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What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts

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ABSTRACT

Although a small set of external factors account for much of the spatial variation in plant and animal diversity, the search continues for general drivers of variation in parasite species richness among host species. Qualitative reviews of existing evidence suggest idiosyncrasies and inconsistent predictive power for all proposed determinants of parasite richness. Here, we provide the first quantitative synthesis of the evidence using a meta-analysis of 62 original studies testing the relationship between parasite richness across animal, plant and fungal hosts, and each of its four most widely used presumed predictors: host body size, host geographical range size, host population density, and latitude. We uncover three universal predictors of parasite richness across host species, namely host body size, geographical range size and population density, applicable regardless of the taxa considered and independently of most aspects of study design. A proper match in the primary studies between the focal predictor and both the spatial scale of study and the level at which parasite species richness was quantified (i.e. within host populations or tallied across a host species' entire range) also affected the magnitude of effect sizes. By contrast, except for a couple of indicative trends in subsets of the full dataset, there was no strong evidence for an effect of latitude on parasite species richness; where found, this effect ran counter to the general latitude gradient in diversity, with parasite species richness tending to be higher further from the equator. Finally, the meta-analysis also revealed a negative relationship between the magnitude of effect sizes and the year of publication of original studies (i.e. a time-lag bias). This temporal bias may be due to the increasing use of phylogenetic correction in comparative analyses of parasite richness over time, as this correction yields more conservative effect sizes. Overall, these findings point to common underlying processes of parasite diversification fundamentally different from those controlling the diversity of free-living organisms.

Key words: body size, geographical range, latitude, meta-analysis, phylogenetic influences, population density.

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I. INTRODUCTION

The search for the determinants of local biodiversity and its spatial variation remains a central aim of modern ecology. A synthesis of published patterns has revealed that a small set of factors, namely temperature, rainfall, evapotranspiration and/or primary productivity, can account for much of the variation in plant and animal species diversity across space (Hawkins *et al.*, 2003). However, a substantial proportion of biodiversity consists of parasitic organisms (Poulin & Morand, 2004; Dobson *et al.*, 2008); elucidating the factors shaping variation in their diversity is crucial to identify disease risks for conservation targets or potential foci of emerging infectious diseases.

Parasite diversity is not randomly distributed among host species, yet the key drivers of parasite diversity remain poorly understood even after much study (Poulin, 1997; Poulin & Morand, 2004). It is true that for certain taxa of hosts, interspecific variation in parasite species richness appears to follow variation in host species traits such as body size, diet breadth or home range size (e.g. Bell & Burt, 1991; Nunn *et al.*, 2003; Lindenfors *et al.*, 2007; Arriero & Møller, 2008; Bordes *et al.*, 2009; Mitchell *et al.*, 2010). However, although several factors have been found to correlate with the richness of parasite species per host species in comparative studies, the significance and direction of these relationships are inconsistent among studies, and the predictive power (i.e. r^2) of the significant ones is often low (see Poulin, 1997; Poulin & Morand, 2004). The conclusions of existing studies raise doubt regarding the existence of a small set of universal factors that can account for variation in parasite species richness across host species regardless of the type of parasitic relationship, the taxa involved, or the geographical area of the study.

Parasite assemblages present certain advantages over those of free-living organisms in biodiversity studies. Their physical boundaries are clearly delimited (the host's body) and their historical relationships can be determined as the phylogeny of their host habitats. These assemblages are therefore potentially good model systems for studies of species richness and its determinants. Parasite assemblages form over evolutionary time as species of parasites are gained or lost by host lineages at different rates depending on the biological characteristics of the host species (Poulin & Morand, 2004). It is therefore reasonable to expect that host species with characteristics promoting the colonization and persistence of parasites should harbour richer parasite faunas than related hosts with different characteristics.

Among the available comparative studies, four main factors emerge as candidate predictors of parasite species richness (PSR), because they often, although not always, correlate with PSR. First, host body size frequently shows a positive correlation with PSR, as larger-bodied host species provide greater space and other resources to parasites, encounter them at higher rates, and also represent longer-lived habitat patches (Guégan *et al.*, 1992; Poulin, 1995). Of course, the independent effect of host body size (or that of the other characters mentioned below) on PSR can be obscured when comparisons are made across hosts with different trophic levels or living in completely different habitats; this may explain to some extent why not all comparative studies detect an effect of host body size. Second, geographical range size also often correlates with PSR, with host species having a broad range being more likely to encounter and be colonised by several parasite species over evolutionary time (Price & Clancy, 1983; Gregory, 1990). Third, host population density is a central parameter of classical epidemiological models (Anderson & May, 1979; May & Anderson, 1979) that determines the likelihood of a parasite persisting in a host population. Thus, host species occurring at high densities should have been more readily colonised by several parasite species, and have higher PSR, than hosts living at low population densities, a prediction for which there is also some empirical support (Morand & Poulin, 1998; Arneberg, 2002). Finally, in addition to the above three host properties, latitude is generally correlated with the diversity of free-living organisms (Willig, Kaufman & Stevens, 2003). As a proxy for the input of solar energy and potential rates of diversification (Turner, Gatehouse & Corey, 1987; Cardillo, 1999), it is also expected to correlate with the diversity of parasitic organisms, and often does so (Lindenfors *et al.*, 2007; Bordes, Guégan & Morand, 2011).

As mentioned earlier, the inconsistent relationships between the above four factors and PSR and their variable predictive power makes it difficult to assess their general importance as determinants of parasite diversity. Meta-analysis provides a rigorous way of synthesizing results from primary studies to identify general patterns and pinpoint sources of heterogeneity among original results (Nakagawa & Poulin, 2012; Koricheva, Gurevitch & Mengersen, 2013). In particular, meta-analysis has proved a useful tool for cutting through the idiosyncratic results of studies addressing various aspects of host-parasite interactions (Poulin & Forbes, 2012). For example, a meta-analysis of the inconsistent associations reported between host group size and the severity of parasitic infections experienced by individuals has revealed that the positive effect of group size depends on the parasite's mode of transmission and the taxa involved, and is only really strong for host species living in large aggregations (Rifkin, Nunn & Garamszegi, 2012).

Here, we perform a set of meta-analyses to evaluate the global empirical support for these four factors as predictors of PSR, and to identify for which types of host or parasite taxa they are more important determinants of PSR. We provide a quantitative review of the current evidence using a meta-regression approach that incorporates multiple factors (i.e. modulators) to account for heterogeneity in data (Thompson & Higgins, 2002). This approach allows estimation of an effect size for separate categories (e.g. across different host or parasite taxa) as well as comparisons of modulators using an information-theoretic framework. We also assess the influence of several aspects of the design of original studies on the strength of the support they found for the four predictors. For example, both sampling effort (Walther *et al.*, 1995) and host phylogenetic relationships (Morand & Poulin, 2003) are known to influence comparisons of PSR across host species, but not all studies have corrected for such confounding variables. In order to seek commonalities among different systems, we employed a broad definition of parasitism which encompasses a wide range of interactions involving plant, animal and fungal hosts; therefore, we included studies on parasitoids, parasitic castrators, directly transmitted parasites, trophically transmitted parasites, vector-transmitted parasites, micro-predators and gall-forming insects. With dozens of comparative analyses now available in the literature, the time is ripe for this particular meta-analysis (Poulin & Forbes, 2012), which complements earlier synthetic quantitative assessments of the drivers of diversity in free-living organisms (Hawkins *et al.*, 2003).

II. METHODS

(1) Data compilation

A dataset was compiled from published comparative studies reporting an effect size for the association between PSR and one or more of the four predictors of interest (host body size, host geographical range size, host population density, and latitude). The search for studies of metazoan hosts began with the references listed in table 4.1 from Poulin & Morand (2004). In addition, in search of plant and fungal host studies, we carried out a search across all years of the ISI *Web of Knowledge*, up to the end of 2012, using the key words: (parasite species richness or insect species richness or pathogen richness) AND (height or size or geographical range or density or latitude) AND (plant or fungi). The ISI *Web of Knowledge* was further searched for articles that cited the references found for metazoan, plant or fungal hosts following the procedures outlined above, for which further citing articles were also cross-checked to form a network of articles connected by citations. The reference lists of all key relevant papers found in this way were also scrutinised to expand the database. Thus, the literature coverage was as close to exhaustive as possible, and spanned all available literature on determinants of parasite and pathogen richness across a range of animal, plant and fungal hosts.

In total, the dataset included 62 comparative studies which examined at least one of the correlates of PSR of interest here; several of these studies contributed more than one data point to our analyses (see online supporting information Tables S32–S35 in Appendix S2). If multiple host-parasite interactions were investigated separately within a single study (e.g. Poulin, 1995), they were treated as independent data points, although dataset identity was controlled for in analyses (see Meta-analytical models section below). Conversely, some results from particular studies were omitted when reported for different taxa of parasites examined on the same hosts at taxonomic levels below those of interest here (e.g. coleopterans and dipterans were pooled as arthropods; Takahashi, Tuno & Kagaya, 2005). To be included, a comparative study had to report a standardised effect size, usually in the form of a correlation coefficient, of the relationship between PSR (number of parasite species of a given type per host species) and one or more of the four predictors. Several otherwise relevant studies had to be omitted because they presented no effect size, and no way of calculating one. Effect sizes other than correlations were converted to correlation coefficients according to Lipsey & Wilson (2001) and Nakagawa & Cuthill (2007). Also, host sample size, i.e. the number of host species (or genera in three cases) involved in the analysis, had to be specified (for computation of sampling variances of the Fisher's z-transformed correlation coefficients, or Zr; see Meta-analytical models section below). In cases where there was a complete overlap of datasets used by distinct studies, we only retained the publications which included the larger dataset, or those that controlled for the most confounding variables (e.g. sample size and/or host phylogeny), to avoid duplication. For example, Luque & Poulin (2007) was included in the analysis of body size as it controlled for sampling effort in terms of publication bias, whereas Luque & Poulin (2008) had an overlapping dataset but did not control for sampling effort. For other studies where a significant degree of overlap in datasets was known (e.g. Poulin, 1995; Gregory, Keymer & Harvey, 1996; Poulin & Mouillot, 2004), the same dataset identifier was allocated and used for analysis (see Tables S32–S35 in online Appendix S2) to control for pseudo-replication. In addition, a few studies on primates were carried out by the same research group to answer slightly different questions; however, the datasets used are likely to be similar, although they involved independent literature searches as well as the use of an online database. Therefore results from Altizer, Nunn & Lindenfors (2007), Nunn *et al.* (2003) and Vitone, Altizer & Nunn (2004) were all assigned the same dataset identifier in the analysis of body size. This assured a more conservative approach than including study identity in the analysis.

For each comparative analysis, additional information was also recorded on several other variables that were treated as modulators in the meta-regression. These included two host-related modulators: (*i*) higher taxon to which the hosts belong, i.e. plants, fungi, or metazoans; and (*ii*) in the case of metazoans, the taxonomic group to which they belong, i.e. gastropods, arthropods, fishes, birds or mammals. We also included four parasite-related modulators: (*i*) higher taxon to which the parasites belong, i.e. metazoans or non-metazoans; (*ii*) in the case of metazoans, the taxonomic group to which they belong, i.e. arthropods or helminths; (*iii*) in the case of helminths, the taxonomic group to which they belong, i.e. monogeneans, trematodes, cestodes, nematodes or acanthocephalans; and (*iv*) whether they were ecto- or endoparasites. Finally, we recorded information on five study-related modulators: (*i*) year of publication of the study; (*ii*) the study's geographical scale, either regional, continental or global, i.e. involving host species from a defined region within a continent, from a significant portion of a continent, or from anywhere in the world; (*iii*) whether the parasite assemblage was measured at the host population or species level, in other words whether PSR was measured in parasite communities from one or a few (averaged) population samples per host species or whether it represents a tally of the whole parasite fauna exploiting a host across its geographical range; (*iv*) whether or not the analysis controlled for the potential influences of host phylogenetic relationships; and (*v*) whether or not the analysis controlled for unequal sampling effort among host species, i.e. unequal numbers of individual hosts examined per species.

(2) Meta-analytical models

Meta-analyses were carried out in R 2.14.1 (R Development Core Team, 2011) using the *metafor* package (Viechtbauer, 2010), and the *nlme* package (Pinheiro *et al.*, 2012) to account for correlated structures arising from dataset identity (Lumley, 2002); see also Nakagawa & Santos (2012). The raw correlation coefficients were transformed to Fisher's z-transformed correlation coefficients, Zr, and their sampling variances were computed using the *escalc* function in the *metafor* package, thereby weighting for differences in the sample size among studies. Based on Zr and the corresponding sampling variances, separate random-effect models were employed to estimate the overall effect size of the relationship between PSR and each of the four proposed determinants (i.e. host body size, geographical range size, host population density, and latitude). We assessed potential publication bias visually using funnel plots and also quantitatively using rank correlation tests for asymmetry (Rothstein, Sutton & Borenstein, 2005). Where a significant level of asymmetry was detected, an adjusted estimate derived from the trim and fill method was calculated (Duval, 2005). Models were also constructed with dataset identifier as a random effect to model correlated structure arising from shared datasets before the modulators were investigated.

Mixed-effects meta-regression models were then employed to account further for heterogeneity in the data. In addition, an information-theoretic approach was used to compare the effect of the modulators, with corrected Akaike Information Criterion, AICc, used to assess model fit (e.g. Jones, Nakagawa & Sheldon, 2009; reviewed in Grueber *et al.*, 2011). Also the measure of heterogeneity I^2 was employed to quantify the amount of between-study variation in relation to the total variance; in our case, the total variance consisted of the between-study variance and the sampling/measurement error variance (Higgins *et al.*, 2003; Nakagawa & Santos, 2012). In the case of host body size and geographical range size, for which a relatively large number of data points was available ($N = 78$ and 44, respectively), we tested the effect of all of the aforementioned host-related, parasite-related and study-related modulators separately while controlling for (*i*) the effect of dataset identity and (*ii*) a subset of other covariates determined from AICc-based model selection using the *dredge* function in the *MuMIn* package (Bartoń, 2012). Because the number of data points for host density and latitude was considerably smaller ($N = 20$ data points in each case with $N_{\mathrm{Density}} = 11$ and $N_{\mathrm{Latitude}} = 10$ independent datasets), we only tested subsets of the modulators after controlling for dataset identity and no model selection procedure was carried out for these potential determinants.

III. RESULTS

Overall, the present meta-analysis examined 62 studies investigating metazoan and non-metazoan parasites that infect fungal, metazoan and plant hosts (Table 1). The full dataset is available in online Appendix S2 (Tables S32–S35). Results of detailed analyses may be found in online Appendix S1 (Tables S1–S31).

(1) Host body size

Overall, host body size had a relatively strong, well-supported positive effect on the number of parasite taxa the host harboured ($Zr = 0.278$, 95% CI = 0.222–0.335, $P < 0.001$, $I^2 = 78.07\%$) (Fig. 1). However, a significant asymmetry was detected in the funnel plot (Rank-test: Kendall's tau = 0.189, $P = 0.015$), which could be indicative of publication bias. After the potential effects of publication bias were accounted for using the trim and fill method, the relationship between host body size and PSR remained positive ($Zr = 0.193$, 95% CI = 0.128–0.259, $P < 0.001$, $I^2 = 85.56\%$). Furthermore, the effect size remained roughly similar after controlling for the effect of dataset identity ($Zr = 0.262$, 95% CI = 0.197–0.328, $P < 0.001$, $I^2 = 61.24\%$).

In all the host kingdoms investigated, host body size exhibited a significantly positive effect on PSR (Fig. 1; online Table S1). Among metazoans, a well-supported positive relationship was found for fishes and mammals, while the confidence intervals of relationships for other taxa included 0 despite the generally positive direction of effect sizes (Fig. 1; online Table S2). Furthermore, the association between host body size and PSR was significantly tighter in fishes when compared pairwise with birds and mammals. Considering different parasite taxa, the association between body size and PSR was significantly positive for both metazoan and non-metazoan parasites regardless of their site of infection, i.e. ecto- or endoparasites (Fig. 1; online Tables S3, S6). At each geographical scale and each level of study, the effect size was significantly positive with no marked difference among them (Fig. 1; online Tables S8, S9). However, although both significantly positive, whether or not studies controlled for the effect of host phylogeny caused a difference in effect sizes: studies that controlled for host phylogeny reported lower effect sizes (Fig. 1; online Table S10). We also uncovered decreasing effect sizes over time (online Table S7), a phenomenon possibly caused by the greater frequency of corrections for host phylogeny in recent studies (see Section IV). Furthermore, the information-theoretic approach suggested that whether or not a study controlled for host phylogeny was a key modulator overall, as it appeared in 6 of the 10 best models, whereas higher parasite taxon accounted

Table 1. Total numbers of effect size values used for each category with the corresponding number of studies and number of datasets, respectively, given in parentheses

Category	Body size	Geographical range	Host density	Latitude
Host taxon				
Metazoans	66 (40, 35)	35 (18, 15)	12 (12, 10)	20 (10, 10)
Arthropods	2 (2, 2)	1 (1, 1)	0	0
Gastropods	1 (1, 1)	0	0	0
Fishes	29 (20, 17)	9 (5, 5)	2 (2, 2)	3 (2, 2)
Birds	8 (6, 5)	4 (2, 2)	1 (1, 1)	5 (3, 3)
Mammals	26 (16, 12)	21 (11, 8)	16 (9, 7)	9 (4, 4)
Fungi	2 (2, 2)	0	1 (1, 1)	0
Plants	10 (9, 8)	9 (8, 8)	0	0
Parasite taxon				
Metazoans	65 (47, 40)	34 (22, 21)	14 (12, 10)	14 (9, 9)
Arthropods	16 (15, 14)	3 (3, 3)	1 (1, 1)	1 (1, 1)
Helminths	40 (26, 22)	24 (12, 11)	13 (11, 10)	11 (8, 8)
Acanthocephalans	2 (2, 2)	1 (1, 1)	—	—
Cestodes	4 (4, 4)	3 (3, 3)	—	2 (2, 2)
Digeneans	5 (5, 5)	3 (3, 3)	—	3 (3, 3)
Monogeneans	2 (2, 2)	1 (1, 1)	—	—
Nematodes	5 (5, 5)	4 (4, 4)	2 (2, 2)	1 (1, 1)
Endoparasites	49 (28, 24)	31 (15, 12)	19 (12, 10)	19 (10, 10)
Ectoparasites	14 (14, 12)	3 (3, 3)	1 (1, 1)	1 (1, 1)
Non-metazoans	13 (8, 7)	10 (6, 4)	6 (3, 3)	6 (3, 3)
Geographical scale				
Regional	20 (15, 14)	13 (9, 9)	4 (4, 4)	1 (1, 1)
Continental	20 (13, 13)	13 (7, 7)	1 (1, 1)	4 (2, 2)
Global	38 (23, 17)	18 (10, 7)	15 (8, 6)	15 (7, 7)
Level of study				
Population	33 (25, 21)	13 (8, 8)	7 (7, 7)	12 (7, 7)
Species	45 (26, 23)	31 (18, 15)	13 (6, 4)	8 (3, 3)
Host phylogenetic relationships				
Controlled	44 (30, 26)	23 (15, 13)	16 (9, 8)	15 (8, 8)
Not controlled	34 (22, 22)	21 (12, 12)	4 (4, 4)	5 (2, 2)
Sampling effort				
Controlled	54 (33, 29)	32 (18, 15)	19 (12, 10)	20 (10, 10)
Not controlled	24 (18, 16)	12 (8, 8)	1 (1, 1)	0
Total	**78 (51, 44)**	**44 (26, 23)**	**20 (13, 11)**	**20 (10, 10)**

Note that numbers are not additive due to several studies contributing to separate categories, as well as some studies being omitted in subsets of the full data (due to a lack of required detail). The totals refer to the full dataset before division into subsets. Dashes under 'Helminths' indicate lack of sufficient details for these subsets while '0' indicates a lack of data points.

for more heterogeneity than other modulators after dataset identity was taken into account (Table 2a).

(2) Host geographical range size

Host geographical range size had a strong, positive association with the number of parasite taxa the host harboured ($Zr = 0.306$, 95% CI = 0.213–0.398, $P < 0.001$, $I^2 = 83.59\%$). Although evidence of asymmetry was detected in the funnel plot (Rank test: Kendall's tau = 0.229, $P = 0.031$), the trim and fill method estimated zero missing studies in the negative direction. Furthermore, the effect size remained similar after controlling for the effect of dataset identity ($Zr = 0.320$, 95% CI = 0.186–0.454, $P < 0.001$, $I^2 = 84.87\%$).

For both metazoan and plant hosts, host geographical range size exhibited a significantly positive effect on PSR, and there was no difference between them (Fig. 2; Table S12). All taxonomic subsets of animal hosts exhibited a significant positive relationship, with the exception of arthropods for which the confidence interval marginally included 0, probably due to limited sample size (online Table S13). Furthermore, host geographical range size had a significantly positive effect on PSR for all parasite taxa examined, while none of the taxonomic groups differed significantly from each other (Fig. 2; online Table S14). However, endoparasites exhibited a greater effect size than ectoparasites after controlling for the effect of dataset identity (online Table S16). With regard to variables associated with study design, the overall effect size of studies carried out at the global level was not significantly different from 0 despite its general positive direction (Fig. 2; online Table S18). In addition, studies that employed parasite richness data at the

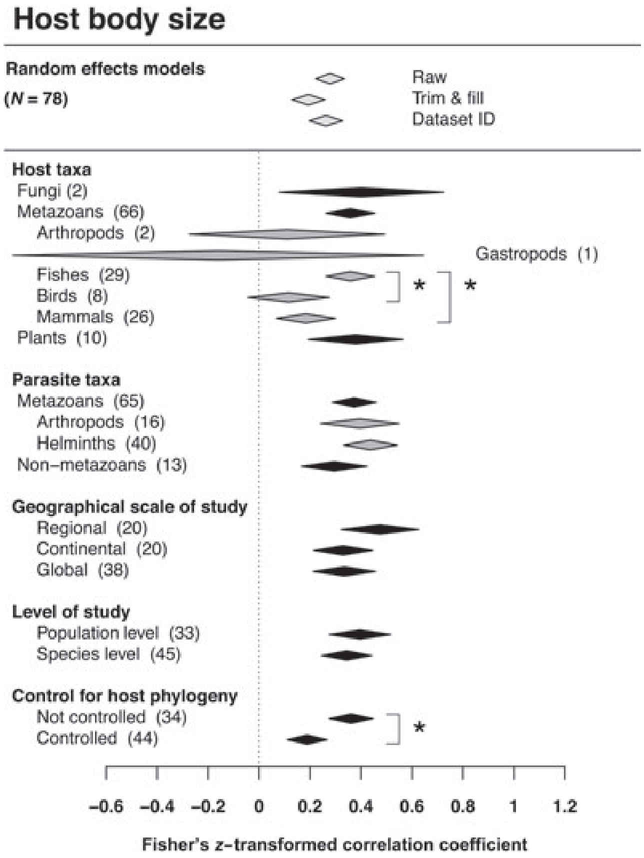

Fig. 1. Forest plot showing the results of 78 comparative estimates examining the relationship between host body size and parasite species richness, overall and for different subsets based on different host-related, parasite-related, and study-related modulators. The results of the random-effect models (raw analysis, trim and fill method and controlled for dataset identity) are shown at the top. All mixed-model effect sizes presented here are controlled for dataset identity and, where applicable, a subset of potential confounders selected according to corrected Akaike Information Criterion (AICc)-based model selection (see online Appendix S1 for results). Sample size in each category (number of effect sizes) is shown inside parentheses. The width of diamonds represents the 95% confidence interval. Asterisks indicate significant pairwise differences at the α level of 0.05.

population level had a non-significant overall effect size (Fig. 2; online Table S19). Again, studies that controlled for host phylogeny reported lower effect sizes than those that did not (Fig. 2; online Table S20).The information-theoretic approach again suggested that whether or not a study controlled for host phylogeny was a key modulator overall, as it appeared in 4 of the 10 best models, while none of the other modulators reduced the heterogeneity markedly (Table 2b).

(3) Host population density

The overall association between host density and PSR was positive ($Zr = 0.236$, 95% CI = 0.132–0.339, $P < 0.001$, $I^2 = 66.78\%$) with an indication of publication bias from the funnel plot (Rank test: Kendall's tau = 0.404, $P = 0.014$). After an addition of one estimated missing study, the positive relationship remained ($Zr = 0.226$, 95% CI = 0.122–0.330, $P < 0.001$, $I^2 = 66.52\%$). Furthermore, the overall effect size remained similar after controlling for the effect of dataset identity ($Zr = 0.275$, 95% CI = 0.128–0.422, $P = 0.004$, $I^2 = 56.29\%$). Host density served as a reliable predictor of PSR for both metazoan and non-metazoan parasites, and at any geographical scale (Fig. 3; online Tables S22, S24). For studies based on population-level measures of PSR, the average effect size was significantly positive, whereas for those using species-level PSR estimates, the effect size was close to statistical significance ($P = 0.056$) after controlling for the effects of dataset identity (Fig. 3; online Table S25).

(4) Latitude

There was a weak, and non-significant, positive association between latitude and PSR overall ($Zr = 0.038$, 95% CI = −0.049–0.125, $P = 0.391$, $I^2 = 69.22\%$), i.e. parasite species richness tended to be higher further from the equator; there was little indication of publication bias from the funnel plot (Rank test: Kendall's tau = 0.081, $P = 0.624$). Furthermore, the overall effect size remained similar after controlling for the effect of dataset identity ($Zr = 0.057$, 95% CI = −0.043–0.156, $P = 0.291$, $I^2 = 39.94\%$). While latitude showed a significantly positive association with PSR for metazoan parasites, the pattern was reversed for non-metazoan parasites with a negative, albeit non-significant, effect size ($P = 0.096$; Fig. 4; online Table S27). For each geographical scale of study, the average effect size was not significantly different from 0, with only a slight positive tendency (Fig. 4, online Table S29). In addition, studies based on population-level measures of PSR exhibited a significantly higher overall effect size than those using species-level PSR estimates (Fig. 4; online Table S30). Finally, the impact of controlling for host phylogeny was minimal (online Table S31).

IV. DISCUSSION

Identifying the main drivers of spatial variability in biodiversity provides key insights toward the identification of underlying mechanisms of diversification, as well as being an essential step for biodiversity conservation. For free-living organisms, a small set of factors emerge as universal predictors of plant and animal diversity (Hawkins *et al.*, 2003). Our meta-analysis indicates that for parasitic organisms, there also exist a small number of universal predictors of variation in parasite species richness across host species, namely host body size, host geographical range size and host population density. Their effects apply regardless of the type of hosts or parasites considered, or the parasites' mode of infection, site of transmission or size relative to the host. This finding contrasts with earlier conclusions based on qualitative reviews of published empirical results (Poulin, 1997; Poulin & Morand,

Table 2. Corrected Akaike Information Criterion (AICc)-based model selection of modulators for the relationship between either (a) host body size or (b) geographical range size and parasite species richness

(a) Host body size				(b) Geographical range size			
Models	I^2(%)	AICc	Δ AICc	Models	I^2(%)	AICc	Δ AICc
(Intercept) + phylogeny	60.2	15.2	0	(Intercept)	84.9	16.3	0
(Intercept)	61.3	18.7	3.46	(Intercept) + phylogeny	80.3	17.1	0.81
(Intercept) + phylogeny + parasite	53.9	20.0	4.76	(Intercept) + effort	81.8	18.1	1.77
(Intercept) + phylogeny + level	60.2	20.6	5.36	(Intercept) + level	83.9	20.0	3.69
(Intercept) + phylogeny + effort	60.6	20.7	5.48	(Intercept) + host	84.9	20.2	3.89
(Intercept) + effort	59.8	21.9	6.67	(Intercept) + phylogeny + effort	79.0	20.4	4.03
(Intercept) + parasite	53.4	22.9	7.69	(Intercept) + parasite	85.4	20.8	4.50
(Intercept) + phylogeny + scale	60.9	23.6	8.41	(Intercept) + phylogeny + level	80.3	21.5	5.17
(Intercept) + phylogeny + year	56.9	23.9	8.73	(Intercept) + phylogeny + host	80.8	21.5	5.19
(Intercept) + level	61.8	24.1	8.88	(Intercept) + scale	83.8	21.6	5.31

I^2 = heterogeneity (the amount of between-study variance in relation to the total variance). Ten models were chosen based on AICc. Modulators included were: host, host taxonomy (metazoans, plants, fungi); parasite, parasite taxonomy (metazoans, non-metazoans); year, year of publication; scale, geographical scale (regional, continental, global); level, whether parasite richness was measured at host population or species level; phylogeny, whether a study controlled for host phylogeny; effort, whether a study controlled for sampling effort. Kingdom-level host taxonomy was used because it produced the lowest AICc. Intercept-only models are the simplest models without modulators. Global model = (intercept) + host + parasite + scale + level + phylogeny + effort + year; (a) AICc = 60.43; (b) AICc = 58.37.

2004), and hints at the action of common underlying processes of community diversification independent of the taxa involved. However, the meta-analysis also reveals that in some cases the effect of these universal predictors depends on either the hierarchical level of study (whether parasite richness is measured within host populations or across the hosts' entire ranges) or on the spatial scale of the study. As discussed below, these highlight issues of mismatch between the chosen level or scale, and the underlying processes of parasite diversification associated with certain predictors.

Host body size is the most widely used predictor of PSR in comparative analyses and the one with the longest history as a suspected determinant of PSR (Price & Clancy, 1983; Kennedy & Southwood, 1984; Poulin & Morand, 2004). The theoretical basis of its potential as a predictor of PSR originates from parallels with island biogeography theory (MacArthur & Wilson, 1967) and species-area relationships (He & Legendre, 1996; Lomolino, 2000). Simply put, larger-bodied host species provide greater space and other resources to parasites, may encounter them at higher rates through contact or food, and/or also represent less ephemeral habitat patches than small-bodied host species. Here, we show that the interspecific relationship between host body size and PSR is universal across host and parasite taxa, and across levels or scales of study. When average effect sizes are computed separately for lower taxonomic groups of hosts or parasites, either effect sizes are stronger for certain host groups than others (e.g. stronger effect sizes for fish hosts than for birds or mammals), or in some cases they are non-significant, though this is most likely due to small numbers of data points and low power (see Fig. 1 and online Table S2). Our results indicate that whether considering fungi, plants or fishes, larger species tend to harbour richer parasite communities, whatever the type of parasites. Therefore, the underlying mechanisms, i.e. greater probability of colonization and persistence on larger and longer-lived resource patches providing more niches, apply generally to most host-parasite associations.

Host geographical range size also often correlates with PSR in comparative studies. The rationale underpinning this relationship is that a host species with a broad range should be more likely to encounter and be colonised by several parasite species over evolutionary time, because its range overlaps with those of other 'source' host species (Gregory, 1990). Broader geographical ranges also encompass a greater diversity of habitats suitable for different parasites and their other required hosts (i.e. vectors, intermediate hosts). Our meta-analysis provides strong support for geographical range size as another universal predictor of PSR, independent of the host or parasite taxa considered. Here again, when average effect sizes are computed for lower taxonomic groups of hosts or parasites, they are sometimes non-significant, most likely because of low power (see Fig. 2 and online Tables S13, S15). Intriguingly, the average effect size of the relationship between geographical range size and PSR is stronger for endoparasites than ectoparasites, a difference with no obvious explanation. Furthermore, our analysis reveals that the effect of host geographical range size depends on the spatial scale of the study: it becomes non-significant for comparative studies performed across a global scale, i.e. contrasting host species from different continents. This is not surprising, as two host species with identical range sizes may experience very different colonization rates by parasites if they inhabit completely different biogeographical realms. For instance, all else being equal small mammals from the Palaearctic (Eurasia) harbour richer ectoparasite faunas for any given local host faunal diversity, than small mammals from the Nearctic (North America) (Krasnov *et al.*, 2007).

In addition, the meta-analysis showed that the effect of host geographical range size is only significant for comparative studies in which PSR was measured at the host species

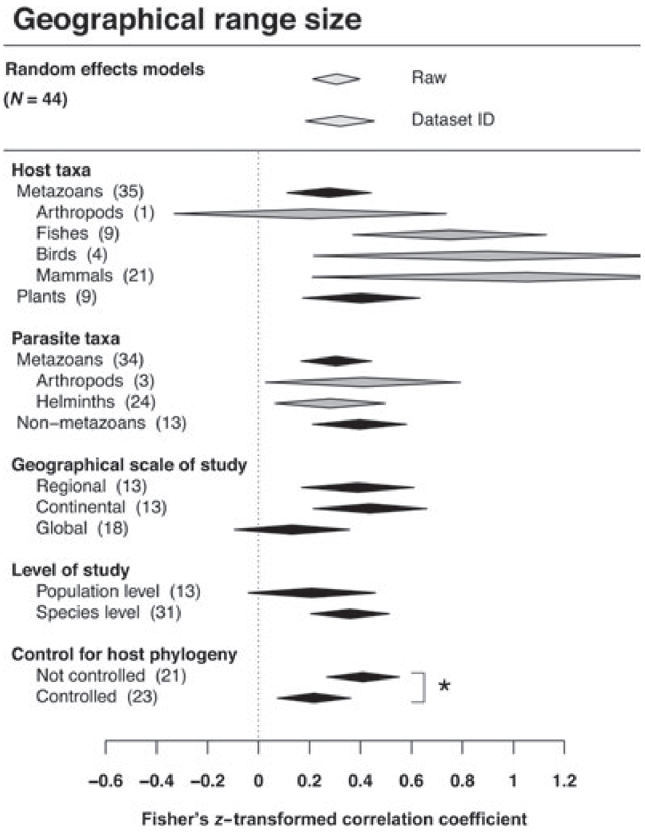

Fig. 2. Forest plot showing the results of 44 comparative estimates examining the relationship between host geographical range size and parasite species richness, overall and for different subsets based on different host-related, parasite-related, and study-related modulators. The results of the random-effect models (raw analysis and controlled for dataset identity) are shown at the top. All mixed-model effect sizes presented here are controlled for dataset identity, and where applicable, a subset of potential confounders selected according to corrected Akaike Information Criterion (AICc)-based model selection (see online Appendix S1 for results). Sample size in each category (number of effect sizes) is shown inside parentheses. The width of diamonds represents the 95% confidence interval. Asterisks indicate significant pairwise differences at the α level of 0.05.

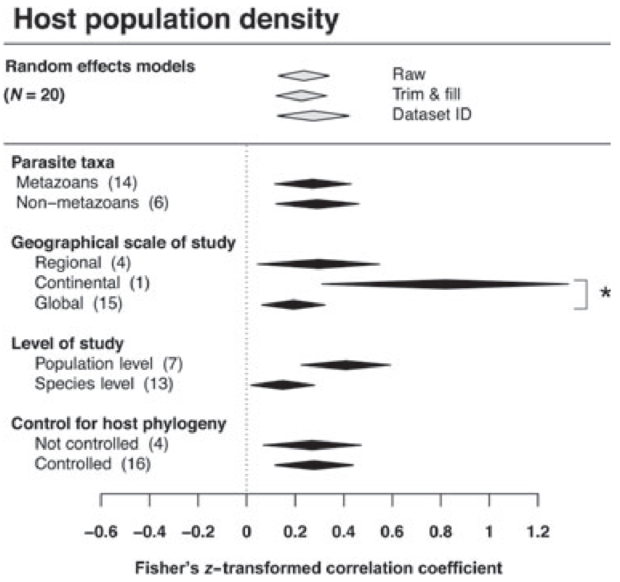

Fig. 3. Forest plot showing the results of 20 comparative estimates examining the relationship between host population density and parasite species richness, overall and for different subsets based on different host-related, parasite-related, and study-related modulators. The results of the random-effect models (raw analysis, trim and fill method and controlled for dataset identity) are shown at the top. All mixed-model effect sizes presented here are controlled for dataset identity, and where applicable, a subset of potential confounders selected according to corrected Akaike Information Criterion (AICc)-based model selection (see online Appendix S1 for results). Sample size in each category (number of effect sizes) is shown inside parentheses. The width of diamonds represents the 95% confidence interval. Asterisks indicate significant pairwise differences at the α level of 0.05.

level, and not at the host population level. The parasite community exploiting a host population is only a subset of the total parasite fauna exploiting this host species across its geographical range. The richness of this local parasite community is determined by both the size of the species pool (the total fauna) and local factors that influence the transmission and persistence of individual species. Therefore, given that the effect of host geographical range size on PSR operates through overlap with other host species and host-switching by parasites (e.g. Beveridge & Spratt, 1996), its influence is most likely manifested at the host species level, and not at a local population level. These results highlight the importance of properly matching the level of a study and its spatial scale with the mechanism linking a focal predictor with PSR, to exclude the influence of additional confounding factors. Most of the inconsistencies among the results of published comparative analyses of PSR appear to be due to mismatches of this kind.

The third seemingly universal predictor of PSR identified by our meta-analysis, host population density, is a central parameter of classical epidemiological models (Anderson & May, 1979; May & Anderson, 1979). Our findings thus corroborate the models' extended prediction that host species occurring at high densities should have higher PSR than hosts living at low population densities (see Morand & Poulin, 1998). In principle, and as observed here, the effect of host density should apply to all types of parasites, whatever their modes of transmission or infection. Not surprisingly, the average effect size tends to be lower for comparative analyses performed at a global scale, again probably because of the extra confounding variables involved when comparing hosts from different biogeographical areas. Also, the average effect size of host population density is higher for comparative studies in which PSR was measured at the host population level, than for those where it was measured at the host species level. Under any set of local conditions, a high-density host population should be more likely to sustain many parasite species than a low-density population. However, local density does not relate to how many different

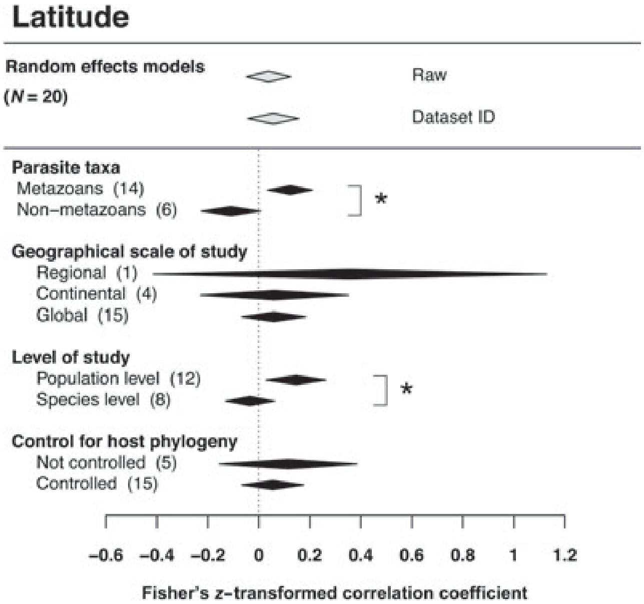

Fig. 4. Forest plot showing the results of 20 comparative estimates examining the relationship between latitude and parasite species richness, overall and for different subsets based on different host-related, parasite-related, and study-related modulators. The results of the random-effect models (raw analysis and controlled for dataset identity) are shown at the top. All mixed-model effect sizes presented here are controlled for dataset identity, and where applicable, a subset of potential confounders selected according to corrected Akaike Information Criterion (AICc)-based model selection (see online Appendix S1 for results). Sample size in each category (number of effect sizes) is shown inside parentheses. The width of diamonds represents the 95% confidence interval. Asterisks indicate significant pairwise differences at the α level of 0.05.

parasite species a host may be exposed to across its entire geographical range, thus accounting for the stronger effect of population density on PSR measured at the more relevant population level than at the species level.

Finally, the latitude at which hosts live did not emerge as an important predictor of PSR across all studies (note, however, the heterogeneity in this dataset was moderately high). However, although not very strong, the average effect size of latitude on PSR was significant for two subsets of studies, those on metazoan parasites and those where PSR was measured at the population level. Intriguingly, these weak but significant effects were positive, hosts at higher latitudes harbouring more parasites than those at lower latitudes (Fig. 4). This goes against the general trend observed for free-living organisms (Cardillo, 1999; Willig *et al.*, 2003). It may be that the overriding effect of other determinants of PSR masks any influence of latitude-associated factors. For instance, among freshwater fish species surveyed for helminth parasites, those of temperate areas are larger-bodied than tropical ones (Poulin, 2001). A more general explanation may be that parasite diversity is decoupled from energy input into a system from solar radiation, and instead driven directly by host characteristics. Studies of human pathogens have reported a more conventional negative relationship between latitude and PSR (Guernier, Hochberg & Guégan, 2004); however, because corrections for socioeconomic factors cannot truly account for latitudinal variation in biomedical practices affecting disease persistence, these are not comparable to studies of non-human hosts.

Some other patterns emerged from the meta-analysis. First, we found that for the two analyses with large numbers of original effect sizes (those for host body size and host geographical range size), average effect sizes adjusted for whether or not the original comparative analyses controlled for host phylogenetic influences were significantly smaller than 'raw' effect sizes (see Figs 1 and 2 and online Tables S10, S20). Different species are not independent data points in comparative studies (Harvey & Pagel, 1991). Controlling for this non-independence often results in lower power, because closely related species with extreme values, such as large-bodied congeneric host species with very high PSR, are not given full weight in the analysis (Morand & Poulin, 2003). Ignoring phylogenetic non-independence among host species clearly inflates estimates of effect size. Second, again focusing on the two analyses with many original studies (host body size and host geographical range size), based on the 'raw' effect sizes, there was a negative relationship between the magnitude of the effect size and the year of publication of original studies. At first glance, this might suggest some form of temporal publication bias (known as time-lag bias; Trikalinos & Ioannidis, 2005), as occasionally seen in evolutionary ecology (Alatalo, Mappes & Elgar, 1997; Poulin, 2000; Santos, Scheck & Nakagawa, 2011). However, in the case of host body size (the effect of whether or not phylogeny has been controlled was lost after controlling for dataset identity in the case of geographical range size), the relationship disappeared once we used effect sizes adjusted for whether or not the original comparative analyses controlled for host phylogeny (online Tables S7, S17). As the use of phylogenetic correction in comparative analyses of PSR has increased over time, these findings probably reflect the more frequent use of phylogenetically correct approaches in more recent studies.

V. CONCLUSIONS

(1) Our analysis identified host body size, host geographical range size and host population density as key universal determinants of interspecific variation in parasite species richness, independent of the types of hosts or parasites considered. Combined, these factors are probably as powerful to explain PSR as temperature, rainfall, evapotranspiration and primary productivity are to explain plant and animal species richness across space (Hawkins *et al.*, 2003).

(2) These three determinants of interspecific variation in parasite species richness are intercorrelated, however. Indeed, macroecological studies have demonstrated that body size and population density are negatively related; similarly, population density and geographical range size

are generally positively related (Damuth, 1987; Brown, 1995; Gaston & Blackburn, 2000). Because these three determinants of PSR are not independent from each other, it is difficult to disentangle their respective effects. Not enough of the original comparative studies included in our meta-analysis considered all three factors to allow us to tackle this issue, and it therefore remains to be addressed.

(3) The general influence of latitude on PSR emerged as weak, and limited to certain subsets of studies. However, because few original effect sizes were available to test the effect of latitude, and because the observed effect, in the two cases where it was significant, was the opposite of the latitudinal gradient in diversity seen in free-living organisms, it is too early to dismiss latitude as a predictor of PSR. Further comparative analyses will be necessary, especially for host taxa that have not received much attention to date (i.e. plants, fungi and invertebrates).

(4) Other predictors of PSR have been proposed in the primary literature, such as host metabolic rate or diet (Bell & Burt, 1991; Morand & Harvey, 2000; see review in Poulin & Morand, 2004), but in too few comparative studies to allow meta-analytic synthesis. Here, too, further comparative tests are necessary before any overall assessment of the strength of these predictors becomes possible.

(5) Our meta-analysis has also identified some aspects of study design that act as artefacts capable of modifying or masking the influence of given predictors of PSR. As others before have done (Morand & Poulin, 2003), we re-emphasize that comparative analyses of PSR must control for host phylogenetic relationships to avoid inflated estimates of effect sizes. Also, it is crucial that both the geographical scale of a comparative study and the level at which PSR is measured (host population or host species) are well matched to its set of predictors.

(6) Overall, our findings highlight the very different drivers of diversity for parasites compared to free-living species. This discrepancy might weaken to some extent if estimates of PSR were obtained per area instead of per host species, although it nevertheless hints at fundamental differences in the processes controlling their diversity.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Results of detailed analyses testing for the effects of all modulators (Tables S1–S31).

Appendix S2. Full datasets for each meta-analysis, including raw effect sizes and information on all modulators (Tables S32–S35).

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