**Methods**

**Measures of host-symbiont phylogenetic congruence**

We considered studies that reconcile host and symbiont phylogeny to test for topological congruence, using knowledge of the associations that exist between symbiont and host tips, where host phylogeny is considered the independent variable and the symbiont phylogeny is considered the dependent variable1. We included reported test statistics from the two most widely applied analytical approaches for estimating host-symbiont phylogenetic congruence (Extended Data Tab. 2): TreeMap2-4, based on estimates of shared discrete macroevolutionary events, and ParaFit5, based on branch-length comparisons to estimate overall similarity. Both approaches adopt a null hypothesis of independent evolution between host and symbiont phylogenetic trees, but they interrogate the hypothesis using different forms of phylogenetic data. Briefly, in TreeMap congruence is assessed by mapping symbiont phylogeny onto host phylogeny and quantifying apparent host-symbiont cospeciation events (out of a maximum of *n* – 1 for a phylogeny of *n* symbiont taxa), versus other events (i.e. independent speciations, host switches, and sorting events). Host and symbiont phylogenies are considered congruent if the total is significantly greater than the distribution of scores observed when symbiont phylogeny is randomized a large number of times and mapped back onto host phylogeny, with the resultant *p* value indicating the level of significance1-4. In contrast, instead of proposing evolutionary scenarios, ParaFit adopts a distance matrix approach to quantifying congruence between host and symbiont phylogenies5. Host-symbiont data is transformed into a distance matrix using the sum of squared distances to quantify the similarity between host and symbiont trees. Together with an incidence matrix describing host-symbiont associations (i.e. ‘H-P links’), this is then compared to the distribution of values obtained by permutating the dataset to determine significance (i.e. the global test of host-symbiont cophylogeny ‘ParaFitGlobal’)5.

Both Parafit and TreeMap presume fully resolved and accurate host and parasite phylogenies, and neither method takes phylogenetic uncertainly into account. Currently, many host and symbiont phylogenies are based on single gene analyses, and there is undoubtedly scope for improvements in phylogenetic accuracy by using multi-gene approaches and accounting for phylogenetic uncertainty. However, there is no evidence to suggest that any errors that may be present in individual host or symbiont phylogenies affect assessments of congruence in a systematic manner.

Phylogenetic congruence arising as a result of cospeciation, and phylogenetic congruence arising via other means that can produce a phylogenetic signature similar to cospeciation (such as successive host-switching across host phylogeny), are not differentiated by Parafit or TreeMap, as this requires accurately dated host and parasite phylogenies, of which relatively few pairs are available currently. However, our analyses were not directed at unravelling among alternative scenarios underlying host and symbiont speciation, but rather towards considering broadscale patterns in phylogenetic congruence.

**Data collection**

*Literature search*

A literature search was performed using Google Scholar on 19th March 2019, which identified 368 citations of the original paper for TreeMap2, and 332 citations for the original paper for Parafit5, resulting in a total of 700 citations that were screened to extract metrics for inclusion in our meta-analysis. Articles that did not contain cophylogenetic analyses were immediately excluded. Studies focussing at the population level were also excluded, as these do not represent true cophylogenetic analyses at the macroevolutionary level. Additionally, studies that included less than 4 taxa were excluded from consideration, as these do not provide sufficient power for inclusion in the meta-analysis, while studies that did not report the test statistic for congruence were also necessarily excluded. After exclusions were applied, a sample of 232 separate host-symbiont cophylogenetic studies remained, upon which our meta-analysis is based (Extended Data Tab. 1).

*Explanation of metrics*

Metrics collected for this study are described below, with reference to Extended Data Tab. 1.

A short citation of each study was recorded under ‘*authors*’, and the year of publication was recorded in ‘*year*’. Hosts and symbionts were classified broadly according to Linnean taxonomy for ‘*host\_tax\_broad’* and ‘*symbiont\_tax\_broad*’ as either: invertebrate, vertebrate, microbe, or plant. Hosts and symbionts were also classified finely for ‘*host\_tax\_fine’* and ‘*symbiont\_tax\_fine’* as: fungus, virus, protist, bacterium, plant, invertebrate or bird..

We adopted the mode of symbiosis and mode of transmission specified by the authors in each individual study considered for ‘*symbiosis*’ and ‘*mode\_of\_transmission*’. In cases where either mode of symbiosis or mode of transmission were not directly specified by authors, we consulted the literature for clarification. In a small number of studies restricted to bacterial intracellular symbionts, the mutualism-parasitism distinction was not defined by the authors and either no further information was available, or a symbiont was cited in the literature as being both a mutualist or a parasite, depending on which study was considered. The nature of the relationship between bacterial intracellular symbionts and their hosts is complex, and in some cases they may display both beneficial and detrimental effects simultaneously6. In conflicting cases or where data were absent, we classified bacterial intracellular symbionts as mutualists as the vast majority of available references indicated this. Meanwhile, if authors did not explicitly state mode of transmission for bacterial intracellular symbionts, we assumed a vertical mode of transmission, on the basis of the majority of available references.

The total number of host tips with a link to a symbiont taxon were summed to provide ‘*host\_tips\_linked*’, which in a very few cases was corrected to remove multiple sampling of the same host species, to provide ‘*host\_tips\_linked\_corrected*’. The total number of symbiont tips with a link to a host taxon were summed to provide ‘*symbiont\_tips\_linked*’, while the total number of individual links between hosts and symbionts was recorded as ‘*total\_host\_symbiont\_links*’. If all symbionts in a phylogeny were strict specialists, such that each one had a single link to a single host, ‘*total\_host\_symbiont\_links*’ would simply equal ‘*symbiont\_tips\_linked*’. However, because symbionts are often associated with more than one host, the value of ‘*total\_host\_symbiont\_links*’ was often higher than the total number of symbionts included in a study. Thus, a measure of symbiont generalism was captured using ‘*host\_range\_link\_ratio*’, defined as ‘*total\_host\_symbioint\_links*’ divided by ‘*symbiont\_tips\_linked*’, providing the mean number of host-symbiont links observed per symbiont taxon, with the measure increasing with increasing generalism. An alternative estimate of symbiont host specificity was captured using ‘*host\_range\_taxonomic\_breadth*’, which considers Linnean taxonomic rank, and was calculated by assigning an incremental score to successive host taxonomic ranks per symbiont in turn (i.e. single host species = 1, multiple host species in the same genus = 2, multiple host genera = 3, multiple host families = 4, multiple host orders = 5), summing the total score across all symbionts, and dividing by ‘*symbiont\_tips\_linked*’ (i.e. the total number of symbionts). Consequently, ‘*host\_range\_taxonomic\_breadth*’ increases with symbiont generalism, such that symbiont phylogenies containing symbionts capable of infecting hosts from a wide range of taxonomic ranks are assigned a greater score.

The number of phylogenetic permutations performed by authors during cophylogenetic analyses was recorded as ‘no\_randomizations’. The resultant *p* value from each study was recorded as ‘*p\_value*’, whereby observed *p* values decrease with a decreasing likelihood of observing host-symbiont cophylogeny by chance alone (i.e. as calculated during permutation tests of host-symbiont phylogenies performed by authors during TreeMap or Parafit analyses).

**Meta-analysis**

We used *p* values obtained from randomization tests that are implemented in ‘TreeMap’ and ‘Parafit’ as measures of incongruence. These *p* values were converted into *r* and its transformation *Zr*. We can calculate *requivalent* via *t* values with *df* = *N* - 2 from *p* values (one-tailed)10, and then, also obtain *Zr*equivalent from *r*equivalent, as follows:

where *N* is sample size, which is, in our case, the sum of the numbers of host and symbiont species included in a randomisation test.

All statistical analyses were conducted using R version 3.5.211. We used multilevel (random-effects) meta-analytic and meta-regression models12, because multiple effect sizes were obtained from some studies (i.e., study IDs were included as a random factor in the models to account for non-independence). All meta-analytic models were implemented using the function, *rma.mv* in the R package, *metafor* version 2.0-013. All model specifications and model selection procedures are found in our electronic supplementary materials (ESM).

**Publication bias and sensitivity analysis**

* egger regression with the full model - say reason why
* truncations due to the number of simulations……
* boundaries due to N (randomization tests) is creating
* sensitivity analysis - two justifications
  1. why we put TreeMap and Parafit data
  2. Truncation are not biasing our main results!!!
  + simulation numbers are not different between parasites and mutualists

**Estimates of effect size**

Discussion on the likely underestimation of effect size.

The modal number of host-symbiont phylogenetic permutations performed by authors in our data set was 999 permutations, which limits the lowest observable *p* value statistic to *p* ≤ 0.001. In practice, the number of permutations performed by authors is constrained by the computational time and resources required to perform large numbers of phylogenetic permutations, particularly for large phylogenies and older studies, when access to high speed computing facilities was more limited. In cases of incongruence, this limitation is not important, since determining exact likelihoods between for example 0.54-0.55 is trivial. However, a consequence of this limitation is that for highly congruent host-symbiont cophylogenies, and particularly those cases involving large numbers of taxa (where there is less chance of observing high congruence by chance alone), the true test statistic is often unknown. In such cases we had to adopt the upperlimit of the reported *p* value, such that in the case of *p* ≤ 0.001, the adopted *p* value would be *p* = 0.001. Since the true likelihood of achieving the observed number of cospeciations by chance alone can be considerably lower than 0.001, particularly in cases of perfect host-symbiont congruence involving many taxa, our analyses thus represent a conservative measure of host-symbiont phylogenetic congruence, and should be considered the lower bound of congruence that exists for the considered studies.

**Further patterns in our data**

Splitting host taxonomy by mode of symbiosis revealed that the observed higher phylogenetic congruence of host-symbiont cophylogenies involving a microbial host is driven primarily by greater congruence between microbial hosts and mutualist symbionts (Fig. 3d). Congruence is also relatively high for invertebrate hosts that harbour a mutualistic symbiont, while congruence appears to be lowest for plant hosts that harbour a parasitic symbiont (Fig. 3d). Splitting symbiont taxonomy by mode of symbiosis revealed much less variation, except for higher congruence exhibited by cophylogenies involving a plant symbiont (which are relatively rare), and the finding that cophylogenies involving a microbial mutualist symbiont are slightly more congruent than the remaining categories (Fig. 3e).

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