Supplementary Information

Soil biota contributions to soil aggregation

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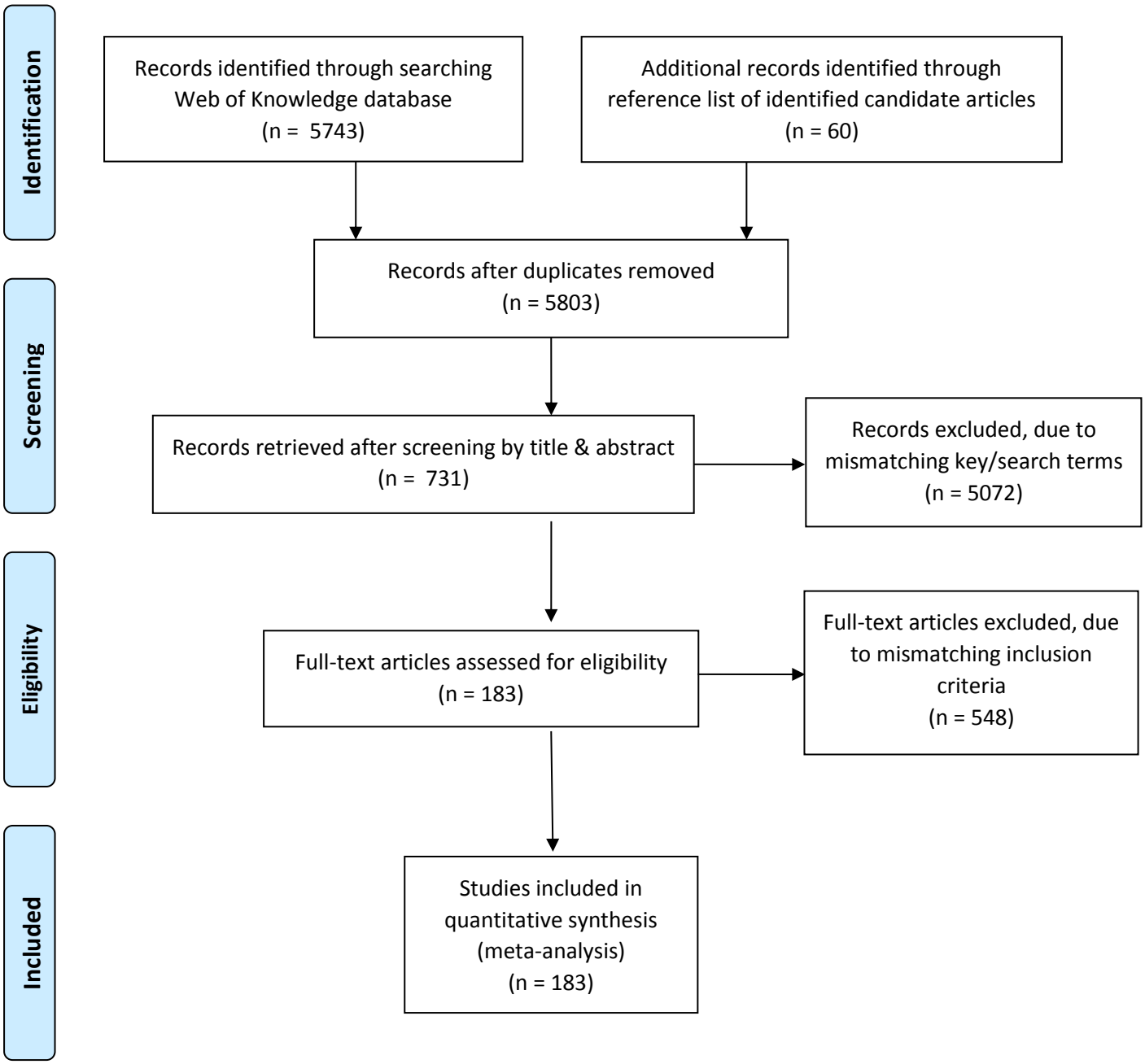
PRISMA 2009 Flow Diagram[1]



Supplementary Figure 1. PRISMA flow diagram illustrating the process of data collection and quality control.

Soil biota traits contributing to soil aggregation

Supplementary Table 1 Compilation of essential soil biota traits contributing to biological, biophysical and –chemical mechanisms of soil aggregation. The traits and mechanisms are assigned to the three major groups (kingdoms/domain) Animalia, Bacteria and Fungi.

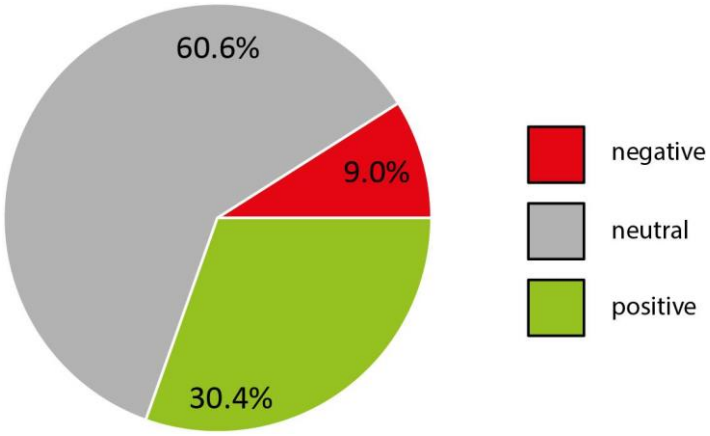
MECHANISMS	*Animalia*	*Bacteria*	*Fungi*	*Refs*
Biochemical	- particle adhering & orientation - cementing & surface sealing	- particle adhering & orientation - surface sealing - surface hydrophobicity	- particle adhering & orientation - cementing & surface sealing - surface hydrophobicity	2-13
By means of	intestinal & extracorporeal biopolymers (mucus enriched with Ca^{2+}, saliva), organic debris (integuments , eggs)	extracellular biopolymers (e.g. polysaccharides, hydrophobins), biofilm	extracellular biopolymers (e.g. polysaccharides, hydrophobins)	14-19
Biophysical	- compaction & compression - grinding & remolding - cast water regime	- none reported	- compaction & compression - entanglement - soil water regime	3,4,6,20-25
By means of	whole body (inside/ outside)	N/A	fungal hyphae/ mycelium	
Biological	- interactions with soil food web (ingest fungi & bacteria) - vector for dispersion of soil microbes	- interaction with plant roots & fungal hyphae	- interactions with plant roots & root-adhering bacteria - interactions with soil food web (e.g. grazers)	9,26-34
By means of	ingestion (geophagus organisms) & movement of soil fauna	signaling (e.g. exo-biopolymers, hormones)	signaling (e.g. exo-biopolymers, hormones)	
Scale of action	- Micron – cm scale (macroaggregates)	- Micron scale (micro-aggregates)	- Micron scale (macro- & micro-aggregates)	
Binding agent	- Transient & temporary binding agents	- Transient binding agent	- Transient & temporary binding agent	

Species composition of Single Taxa dataset

Supplementary Table 2 Overview of number of different species used in experiments of the studies included in this meta-analysis.

Domain	Kingdom	Phylum	*of these are*	No. of species
Eukaryota	Animalia	Annelida		33
			earthworm	*30*
			enchytraeids	*3*
		Arthropoda		26
			mite	*3*
			termite	*16*
			ant	*3*
			beetle	*1*
			millipede	*2*
			collembola	*1*
		Nematoda		1
Bacteria		Actinobacteria		12
		Bacteroidetes		2
		Cyanobacteria		13
		Firmicutes		38
		Proteobacteria		29
Eukaryota	Fungi	Ascomycota		75
			yeasts	*5*
		Basidiomycota		19
			yeasts	*3*
		Glomeromycota		24
		Mucoromycotina		7
		In total		279

Effect sizes composition



Supplementary Figure 2. Percentage of negative, neutral and positive effect size values in Single Taxa Dataset. For further detail, see **Fig. 2**.

The majority of trials provided effect sizes values for which the corresponding variance overlapped zero, meaning that there was a neutral effect when comparing treated (soil biota) and untreated (control) samples.

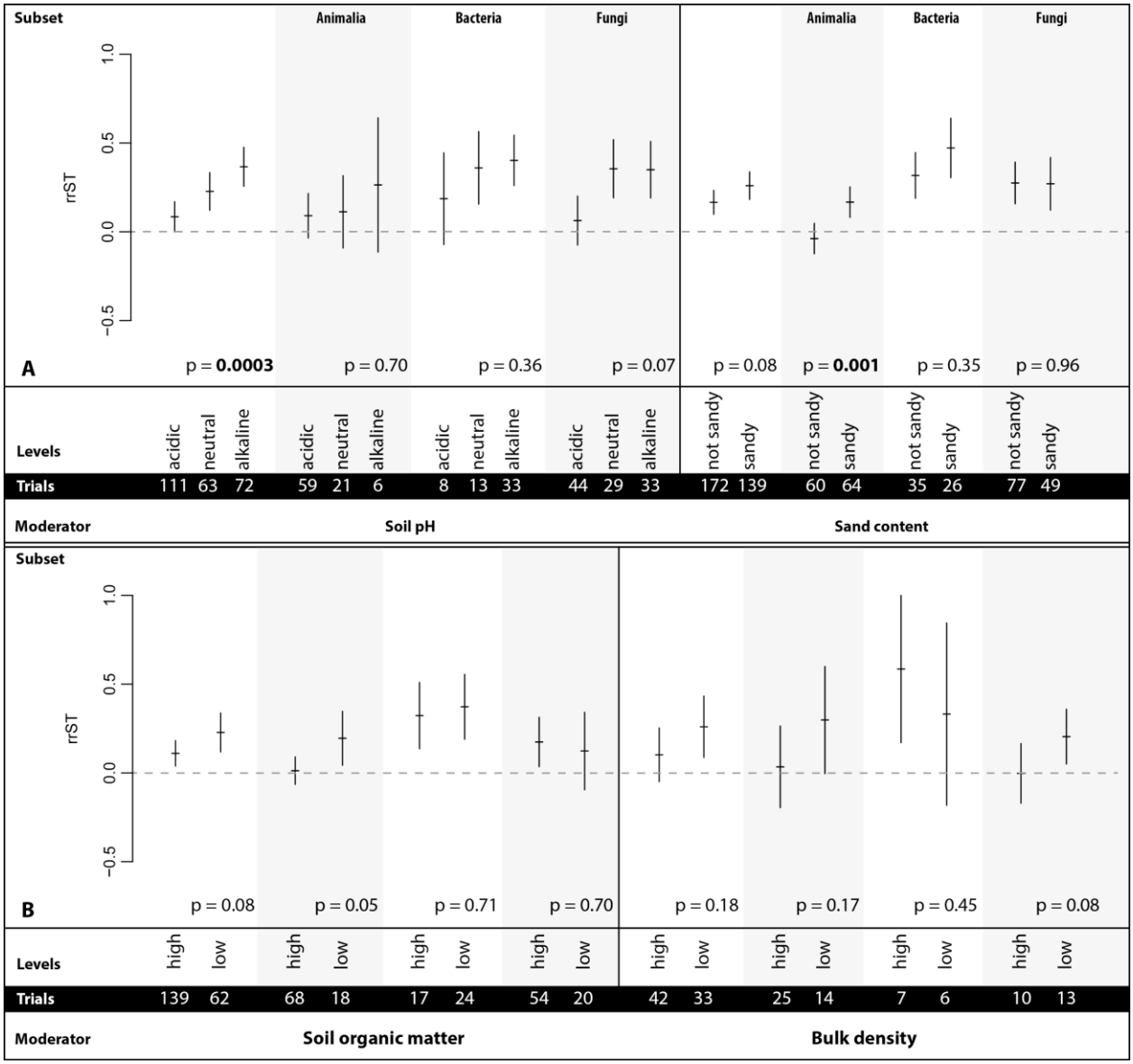
Soil- and experiment-related factors

The edaphic factors were all analyzed as categorical variables. **Soil pH** had three levels (acidic, neutral and alkaline) which followed the classification by USDA criteria (*soils. usda.gov*): acidic <6.5, neutral: 6.6 - 7.3 and alkaline >7.4. Data were converted to $CaCl_2$ to allow for comparison among different reagents (*eusoils.jrc.ec.europa.eu*). The values for soil pH ranged from 3.7 to 10. For **sand content**, values ranged from 3.8 to 97.4 %; these were grouped into two levels (sandy and not sandy). Data were either presented directly or deduced from the soil texture via the USDA soil triangle [35]. All soil textures with a sand content > 50% were grouped in the moderator level sandy. **Soil organic matter** had two levels (low and high). The level low comprised all trials with soil organic matter content < 2%. Soil organic matter content ranged from 0.02 to 56.9 %. **Bulk density** had two levels (low and high). The level high comprised all trials with soil organic matter content >1. 2%. Bulk density of test soils ranged from 0.8 to 2.7 g cm^{-3}. In the analyses, we log-transformed this variable to improve data distribution.

The experimental factors were all analyzed as categorical variables. **Setting** had three levels (in vitro system, pot and field) representing the degree of environmental control which is lowest for field studies and highest for in vitro systems. The latter comprised all enclosed experimental units (in vitro systems) that were loaded under sterile conditions and could be sealed off for the duration of the experiment (e.g. Petri dishes, bioreactors and sealed jars). **Experimental duration** had three levels (short (<56 days), medium (56-112 days) and long (>112 days)) which followed the classification used in previous works [36,37]. Only data from the last harvest were included. The three variables **additional organic matter** application, **plant**, **sterilization** of growth substrate all had two levels (yes and no). These moderators were tested to check for any potential biases introduced by such practices. If there was an option, studies with sterilized growth substrate and no additional organic matter application or plant in the test system were included during data collection.

Analysis outcomes for soil- and experiment-related factors

We tested soil- and experiment-related factors to evaluate their impact on the effect size rrST in the Single Taxa dataset since there were not sufficient data available to conduct robust analyses in the Interacting Species dataset for the effect size rrIT.



Supplementary Figure 3. Effect of soil-related factors (soil pH, sand content, soil organic matter and bulk density) on the effect size rrST. For each variable an overall summary effect and results of HTC-specific subset analyses are presented. Effects are represented as means and 95% CIs; below the p-values, moderator levels and number of trials included in the analysis can be found. Significance test for between-level differences of moderators were based on a permutation test (random effects design); $p < 0.05$ were significant and marked in bold.

For the soil-related factors, we found a significant overall relationship for the moderator variables soil pH and a trend for sand content (**Supplementary Figure 3**). For sand content, we found a significant effect in the Animalia subset. Thus soils with high pH and sand content favored soil biota mediated effects on soil aggregation.

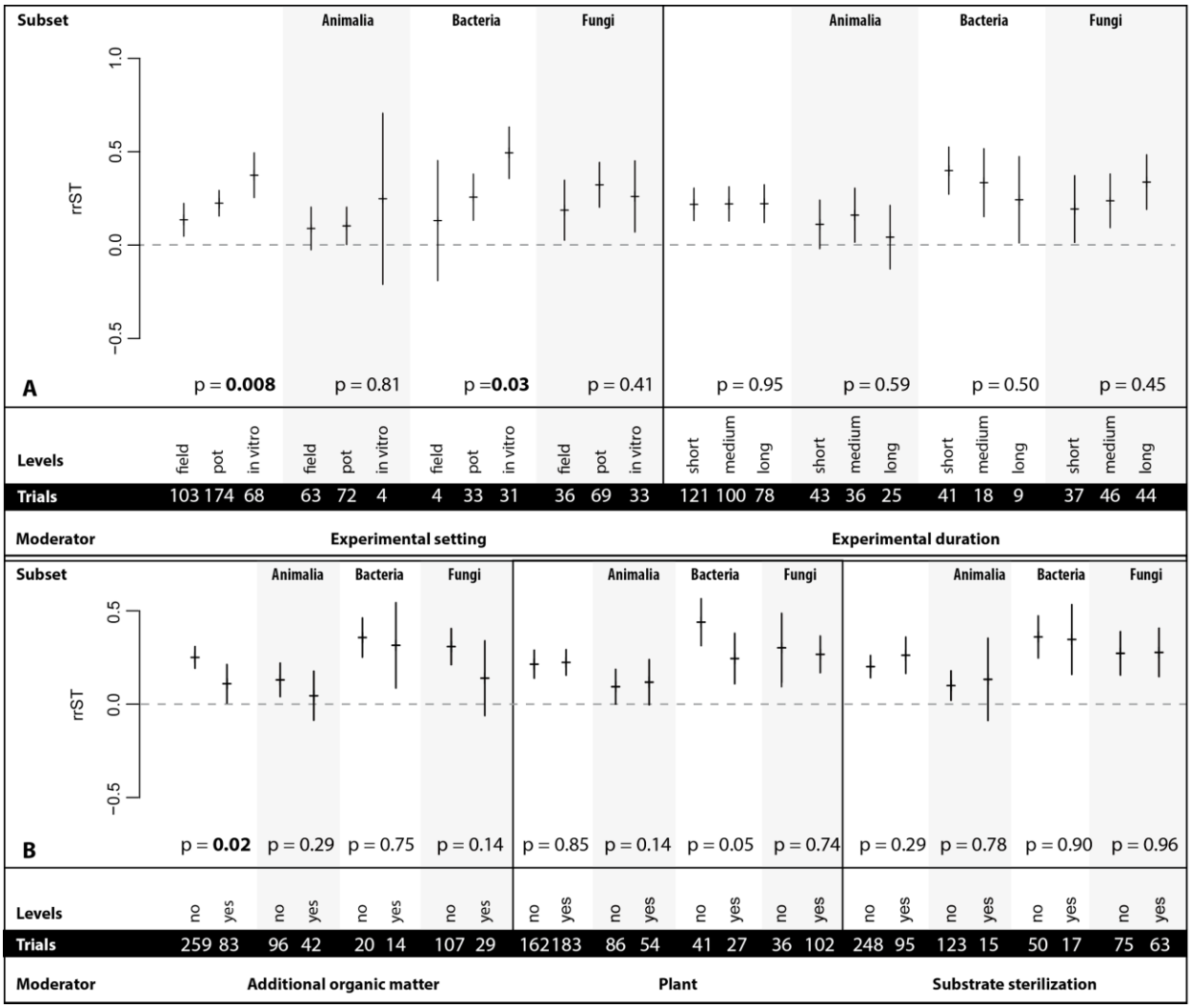
In our analyses we found that only the two soil-related moderator variables soil pH and sand content modulated the soil biota effects on soil aggregation. Higher soil pH leads to increased concentrations of negative charges and hence increased repulsive forces between particles resulting in dispersion [38]. The detected positive soil biota mediated effect suggested that their actions in soil could counteract the negative impact of increasing soil pH on soil aggregation. Coarsely textured soils high in sand content were more positively affected by soil biota than fine textured soils with a low amount of sand particles. In soils rich in clay particles swelling and dispersion processes might override soil biota contribution to soil aggregation [39].

For the experiment-related factors, we found a significant overall impact of additional organic matter application and experimental setting on the effect size rrST (**Supplementary Figure 4**). For the latter one, the same and also significant effect was detectable for bacteria. For Animalia, this pattern was present but not significant. In the Bacteria subset the between-level differences were significant.

In our analyses we found that only the two experiment-related moderator variables experimental setting and additional organic matter application modulated the soil biota effects on soil aggregation.

Soil organic matter itself functions as a binding agent and aggregate nucleation sites during the process of soil aggregation [40]. Thus additional application of organic matter diminished the soil biota effect on soil aggregation.

The experimental setting affected the soil biota mediated effect on soil aggregation; the more controlled the setting the higher were the resulting effects. This finding was in accordance with other studies comparing field and lab studies e.g. [41]. To evaluate if the identified moderator variables are potentially confounding factors, we re-analyzed our data while excluding all trials of experiments with application of in vitro experiments, application of additional organic matter, acidic or not sandy (sand content < 50%) soil. For further information, see paragraph “Evaluation of potential confounding effect by “experimental setting” below (**Supplementary Figure 5**).

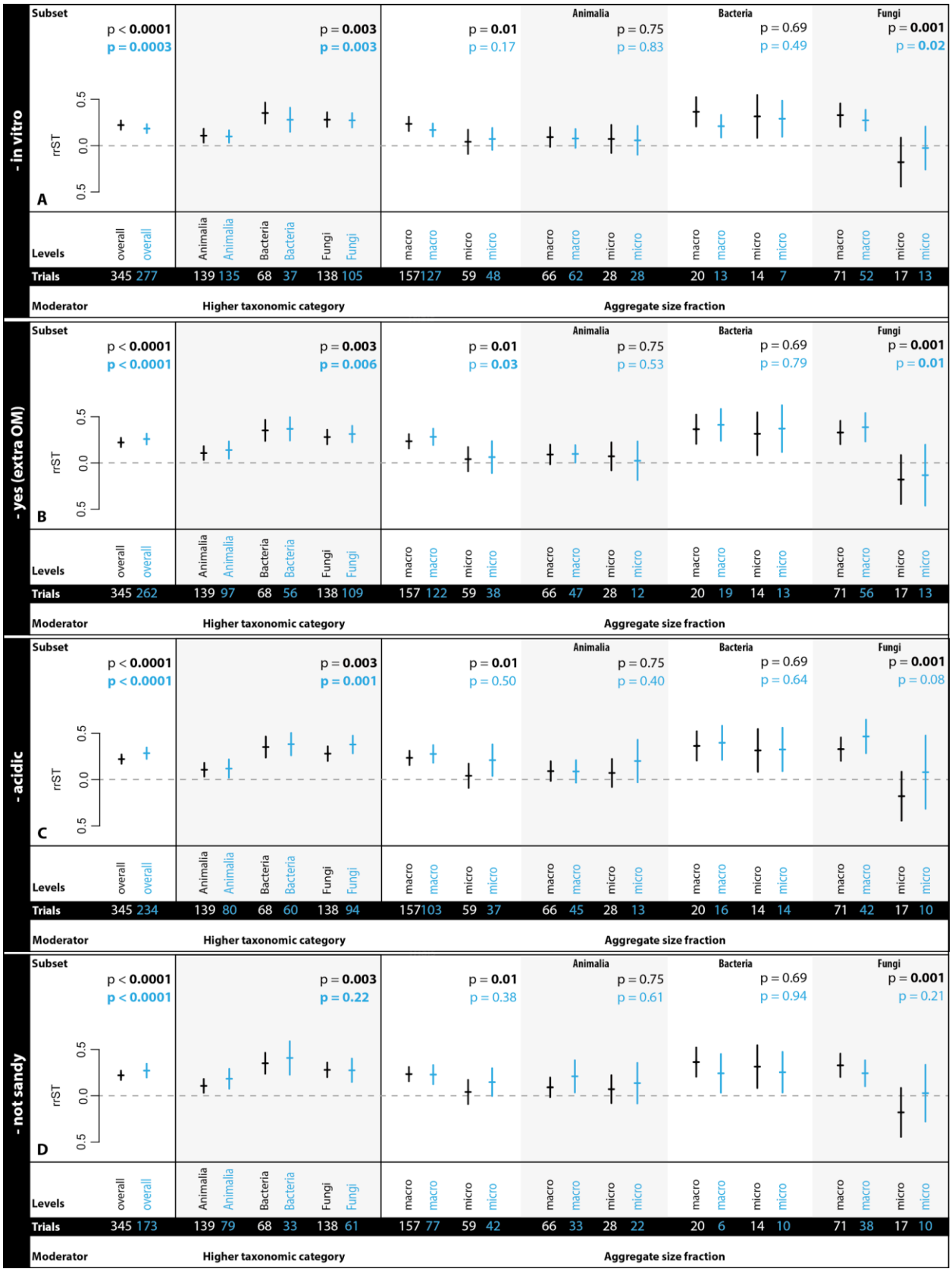


Supplementary Figure 4. Effect of experiment-related factors (experimental duration and setting, additional organic matter application, plant as co-occurring organism and pre-sterilization of growth substrate) on the effect size rrST. For each variable an overall summary effect and results of HTC-specific subset analyses are presented. Effects are represented as means and 95% CIs; below the p-values, moderator levels and number of trials included in the analysis can be found. Significance test for between-level differences of moderators were based on a permutation test (random effects design); $p < 0.05$ were significant and marked in bold.

Sensitivity analyses I: Evaluation of potential confounding variables

As depicted in **Supplementary Figure 3** and **Supplementary Figure 4**, the moderators soil pH, sand content and experimental setting had a clear influence on our effect size rrST: with increasing environmental control, application of additional organic matter, decreasing soil pH and sand content the effect sizes increased. To evaluate how these potential confounding factors (use of in vitro experiments, application of additional organic matter, acidic or not sandy (sand content < 50%)) soil influenced our results - with the potential to over- or underestimate soil biota effects on soil aggregation - we re-analyzed our data while excluding all trials derived from the respective experiments (**Supplementary Figure 5**).

When excluding “in vitro” trials, we found for the overall summary effect a reduced but still pronounced positive effect (Single Taxa dataset: 24% [CI: 18-31%]; Single Taxa dataset - in vitro trials: 20% [CI: 14-26%]). The exclusion of “acidic”, “not sandy” or “extra OM-yes” trials led to an increase of the overall summary effect (Single Taxa dataset - acidic trials: 33% [CI: 25 to 41%], Single taxa dataset - not sandy trials: 31% [CI: 22 to 41%], Single Taxa dataset - extra OM-yes: 28% [CI: 21 to 36%]) which still remained positive. The exclusion of respective trials only marginally altered the patterns we found (**Supplementary Figure 5**). Thus, by including in vitro experiments we only slightly overestimated while by including acidic and sandy soil trials and trials with additional organic matter application we slightly underestimated soil biota mediated effects on soil aggregation.

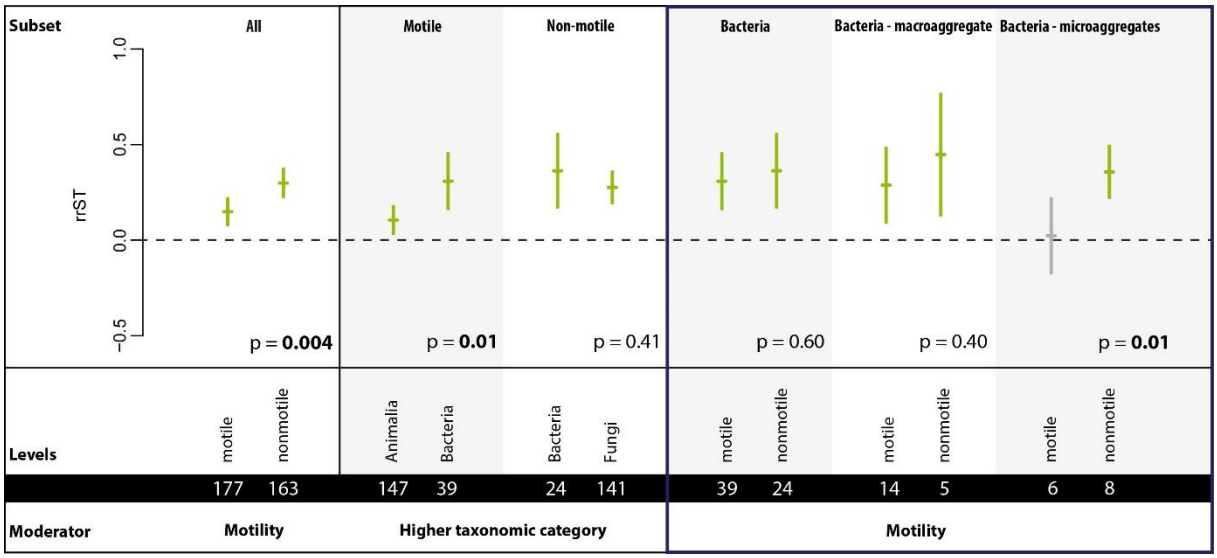


Supplementary Figure 5. Comparison of analysis outcomes for effect size rrST with (black) and without (blue) trials extracted from "in vitro", "extra organic matter (yes)", "acidic soil" and "not sandy soil" experiments for overall effect, higher taxonomic category (HTC) and aggregate size fraction (for overall and HTC-specific subsets). Effects are represented as means and 95% CIs; below the p-values, moderator levels and number of

trials included in the analysis can be found. Significance test for between-level differences of moderators were based on a permutation test (random effects design); $p < 0.05$ were significant.

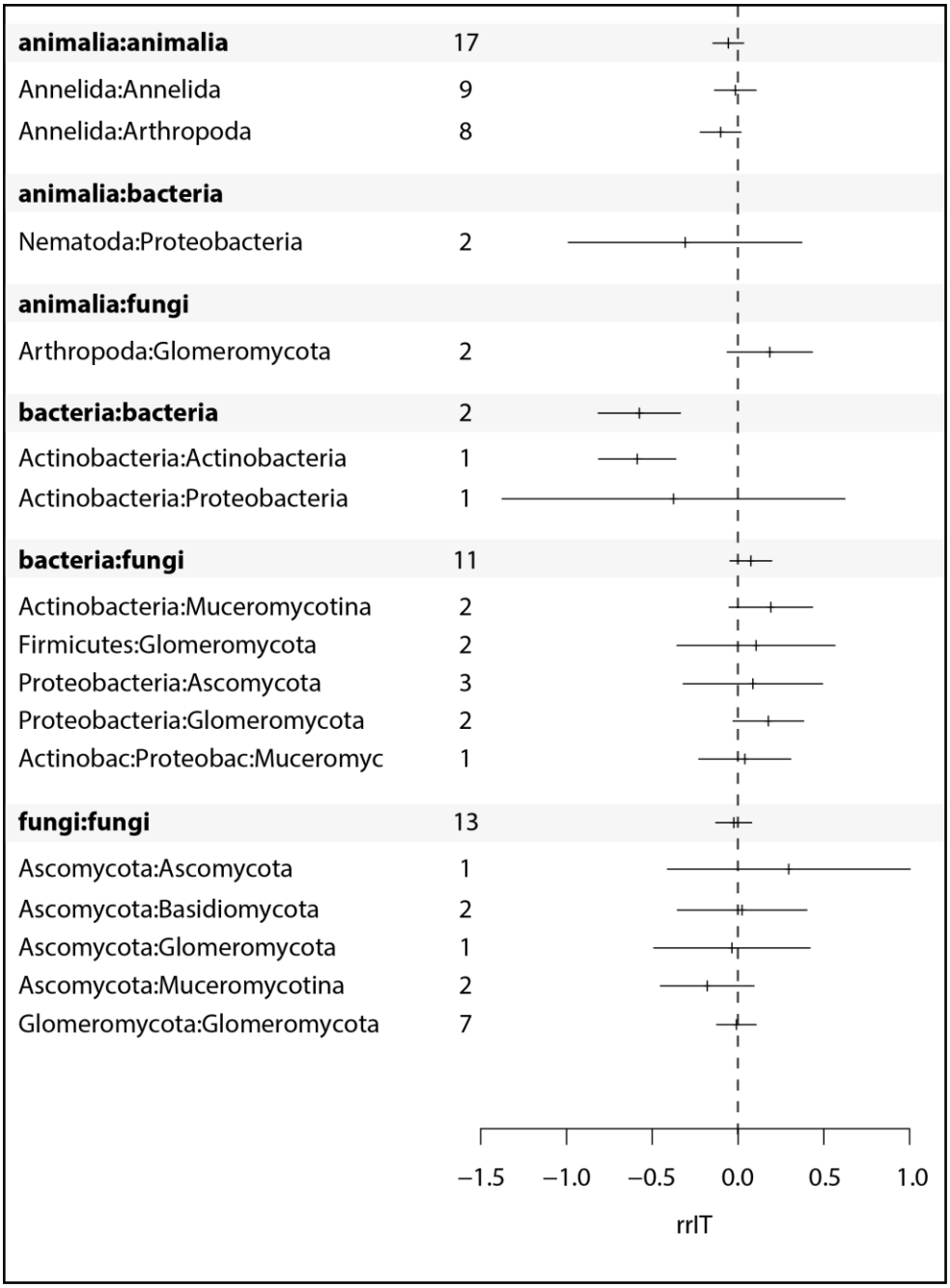
Investigation of soil biota 'motility' trait

While testing for the impact of motility on soil biota contribution to soil aggregation, we found that nonmotile organisms had higher effects on rrST (**Fig. 3, Supplementary Figure 6**). However, when investigated in more detail, it became apparent that this finding was confounded by taxonomic groups: motile soil animals showed lower rrST than nonmotile fungi. Since bacteria were the only taxonomic group comprising both motile and nonmotile species, we re-analyzed their impact on soil aggregation on "bacteria"- and "aggregate size fraction"-subsets. We found that nonmotile bacteria more positively contribute to soil aggregation than motile species and that this pattern is especially evident at the microaggregate scale. Due to their small body size and hence restricted area of influence, bacteria have a stronger impact on microaggregates [42] which is even more pronounced when species concerned are nonmotile. Thus at the microscale, bacteria contributed more strongly to soil aggregation when attached to surfaces (providing their binding agents, e.g. exo-biopolymers and formation of biofilms) compared to motile forms.



Supplementary Figure 6. Analysis outcomes of the effect size rrST for motility trait for complete dataset and various subsets to investigate potential confounding effect of taxonomic groups on our results. In the blue-framed compartment, data and subset analyses for the taxonomic group bacteria only are presented. Effects are represented as means and 95% CIs; below the p-values, moderator levels and number of trials included in the analysis can be found. Significance test for between-level differences of moderators were based on a permutation test (random effects design); $p < 0.05$ were significant.

Taxonomic group combinations both on HTC and phylum level



Supplementary Figure 7. Overview of the impact of taxonomic group combinations (on higher taxonomic category or phylum level) on the effect size rrIT. Effects are represented as means and 95% CIs with number of trials for each grouping.

Composition of inoculum for monoculture and species mixtures

Supplementary Table 3. Biomass of inoculum for monocultures and mixtures. In the column "phyla", those species combinations are marked in green which revealed a positive effect size mean as presented in **Supplementary Figure 7**.

phyla	organism groups	biomass of group1	biomass of group2	biomass of group3	biomass of group 4	biomass of groups in mixture
glomeromycota:glomeromycota	Glomus claroideum:mix	5% (v:v)	NA	NA	NA	5% (v:v)
firmicutes:glomeromycota	Glomus mosseae:Bacillus	1000 spores & 500 root fragments	10^9 cfu	NA	NA	NA
firmicutes:glomeromycota	Glomus mosseae:Bacillus (Bacillus sp. & Rhizobium leguminosarum)	1000 spores & 500 root fragments	20 ml, 10^9 cells * ml–1	10 ml, 10^8 cells ml –1	NA	NA
ascomycota:glomeromycota	Glomus intra:Aspergillus	5% (v:v)	3% (1.2 × 10^7)	NA	NA	NA
ascomycota:basidiomycota	Scleroderma:Aspergillus	10^6 spores per container (1:10 inoculum:substrate)	3% (1.2 × 10^7)	NA	NA	NA
proteobacteria:ascomycota	Enterobacter:Sordaria	10^9 bacteria cells	1 agar block	NA	NA	NA
ascomycota:ascomycota/basidiomycota	Rhodotorula rubra:Sordaria	10^8 yeast cells	1 agar block	NA	NA	NA
nematoda:proteobacteria	Meloidogyne jav:Pasteuria penetrans:Pseudomonas men	300 juveniles	13.5 x 10^6 cells	> 10^8 cells ml-1	NA	300 + 13.5 x 10^6 + "strains"
annelida:annelida	Amynthas:Lumbricus	140 individuals	140 individuals	NA	NA	70 + 70 individuals
annelida:annelida	Millsonia:Hyperiodrilus:Dichogaster	206 individuals m -2	206 individuals m -2	206 individuals m -2	NA	206 individuals m -2
annelida:annelida	Eisenia:Lumbricus	2 individuals	1 individual	NA	NA	NA
proteobacteria:glomeromycota	Glomus:Pseudomonas	5% (v:v)	10^9 CFU	NA	NA	NA
proteobacteria:glomeromycota	Glomus:Pseudomonas	5% (v:v)	10^9 CFU	NA	NA	NA
glomeromycota:glomeromycota	Glomus mix	55 spores of G. intraradices g -1	NA	NA	NA	64 spores (including group1 and 3

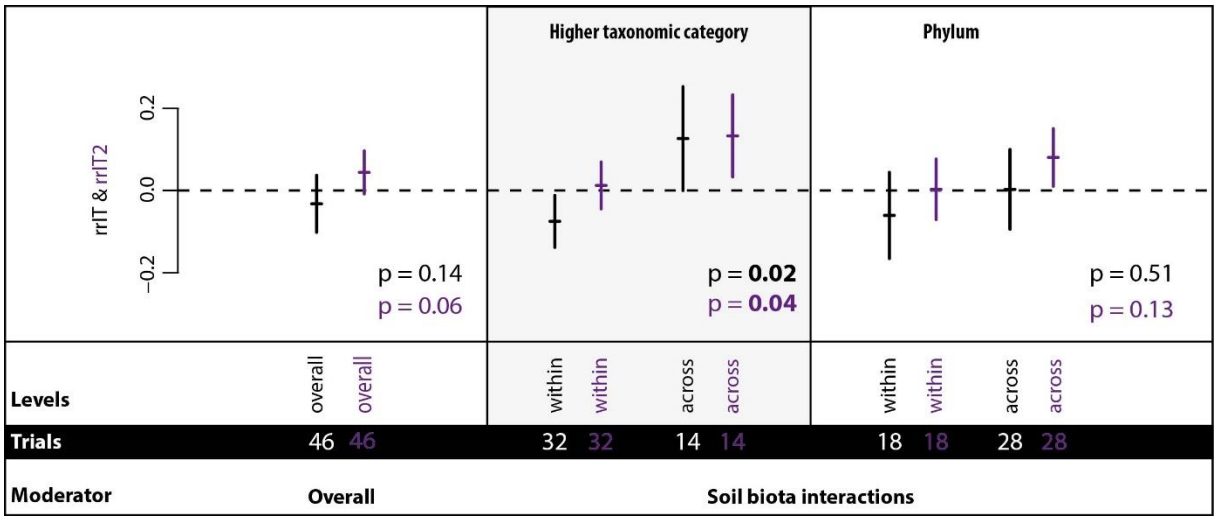
						additional species)
proteobacteria:ascomycota	Azotobacter:Trichoderma	not specified	not specified	NA	NA	NA
ascomycota:muceromycotina	Mucor:Penicillium	not specified	not specified	NA	NA	NA
arthropoda:glomeromycota	Proisotoma:AMF	extracted from 300 g of soil	80 individuals Proisotoma minuta (Collembola: Isotomidae) per pot	NA	NA	300g-extract + 80 Ind.
arthropoda:glomeromycota	Proisotoma:AMF	extracted from 300 g of soil	80 individuals Proisotoma minuta (Collembola: Isotomidae) per pot	NA	NA	300g-extract + 80 Ind.
actinobacteria:proteobacteria	Micrococcus:Pseudomonas:Actinomyces:Absidia	not specified	not specified	not specified	not specified	NA
anneldida:arthropoda	Pseudopolydesmus:Amynthas	1 large (0.156 g) or 2 small (0.045 g each)	4 earthworms per microcosm (0.865 g each)	NA	NA	NA
glomeromycota:glomeromycota	G.etunicatum:G.mosseae:Gi.margarita:A.lacunosa:G.aggregatum:G.versiforme	7000 IPU	7000 IPU	7000 IPU	7000 IPU	7000 IPU
glomeromycota:glomeromycota	G.etunicatum:G.mosseae:Gi.rosea	500 spores	500 spores	1000 spores	NA	250, 250 & 500 spores of each fungus
anneldida:annelida	Apporectodea:Lumbricus	1.82 g of A. caliginosa (6 adults)	1.98 g of L. rubellus (6 adults)	NA	NA	1.93 g of A. caliginosa+L. rubellus (3 of each species)
anneldida:annelida	Apporectodea:Allolobophora	1.37 g biomass	1.15 g biomass	NA	NA	1.70 g biomass
annelida:arthropoda	enchytrae:mite	50 individuals	400 individuals	NA	NA	50 + 400
annelida:arthropoda	enchytrae:mite:mite	50 individuals	3 individuals	400 individuals	NA	50 + 3 + 400

5

6

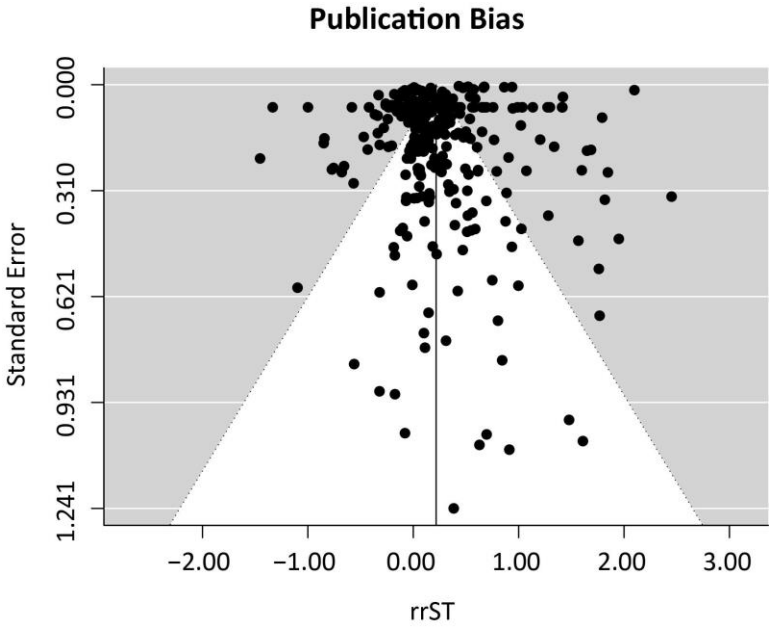
Alternative effect size for Interacting Taxa dataset

To evaluate the choice of our effect size rrIT, we calculated an alternative effect size. We used instead of the best performing monoculture the average of soil aggregation data for all the presented monocultures; the resulting effect size will be called hereafter rrIT2. We found that this alternative effect size yielded more positive analysis outcomes than rrIT while the moderator analyses showed comparable patterns and significance levels. Thus our conclusions are robust to the particular choice of effect size.



Supplementary Figure 8. Impact of soil biota interactions in mixtures across and within taxonomic groups (HTC and phylum level, respectively) on soil aggregation presented for the original effect size rrIT (in black) and the alternative effect size rrIT2 (in purple). Effects are represented as means and 95% CIs; below the p-values, moderator levels and number of trials included in the analysis can be found. Significance test for between-level differences of moderators were based on a permutation test (random effects design); $p < 0.05$ were significant.

Sensitivity analyses II: Publication bias



Supplementary Figure 9. Test for publication bias by funnel plot. Observed pattern indicated no sign of publication bias.

We tested our datasets for publication bias by plotting the effect size rrST against the sample size (replicates) and variance (within-study variance; [43]). There was no pattern suggesting the existence of a publication bias, as would be evident by funnel asymmetry [44].

Applied soil aggregation stability test

The soil aggregation data extracted from articles reflected the stability of treated/ untreated soil. The stability tests varied by the type of applied disintegrating force (e.g. water, abrasion, drop impact). The majority of studies used water as disintegrating force. In rarer cases abrasion on a sieve or drop impact were used as disintegrating force (impact of aggregates on surface after fall from 1.5m height). Only in 12 studies no appropriate information was given about the disintegrating force. In general, the type of disintegrating force did not cause a change in the effect size outcome (**Supplementary Table 4**), thus we did not exclude any disintegrating force type from our analyses.

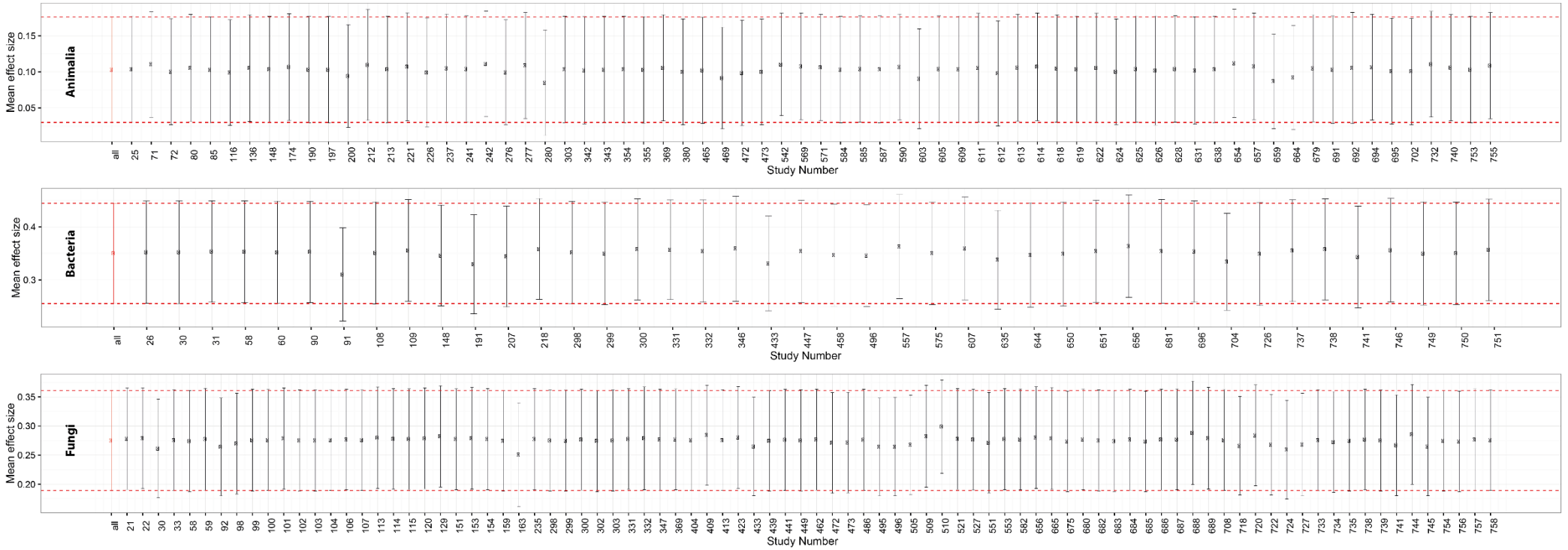
Supplementary Table 4 Overview of types of disintegrating forces applied to test aggregate stability throughout the 183 studies included in the Single Taxa dataset

disintegrating force	**mean (rrST)**	**lbCI** [b]	**ubCI** [b]	**trials**	**P** [a]
abrasion	0.21	-0.03	0.45	17	0.86
drop impact	0.06	-0.30	0.42	6	
no info	0.22	-0.05	0.50	12	
water	0.22	0.17	0.27	310	

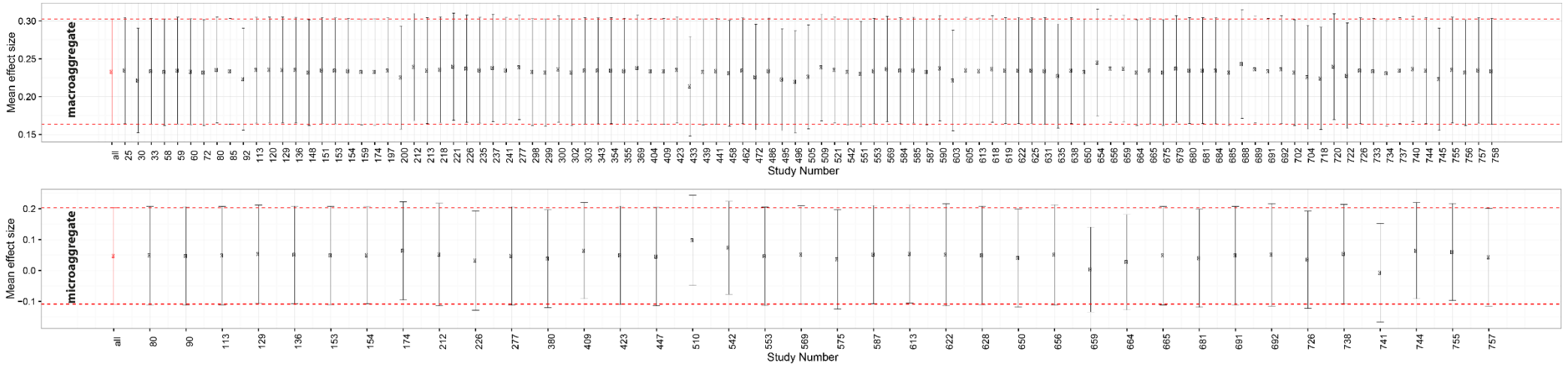
[a] significance for between-level differences; $p < 0.05$ were significant

[b] lower and upper border of the 95% confidence intervals

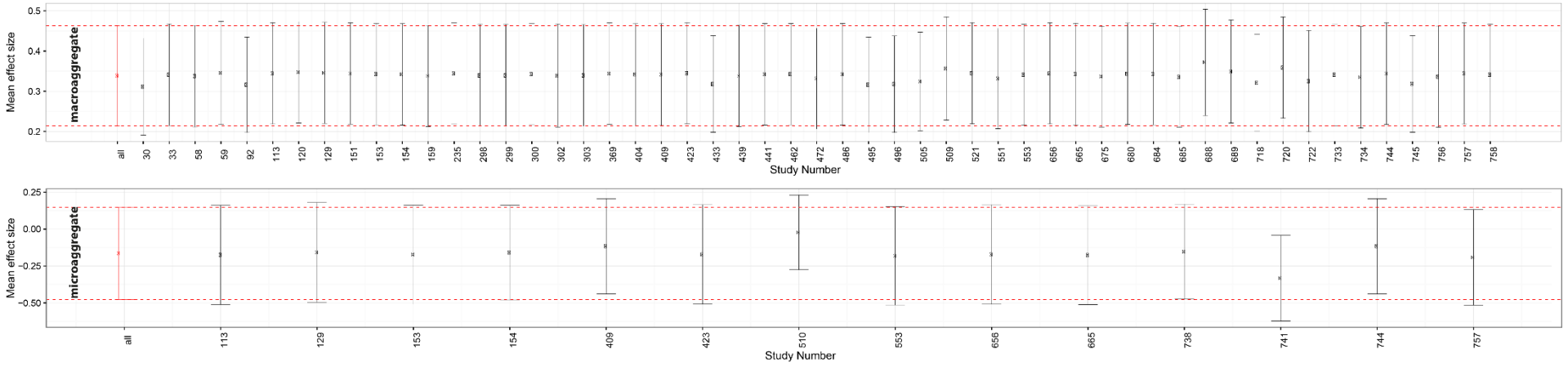
Sensitivity analysis III: 'Disproportional impact of studies' approach



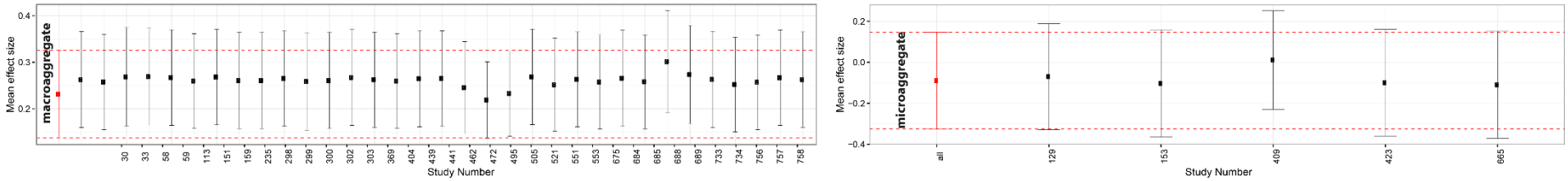
Supplementary Figure 10. Test for disproportional impact of studies on the effect size rrST for the moderator variable Higher taxonomic category (levels: Animalia, Bacteria, Fungi; see **Fig. 2B**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



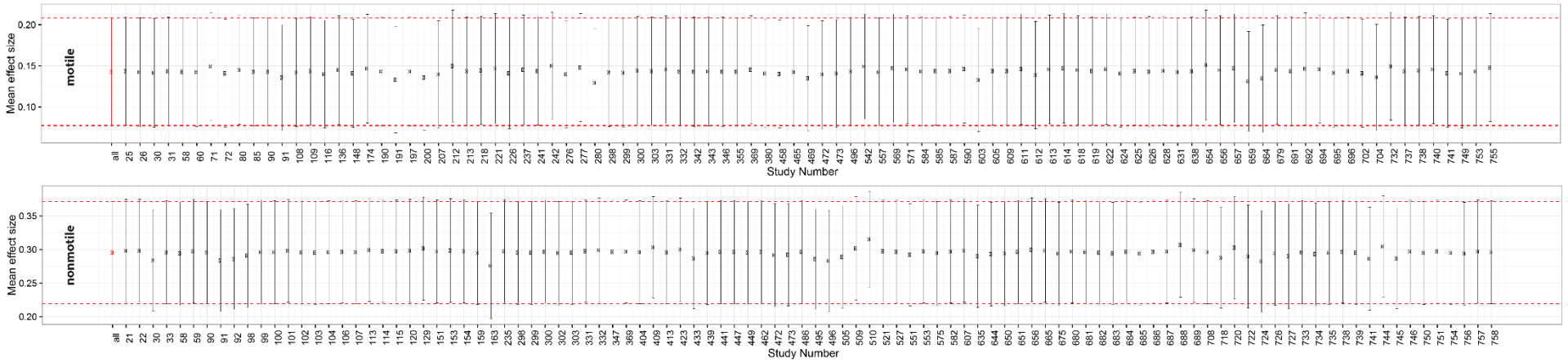
Supplementary Figure 11. Test for disproportional impact of studies on the effect size rrST for the moderator variable Aggregate size fraction (levels: macroaggregate, microaggregate; see **Fig. 2C**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



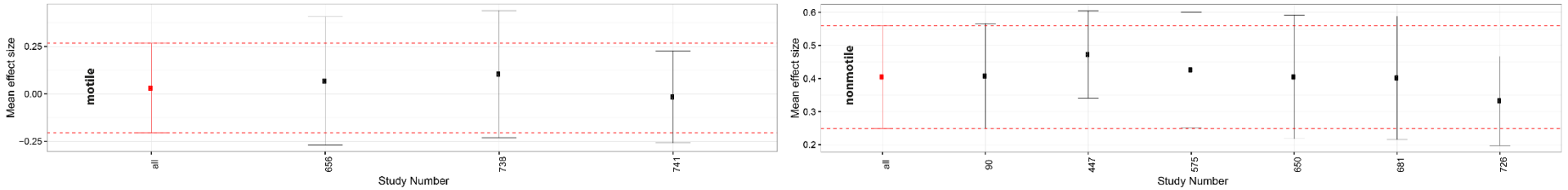
Supplementary Figure 12. Test for disproportional impact of studies on the effect size rrST for the moderator variable Aggregate size fraction (levels: macroaggregate, microaggregate; see **Fig. 2C**) in the subset "Fungi". No disproportional impact was detected; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



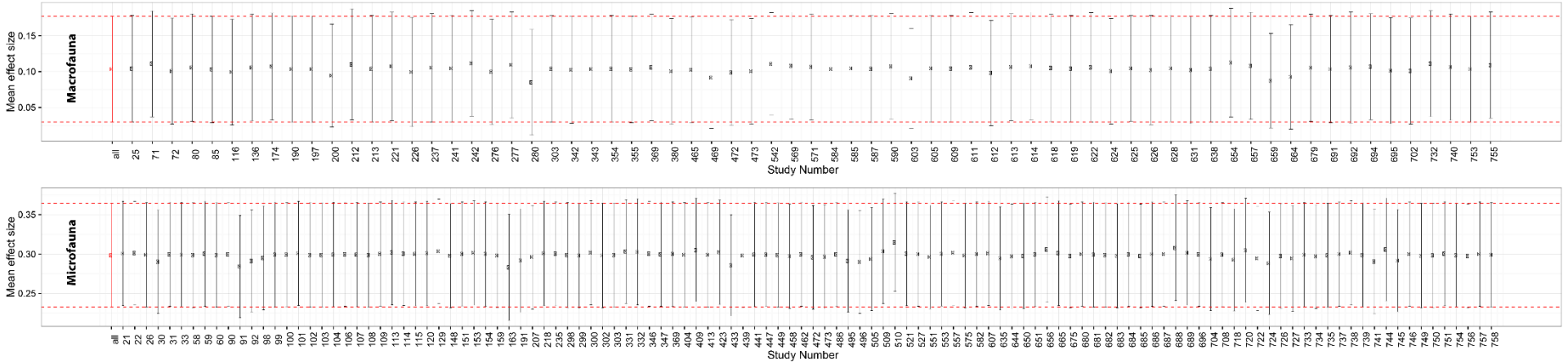
Supplementary Figure 13. Test for disproportional impact of studies on the effect size rrST for the moderator variable Aggregate size fraction (levels: macroaggregate, microaggregate; see **Fig. 2C**) in the subset "Glomeromycota". No disproportional impact was detected; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



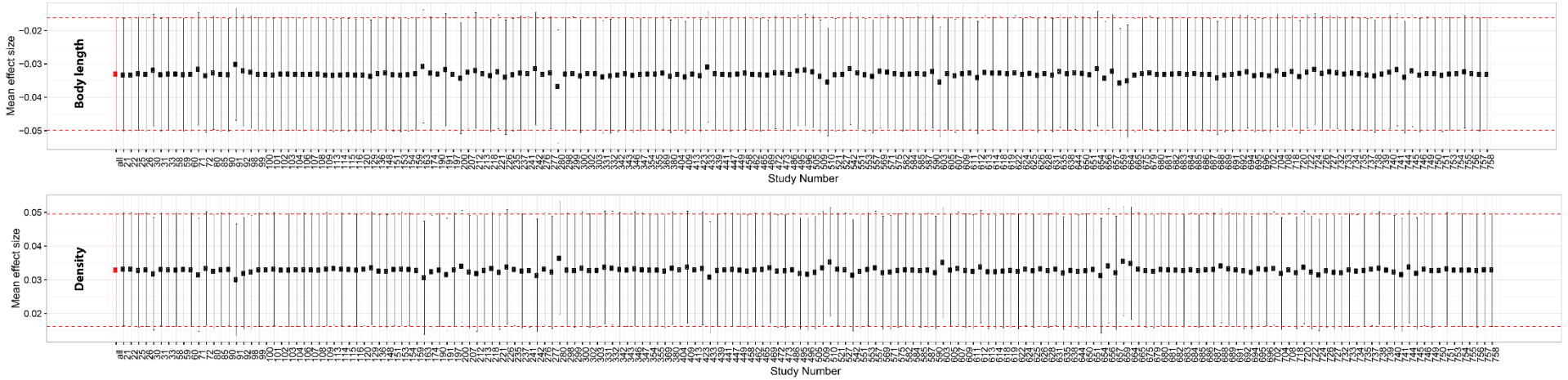
Supplementary Figure 14. Test for disproportional impact of studies on the effect size rrST for the moderator variable Motility (levels: motile, nonmotile; see **Fig. 3A**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



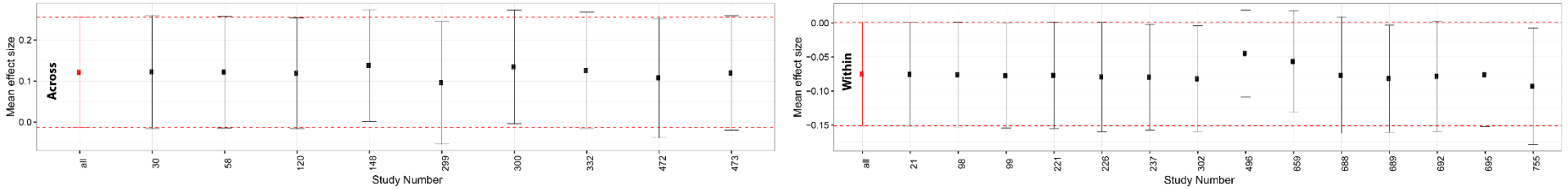
Supplementary Figure 15. Test for disproportional impact of studies on the effect size rrST for the moderator variable Motility (levels: motile, nonmotile; see **Fig. 3A**) in the subset "Bacteria & Microaggregate". No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



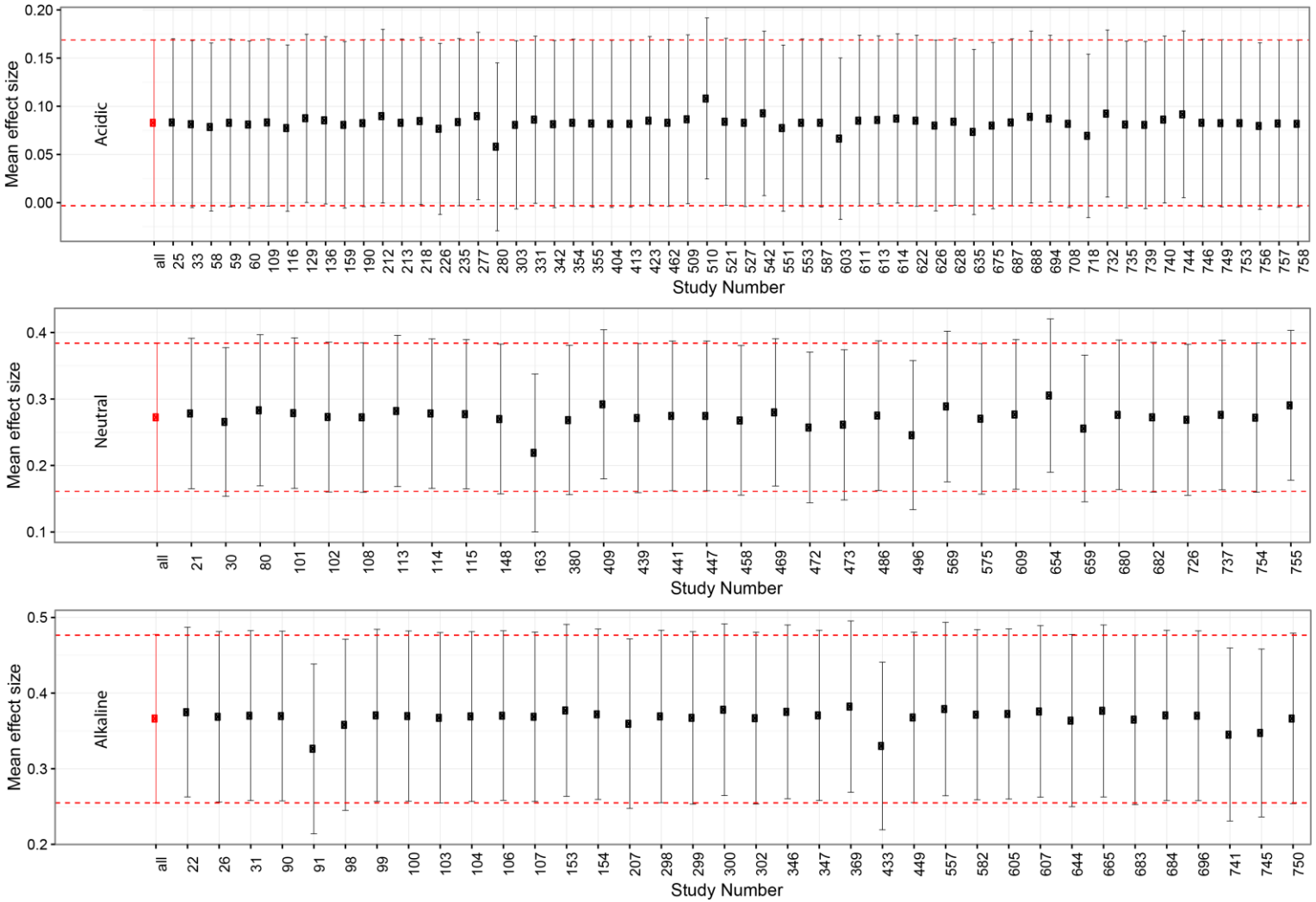
Supplementary Figure 16. Test for disproportional impact of studies on the effect size rrST for the numeric moderator variables Body Size (see results in main text and **Fig. 3B** and **C**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



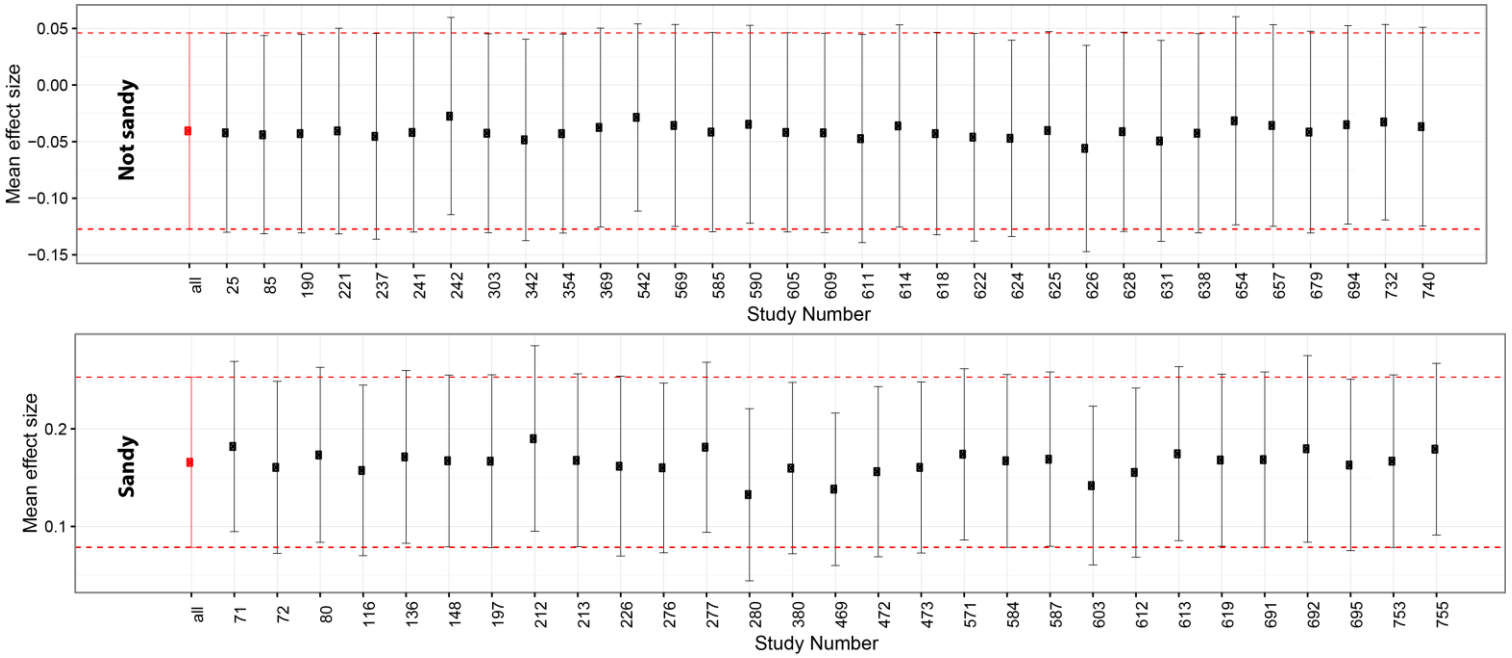
Supplementary Figure 17. Test for disproportional impact of studies on the effect size rrST for the numeric moderator variables Body length and Density (see **Fig. 3B** and **C**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the CI limits (red, dashed line) of the original set of studies.



Supplementary Figure 18. Test for disproportional impact of studies on the effect size rrIT for the moderator variable Soil biota interactions for HTC (see **Fig. 4**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.

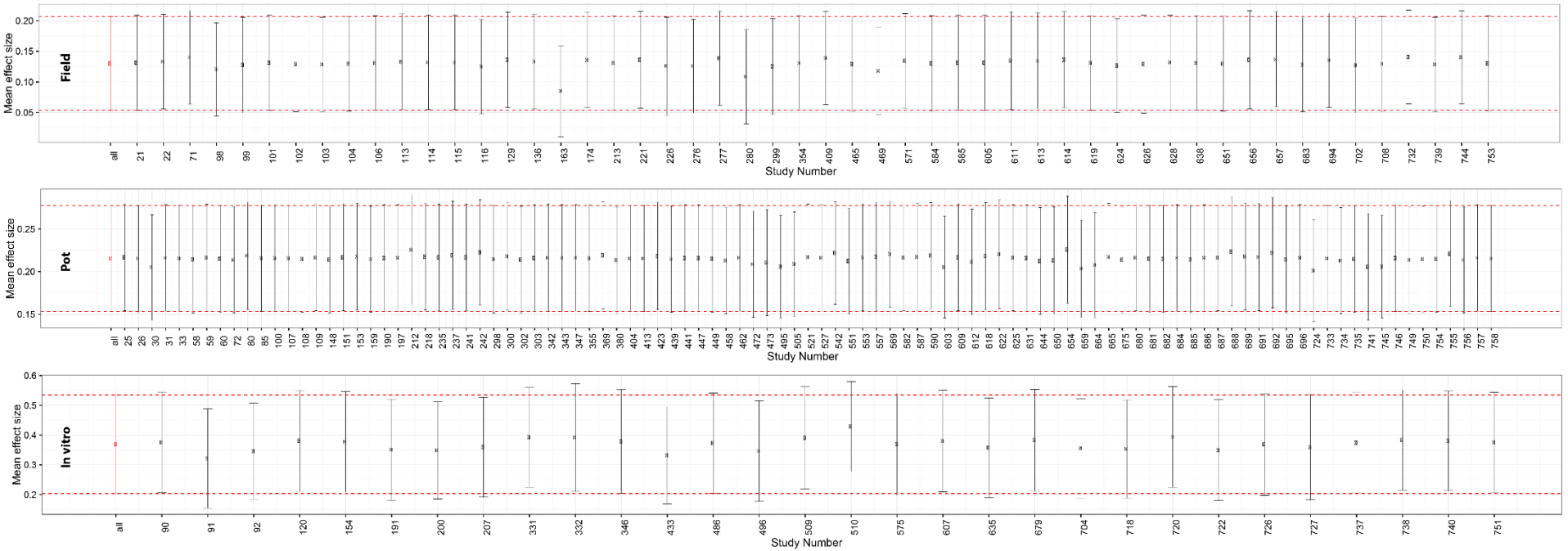


Supplementary Figure 19. Test for disproportional impact of studies on the effect size rrST for the moderator variable soil pH (levels: acidic, neutral, alkaline; see **Fig. S3**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.



92

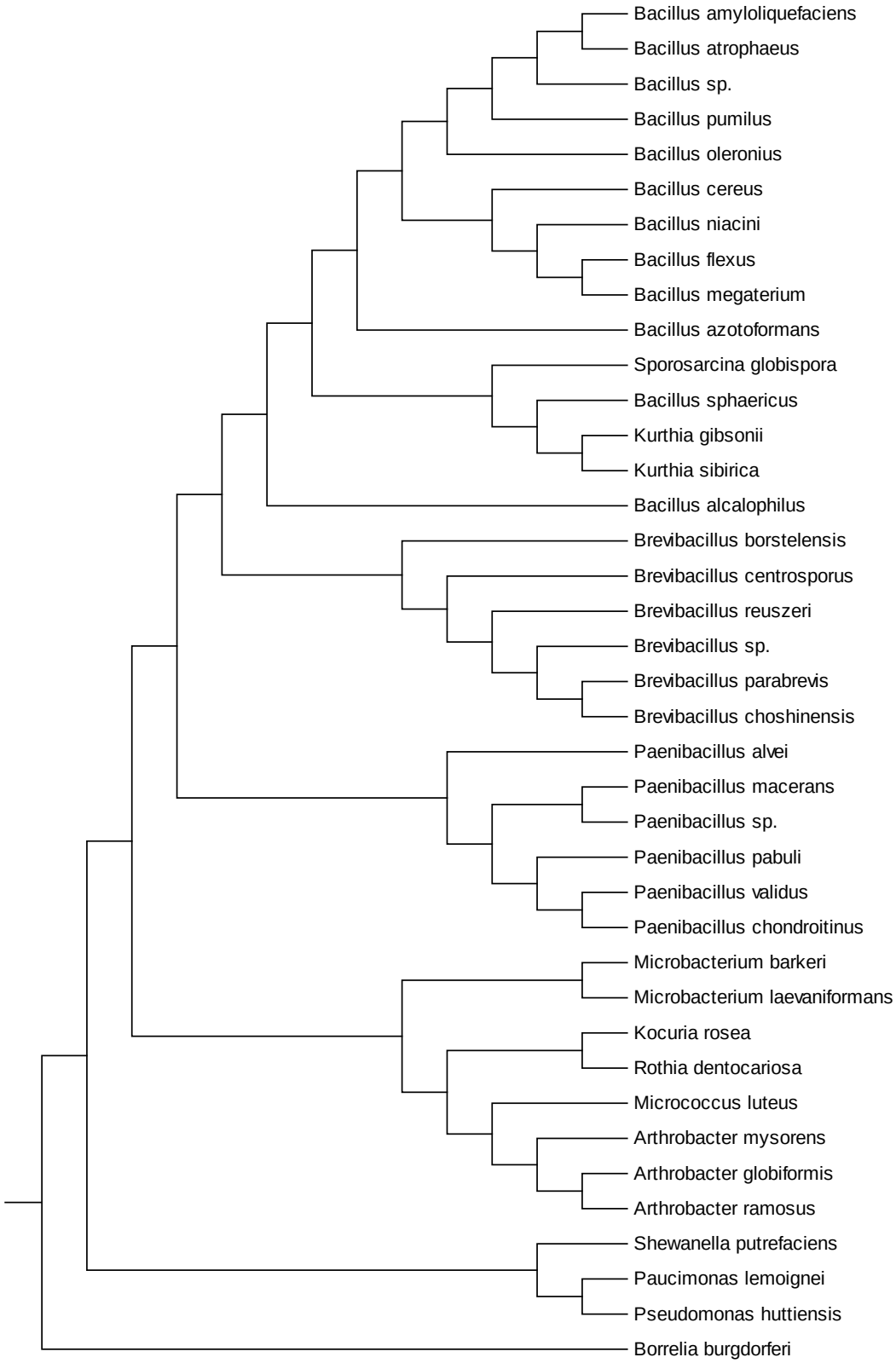
93 **Supplementary Figure 20.** Test for disproportional impact of studies on the effect size rrST for the moderator variable sand content (levels: not sandy, sandy;
94 see **Supplementary Figure 3**) in the subset “Animalia”. No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to
95 move outside the 95% CI limits (red, dashed line) of the original set of studies.



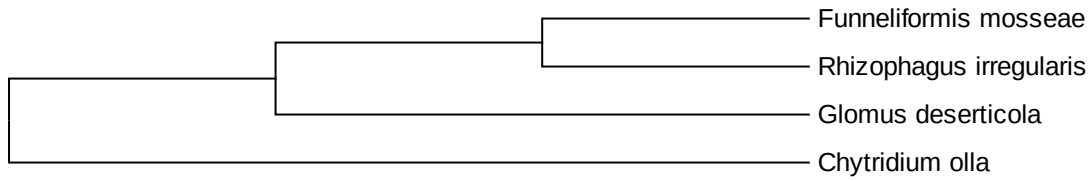
Supplementary Figure 21 Test for disproportional impact of studies on the effect size rrST for the moderator variable setting (levels: field, pot, in vitro; see **Supplementary Figure 4**). No disproportional impact was detectable; the exclusion of a study did not cause the mean effect size to move outside the 95% CI limits (red, dashed line) of the original set of studies.

Constructed maximum likelihood trees

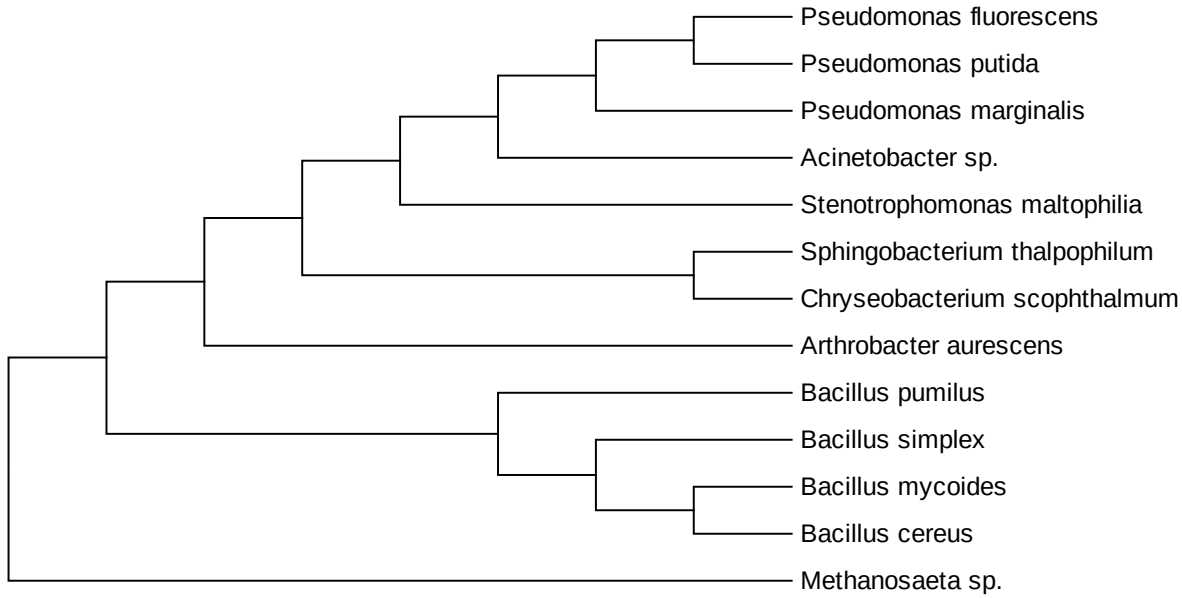
For the phylogenetic merging approach, species' names (EOL encyclopedia of life, MycoBank) and availability of DNA sequences were checked and retrieved from GenBank by using the species specific spacer regions 28S (earthworms and enchytraeids), ITS1 and 2 (fungi), 16S (bacteria). Unavailable sequences were replaced by congeneric species. Aligned sequences and Maximum Likelihood Trees (calculated by best fitted model and bootstrapping with 1000 iterations) were constructed in MEGA 2.6 (for calculated trees, see following graphics). The final merging procedure was conducted in R v.3.3.1 [45] via the rma.mv() function in the 'metafor' package [46]. Here the rma.mv() function was used to build a model with species as random factor and the implemented phylogenetic correlation matrix constructed by the 'phytools' package [47].



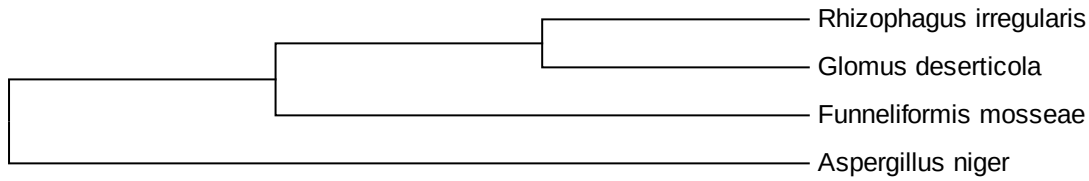
Maximum likelihood tree for study 90



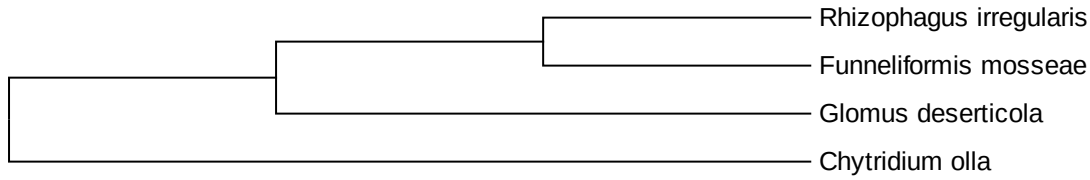
Maximum likelihood tree for studies 22 & 683



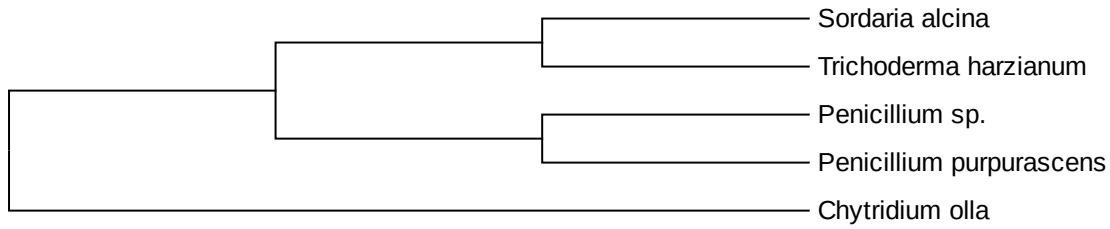
Maximum likelihood tree for study 91



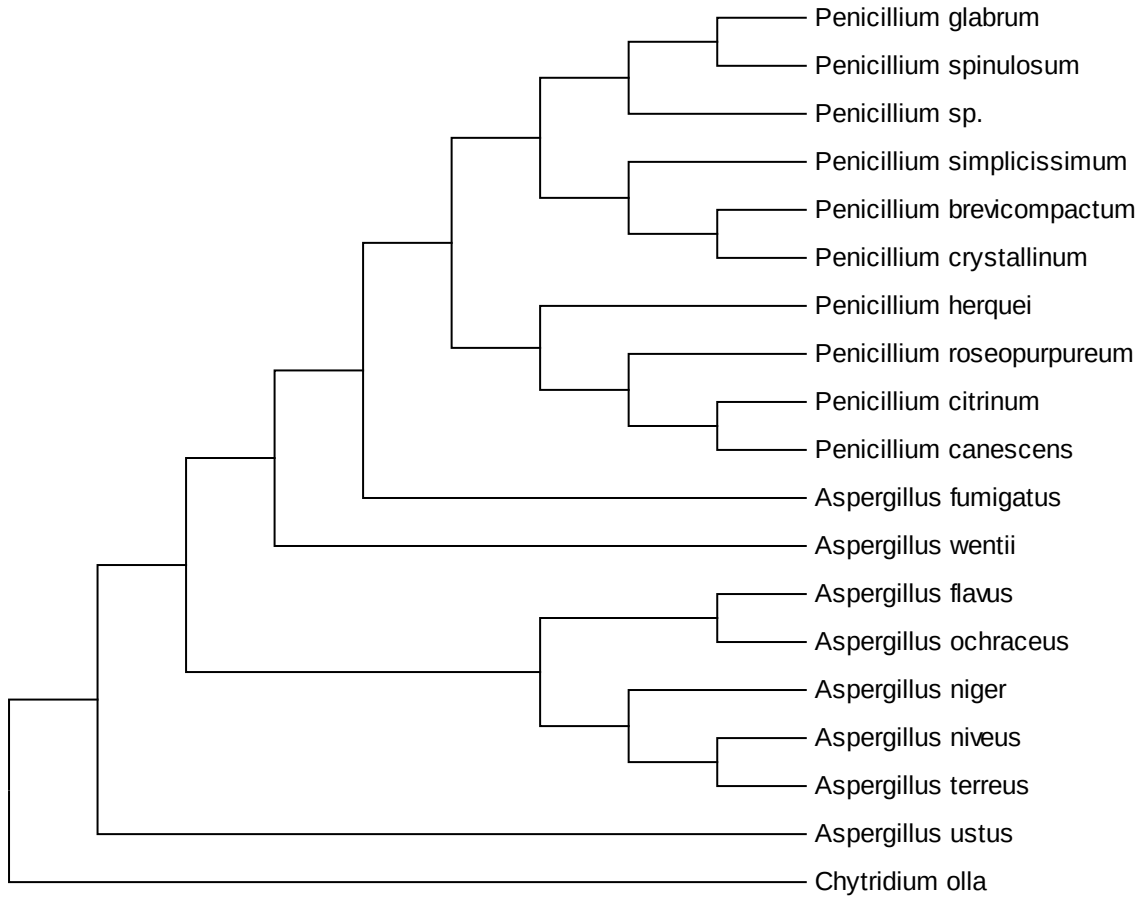
Maximum likelihood tree for study 98



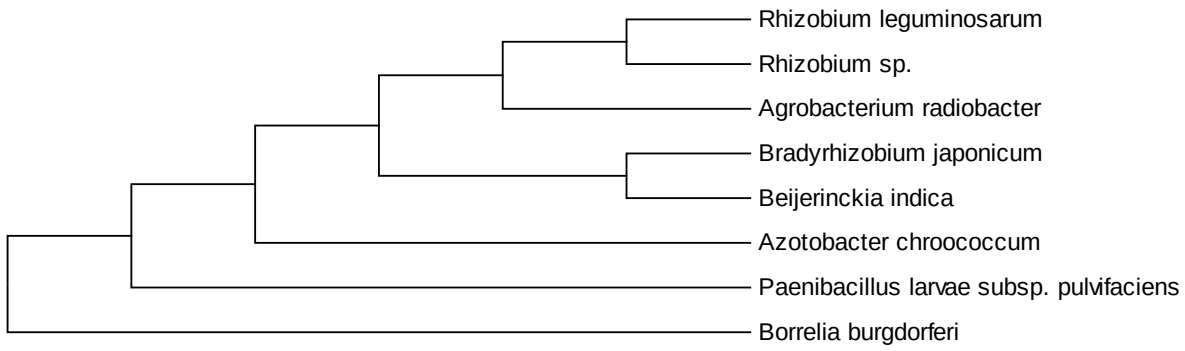
Maximum likelihood tree for study 107



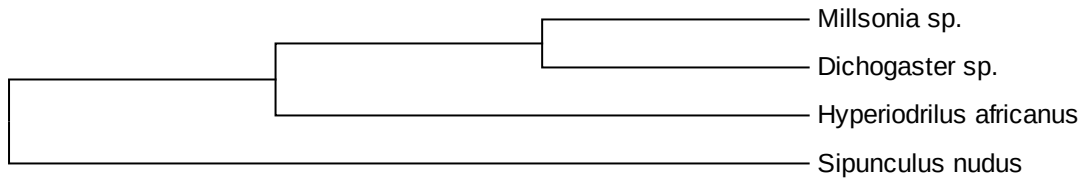
Maximum likelihood tree for study 120



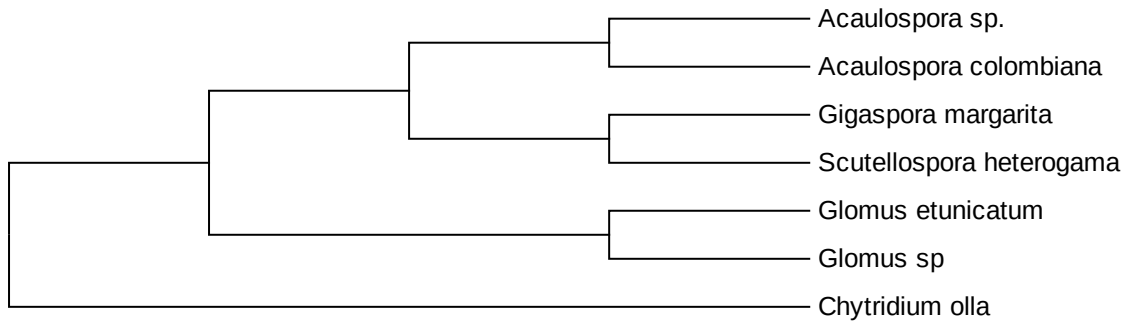
Maximum likelihood tree for study 154



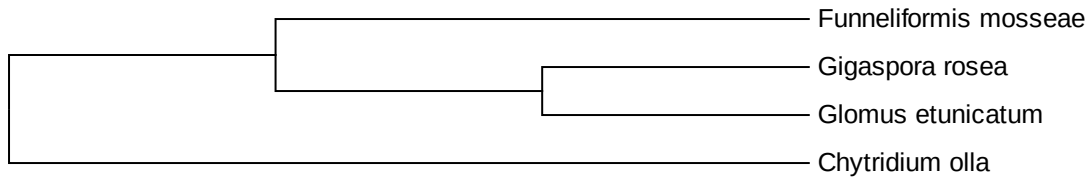
Maximum likelihood tree for study 207



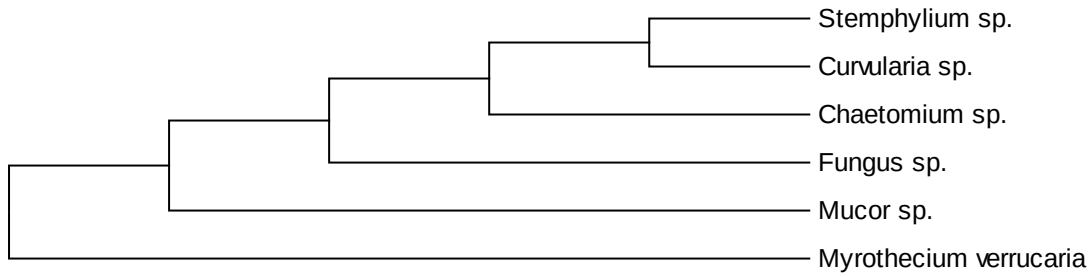
Maximum likelihood tree for study 226



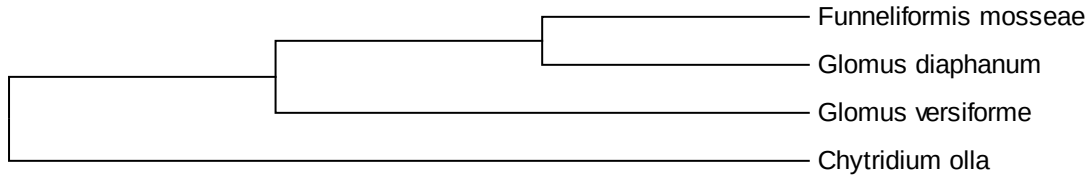
Maximum likelihood tree for study 439



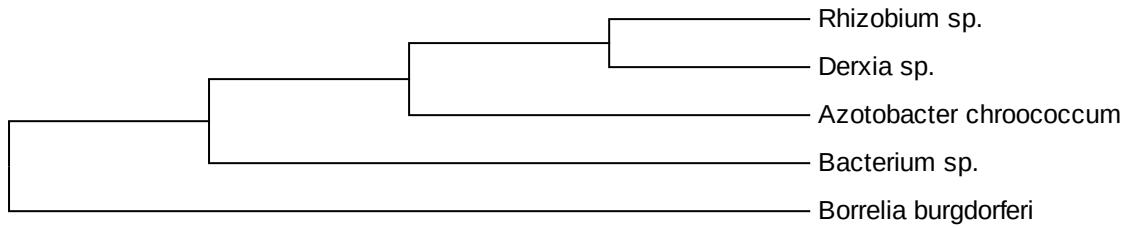
Maximum likelihood tree for study 462



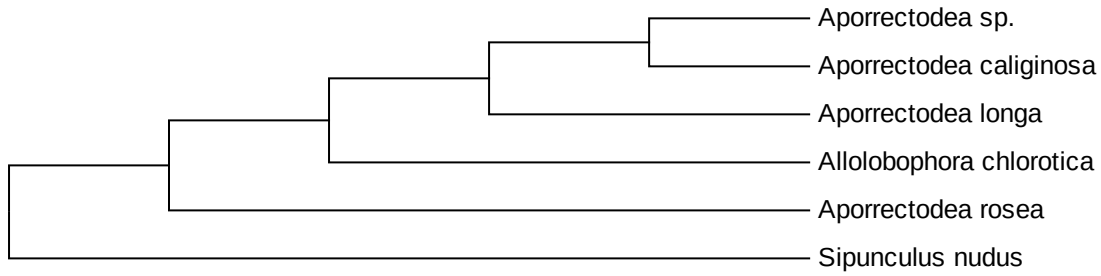
Maximum likelihood tree for study 509



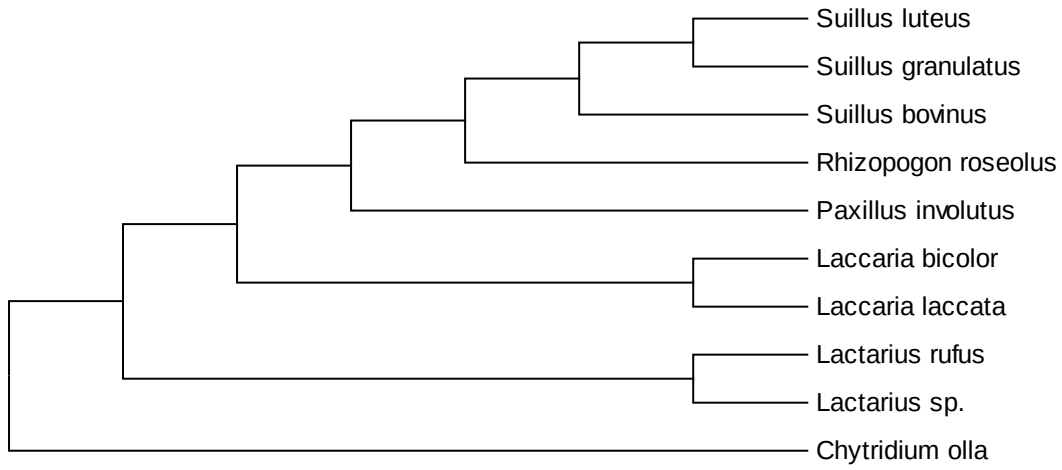
Maximum likelihood tree for study 533



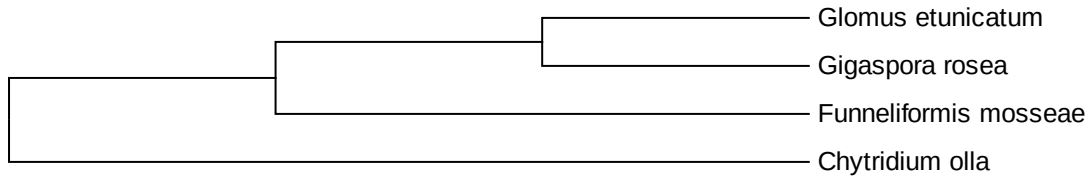
Maximum likelihood tree for study 557



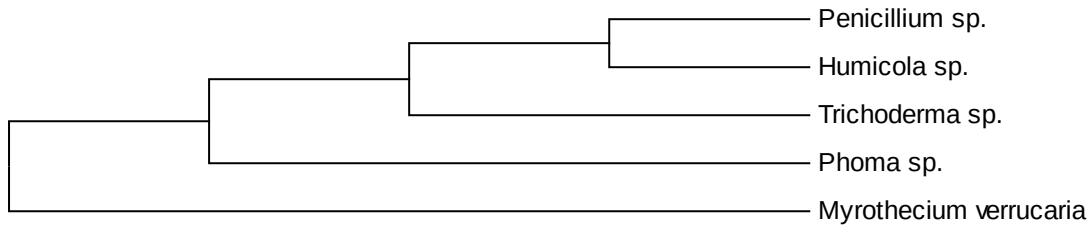
Maximum likelihood tree for study 622



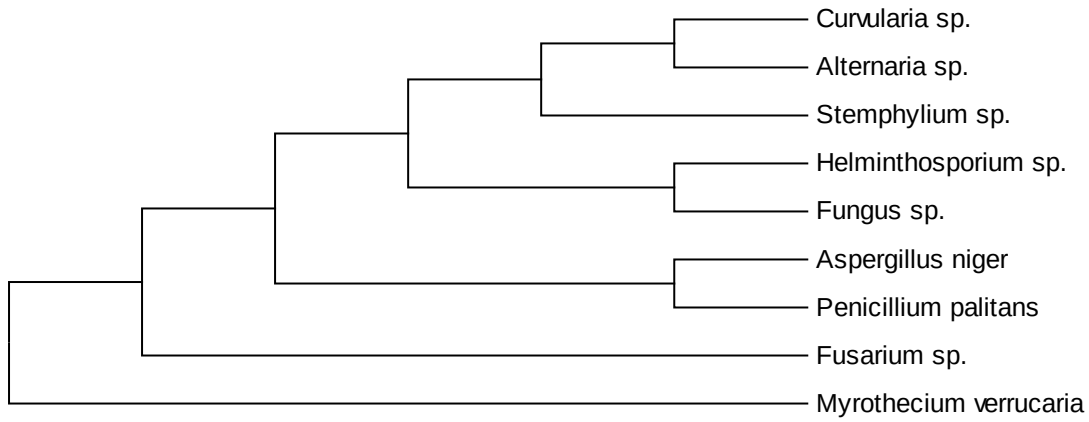
Maximum likelihood tree for study 680



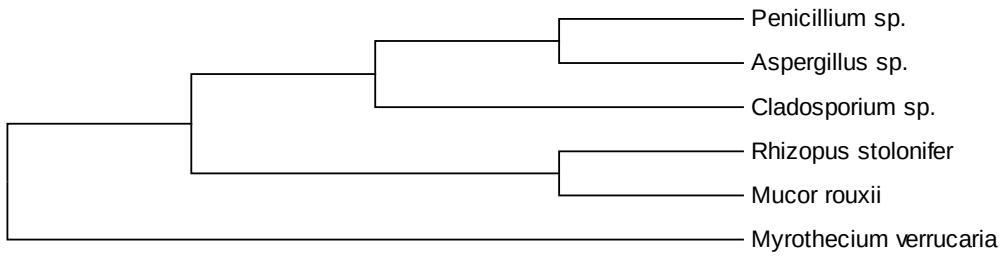
Maximum likelihood tree for study 689



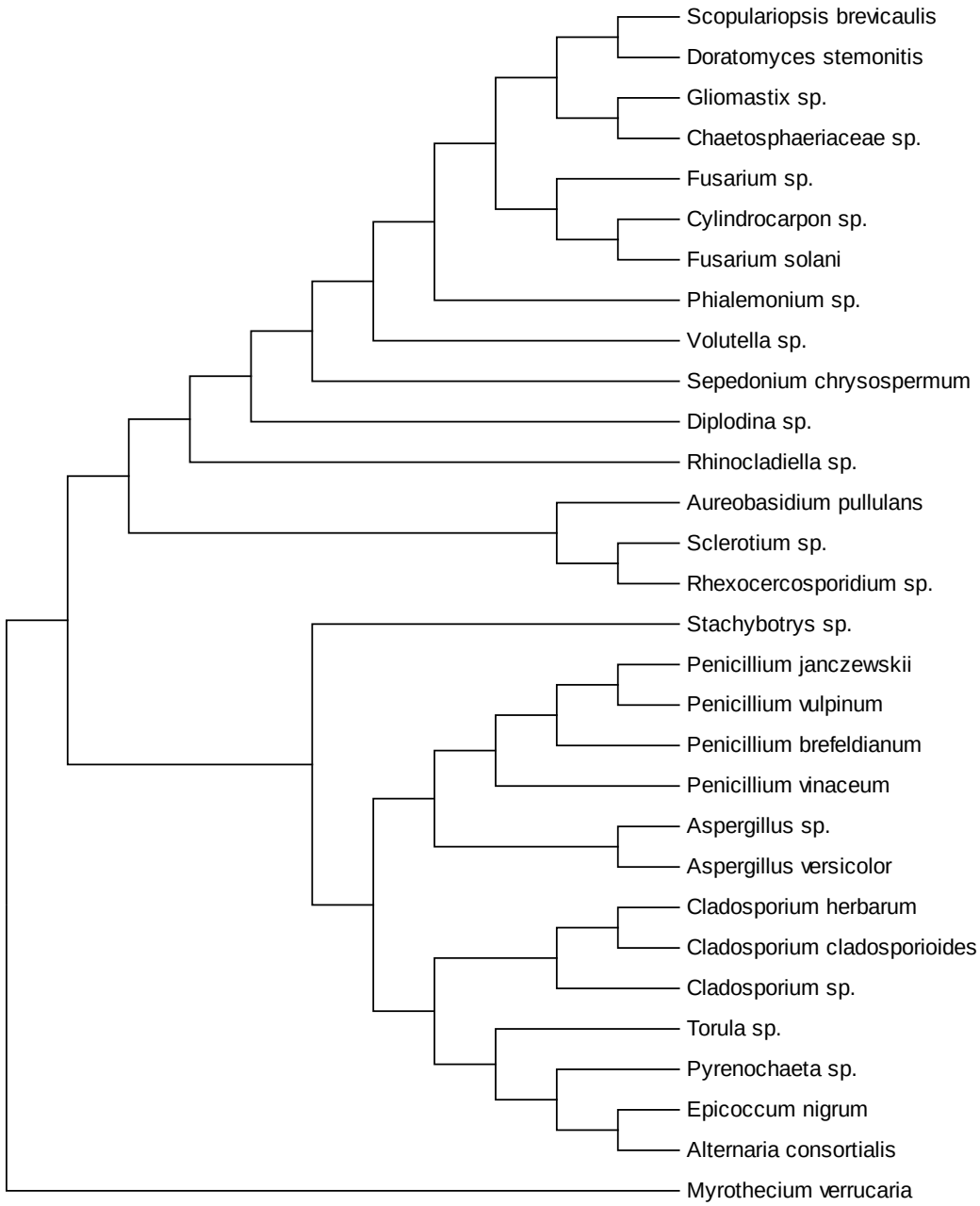
Maximum likelihood tree for study 718



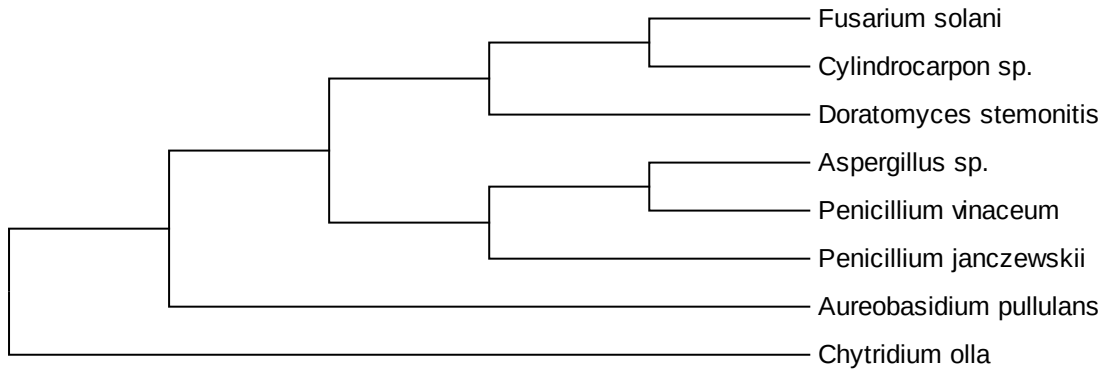
Maximum likelihood tree for study 720



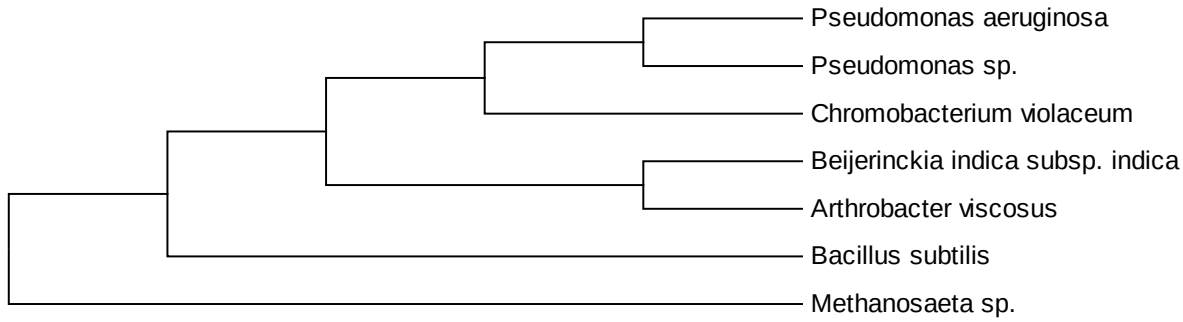
Maximum likelihood tree for study 722



Maximum likelihood tree for study 727



Maximum likelihood tree for study 738



Maximum likelihood tree for study 741

References

1 Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G. & Group, T. P. Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *PLoS Med* **6** (2009).

2 Chenu, C. Influence of a fungal polysaccharide, scleroglucan, on clay microstructure. *Soil Biol. Biochem.* **21**, 299-305 (1989).

3 Daynes, C. N., Zhang, N., Saleeba, J. A. & McGee, P. A. Soil aggregates formed in vitro by saprotrophic Trichocomaceae have transient water-stability. *Soil Biol. Biochem.* **48**, 151-161 (2012).

4 Edwards, C. A. & Bohlen, P. J. (Chapman & Hall, London, 1996).

5 Epstein, A. K., Pokroy, B., Seminara, A. & Aizenberg, J. Bacterial biofilm shows persistent resistance to liquid wetting and gas penetration. *Proc. Natl. Acad. Sci. USA* **108**, 995-1000 (2011).

6 Gupta, V. & Germida, J. J. Distribution of microbial biomass and its activity in different soil aggregate size classes as affected by cultivation. *Soil Biol. Biochem.* **20**, 777-786 (1988).

7 Jeanson, C. in *Soil Micromorphology Proceedings of the Second International Work Mett on Soil Micromorphology* (ed A. Jongerius) (Elsevier Publishing Company, Arnhem, the Netherlands, 1964).

8 Rillig, M. C., Mardatin, N. F., Leifheit, E. F. & Antunes, P. M. Mycelium of arbuscular mycorrhizal fungi increases soil water repellency and is sufficient to maintain water-stable soil aggregates. *Soil Biol. Biochem.* **42**, 1189-1191 (2010).

9 Santaella, C., Schue, M., Berge, O., Heulin, T. & Achouak, W. The exopolysaccharide of Rhizobium sp. YAS34 is not necessary for biofilm formation on Arabidopsis thaliana and Brassica napus roots but contributes to root colonization. *Environ. Microbiol.* **10**, 2150-2163 (2008).

10 Schantz, E. C. & Piemeisel, F. J. Fungus fairy rings in Eastern Colorado and their effect on vegetation. *J. Agr. Res.* **11**, 1-10 (1917).

11 Sutton, J. C. & Sheppard, B. R. Aggregation of sand-dune soil by endomycorrhizal fungi. *Can. J. Bot./Rev. Can. Bot.* **54**, 326-333 (1976).

12 Tisdall, J. M. & Oades, J. M. Stabilization of soil aggregates by the root systems of ryegrass. *Aust. J. Soil Res.* **17**, 429-441 (1979).

13 York, C. A. & Canaway, P. M. Water repellent soils as they occur on UK golf greens. *J. Hydrol.* **231**, 126-133 (2000).

14 Bonfantefasolo, P. & Gianinazzipearson, V. Ultrastructural aspects of endomycorrhiza in the Ericaceae. 3. Morphology of the dissociated symbionts and modifications occuring during their reassaciation in axenic culture. *New Phytol.* **91**, 691-704 (1982).

15 Caesar-TonThat, T. C., Caesar, A. J., Gaskin, J. F., Sainju, U. M. & Busscher, W. J. Taxonomic diversity of predominant culturable bacteria associated with microaggregates from two different agroecosystems and their ability to aggregate soil in vitro. *Appl. Soil Ecol.* **36**, 10-21 (2007).

16 Dangerfield, J. M., McCarthy, T. S. & Ellery, W. N. The mound-building termite Macrotermes michaelseni as an ecosystem engineer. *J. Trop. Ecol.* **14**, 507-520 (1998).

17 Linder, M. B., Szilvay, G. R., Nakari-Setala, T. & Penttila, M. E. Hydrophobins: the protein-amphiphiles of filamentous fungi. *FEMS Microbiol. Rev.* **29**, 877-896 (2005).

18 Maass, S., Caruso, T. & Rillig, M. C. Functional role of microarthropods in soil aggregation. *Pedobiologia* **58**, 59-63 (2015).

19 Watt, M., McCully, M. E. & Jeffree, C. E. Plant and bacterial mucilages of the maize rhizosphere - comparison of their binding-properties and histochemistry in a model system. *Plant Soil* **151**, 151-165 (1993).

20 Auge, R. M. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* **11**, 3-42 (2001).

21 Barois, I. & Lavelle, P. Changes in respiration rate and some physicochemical properties of a tropical soil during transit through Pontoscolex corethrurus (Glossoscolecidae, Oligochaeta). *Soil Biol. Biochem.* **18**, 539-541 (1986).
22 Marjanovic, Z. & Nehls, U. in *Mycorrhiza - State of the Art, Genetics and Molecular Biology, Eco-Function, Biotechnology, Eco-Physiology, Structure and Systematics* (ed A. Varma) (Springer Verlag, Germany, 2008).
23 Meadows, A., Meadows, P. S., Wood, D. M. & Murray, J. M. H. Microbiological effects on slope stability - an experimental analysis. *Sedimentology* **41**, 423-435 (1994).
24 Money, N. P. in *The Mycota I - Growth, differentiation and sexuality* (eds J.G.H. Wessels & F. Meinhardt) (Springer Verlag, Germany, 1994).
25 Shipitalo, M. J. & Protz, R. Chemistry and micromorphology of aggregation in earthworm casts. *Geoderma* **45**, 357-374 (1989).
26 Caravaca, F., Alguacil, M. M., Azcon, R., Diaz, G. & Roldan, A. Comparing the effectiveness of mycorrhizal inoculation and amendment with sugar beet, rock phosphate and Aspergillus niger to enhance field performance of the leguminous shrub Dorycnium pentaphyllum L. *Appl. Soil Ecol.* **25**, 169-180 (2004).
27 Caravaca, F. *et al.* Establishment of two ectomycorrhizal shrub species in a semiarid site after in situ amendment with sugar beet, rock phosphate, and Aspergillus niger. *Microb. Ecol.* **49**, 73-82 (2005).
28 Hutchinson, S. A. & Kamel, M. The effect of earthworms on the dispersal of soil fungi. *J. Soil Sci.* **7**, 213-218 (1956).
29 Parle, J. N. A microbiological study of earthworm casts. *J. Gen. Microbiol.* **31**, 13-22 (1963).
30 Rillig, M. C. & Mummey, D. L. Mycorrhizas and soil structure. *New Phytol.* **171**, 41-53 (2006).
31 Siddiky, M. R. K., Kohler, J., Cosme, M. & Rillig, M. C. Soil biota effects on soil structure: Interactions between arbuscular mycorrhizal fungal mycelium and collembola. *Soil Biol. Biochem.* **50**, 33-39 (2012).
32 Siddiky, M. R. K., Schaller, J., Caruso, T. & Rillig, M. C. Arbuscular mycorrhizal fungi and collembola non-additively increase soil aggregation. *Soil Biol. Biochem.* **47**, 93-99 (2012).
33 Tisdall, J. M. Possible role of soil-microorganisms in aggregation in soils. *Plant Soil* **159**, 115-121 (1994).
34 Wolter, C. & Scheu, S. Changes in bacterial numbers and hyphal lengths during the gut passage through Lumbricus terrestris (Lumbricidae, Oligochaeta). *Pedobiologia* **43**, 891-900 (1999).
35 Juma, N. G. in *The pedosphere and its dynamics: a systems approach to soil science* (Salman Productions, Canada, 1999).
36 Lehmann, A. & Rillig, M. C. Arbuscular mycorrhizal contribution to copper, manganese and iron nutrient concentrations in crops - A meta-analysis. *Soil Biology & Biochemistry* **81**, 147-158 (2015).
37 Lehmann, A., Veresoglou, S. D., Leifheit, E. F. & Rillig, M. C. Arbuscular mycorrhizal influence on zinc nutrition in crop plants - A meta-analysis. *Soil Biol. Biochem.* **69**, 123-131 (2014).
38 Roth, C. H. & Pavan, M. A. Effects of lime and gypsum on clay dispersion and infiltration in samples of a Brazilian oxisol *Geoderma* **48**, 351-361 (1991).
39 Bronick, C. J. & Lal, R. Soil structure and management: a review. *Geoderma* **124**, 3-22 (2005).
40 Six, J., Bossuyt, H., Degryze, S. & Denef, K. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil Till. Res.* **79**, 7-31 (2004).
41 Leifheit, E. F., Veresoglou, S. D., Lehmann, A., Morris, E. K. & Rillig, M. C. Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation-a meta-analysis. *Plant Soil* **374**, 523-537 (2014).
42 Tisdall, J. M. & Oades, J. M. Organic-matter and water-stable aggregates in soils. *J. Soil Sci.* **33**, 141-163 (1982).
43 Egger, M., Smith, G. D., Schneider, M. & Minder, C. Bias in meta-analysis detected by a simple, graphical test. *Br. Med. J.* **315**, 629-634 (1997).

44 Nakagawa, S. & Santos, E. S. A. Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* **26**, 1253-1274 (2012).
45 R: A Language and Environment for Statistical Computing, Vienna, Austria (2014).
46 Viechtbauer, W. Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Softw.* **36**, 1-48 (2010).
47 Revell, L. J. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217-223 (2012).