



# Host diversity drives parasite diversity: meta-analytical insights into patterns and causal mechanisms

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Statistical correlations of biodiversity patterns across multiple trophic levels have received considerable attention in various types of interacting assemblages, forging a universal understanding of patterns and processes in free-living communities. Host–parasite interactions present an ideal model system for studying congruence of species richness among taxa as obligate parasites are strongly dependent upon the availability of their hosts for survival and reproduction while also having a tight coevolutionary relationship with their hosts. The present meta-analysis examined 38 case studies on the relationship between species richness of hosts and parasites, and is the first attempt to provide insights into the patterns and causal mechanisms of parasite biodiversity at the community level using meta-regression models. We tested the distinct role of resource (i.e. host) availability and evolutionary co-variation on the association between biodiversity of hosts and parasites, while spatial scale of studies was expected to influence the extent of this association. Our results demonstrate that species richness of parasites is tightly correlated with that of their hosts with a strong average effect size ( $r = 0.55$ ) through both host availability and evolutionary co-variation. However, we found no effect of the spatial scale of studies, nor of any of the other predictor variables considered, on the correlation. Our findings highlight the tight ecological and evolutionary association between host and parasite species richness and reinforce the fact that host–parasite interactions provide an ideal system to explore congruence of biodiversity patterns across multiple trophic levels.

Understanding patterns in species diversity and distribution, and evaluating the role of biodiversity in ecosystem function, remain key goals for contemporary ecologists (Sutherland et al. 2006). As a consequence, congruence of biodiversity patterns across multiple trophic levels has received considerable attention in various types of interacting communities including plant–herbivore (Siemann et al. 1998), plant–pollinator (Biesmeijer et al. 2006), predator–prey (Nilsson et al. 2008), and host–parasite (Hechinger and Lafferty 2005) relationships. These associations may be mediated through ‘bottom-up’ processes whereby diversity at higher trophic levels is governed by diversity at lower trophic levels (in addition, ‘top-down’ control via consumption by higher trophic levels may operate simultaneously in some systems) (Hunter and Price 1992). For the best documented plant–herbivore relationships, a series of independent experimental studies have validated the ‘bottom-up’ causal link between manipulated plant species richness and herbivorous arthropod richness (Siemann et al. 1998, Haddad et al. 2009, Scherber et al. 2010, Rzanny and Voigt 2012), while recent meta-analyses have corroborated the effect of plant diversity on the taxonomic richness of a wide range of functional groups at the community level (Castagneyrol and Jactel 2012).

Although patterns of species diversity have been studied predominantly in free-living organisms, host–parasite interactions present an ideal model system for studying ‘bottom-up’ richness associations. Indeed, obligate parasites are strongly, if not completely, dependent upon the availability of their hosts for survival and reproduction. This has strong parallels with the positive association between habitat diversity or heterogeneity and species richness reported for a variety of plants and animals (i.e. habitat heterogeneity hypothesis) (Kohn and Walsh 1994, Kerr and Packer 1997); just as a diverse habitat can support a diverse community of birds (MacArthur 1964), a species-rich community of host organisms should provide resource-rich habitats capable of supporting a diverse community of parasites. Parasitism also rules as the most common lifestyle choice among extant species on Earth, constituting a vital part of ecosystem functioning (Poulin and Morand 2004). It is therefore not surprising that the response of parasite communities to extinctions of free-living species has been recognized as an essential aspect of the current biodiversity crisis (Dobson et al. 2008, Keesing et al. 2010). Recent mathematical models and simulations using independent empirical food webs have suggested that the loss of host species may lead to a disproportionate loss of

parasites than previously thought (Lafferty 2012). Therefore, further elucidation of patterns and mechanisms associated with biodiversity of host–parasite communities is not only valuable as a model case for the ‘bottom-up’ control of biodiversity, but may also be important for biodiversity conservation and in predicting the future distribution of zoonotic diseases.

We extracted 38 case studies from 21 reports in the primary literature in which the relationship between host and parasite richness has been investigated. Cited references generally employed 1 of the following 2 approaches. On the one hand, studies derive correlation coefficients between the number of host and parasite species present within patches of the target study areas (‘area-based studies’ hereafter) (Hechinger and Lafferty 2005, Thielges et al. 2011). On the other hand, ‘taxon-based studies’ investigate the number of parasite species or genera per host clade across host clades that vary in richness (e.g. the number of species in genera and the number of genera in families: Hawkins and Lawton 1987, Vas et al. 2012). Even though a positive correlation between richness of hosts and that of parasites is expected a priori for both approaches, the former approach aims to capture the contemporary associations among ecological communities whereas the latter has the scope to infer co-diversification among taxa. Statistical correlations between richness of multiple trophic levels suggest multiple causal mechanisms that are non-mutually exclusive. Firstly, the correlations may be a mere reflection of current resource availability across trophic levels (e.g. availability of host plants for herbivores and host birds for parasitic flatworms). In such a case, consistent positive correlations between resource (e.g. host) and consumer (e.g. parasite) richness are expected across the ‘area-based’ studies. Secondly, co-evolutionary diversification may produce correlated patterns of species richness between host and parasite clades (i.e. Eichler’s rule (1942)). Given the relatively high host specificity of many parasites, and even assuming only modest rates of cospeciation between hosts and parasites (Paterson and Gray 1997), highly diversified host clades should provide a wide range of niches for parasites over an evolutionary time scale (Hawkins and Lawton 1987). The role of evolutionary co-variation can then be tested using the ‘taxon-based’ studies.

Additionally, the spatial scale of the ‘area-based’ studies was expected to influence the degree of the association between species richness of hosts and parasites; we would expect field surveys carried out at smaller scales to exhibit stronger correlations than large-scale studies because pooling of data from a large geographical region might mask the region-specific factors that influence the relationship among different communities (Fleming et al. 1987).

While causal relationships can be empirically validated through experiments only, manipulation of host or parasite richness will prove extremely difficult in the context of community interactions. Given the success and potential of meta-regression models as a means of empirical hypothesis testing (Nakagawa and Poulin 2012), the present meta-analysis aims to provide meta-analytical insights into the role of host availability and evolutionary co-variation in determining parasite species richness, as well as quantitatively

review the host–parasite richness relationship as a model case of the ‘bottom-up’ control of biodiversity.

## Methods

### Data collection

We searched the literature for articles and proceedings papers that reported the relationship between host and parasite taxonomic richness at either the host community or host clade level. Since species richness presents a convenient and widely available measure of biodiversity, our analysis focused on the relationship between species richness of animal hosts and that of their parasites, with some exceptions where only parasite generic richness was available. The following keywords (‘parasite species richness OR parasitoid species richness OR pathogen species richness’) AND host species richness’ were used for searches on ISI Web of Science in January and February 2013 and yielded 771 results. Articles were assessed for relevance to the present analysis, firstly by their title and then by the content of their abstract. Through the keyword search, we identified 11 relevant publications which served as the basis for the forward (i.e. articles that cite the article of interest) and reverse (i.e. articles that are cited by the article of interest) reference searches. The first round of citation searches yielded 6 additional articles while the forward and reverse searches on those additional articles added 4 more papers; refer to the flow chart for details of the data collection procedure (Supplementary material Appendix 1, Fig. A1). In addition, a short list of related articles excluded and the rationale for their exclusion may be found in the Supplementary material Appendix 1, Table A1.

In total, the dataset included 21 articles that provided a total of 38 case studies. TK conducted the original data extraction process while KoD independently validated the data points subsequently. If multiple effect sizes were reported separately within a single article, they were treated as separate data points to ensure maximal statistical power, though study identity was controlled for in the analysis (see below). Each article reported at least 1 standardised effect size, usually in the form of a correlation coefficient, of the relationship between host and parasite richness, which were derived from samples across the target study areas (i.e. ‘area-based’ studies) or host clades (i.e. ‘taxon-based’ studies); the only 2 exceptions both involved studies of the richness of parasitoids and their insect hosts that treated taxa of host plants as samples (Compton and Hawkins 1992, Sato et al. 2002). Effect sizes other than measures of correlation or the equivalent (i.e. anything other than Pearson’s correlation, Spearman’s correlation, (semi) partial correlation, or beta weight, which approximates a correlation coefficient (Schielzeth 2010)) were converted to correlation coefficients according to Lipsey and Wilson (2001) and Nakagawa and Cuthill (2007). Also, the sample size (i.e. the number of surveyed patches for the ‘area-based’ studies, the number of host clades for the ‘taxon-based’ studies and the number of host taxa for the 2 exceptions) was required for each case study to compute sampling

variances of the Fisher's  $z$ -transformed correlation coefficients, or  $Zr$ .

For each case study, additional information was recorded on several other variables that were treated as predictors in the meta-regression analyses described below. These included 9 variables: 1) host taxon, i.e. arthropods, birds, gastropods, mammals or fishes; 2) Kingdom to which the parasites belong (i.e. Metazoa or Protozoa); 3) in the case of metazoans, the taxonomic group to which those parasites belong (i.e. arthropods, trematodes, or unionid bivalves, since these were the only well-studied taxa); 4) parasite life cycle patterns (i.e. simple or complex life cycle), which corresponds to whether they require 1 or multiple host species, respectively, to complete 1 generation; 5) parasite niches (i.e. whether they were ecto- or endoparasites); 6) unit of study (i.e. 'area-based', 'taxon-based' or 'plant-taxon-based' study); 7) type of study (i.e. field survey, field experiment, or literature survey) from which data were compiled; 8) year of publication of the study; and 9) sample size (i.e. the number of patches or host clades such as families or genera examined). Additionally for 'area-based' studies, the distance between the two most distant patches was recorded as a measure of the spatial scale of the study.

## Meta-analytic procedures

Meta-analyses along with associated statistical analyses were carried out in R 2.15.1 (R Development Core Team). We used the nlme package (Pinheiro et al. 2012) to account for correlated structures arising from study identity (Lumley 2002, Nakagawa and Santos 2012); that is, we included study identity as a random effect in meta-analytic models. The raw correlation coefficients ( $r$ ) were transformed to Fisher's  $z$ -transformed correlation coefficients,  $Zr$ , and their sampling variances were computed using equations provided by Nakagawa and Cuthill (2007), thereby weighing for differences in sample sizes among studies. Based on  $Zr$  and the corresponding sampling variances, a random-effects meta-analysis was employed to estimate the overall effect size of the relationship between species richness of hosts and that of parasites. A measure of heterogeneity,  $I^2$  (i.e. the degree of inconsistency among studies) was calculated from the random effects model (Higgins et al. 2003). Here, we note that  $r$  ( $Zr$ ) values of 0.1 (0.1), 0.3 (0.31) and 0.5 (0.55) are considered as small, medium, and large effects, respectively (Cohen 1988) while  $I^2$  values of 25, 50 and 55% are considered as low, moderate, or high, respectively (Higgins et al. 2003).

A series of meta-regression models were then constructed in an attempt to account for the observed heterogeneity in the data and examine effect sizes at separate levels for each predictor listed above. The sample size for each model may be found in Supplementary material Appendix 1, Table A2 to A9. An information-theoretic approach was employed to compare the effect of the predictors based on AICc (Burnham and Anderson 2010, Grueber et al. 2011) using the dredge function in the MuMIn package (Bartoń 2012). To assess the influence of spatial scales of studies, the effect sizes ( $Zr$ ) for the 'area-based' studies were regressed

against the spatial scale of studies (log-transformed) in a separate meta-regression model.

The reliability of results from both meta-analytic and meta-regression models depend on the assumption that our data set was clear of publication bias whereby statistically significant results are more likely to be published (reviewed by Rothstein et al. 2005). We assessed potential publication bias visually for asymmetry in funnel plots of both raw effect sizes and 'meta-analytic residuals' against the precision (or the inverse of sampling standard errors); residuals from the random-effects meta-analytic model consisted of within-study effects and sample errors (or what was left after taking the mean and between-study effects from the effect sizes; Nakagawa and Santos 2012). Funnel asymmetry in raw data can indicate heterogeneity among studies rather than publication bias (Egger et al. 1997) so that a funnel plot with residuals may be preferable. We also quantitatively assessed publication bias using a rank correlation test between meta-analytic residuals and the inverse of sample variance (cf. Begg and Mazumdar 1994). We note that meta-analytic residuals, but not raw effect sizes, are free from correlated structures due to shared study identities and, therefore, such residuals are more suited for this test.

## Results

We examined 38 case studies that investigated metazoan and protozoan parasites that infect animal hosts (Table 1). Overall, there was a strong, positive correlation between species richness of hosts and parasites with an average effect size ( $r$ ) of 0.550 ( $Zr=0.618$ , 95% CI: 0.474–0.763,  $p<0.001$ ; Fig. 1). Furthermore the heterogeneity was moderate ( $I^2=40.914\%$ ). Detailed results of the meta-regression analyses can be found in Supplementary material Appendix 1, Table A2 to A10.

Strong positive correlations between richness of hosts and that of parasites were found among both 'area-based' studies ( $r=0.561$ ) and 'taxon-based' studies ( $r=0.506$ ), supporting the role of host availability and evolutionary co-variation in determining the correlation between host and parasite species richness (Fig. 1; Supplementary material Appendix 1, Table A7). However, we found no evidence among the studies included here that the correlation between host richness and parasite richness in 'area-based' studies was influenced by the spatial scale of studies (meta-regression:  $b_{[\log(\text{study scale}) \text{ for overall}]} = 0.014$ , SE = 0.043,  $p\text{-value} = 0.744$ ;  $b_{[\log(\text{study scale}) \text{ for field surveys}]} = 0.033$ , SE = 0.044,  $p\text{-value} = 0.477$ ;  $b_{[\log(\text{study scale}) \text{ for literature surveys}]} = -0.369$ , SE = 0.224,  $p = 0.198$ ; Fig. 2).

The most parsimonious model to explain the relationship between host species richness and parasite species richness was the null (intercept) model (Supplementary material Appendix 1, Table A11). Nonetheless, among the host taxa examined, the average effect size for gastropods ( $r=-0.212$ ) was significantly lower than those for arthropods ( $r=0.576$ ), birds ( $r=0.653$ ) or fishes ( $r=0.624$ ) (Fig. 1; Supplementary material Appendix 1, Table A2). Also, birds exhibited a significantly higher effect size than

Table 1. Host–parasite interactions included in the analyses. See the text for definitions.

Publication	Host	Parasite	Parasite life cycle	Parasite niche	N	Reported statistic	R	Location	Study type	Study unit	Spatial scale (km)
Hawkins and Lawton 1987	Arthropods (insects)	Arthropods (parasitoids)	Simple	Endoparasites	158	$R^2 = 0.022$	0.148	UK	Literature survey	Taxon	
Compton and Hawkins 1992	Arthropods (wasps)	Arthropods (parasitoids)	Simple	Endoparasites	24	$R = 0.751$	0.751	Southern Africa	Field survey	Plant taxa	
Watters 1992	Fishes	Unionids	Simple	Ectoparasites	38	$R^2 = 0.92$	0.959	Ohio	Literature survey	Area	439
Salvo and Valladares 1999	Arthropods (Diptera)	Arthropods (parasitoids)	Simple	Endoparasites	10	$R^2 = 0.39$	0.624	Central Argentina	Field survey	Taxon	
Vaughn and Taylor 2000	Fishes	Unionids	Simple	Ectoparasites	36	$R = 0.31$	0.310	South central USA	Field survey	Area	257
Sato et al. 2002	Arthropods (Lepidoptera)	Arthropods (parasitoids)	Simple	Endoparasites	6	$R = 0.686$	0.686	Japan	Field survey	Plant taxa	
Krasnov et al. 2004	Mammals	Arthropods (fleas)	Simple	Ectoparasites	36	$R = 0.47$	0.470	Worldwide	Literature survey	Area	20038
Hechinger and Lafferty 2005	Birds	Trematodes	Complex	Endoparasites	6	$R = 0.88$	0.880	California	Field survey	Area	930
Hechinger and Lafferty 2005	Birds	Trematodes	Complex	Endoparasites	7	$R = 0.79$	0.790	California	Field survey	Area	930
Felso and Rozsa 2006	Birds	Arthropods (lice)	Simple	Ectoparasites	22	$T = 1.15$	0.249	Worldwide	Literature survey	Taxon	
Tylianakis et al. 2006	Arthropods (Hymenoptera)	Arthropods (parasitoids)	Simple	Endoparasites	48	$F = 4.22$	0.628	Southwest Ecuador	Field survey	Area	47
Felso and Rozsa 2007	Mammals	Arthropods (lice)	Simple	Ectoparasites	38	$F = 36.536$	0.720	Worldwide	Literature survey	Taxon	
Hechinger et al. 2007	Annelids, Crustaceans and Molluscs	Trematodes	Complex	Endoparasites	27	$F = 8.13$	0.640	California and Mexico	Field survey	Area	468
Hechinger et al. 2007	Fishes	Trematodes	Complex	Endoparasites	30	$F = 2.09$	0.263	California and Mexico	Field survey	Area	468
Hechinger et al. 2007	Crustaceans and Molluscs	Trematodes	Complex	Endoparasites	30	$F = 21.2$	0.656	California and Mexico	Field survey	Area	468
Krasnov et al. 2007	Mammals	Arthropods (fleas)	Simple	Ectoparasites	26	$F = 14.9$	0.616	Palaeoartic	Literature survey	Area	9192
Krasnov et al. 2007	Mammals	Arthropods (fleas)	Simple	Ectoparasites	19	$F = 1.1$	0.265	Nearctic	Literature survey	Area	6208
Merino et al. 2008	Birds	Protozoans (Haemoproteus)	Complex	Endoparasites	5	$F = 0.0006$	0.012	Chile	Field survey	Area	2419
Merino et al. 2008	Birds	Protozoans (Plasmodium)	Complex	Endoparasites	5	$F = 0.34$	0.280	Chile	Field survey	Area	2419
Merino et al. 2008	Birds	Protozoans (Leucocytozoon)	Complex	Endoparasites	4	$F = 18.60$	0.928	Chile	Field survey	Area	2419
Elizalde and Folgarait 2010	Arthropods (ants)	Arthropods (parasitoids)	Simple	Endoparasites	12	$Rho = 0.8$	0.800	South America	Field survey	Area	1271
Ishtiaq et al. 2010	Birds	Protozoans	Complex	Endoparasites	20	$b = 0.65$	0.650	Vanuatu archipelago	Field survey	Area	905
Krebs et al. 2010	Fishes	Unionids	Simple	Ectoparasites	9	$R = 0.5$	0.500	Ohio	Field survey	Area	276
Thieltges et al. 2011	Birds, Mammals and Reptiles	Trematodes (allogenic)	Complex	Endoparasites	25	$T = 5.191$	0.735	Europe	Literature survey	Area	3703
Thieltges et al. 2011	Fishes	Trematodes (autogenic)	Complex	Endoparasites	25	$T = 3.755$	0.617	Europe	Literature survey	Area	3703

(Continued)

Table 1. Continued.

Publication	Host	Parasite	Parasite life cycle	Parasite niche	N	Reported statistic	R	Location	Study type	Study unit	Spatial scale (km)
Thieltges et al. 2011	Gastropods	Trematodes (allogenic)	Complex	Endoparasites	25	$T = -1.839$	-0.358	Europe	Literature survey	Area	3703
Thieltges et al. 2011	Gastropods	Trematodes (autogenic)	Complex	Endoparasites	25	$T = -0.384$	-0.080	Europe	Literature survey	Area	3703
Vas et al. 2011	Birds	Arthropods (lice: Amblycera)	Simple	Ectoparasites	107	$R = 0.65$	0.650	Worldwide	Literature survey	Taxon	
Vas et al. 2011	Birds	Arthropods (lice: Ischnocera)	Simple	Ectoparasites	107	$R = 0.62$	0.620	Worldwide	Literature survey	Taxon	
Ebeling et al. 2012	Arthropods (bees)	Arthropods (parasitoids)	Simple	Endoparasites	78	$F = 0.702$	0.091	Germany	Field experiment	Area	2
Ebeling et al. 2012	Arthropods (wasps)	Arthropods (parasitoids)	Simple	Endoparasites	78	$F = 14.9$	0.403	Germany	Field experiment	Area	2
Vas et al. 2012	Birds	Arthropods (lice: Amblycera)	Simple	Ectoparasites	174	$R^2 = 0.46$	0.678	Worldwide	Literature survey	Taxon	
Vas et al. 2012	Birds	Arthropods (lice: Ischnocera)	Simple	Ectoparasites	174	$R^2 = 0.34$	0.583	Worldwide	Literature survey	Taxon	
Vas et al. 2012	Mammals	Arthropods (lice: Amblycera)	Simple	Ectoparasites	146	$R^2 = 0.11$	0.316	Worldwide	Literature survey	Taxon	
Vas et al. 2012	Mammals	Arthropods (lice: Anoplura)	Simple	Ectoparasites	146	$R^2 = 0.20$	0.447	Worldwide	Literature survey	Taxon	
Vas et al. 2012	Mammals	Arthropods (lice: Ischnocera)	Simple	Ectoparasites	146	$R^2 = 0.08$	0.283	Worldwide	Literature survey	Taxon	
Negishi et al. 2013	Fishes	Unionids	Simple	Ectoparasites	13	$R^2 = 0.17$	0.412	Japan	Field survey	Area	5
Negishi et al. 2013	Fishes	Unionids	Simple	Ectoparasites	13	$R^2 = 0.36$	0.600	Japan	Field survey	Area	5

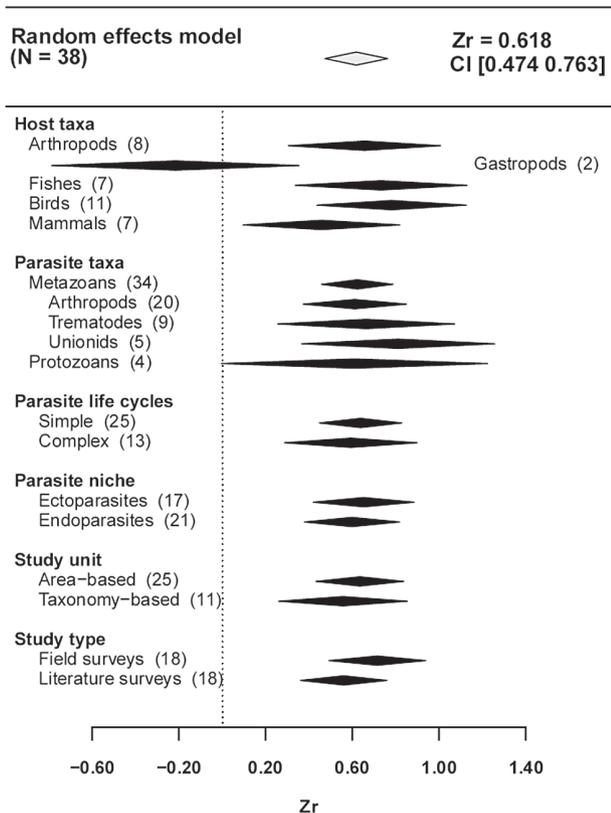


Figure 1. Forest plot showing the results of the meta-analysis examining the relationship between host species richness and parasite species richness, overall and for different subsets based on predictors. The result of the random effects model is shown at the top with a 95% confidence interval. Sample size in each category (number of effect sizes) is shown inside the parentheses. The width of diamonds represents a 95% confidence interval.

mammals ( $r = 0.428$ ) on average (Fig. 1). However, these statistically significant results are based on smaller sample sizes in each taxonomic group; therefore, the results should be interpreted cautiously. For the remaining categories associated with the tested predictors, the mean effect size for each category was consistently positive and statistically significant regardless of parasite taxa, parasite life cycle patterns, parasite niches, study designs, year of publication and/or sample size of the study (Fig. 1; Supplementary material Appendix 1, Table A3–A10).

Funnel plots revealed little indication of asymmetry (Supplementary material Appendix 1, Fig. A2). Also, the rank correlation between meta-analytic residuals and the inverse of sampling variance showed little evidence for publication bias (Kendall's tau =  $-0.142$ ,  $p = 0.213$ ). Therefore, our results from meta-analytic and meta-regression models are likely to be robust.

## Discussion

A growing realisation is now emerging that parasites can dominate food web links (Lafferty et al. 2006), and perform vital roles in ecosystem functioning from acting as ecosystem engineers (Thomas et al. 1999) to providing a

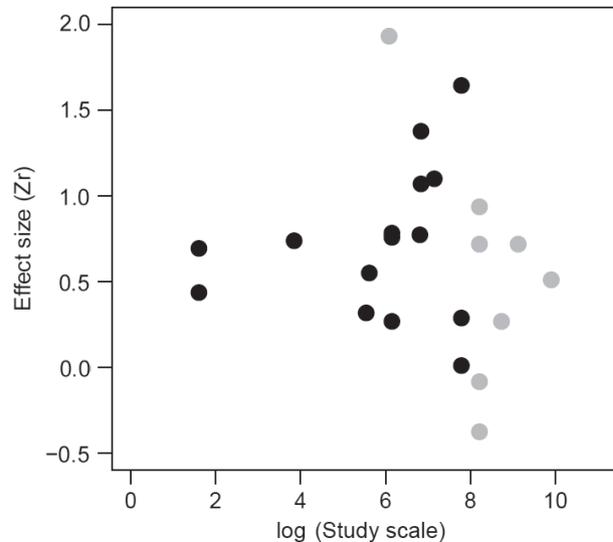


Figure 2. The effect size plotted against the log-transformed spatial scale of study. Black dots indicate field surveys ( $n = 15$ ) and grey dots are of literature surveys ( $n = 8$ ).

source of food (Johnson et al. 2010). Given also that biodiversity may impact the risk of infectious diseases and thus affect public health (Daszak et al. 2000, Keesing et al. 2006, Jones et al. 2008, Salkeld et al. 2013) patterns linking the biodiversity of parasites and their hosts and the underlying causal mechanisms are of both fundamental and applied ecological relevance. The present meta-analysis demonstrates that species richness of parasites is strongly correlated with that of their hosts, matching patterns between resource diversity and consumer diversity seen among free-living communities (Scherber et al. 2010, Castagnyrol and Jactel 2012); however, we found little evidence that spatial scale of studies affects the strength of this association. Furthermore, the present meta-analysis provides strong support for both the role of host availability and evolutionary co-variation in shaping host–parasite diversity relationships.

As hypothesised, we found a strong positive correlation among ‘area-based’ studies, meaning diverse communities of host species support more parasite species, regardless of the taxa involved. Our findings support the application of the ‘habitat heterogeneity hypothesis’ (Lawton 1983) which proposes that greater environmental diversity (in this case, host diversity) supports greater biological diversity. However, instead of overall habitat heterogeneity, Tews et al. (2004) point out the importance of ‘keystone structures’ that provide distinct resources, shelters or services, which may attract corresponding groups of animal species. In the context of host–parasite community interactions, certain host species may be considered as ‘keystone host species’ that attract disproportionate numbers of dependant parasite species, thereby boosting the total number of parasite species per area. Although the literature support for the role of host availability seems much more consistent than that for the ‘habitat heterogeneity hypothesis’ (cf. Tews et al. 2004), an assessment of the relative importance of overall host diversity versus that of ‘keystone host species’ will be

necessary for a fuller understanding of causal links between the biodiversity of parasites and their host communities. Nonetheless, given the tight statistical correlation between the number of host and parasite species across areas, loss of host biodiversity will inevitably be accompanied by loss of their parasites (Colwell et al. 2012). In fact, depending on host specificity and life cycle complexity, a decline in parasite diversity may be disproportionately steeper than that for their host species (Dobson et al. 2008). Furthermore, parasites constitute a significant part of food web interactions (Lafferty et al. 2006); their loss will result in a loss of food web links, the indirect impacts of which are still poorly understood. The meta-analytic mean values are likely to be useful for future modelling approaches, which attempt to understand parasite species loss in relation to that of host species.

An evolutionary aspect of the association between host and parasite diversity was also evident in the present analysis; richer host clades harboured richer parasite assemblages as expected by Eichler's rule (Eichler 1942). Although phylogenetic congruence between parasite phylogenetic trees and corresponding host trees is far from universal among host–parasite systems (Poulin and Morand 2004, de Vienne et al. 2013), for any given host lineage, the richness of parasite and host clades is expected to co-vary through co-diversification. Such co-variation is true, even if rates of speciation between parasites and their hosts are low. Our result is also consistent with the findings that parasite communities of endangered hosts generally undergo a bottleneck, resulting in reduced parasite biodiversity (Altizer et al. 2007). Considering the fact that certain clades are more likely to go extinct than others (Cardillo et al. 2005), it follows then that the evolutionary co-variation of host and parasite biodiversity is likely to be maintained through co-extinction as well as co-speciation events. Nonetheless, the mechanisms underlying host–parasite evolutionary diversification likely are complicated (Nunn et al. 2004) and deserve further investigation.

Finally, we found no evidence to suggest that the spatial scale of a study influences the host–parasite diversity relationships, a pattern consistent with those for free-living communities (Castagneyrol and Jactel 2012). Spatial scale was identified as a key factor because diversity relationships are expected to be driven by different ecological forces depending on scale: trophic interactions should matter at the local scale while environmental constraints would be more important at larger scales (Crawley and Harral 2001). Another assumption was that shared environmental constraints help to maintain the host–parasite diversity relationship; for instance, environmental conditions, such as habitat characteristics, have been linked to patterns of parasite community assembly (Krasnov et al. 1997). However, the role of environmental constraints may arise from their spatial variability, or predictability, instead of their average across areas. For example, differences in spatio-temporal predictability affect the relationships between the diversity of resource plants and their mutualist birds and bats (Fleming 2005); higher spatio-temporal predictability should drive consumers into specialisation, whereas lower predictability (i.e. high variability) may favour generalist strategies. Therefore, the strength of

the 'bottom-up' control of parasite diversity may be mediated through not only the mean values of shared environmental conditions, but also their predictability across different habitats. Yet in our meta-analysis, the relationship between host diversity and parasite diversity proved to be independent of study scale, suggesting that the importance of resource availability and co-diversification processes may override any spatial scale effects.

At the individual host species level, parasite biodiversity has traditionally been studied in relation to host body size (Price and Clancy 1983), geographical range (Dritschilo et al. 1975), population density (Morand et al. 2000), latitudinal distribution (Poulin 2001), and diet (Bell and Burt 1991) using interspecific comparisons among host species. In a recent meta-analysis, we identified host body size ( $r=0.256$ ), geographical range size ( $r=0.310$ ) and population density ( $r=0.268$ ) as significant correlates of parasite diversity at the level of individual host species (Kamiya et al. 2013). The present analysis is the first to provide meta-analytical insights into the patterns of parasite biodiversity at the broader community level. In comparison to species level determinants, the community level effect of host species richness as a predictor of parasite species richness was at least 1.9 times higher on average (in  $Z$ -transformed scale) than the best species level predictor (i.e. geographical range size), highlighting the importance of community level interactions in mediating biodiversity. The tight association between host and parasite biodiversity reported in the present analysis was independent of all the predictor variables tested, underscoring the generality of this relationship. This finding corroborates the widespread correlation of biodiversity between resource and consumer levels in free-living communities (Siemann et al. 1998, Biesmeijer et al. 2006, Nilsson et al. 2008). Furthermore the average effect size ( $r$ ) of 0.55 for the host–parasite diversity relationships was greater than that of the recent meta-analysis of plant–animal diversity relationships, which reported an average effect size ( $r$ ) of 0.45 (Castagneyrol and Jactel 2012), re-emphasising that host–parasite interactions provide an ideal system for studying congruence of biodiversity patterns across multiple trophic levels.

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Supplementary material (Appendix ECOG-00571 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1.