isla de la Cartuja, E-41092 Sevilla, Spain

*Correspondence: liam.k.kendall@gmail.com

Thoughts and ideas

##lets try get it in the functional ecology special issue~ https://besjournals.onlinelibrary.wiley.com/page/journal/13652435/homepage/call_for_papers:animal_functional_traits

150 word abstract - due by April 30 Paper - due by 31 July

- Is distance the right word? I cant decide between distance or range, range seems more synonymous with resource use and therefore maybe better i.e. they will forage within this range, rather than at this distance

- I think the physiological ~ functional split in estimates (feeder and homing vs. all others) is very interesting. I am open to ideas regarding the names - maybe behavioural is better than functional?

- I didn't find an effect of polylecty for either maximum or typical distances - i thought there was one but there were a few estimates which were incorrectly coded - and after fixing these,there was no effect. Do we keep lecty stuff in paper?

- Not enough coverage to use Family as a predictor #see table(forage.traits$Family$, $forage.traits$distance_type2)

- Henrik had an interesting idea - use colony size instead of categorical eusociality

- perhaps one additional analysis with bumblebees split out?

Abstract

1. The foraging distance of bees structures the scale at which bee ~ plant interactions, pollination and other associated ecosystem functions occur. Previous studies have demonstrated that foraging distance is positively allometric (i.e larger bees can forage at greater distances than smaller bees), yet how foraging distance is related to other functional traits important to foraging behavior, such as eusociality and floral specialisation remains unknown.

2. We conducted a systematic review of known bee foraging distances, compiling 411 estimates for 100 species. We divided estimates firstly into *typical* or *maximum* foraging distances and then into physiological (i.e. homing ability) and functional estimates (e.g. molecular methods, nest- plant association studies). For each bee species, we collected information on their body size (intertegular distance), level of eusociality (highly eusocial, primitively eusocial or solitary) and floral specialization (oligolectic vs. polylectic).

3. We then conducted a phylogenetic un-weighted meta-analysis of typical and amximum bee foraging distances in relation to body size and functional traits.

4. We found that body size was only weakly predictive of both typical and maximum foraging distances: R^2:0.12 & 0.16).

5. However, models that included distance type (i.e. physiological and functional foraging distances), in conjunction with eusociality greatly improved predictions of foraging distances (R^2s:0.36 & 0.37).

6. Physiological estimates of foraging distances increased more steeply than functional estimates in relation to body size. Further, highly eusocial species can forage at greater distances per unit body mass (ITD) than primitively eusocial or solitary bee species. In contrast, we found no relationship between floral specialisation and foraging distances in solitary species.

7. The greater foraging distances in highly eusocial species suggests...
Physiological estimates are likely to overestimate foraging range...
In contrast, the shallow slope of functional estimates means that the majority of bee species forage within 403.4287935 ...
Functional ranges/distances rather physiological esimates should be used in conservation planning and crop pollinator management...

Introduction

Paragraph One: Ecological significance of foraging in terms of ecosystem function. Effects on foraging - landscape context etc -links to body size

Types of measurements Structure that feeder and homing as physiological measures - others as functional

Why should this be revisited? -Many more studies -new analytical methods -need to incorporate things like phylogeny etc

Research questions

1) How accurate is body size in predicting foraging distance in bees?

2) How do functional and physiological measurements of bee foraging distance/range scale allometrically?

3) Do the functional and physiological measurements of foraging distance differ between eusocial and solitary bee species?

4) Does floral specialisation affect foraging distances in solitary bee species?

Materials and Methods

To identify relevant publications for our review and meta-analysis, we first compiled foraging distance estimates from a previous meta-analysis by Greenleaf et al. 2007 and a review by Zurbuchen et al. 2010. We then undertook a systematic Scopus database search with the following search terms: TITLE-ABS-KEY ((bee OR apoid*) AND (forag* AND distanc*) OR "flight range"). As of 12 March 2021, this returned 643 articles. We then subsetted this database to articles published post-2006 (to coincide with Greenleaf et al. 2007) and screened all articles for foraging distance estimates (n = 180 articles). We focussed solely on

female bee foraging patterns, excluding all studies that studied male and/or queen dispersal distances. From this search, we identified 114 articles. For each estimate, we defined the type of distances measured (maximum, typical or observed) and methodology used to measure foraging distance (see Table 1 for definitions), following Greenleaf et al. 2007.

Group	Type	Type2	Definition
Type of distance	**Typical**		Typical foraging distance was defined as the mean, median or mode foraging distance by a species within a study
	Maximum		Maximum foraging distance was defined as the maximum distance or distances observed within a experiment or study
	Observed		Observed foraging distances were those estaimtes that could not be defined as either typical or maximum distances. For example. A...B...
Method	**Functional**	**Associative**	Associative studies were those that measured foraging distance by associating known nests / hives and floral resources..
		Mark-recapture	Mark-recapture...
		Molecular	Molecular...
		Tracking	Tracking...
		Waggle dance	Dancing...
	Physiological	**Feeder**	Feeder studies involved...
		Homing	Homing studies...

Table 1. Types of bee foraging estimates and methodologies..

Species taxonomy and functional traits

We checked the validity of species' names using (Zach to fill X, Y, and Z). We then collected the following traits for each species: female body size (measured as the intertegular distance, Cane et al. 1987), level of eusociality and floral specialisation. We obtained body size from literature sources (i.e. pollimetry, brazilian trait dataset, traitbase) and by directly contacting researchers. Where multiple ITD measurements for a given species were found, we took the mean value. For eusocial species, where applicable, we obtained ITD measurements for the caste used within the study (i.e. workers or queens).

We delimited species into three levels of sociality: *obligate solitary*, *primitively eusocial* or *highly eusocial*. Obligate solitary species were those bee species that provision their own nest cells. This group includes species that live communally or in aggregations. Primitively eusocial species were those species that have non-permanent colonies and that are founded by a single female. This group included bumblebees *Bombus* species, as well as socially flexible *Lasioglossum* species, and those with overlapping generations e.g. *Xylocopa* species. Highly eusocial species were those species that had permanent colonies, which reproduce by budding. This group included all honeybees *Apis* species, and stingless bees (Meliponini).

Lastly, we grouped species, based on their level of floral specialisation, as either *oligolectic* or *polylectic*. Oligolectic speies were defined as those species who consistently collect pollen from a single plant species or group of similar or related plant species, even the presene of other pollen sources. Polylectic species were defined as those that use multiple, unrelated species for pollen.

Statistical analysis

All statistical analyses were undertaken in *R* (citation).

We used Bayesian generalized linear mixed effect models to analyze bee foraging distances as a function of body size and functional traits. We chose to use an un-weighted model as the vast majority of studies did not provide variance components for typical foraging distances. Further, the nature of maximum foraging distance (i.e. the largest distance observed within a species) is incompatible with a meta-analytical model as it lacks a definable variance. We modeled typical and maximum foraging distance separately. Observed foraging distances were excluded from analyses, as were all estimates with unknown metholology. As is typical in allometric studies, we log-transformed foraging distance prior to analyses. However, as intertegular distance is logarithmically related to body size (Cane et al. 1987; Kendall et al. 2019), we compared the predictive accuracy (R^2) of models with and without log-transformed ITD. The raw ITD was considerably more predictive than ln(LTD), thus we present those models.

For these purposes we specified the following models (for both typical and maximum foraging distance): * 1) Distance ~ ITD * 2) Distance ~ ITD * Metric type (categorical, physiological or functional) * 3) Distance ~ ITD * Metric type * eusociality (categorical, three levels)

In addition, we also modelled distance ~ ITD * Lecty for solitary bees species.

For all models, the random effect structure consisted of random effects for i) publication, ii) a random intercept and slope for metric, iii) a phylogenetic effect, which consisted of a phylogenetic relatedness correlation matrix between bee genera and iv) a non-phylogenetic species level effect. For the phylogenetic effect, we constructed a bee phylogeny using an available bee genera tree (Hedtke, Patiny, & Danforth, 2013). We removed non-represented genera and then fitted a chronogram from this phylogeny by penalized likelihood, and a correlated rate model (Paradis et al. 2004). We then converted this to a phylogenetic correlation matrix.

We assessed the significance of the main- and interactive effects in each models by assessing whether 95% credible intervals bracketed zero. In the case of insignificant interactive effects in *Model 3*, we removed the interactions including eusociality (i.e. ITD * eusociality and Metric type * eusociality) and refitted a reduced model with eusociality as an addictive effect.

We parameterised each model with a *Gaussian* distribution, which was run for 2000 iterations, and a burn-in of 1000 iterations. We set weakly informative priors and manipulated Δ and maximum tree depth to avoid divergent transitions. We visualised posterior predictive checks using bayesplot (v1.6.0, Gabry & Mahr 2017) and assessed chain convergence for each sub-model separately. We considered effects were considered significant when 95% credible intervals did not bracket zero.

Results

Summary

In total, we included 352 estimates of foraging distance (typical, n = 159) & maximum, n = 193) in our analyses. We excluded 32 'observed' foraging distance estimates from analyses. Typical and maxmium foraging distance estimates included 78 species, 29 genera and 6 families. Honeybees *Apis* spp. (124 estimates) and bumblebees *Bombus* spp. (98 estimates) were the most commonly studied taxa. Maximum foraging distance estimates ranged from 83 metres (*Andrena hattorfiana*) to 23 kilometres (*Eufriesea surinamensis*). Typical foraging distance estimates ranged from 23.8 metres (*Bombus flavifrons*) to 7.5 kilometres (*Xylocopa virginica*).

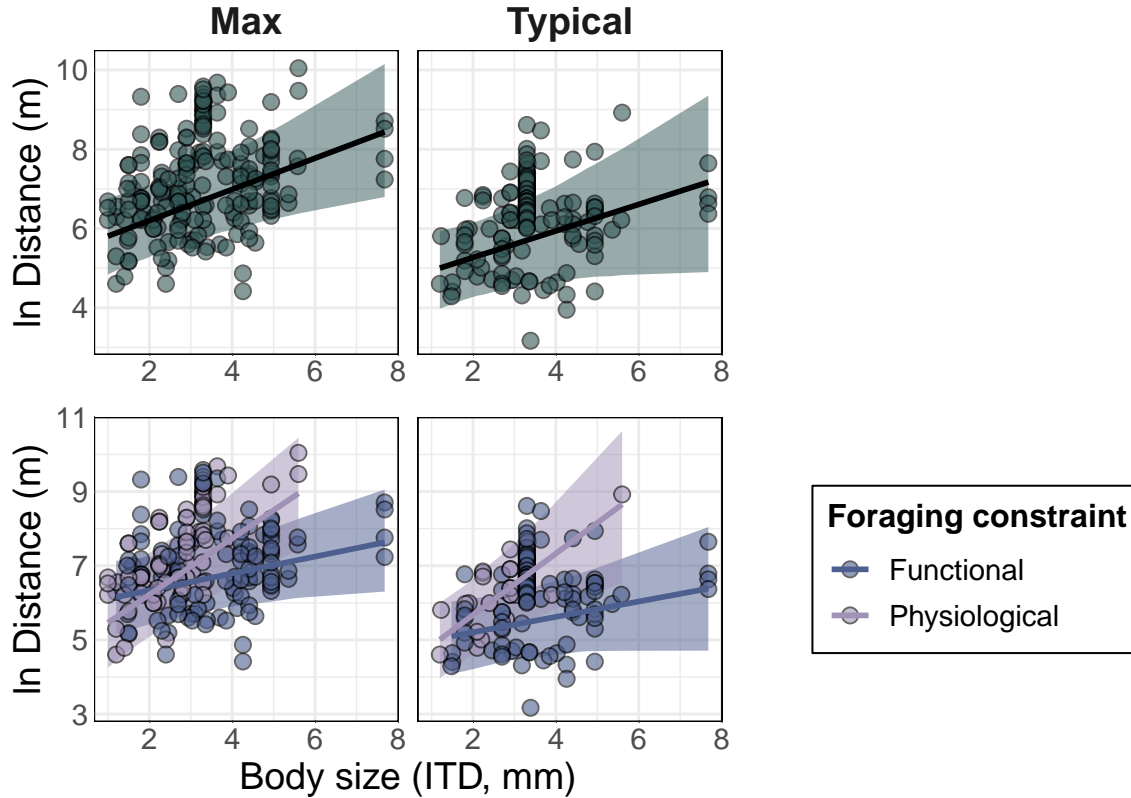ADD TABLE OF ESTIMATES -species summary

Figure 1: Relationship between bee foraging distance (log-transformed metres) and body size (ITD: intertegular distance). Top: Overall trend, bottom: type of measurement used to estimate foraging distance: physiological (feeder or homing experiments) or functional (other methods, see **Table 1**). Bold lines and ribbons indicate lines of best fit and corresponding 95% credible intervals. Circles denote raw data.
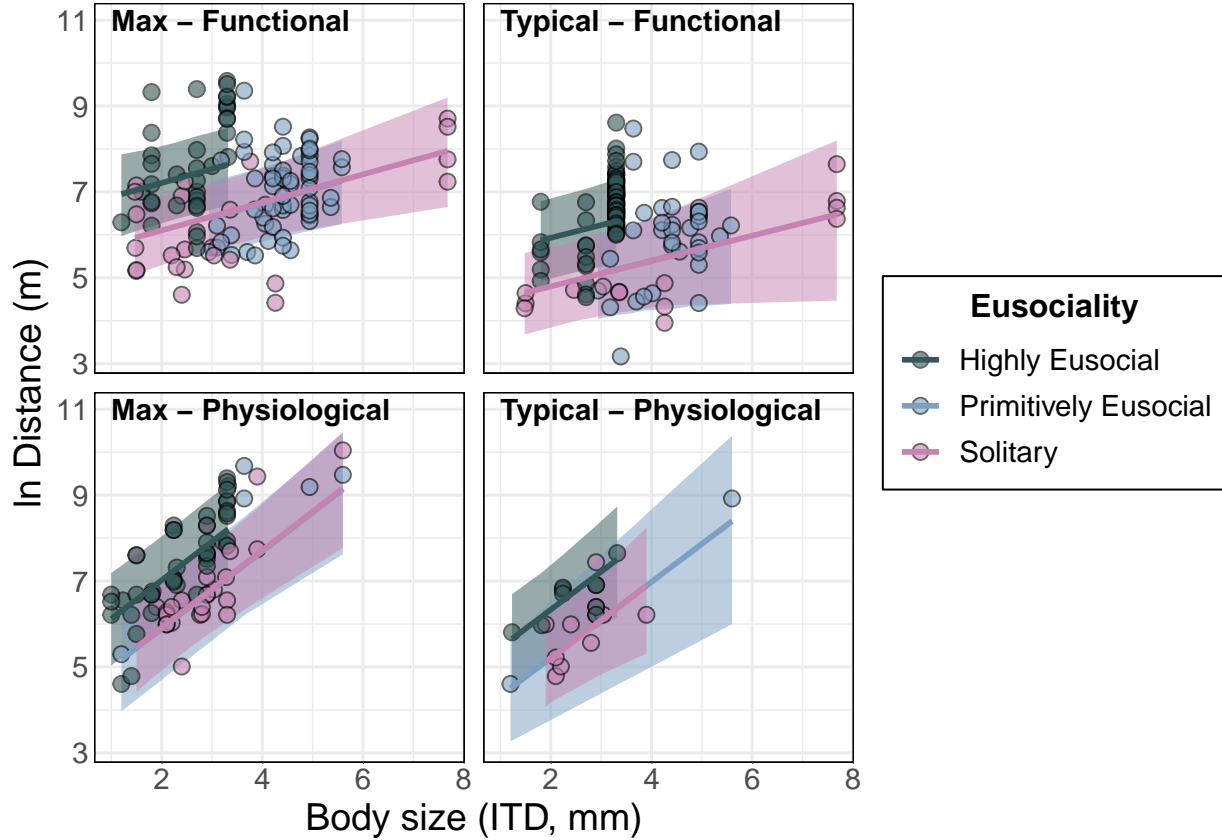
Figure 2: Relationship between phyisiological or functional bee foraging distances (log-transformed metres), body size (ITD) and eusociality. Bold lines and ribbons indicate lines of best fit and corresponding 95% credible intervals. Circles denote raw data.

Allometry of foraging distance

Overall, body size was positively related to both maximum (*Marginal R^2 = 0.16*) and typical (*Marginal R^2 = 0.12*) foraging distances (Figure 1).

We found that physiological and functional constraints/measurements upon foraging distances differ in their relationship (slope) with body size (Model table, Figure 2). Specifically, physiological measurements of foraging distances increased at a greater rate per unit ITD than functional constraints/measurements (significant interaction with ITD, steeper slope). For example, in small bees (e.g. ITD of 2mm), physiological and functional measurements of foraging distance are similar (e.g. Typical: *functional* 182.37, *physiological* 290.44; Maximum: *functional* 564.3, *physiological* 502.57). However, in larger bees (ITD: 4mm), whereas physiological limits upon forging distance increase considerably, typical - 1522.51m, maximum - 2290.54m, functional limits do not: typical, 276.08m; maximum, 889.87m.

Eusociality was also highly important in structuring species differences in both functional and physiological bee foraging distances (*Marginal R^2*: Typical distance: 0.36, Maximum distance: 0.37. In particular, highly eusocial bees (*Apis* species and stingless bees (Tribe: Meliponini)) exhibited significantly higher physiological and functional foraging distances than either primitively eusocial or solitary species (MODEL TABLE of "max.euc.phylo.reduced.brm"). Primitively eusocial and solitary species exhibited near-identical foraging distance estimates. For example, a European honeybee *Apis mellifera* (ITD:) is expected to have a physiological foraging distances of between 1778.52 and 3604.21m. In contrast, a primitively eusocial or solitary bee of the same size, such as *Osmia pedicornis*, is expected to have a physiological foraging distances of between 573.02 and 1193.93m.

We found no effect of floral specialization on either typical and maximum foraging distance in solitary bee

species (See Table S7 & S8). **Table SX-XX. Model tables**

Table S1. Mean distance ~ ITD model

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov = Bg))
##    Data: forage.traits.mean (Number of observations: 159)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##          total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 47)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.53      0.11     0.33     0.77 1.00      940     2086
##
## ~Genus (Number of levels: 17)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.89      0.44     0.11     1.81 1.00     1233     1292
##
## ~Metric2 (Number of levels: 6)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.42      0.34     0.01     1.28 1.00     2731     2391
## sd(ITD)               0.28      0.16     0.06     0.67 1.00     1195     1417
## cor(Intercept,ITD)   -0.22      0.57    -0.98     0.91 1.00      971     1591
##
## ~spp (Number of levels: 47)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.46      0.11     0.25     0.70 1.00     1188     2051
##
## Population-Level Effects:
##           Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept     4.60      0.59     3.44     5.73 1.00     3019     2867
## ITD           0.33      0.18    -0.02     0.68 1.00     2007     1992
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.45      0.03     0.39     0.51 1.00     2661     2644
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Table S2. Max distance ~ ITD model

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov = Ag))
##    Data: forage.traits.max (Number of observations: 193)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##          total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 81)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.55      0.09     0.39     0.73 1.01     1015     1849
```

```
##
## ~Genus (Number of levels: 29)
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)    1.21      0.34     0.61     1.95 1.00     1509     1731
##
## ~Metric2 (Number of levels: 7)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.70      0.44     0.05     1.72 1.00      765      932
## sd(ITD)               0.21      0.13     0.02     0.53 1.00      627      717
## cor(Intercept,ITD)   -0.27      0.54    -0.94     0.89 1.00     1008     1548
##
## ~spp (Number of levels: 78)
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)    0.39      0.08     0.24     0.56 1.01     1238     1814
##
## Population-Level Effects:
##           Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept     5.41      0.56     4.33     6.53 1.00     2277     2615
## ITD           0.39      0.13     0.12     0.67 1.00     2226     2578
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.51      0.04     0.43     0.59 1.00     1084     2115
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Table S3. Mean - metric type - distance model

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * limits + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov =
##    Data: forage.traits.mean (Number of observations: 159)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##         total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 47)
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)    0.53      0.10     0.34     0.75 1.00     1214     2336
##
## ~Genus (Number of levels: 17)
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)    0.78      0.42     0.06     1.66 1.00     1172     1480
##
## ~Metric2 (Number of levels: 6)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.37      0.30     0.02     1.15 1.00     2251     1795
## sd(ITD)               0.14      0.11     0.01     0.43 1.00     1332     2001
## cor(Intercept,ITD)   -0.14      0.58    -0.96     0.93 1.00     2152     2404
##
## ~spp (Number of levels: 47)
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)    0.46      0.11     0.25     0.70 1.00     1133     1402
```

```
##
## Population-Level Effects:
##                 Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept           4.79      0.62     3.55     5.95 1.00     2524     2833
## ITD                 0.21      0.14    -0.07     0.50 1.00     2213     2463
## limitsphysio       -0.78      0.67    -2.11     0.53 1.00     2890     2837
## ITD:limitsphysio    0.62      0.25     0.13     1.10 1.00     2593     2242
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.44      0.03     0.39     0.51 1.00     2787     2798
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Table S4. Max - metric type - distance model

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * limits + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov =
##    Data: forage.traits.max (Number of observations: 193)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##         total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 81)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.55      0.08     0.39     0.72 1.00     1448     2177
##
## ~Genus (Number of levels: 29)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     1.11      0.33     0.55     1.86 1.00     2009     2696
##
## ~Metric2 (Number of levels: 7)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.76      0.36     0.24     1.63 1.00     1628     1863
## sd(ITD)               0.10      0.09     0.00     0.32 1.00     1485     1875
## cor(Intercept,ITD)   -0.37      0.56    -0.99     0.87 1.00     2874     2729
##
## ~spp (Number of levels: 78)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.38      0.08     0.24     0.54 1.00     1467     2349
##
## Population-Level Effects:
##                 Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept           5.88      0.57     4.74     7.01 1.00     2904     2772
## ITD                 0.23      0.12    -0.00     0.45 1.00     2884     2792
## limitsphysio       -1.18      0.64    -2.45     0.08 1.00     3319     3004
## ITD:limitsphysio    0.53      0.17     0.20     0.86 1.00     2688     2776
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.50      0.04     0.43     0.59 1.00     1928     2417
##
```

```
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Table S5. Mean - metric type - eusociality distance model

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * limits + social_tree + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | g
##    Data: forage.traits.mean (Number of observations: 159)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##          total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 47)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.49      0.10     0.31     0.71 1.00     1230     2012
##
## ~Genus (Number of levels: 17)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.44      0.34     0.01     1.26 1.00     1696     1694
##
## ~Metric2 (Number of levels: 6)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.40      0.32     0.02     1.23 1.00     2455     2305
## sd(ITD)               0.16      0.13     0.01     0.51 1.00     1185     1831
## cor(Intercept,ITD)   -0.15      0.58    -0.97     0.92 1.00     2035     2643
##
## ~spp (Number of levels: 47)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.44      0.11     0.24     0.67 1.00     1168     1823
##
## Population-Level Effects:
##                               Estimate Est.Error l-95% CI u-95% CI Rhat
## Intercept                         5.34      0.57     4.16     6.47 1.00
## ITD                               0.30      0.15    -0.02     0.58 1.00
## limitsphysio                     -0.78      0.64    -2.02     0.48 1.00
## social_treePrimitivelyEusocial   -1.12      0.40    -1.88    -0.30 1.00
## social_treeSolitary              -1.13      0.39    -1.88    -0.38 1.00
## ITD:limitsphysio                  0.59      0.25     0.05     1.07 1.00
##                               Bulk_ESS Tail_ESS
## Intercept                         2526     2421
## ITD                               1955     2093
## limitsphysio                      3040     2981
## social_treePrimitivelyEusocial    2588     2744
## social_treeSolitary               2584     2667
## ITD:limitsphysio                  2089     2327
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.44      0.03     0.39     0.51 1.00     2724     3038
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Table S6. Max- metric type - eusociality distance model

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * limits + social_tree + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 |
##    Data: forage.traits.max (Number of observations: 193)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##          total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 81)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.57      0.08     0.41     0.74 1.00     1280     2034
##
## ~Genus (Number of levels: 29)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.47      0.32     0.03     1.22 1.00     1004     2177
##
## ~Metric2 (Number of levels: 7)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.74      0.35     0.24     1.60 1.00     1254     1038
## sd(ITD)               0.10      0.08     0.00     0.30 1.00     1770     2133
## cor(Intercept,ITD)   -0.36      0.56    -0.99     0.87 1.00     2494     2772
##
## ~spp (Number of levels: 78)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.38      0.08     0.23     0.54 1.00     1257     2236
##
## Population-Level Effects:
##                              Estimate Est.Error l-95% CI u-95% CI Rhat
## Intercept                        6.56      0.54     5.47     7.60 1.00
## ITD                              0.33      0.11     0.10     0.55 1.00
## limitsphysio                    -1.34      0.62    -2.61    -0.14 1.00
## social_treePrimitivelyEusocial  -1.13      0.33    -1.76    -0.47 1.00
## social_treeSolitary             -1.10      0.32    -1.69    -0.43 1.00
## ITD:limitsphysio                 0.57      0.16     0.26     0.88 1.00
##                              Bulk_ESS Tail_ESS
## Intercept                        2387     2577
## ITD                              2822     2543
## limitsphysio                     3038     2611
## social_treePrimitivelyEusocial   2819     2969
## social_treeSolitary              2560     2973
## ITD:limitsphysio                 2768     2428
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.50      0.04     0.43     0.58 1.00     1662     2813
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Table S7. Mean - lecty distance model

```
##  Family: gaussian
```

```
##   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * Lecty + (ITD | Metric2) + (1 | Authors) + (1 | spp) + (1 | gr(Genus, cov =
##     Data: forage.traits.mean.sol (Number of observations: 24)
## Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1;
##          total post-warmup samples = 8000
##
## Group-Level Effects:
## ~Authors (Number of levels: 9)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.40      0.30     0.02     1.11 1.00     3176     4704
##
## ~Genus (Number of levels: 10)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.75      0.43     0.05     1.70 1.00     2668     2822
##
## ~Metric2 (Number of levels: 3)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.72      0.54     0.03     2.02 1.00     6183     3895
## sd(ITD)               0.47      0.37     0.03     1.44 1.00     3023     4171
## cor(Intercept,ITD)    0.01      0.57    -0.94     0.95 1.00     4452     4963
##
## ~spp (Number of levels: 17)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.16      0.14     0.00     0.53 1.00     4377     3901
##
## Population-Level Effects:
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS
## Intercept             4.08      1.19     1.64     6.38 1.00     5309
## ITD                   0.30      0.40    -0.60     1.03 1.00     2964
## LectyOligolectic      0.04      1.14    -2.22     2.22 1.00     3082
## ITD:LectyOligolectic  0.05      0.42    -0.75     0.87 1.00     3021
##                   Tail_ESS
## Intercept             5198
## ITD                   3001
## LectyOligolectic      4438
## ITD:LectyOligolectic  4051
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.40      0.09     0.26     0.61 1.00     4103     5349
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Table S8. Max - lecty distance model

```
##   Family: gaussian
##     Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * Lecty + (ITD | Metric2) + (1 | Authors) + (1 | spp) + (1 | gr(Genus, cov =
##     Data: forage.traits.max.sol (Number of observations: 48)
## Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1;
##          total post-warmup samples = 8000
##
## Group-Level Effects:
```

```
## ~Authors (Number of levels: 26)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.84      0.20     0.44     1.27 1.00     2114     2372
##
## ~Genus (Number of levels: 16)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.49      0.39     0.02     1.46 1.00     2320     3831
##
## ~Metric2 (Number of levels: 4)
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)         0.54      0.43     0.02     1.61 1.00     5568     4312
## sd(ITD)               0.34      0.26     0.03     1.00 1.00     2271     2867
## cor(Intercept,ITD)   -0.09      0.57    -0.96     0.93 1.00     4157     4917
##
## ~spp (Number of levels: 28)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     0.18      0.14     0.01     0.52 1.00     2790     3986
##
## Population-Level Effects:
##                     Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS
## Intercept               4.88      0.91     3.03     6.71 1.00     4940
## ITD                     0.49      0.29    -0.11     1.03 1.00     3744
## LectyOligolectic        0.86      0.98    -1.08     2.78 1.00     4192
## ITD:LectyOligolectic   -0.42      0.36    -1.13     0.30 1.00     4333
##                     Tail_ESS
## Intercept               5522
## ITD                     4014
## LectyOligolectic        5094
## ITD:LectyOligolectic    5100
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     0.48      0.09     0.33     0.70 1.00     1876     2831
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Discussion