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HOW DOES SPACE INFLUENCE THE RELATIONSHIP BETWEEN HOST AND PARASITE DIVERSITY?

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ABSTRACT: Host species richness and parasite species richness are often positively correlated, but the strength of this relationship varies from study to study. What accounts for this variability? Here, we explore the role of spatial scale in mediating the commonly reported positive relationship between host and parasite diversity. Building from ecological theory, we lay out a series of hypotheses for how spatial grain size might influence both the strength and slope of this relationship. Most significantly, we consider how variability in spatial grain size may result in differences in sampling effort that affect estimates of host and parasite richness differently, and we explore the potential for spatial grain to have divergent effects on strength versus slope of the relationship between host and parasite richness. Finally, we examine what empirical data exist to test the outlined hypotheses and conduct a meta-regression of published studies. Our analyses—which detected no significant associations—highlight several factors that compromise our ability to robustly compare the host–parasite richness relationship across contexts, including mismatches between absolute spatial scale and spatial scale of ecological processes as well as variability across and within studies with respect to spatial grain size, taxonomic resolution, definitions of "hosts" and "parasites," and sampling effort. This work suggests that questions regarding the spatial dependence of the host diversity–parasite diversity relationship may be most-effectively addressed within a single multi-host–multi-parasite system.

Where hosts go, parasites follow. This idea, called the "host diversity begets parasite diversity" hypothesis (Hechinger and Lafferty, 2005), posits that increasing host genetic, taxonomic, and functional richness increases parasite species richness through both ecological and co-evolutionary processes. Ecologically, increasing host diversity increases the variety of niches for parasites, facilitating colonization by diverse parasite species (the "habitat heterogeneity" hypothesis; MacArthur,1958, 1964; Krasnov et al., 2004). Evolutionarily, increasing host speciation rates can drive co-speciation for associated parasites (Eichler's rule; Eichler, 1942; Vas et al., 2012). Recently, strong empirical evidence has accumulated to support the "diversity begets diversity" pattern (Poulin, 2007, 2014; Kamiya et al., 2014). A meta-analysis found strong support for a positive correlation between host and parasite diversity, with an average effect size across 38 case studies of Pearson's $r = 0.55$ (Kamiya et al., 2014). But although this mean effect size for the correlation of host and parasite taxonomic diversity relationship is large, individual effect sizes vary from –0.36 to 0.959 (Kamiya et al., 2014); none of the correlates included in this analysis (e.g., host taxon, parasite taxon, parasite transmission patterns, parasite micro-habitat) could account for this variation. In this paper, we use ecological theory to develop hypotheses about the mechanisms through which spatial scale influences the relationship between host and parasite diversity, how such patterns are likely to manifest empirically, and then examine what, if any, data are available to test these ideas. A key goal of our effort is to highlight the inadequacy of available data and to identify the types of data necessary to test for effects of spatial scale on the host diversity–parasite diversity relationship.

It should not come as a surprise that the correlation between host species richness and parasite species richness is typically positive (e.g., for 36 of 38 effect sizes calculated in Kamiya et al., 2014). This positive correlation means that host diversity determines a large proportion of the variance in parasite diversity, and this value is constrained between 1 (perfect positive correlation, or addition of 1 host species leads to addition of a fixed number of parasite species, with no variation in that number) and –1 (perfect negative correlation, or addition of 1 host species leads to loss of a fixed number of parasite species). Positive values would naturally be expected because parasites are—by definition—dependent on their hosts. Negative correlations between host and parasite diversity are unlikely but possible; they might arise, for example, if increasing host diversity had strong negative effects on parasite transmission such that increasing host diversity drove parasites locally extinct (i.e., an extreme dilution effect; Keesing et al., 2006). Similarly, high parasite diversity might drive hosts locally extinct (Krasnov et al., 2004), or anthropogenic disturbances that increase the susceptibility of hosts to infection by multiple parasite species (e.g., pollution that reduces host resistance) might simultaneously reduce host diversity and increase parasite diversity. Nonetheless, the evidence suggests that a positive relationship between host and parasite diversity is common (Kamiya et al., 2014).

Despite the apparent commonness of the positive host diversity–parasite diversity relationship, numerous empirical as well as theoretical questions about this relationship remain poorly understood. To date, the only property to be rigorously considered is the strength of the correlation between host and parasite diversity—that is, Pearson's r, R^2, or some other metric that quantifies how consistently 1 variable changes in response to change in the other. This is the metric used by Kamiya et al. (2014), and it is the only metric used to describe the host diversity–parasite diversity relationship in the majority of studies included in their meta-analysis. But another property that should be considered is the slope of the relationship between host and parasite species richness, which quantifies the degree to which 1 variable changes in response to change in the other. Put simply, the strength of the correlation tells us whether host and parasite diversity are significantly related, and the slope tells us how many parasite species are added (or subtracted, in the case of a negative correlation) for each host species; these are vastly different properties of the same relationship. Slope is of particular interest because it can inform estimates of the total number of parasite

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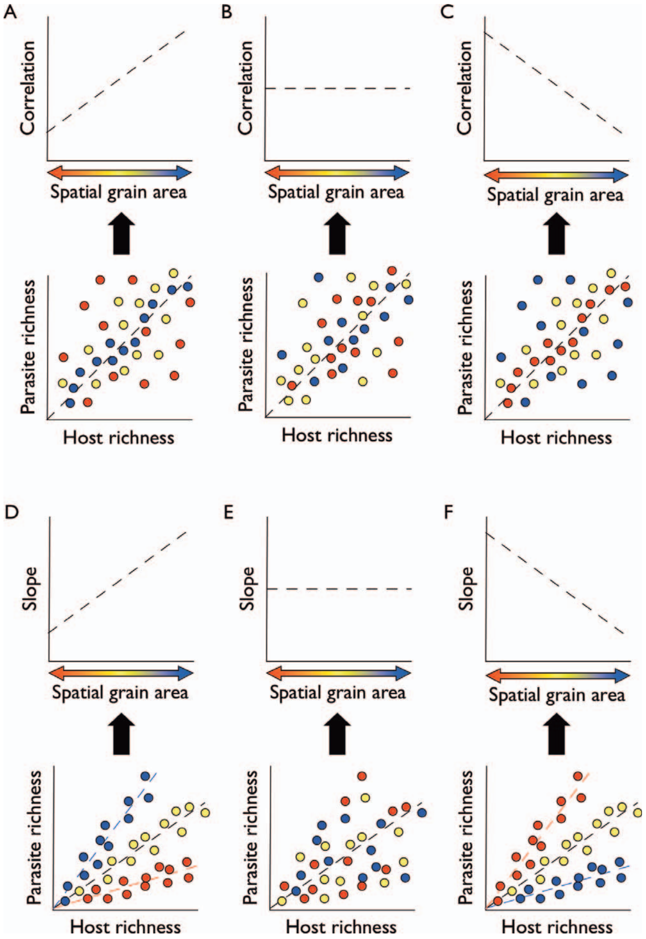

FIGURE 1. The correlation between host and parasite species richness may (**A**) increase, (**B**) remain the same, or (**C**) decrease with increasing spatial grain area. Similarly, the slope of the relationship between host and parasite species richness may (**D**) increase, (**E**) remain the same, or (**F**) decrease with increasing spatial grain area. Red indicates small grains, yellow indicates grains of intermediate size, and blue indicates large grains.

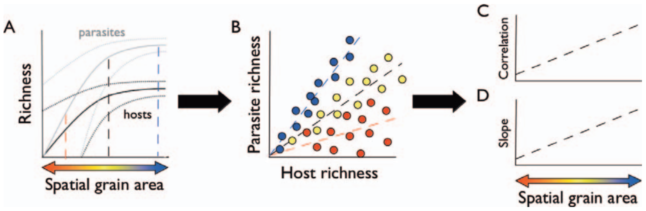

FIGURE 2. Processes contributing to a positive relationship between spatial scale and the strength of the correlation between host and parasite richness. Because parasites are over-dispersed across host individuals, parasite richness may saturate at larger sampling areas than might host richness (**A**). As a result, host richness–parasite richness relationships developed at different sampling grains will differ in both slope and correlation (**B**). Because variability in the number of parasite and host species declines as spatial grain increases (A), the correlation (**C**) and slope (**D**) of the host diversity–parasite diversity relationship will tend to be stronger at larger spatial grains. Red indicates small grains, yellow indicates grains of intermediate size, and blue indicates large grains.

species on Earth (Dobson et al., 2008; Poulin, 2014) and may be helpful in assessing patterns of parasite specialization on hosts (Poulin and Mouillot, 2003; Mouillot et al., 2006).

Spatial scale is a central concept in ecology and one that shapes our understanding of the diversity and distributions of free-living organisms (Levin, 1992); increasingly, evidence is accumulating to suggest that spatial scale is equally important in determining the diversity and distribution of parasites (Poulin, 2014). "Spatial scale" can be defined in many ways and may strongly affect ecological inference (Csillag et al., 2000; Schneider, 2001; Dungan et al., 2002). Consistent with recommendations (Csillag et al., 2000; Dungan et al., 2002), Kamiya et al. (2014) defined spatial extent as the distance between the 2 most distant sampling points and found no relationship between this variable and their effect size (strength of the correlation between host and parasite diversity; slope = 0.014, SE = 0.043, P = 0.744; figure 2 in Kamiya et al., 2014). However, we argue that—when considering the scale-dependence of the correlation between host and parasite diversity—the more important metric is spatial grain. While spatial extent describes the boundaries of the study area (e.g., area in which quadrats were randomly placed, the distance between the 2 most distant quadrats), spatial grain describes the area of observational units (e.g., area of quadrat). "Fine" grains are those at which individuals have the opportunity to interact directly with one another and where within-unit environmental heterogeneity and heterogeneity in dispersal processes are minimized (Fridley et al., 2007). Spatial grain is more likely than spatial extent to influence the strength of the correlation between host and parasite diversity because grain has a direct and predictable influence on the mean and variance of the species richness of hosts and parasites, whereas extent does not (Dungan et al., 2002). For example, 2 quadrats of different areas (i.e., spatial grains) effectively "sample" hosts and parasites differently due to the species–area relationship, with the larger quadrat yielding both more hosts and more parasites; changing spatial extent does not have the same sampling effect. These processes are based on well-known relationships between species richness and area (Rosenzweig, 1995) which hold for host and parasite species alike (Guilhaumon et al., 2012; Poulin, 2014). Here, we consider some potential scale-dependencies of the host diversity–parasite diversity relationship.

Hypotheses for scale-dependence of the correlation between host and parasite diversity

There are good reasons to expect that the strength of the correlation between host and parasite richness may increase (Fig. 1A), decrease (Fig. 1C), or remain unchanged (Fig. 1B) as the size of the sampling grain is increased; the same is true for the slope of the relationship between host and parasite richness (Fig. 1D–F). We begin by considering the processes that might produce a positive relationship between spatial grain size and both (1) the strength of the correlation between host and parasite richness and (2) the slope of this relationship. The first process arises from the fact that host and parasite richness saturate at large spatial grains. As area sampled (i.e., spatial grain) increases, species richness increases until it reaches a saturation point at which all species actually present are detected by sampling (Fig. 2A). At small spatial grains, there will be strong grain-to-grain variability in the number of parasite species and the number of host species, producing variability along the x- (host-) and y- (parasite-) axes of the host diversity–parasite diversity plot. For grain sizes sufficiently large to reach saturation, this variability will be reduced (Fig. 2B). Therefore, as spatial grain increases, we should observe an increase in the correlation between host and parasite diversity (Fig. 2C). Because parasites are over-dispersed across host individuals (Gregory and Woolhouse, 1993; Shaw et al., 1998; Zelmer and Esch, 1999), it is likely that larger sampling grains are needed to achieve parasite richness saturation than are required for host richness saturation (Fig. 2A), meaning that the magnitude of the slope of the host richness–parasite richness relationship may increase as spatial grain area increases (Fig. 2D). A similar and non-mutually exclusive mechanism that may produce the same pattern arises from the fact that increasing spatial grain size increases the amount of environmental heterogeneity encompassed in each sample. This might produce a reduction in sample-to-sample variability with increasing spatial grain (Fig. 2A). This would also produce more-consistent values of the host richness–parasite richness relationship as spatial scale is increased (Fig. 2C).

Other processes might produce a negative relationship between spatial grain area and correlation or slope of the host richness–parasite richness relationship. For example, at spatial grain areas greater than that at which the saturation point of both host and parasite richness are reached (Fig. 3A), values of host and parasite diversity are likely to be highly consistent from unit to unit (Fig. 3B); within this truncated range of species richness values, the "signal" of the host richness–parasite richness relationship may be weak compared to background "noise" of error. This would result in a reduction in the strength of the positive correlation between host and parasite diversity with increase in spatial grain (Fig. 3C), even as the slope increases due to the later saturation point of the parasite species–area relationship relative to the host species–area relationship (Fig. 3D). Krasnov et al. (2007) recognized this possibility, writing that "pooling could mask the true region-specific relationship between parasite and host diversity." Finally, we may see a negative relationship between spatial grain area and the correlation/slope of the host diversity–parasite diversity relationship because of shifts in the importance of different ecological processes across spatial grains. At small spatial grains, local-scale processes such as species interactions (e.g., host diversity) may be important determinants of parasite diversity; at larger spatial grains, other processes—for example, climate and evolutionary history—may swamp local-scale effects and disconnect parasite species richness from host species richness (Fig. 3E). This would result in a weakening of the correlation between host and parasite richness (Fig. 3F) and a reduction in the slope of that relationship as spatial grain is increased (Fig. 3G).

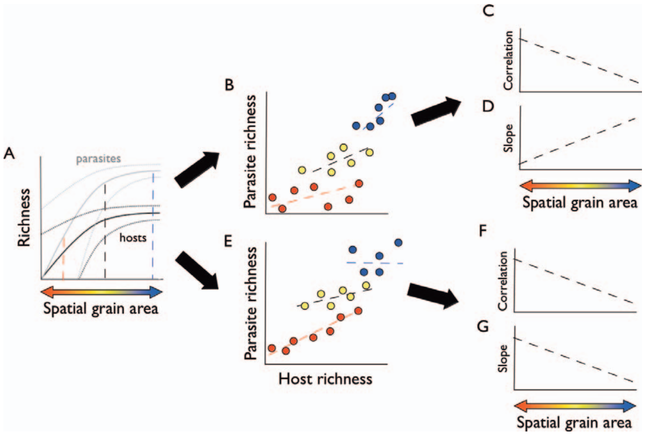

FIGURE 3. Processes contributing to a negative relationship between spatial scale and the strength of the correlation between host and parasite richness. Because parasites are over-dispersed across host individuals, parasite richness may saturate at larger sampling areas than might host richness (**A**). As a result of these divergent species–area curves, both slope and strength of correlation between host and parasite species richness may vary across spatial grains. Larger spatial grains are likely to have truncated ranges of both host and parasite richness (**B**). This may reduce the signal-to-noise ratio for greater spatial grains, resulting in a weakening of correlation with increasing spatial grain (**C**), even as slope increases (**D**), because the number of parasite species added outstrips the number of host species added for each unit increase in spatial grain area. Alternately, host and parasite richness may become decoupled at larger spatial grains (**E**), where processes operating across broad scales (e.g., climate) become more important in determining parasite richness than the local-scale processes (e.g., species interactions like parasitism). This would result in reductions of both correlation (**F**) and slope (**G**). Red indicates small grains, yellow indicates grains of intermediate size, and blue indicates large grains.

Empirical analysis of spatial scale and the diversity-begets-diversity relationship

To further investigate the scale-dependence of the relationship between host and parasite diversity, we updated the analysis conducted by Kamiya et al. (2014) by explicitly testing the influence of spatial grain and extent on the correlation between host and parasite diversity and the slope of the host diversity–parasite diversity relationship. Our paper is a hypothesis-development piece where we consider the mechanistic links among spatial scale, host diversity, and parasite diversity. It differs from Kamiya et al. (2014) in 3 key ways: (1) we consider both spatial grain and spatial extent, whereas Kamiya et al. (2014) considered only spatial extent; (2) we consider the effects of space on both the strength of the correlation and the slope of the relationship between host diversity and parasite diversity, whereas Kamiya et al. (2014) considered only strength of the correlation; and (3) we explore the topic of space exclusively, positing clear hypotheses for the influence of space on the host diversity–parasite diversity relationship, identify appropriate sources of data to test these hypotheses, and discuss whether and how the data support these hypotheses, whereas Kamiya et al. (2014) considered space briefly alongside other potential drivers of the host diversity–parasite diversity relationship.

To perform this meta-regression, we used the exhaustive list of relevant papers compiled by Kamiya et al. (2014). This was accomplished by Kamiya et al. (2014) using a Web of Science search, followed by forward and reverse reference searches of all the appropriate studies yielded by Web of Science. We included only those studies that Kamiya et al. designated as "area-based" for a total of 14 studies and 25 replicates (i.e., some studies reported more than one relationship between host and parasite diversity; study identity was accounted for in our analysis, see below). Kamiya et al. (2014) focused on studies of animal hosts and their parasites and included only those studies where hosts and parasites were identified to species, morpho-species, or (in a handful of cases) family. For the purposes of investigating the role of spatial scale, we adopted rules for inclusion that were slightly more restrictive than those used by Kamiya et al. (2014):

(1) Measurements of host diversity and parasite diversity were made with specific reference to 2-dimensional space. For example,

we excluded any study that used timed counts (e.g., mist-netting for 2 hr).

(2) Spatial grain and spatial extent can be derived from the paper, other papers on the same dataset, or from direct communication with the original authors.

(3) Replicates were independent of one another.

We extracted values for *r* for each of the included studies, which Kamiya et al. (2014) calculated by transforming raw correlation coefficients to Fisher's *z*-transformed correlation coefficients (Table I). Because values for sampling variance were not reported in Kamiya et al., we calculated the variance associated with each effect size (*r*) value using their given method (Nakagawa and Santos, 2012):

$$se = \frac{1}{\sqrt{(n-3)}}.$$

We also calculated a different metric—the slope of that relationship (β), which describes the number of parasite species added for each additional host species. Few of the included studies reported this metric, so we extracted values from graphs where host richness was represented on the x-axis and parasite richness was represented on the y-axis using PlotDigitizer (http://plotdigitizer.sourceforge.net). Where possible, we used graphs that presented values for richness that were corrected for sampling effort. After extracting data points, we derived the slope of the relationship and its associated error by performing a simple, fixed-effects linear model in R v.1.16 (R Foundation for Statistical Computing, Vienna, Austria) in which host richness was the predictor and parasite richness was the response. In some graphs, data points were partitioned into groups (e.g., sites); in these cases (Hechinger et al., 2007) we used a linear mixed-effects model with a random effect of group included to account for the hierarchical nature of the data. Using graphs to infer values from prior studies makes our meta-analysis vulnerable to publication bias; that is, graphs are more likely to be included in a paper if they show a significant result (although several graphs did display non-significant results, e.g., Hechinger et al., 2007; Krasnov et al., 2007; Thieltges et al., 2011). This important limitation must be borne in mind when interpreting results for slope.

For each of the replicate effect sizes, we estimated the spatial grain of analysis and the spatial extent of analysis. We defined spatial grain as the area of each replicate in which host and parasite species richness was assessed. In some cases, hosts and parasites were evaluated at different spatial grains within the same study (e.g., Hechinger and Lafferty, 2005; Negishi et al., 2013). In those cases, we analyzed the host and parasite spatial grains separately. In some studies, spatial grain area varied among replicates; in those cases we took the mean spatial grain area where available (i.e., either from the paper, the supplementary materials, other papers describing the same dataset, or via direct communication with authors). We excluded any studies for which data on spatial grain of replicates were not available. We defined spatial extent as the distance between the 2 most distant replicates and measured this parameter using the ruler tool in Google Earth. Our definition of spatial extent is identical to the one used by Kamiya et al. (2014), but some values that we obtained diverged from those derived by Kamiya et al. (2014). Thus, we track our estimates separately from those of Kamiya et al. (2014) in Table I.

We performed several meta-regressions to investigate the influence of spatial scale on the strength of the host diversity–parasite diversity relationship and the slope of that relationship. All analyses were carried out using the *metafor* package (Viechtbauer, 2010) in R and included study identity as a random effect to account for correlation between replicates within studies. We assessed the influence of spatial grain and spatial extent (log-transformed) on effect sizes with separate meta-regressions. For spatial grain, we used both spatial grain as measured for parasites and that measured for host (see Table I).

Of the 14 area-based studies used in Kamiya et al. (2014), 8 matched our criteria for inclusion. These 8 studies yielded 16 independent measures of the correlation between host and parasite richness. For these studies, neither spatial grain (parasite grain estimate ± SE = –0.0129 ± 0.0113, $z = -1.14$, $P = 0.2531$; host grain estimate ± SE = –0.0109 ± 0.0098, $z = -1.11$, $P = 0.2683$; Fig. 4A, B) nor spatial extent (our estimate of extent ± SE = –0.0403 ± 0.0432, $z = -0.93$, $P = 0.3503$; Kamiya et al. [2014] estimate of extent ± SE = –0.0289 ± 0.0519, $z = -0.56$, $P = 0.5785$; Fig. 5A, B) were significant predictors of the strength of the correlation between host and parasite species richness.

Of the 8 included studies, 6 contained 1 or more graphs from which data on the slope of the relationship between host and parasite richness could be extracted. These 6 studies yielded 10 independent measures of slope. Across these independent measures and controlling for study identity, slope was significantly positive (mean ± SE = 0.4390 ± 0.1203, $z = 3.65$, $P = 0.0003$), indicating that about 0.44 parasites are added for each additional host species across these studies. Neither spatial grain (parasite grain estimate ± SE = –0.0101 ± 0.0100, $z = -1.01$, $P = 0.3102$; host grain estimate ± SE = –0.0084 ± 0.0090, $z = -0.93$, $P = 0.3509$; Fig. 6A, B) nor spatial extent (our estimate of extent ± SE = –0.0354 ± 0.0385, z = –0.92, $P = 0.3580$; Kamiya et al. [2014] estimate of extent ± SE = –0.0704 ± 0.0702, $z = -1.00$, $P = 0.3162$; Fig. 7A, B) were significant predictors of the slope of the relationship between host and parasite species richness.

Future directions for testing the scale dependency of the diversity-begets-diversity relationship

Interest in the relationship between biodiversity and disease has grown rapidly in recent years, but few studies have considered how the spatial scale of observation may affect the magnitude and direction of this relationship. Here, we build from ecological theory to derive a suite of alternative hypotheses for the spatial dependency of the relationship between host and parasite diversity. Only 1 previous study has empirically tested this spatial dependency (Kamiya et al., 2014); similar to this previous study, we found a strong, positive relationship between host and parasite diversity with no dependence on space. Here we discuss some potential limitations on our ability to detect scale-dependence of correlation and slope and suggest additional factors that might influence the host diversity–parasite diversity relationship—including mismatches between absolute spatial scale and spatial scale of ecological processes, variability in spatial grain size, taxonomic resolution, defining "hosts" and "parasites," sampling effort, and the effects of anthropogenic disturbance on the species–area relationship.

Our analysis confirms that "host diversity begets parasite diversity"; according to our meta-regression, each 1-species increase in host diversity begets 0.44 species of parasites. This finding complements the results of Kamiya et al. (2014) who found that the average correlation strength between host and parasite diversity was $r = 0.55$. However, like Kamiya et al. (2014), we were unable to link variability in the host diversity–parasite diversity relationship to spatial scale. In our analysis, neither spatial extent nor spatial grain were significant predictors of correlation or slope.

Spatial grain and extent are metrics that are straightforward, well defined, and easy to measure, but comparing these metrics across studies may still amount to comparing apples and oranges; this is because the scale-dependence of ecological patterns depends upon the scale of processes underlying those patterns. For example, Hechinger et al. (2007) showed that the diversity of large benthic host species was more-closely linked to trematode diversity than was the diversity of fish hosts. They reasoned that, because fish hosts are more vagile than benthic invertebrates, their measurements of fish diversity, taken at small spatial scales, did not adequately capture spatial heterogeneity in fish diversity. In this way, both the strength of the correlation between host and parasite diversity and the slope of that relationship may depend on how well the spatial scale of sampling matches the scale of the ecological processes that govern host and parasite diversity. We used consistent measures of spatial scale to characterize the studies included in our meta-regression (Table I), but studies differed substantially in the kinds of hosts and parasites studied. Hosts included species with extremely low (e.g., cavity-nesting bees and wasps) and extremely high rates of dispersal (e.g., riverine fishes), and parasites included species that are directly transmitted among hosts with small home ranges (e.g., fleas on small mammals) as well as those with complex life cycles that include dispersive stages in vagile hosts (e.g., trematodes with bird definitive hosts). The underlying complexity of ecological processes occurring at variable scales is likely to influence the scale-dependence of the host diversity–parasite diversity relationship.

An additional limitation concerns variability in spatial grain size within studies. For several of the analyses included in our meta-regression, spatial grain size differed among replicates (see grain size in Table I) because the studies compiled data from different sources (Krasnov et al., 2004, 2007; Thieltges et al., 2011) or due to structural differences among sites (Hechinger and Lafferty, 2005; Hechinger et al., 2007; Negishi et al., 2013). This variability probably compromises the power of this dataset to detect effects of space on the host diversity–parasite diversity relationship. Spatial grain size also differed between hosts and parasites within a study, usually because host and parasite diversity were quantified using different methods (Hechinger and Lafferty, 2005; Hechinger et al., 2007; Negishi et al., 2013). For this reason, we analyzed host and parasite spatial grain separately, but neither revealed an effect of space on the host diversity–parasite diversity relationship.

Properties of the host diversity–parasite diversity relationship naturally depend on how we define "host" and "parasite." Both taxonomic resolution and taxonomic identity are likely to be important determinants of the correlation and slope of the host diversity–parasite diversity relationship. For example, if hosts are identified to species while parasites are identified to genus, this will result in a shallowing of the slope of the host diversity–parasite diversity relationship and, probably, a reduction in the strength of the correlation. Most studies included here are taxonomically resolved to species, but several identify a subset of parasites only to family (e.g., Ebeling et al., 2012) or morphospecies (e.g., Tylianakis et al., 2006). Similarly, the slope of the host diversity–parasite diversity relationship will be artificially inflated if parasites are identified to a lower taxonomic resolution than their hosts, as when parasites are identified to lineage and hosts are identified to species (e.g., Merino et al., 2008). Another, perhaps more important factor concerns how boundaries are drawn to define "hosts" and "parasites." Studies included here evaluated the host diversity–parasite diversity relationship for: (1) a suite of hosts and the parasites detected within these same hosts (Elizalde and Folgarait, 2010); (2) a suite of upstream hosts and the parasites detected within a single downstream host species (e.g., Hechinger and Lafferty, 2005; Thieltges et al., 2011); and (3) a suite of hosts and parasites detected in their free-living stages (e.g., Negishi et al., 2013). "Hosts" sometimes included all species known to host 1 or more parasites (e.g., Krasnov et al., 2007) or merely all of the species belonging to a large taxonomic group, regardless of whether those species have known associations with parasites (e.g., fishes in Hechinger et al., 2007). In most of the studies included in our meta-regression, the "host" variable does not include all of the known hosts of the "parasites" but merely a subset; for example, complex life cycle parasites use many different host species, but most studies considered only the following relationships: first intermediate host–parasite, second intermediate host–parasite, and definitive host–parasite. This inevitably results in steepening of the slope of the host diversity–parasite diversity relationship. Any of these choices regarding taxonomic resolution and identity is defensible but comparing across studies that differ in the way they define "host" and "parasite" may not be. We suggest that these issues of taxonomic resolution and identity be explored—that "hosts" and "parasites" must be carefully circumscribed before attempting generalizations about the relationship between host diversity and parasite diversity. Given that "hosts" and "parasites" are likely to be defined differently *among* host–parasite systems, questions regarding the spatial dependence of the host diversity–parasite diversity relationship may be most effectively addressed within a single host–parasite system. For example, we have used trematode parasites of amphibian hosts in ponds of central California to explore how the host diversity–parasite diversity relationship changes with increasing spatial grain, where spatial grains are defined both categorically (i.e., within individual hosts, among host populations, and among ponds) and continuously (i.e., using a neighborhood-based approach that combines communities together into progressively larger neighborhoods of sites; Johnson et al., 2016). By using a single dataset to explore the influence of spatial scale, many of the analytical problems of our meta-regression—that is, the problems associated with variability among studies (e.g., in taxonomic resolution, in defining "hosts" and "parasites")—can be eliminated.

Measures of species diversity are sensitive to the effects of sampling effort (e.g., Gotelli and Colwell, 2001). This is especially true for parasites, which tend to be aggregated in their hosts, with the result that a greater sampling effort is often required to detect parasites than to achieve the same detection probability for free-living species (Gregory and Woolhouse, 1993; Shaw et al., 1998; Zelmer and Esch, 1999). Researchers may choose to examine the effects of sampling effort on estimates of parasite species richness by plotting effort (e.g., number of hosts dissected, number of parasites counted) versus cumulative parasite species richness; an

TABLE I. Properties of the area-based studies included in Kamiya et al. (2014). Bold-faced column headers indicate values derived by our group.

Publication	Group for which statistic was derived (by original authors)	Statistic (reported by original authors)	R (calculated by Kamiya et al., 2014)	N (reported by original authors)	**SE of R (calculated using Kamiya et al., method)**	**Slope (extracted with Plot-Digitizer)**	**SE of slope (extracted with Plot-Digitizer)**	**Grain size (m^2)**	Spatial extent (derived by Kamiya et al., 2014; km)	**Spatial extent (km)**	Included in present study?
Elizalde and Folgarait, 2010		Rho = 0.8	0.800	14	0.30151134	Not plotted	n/a	10,000	1,271	430.0	Y
Hechinger and Lafferty, 2005	Channels	$R = 0.88$	0.880	6	0.57735027	0.6140	0.1648	**Parasite**: 0.15 **Host**: range = 13.2–19.6, mean = 16.4	930	1.93	Y
Hechinger and Lafferty, 2005	Pans	$R = 0.79$	0.790	7	0.5	0.5013	0.1763	**Parasite**: 0.15 **Host**: range = 12.2–34.4, mean = 23.3	930	1.93	Y
Hechinger et al., 2007	Large benthic organisms (e.g., crabs and bivalves)	$F = 8.13$	0.640	32	0.18569534	0.6115	0.2008	**Parasite**: 420 **Host**: mean = 0.00785	468	210.6	Y
Hechinger et al., 2007	Fishes	$F = 2.09$	0.263	32	0.18569534	0.2441	0.2491	**Parasite**: 420 **Host**: mean = 210	468	210.6	Y
Hechinger et al., 2007	Small benthic organisms (e.g., amphipods and polychaetes)	$F = 21.2$	0.656	32	0.18569534	0.4409	0.1424	**Parasite**: 420 **Host**: mean = 0.00196	468	210.6	Y
Tylianakis et al., 2006		$F = 4.22$	0.628	48	0.1490712	Not plotted	n/a	2,500	47	49.19	Y
Krasnov et al., 2004		$R = 0.47$	0.470	37	0.17149859	0.50838	0.48324	Range: 720–2.52E+12, mean = 1.22E+11	20,038	20,039.0	Y
Krasnov et al., 2007	Palaeoarctic	$F = 14.9$	0.616	26	0.30851441	0.88570	0.22923	Range: 2.50E+7–1.14E+12, mean = 2.23E+10	9,192	10,229.0	Y
Krasnov et al., 2007	Nearctic	$F = 1.1$	0.265	19	0.25	0.50838	0.48324	Range: 150,000–1.70E+11, mean = 8.05E+10	6,208	7,297.0	Y
Negishi et al., 2013	Drainage channels, August 2010	$R^2 = 0.17$	0.412	13	0.31622777	Not plotted	n/a	**Parasite**: range = 2.5–13.8, mean = 7.3 **Host**: range = 7.2–51.2, mean = 27.0	5	5.0	Y
Negishi et al., 2013	Drainage channels, June 2010	$R^2 = 0.36$	0.600	13	0.31622777	1.01038	0.26544	**Parasite**: range = 2.5–13.8, mean = 7.3 **Host**: range = 7.2–51.2, mean = 27.0	5	5.0	Y

TABLE I. Continued.

Publication	Group for which statistic was derived (by original authors)	Statistic (reported by original authors)	R (calculated by Kamiya et al., 2014)	N (reported by original authors)	**SE of R (calculated using Kamiya et al., method)**	**Slope (extracted with Plot-Digitizer)**	**SE of slope (extracted with Plot-Digitizer)**	**Grain size (m^2)**	Spatial extent (derived by Kamiya et al., 2014; km)	**Spatial extent (km)**	Included in present study?
Thieltges et al., 2011	Birds, mammals, and reptiles	$T = 5.191$	0.735	25	0.21320072	3.0301	0.7049	Range: 4.95E+10–2.32E+12; mean = 4.00E+11	3,703	4,378.0	Y
Thieltges et al., 2011	Fishes	$T = 3.755$	0.617	25	0.21320072	0.3294	0.1100	Range: 4.95E+10–2.32E+12; mean = 4.00E+11	3,703	4,378.0	Y
Thieltges et al., 2011	Gastropods with allogenic trematodes	$T = -1.839$	–0.358	25	0.21320072	–0.1922	0.3561	Range: 4.95E+10–2.32E+12; mean = 4.00E+11	3,703	4,378.0	Y
Thieltges et al., 2011	Gastropods with autogenic trematodes	$T = -0.384$	–0.080	25	0.21320072	0.006831	0.063524	Range: 4.95E+10–2.32E+12; mean = 4.00E+11	3,703	4,378.0	Y
Ebeling et al., 2012	Bees	$F = 0.702$	0.091	78	0.11547005	Not plotted	n/a	Sampling not area-based	2	0.5	N
Ebeling et al., 2012	Wasps	$F = 14.9$	0.403	78	0.11547005	0.3790	0.1357	Sampling not area-based	2	0.5	N
Ishtiaq et al., 2010b		$b = 0.65$	0.650	16	0.2773501	Not plotted	n/a	Sampling not area-based	905	930.32	N
Krebs et al., 2010		$R = 0.5$	0.500	9	0.40824829	0.2006	0.1958	Reported as watershed area, not sampling area	276	49.57	N
Merino et al., 2008	*Haemoproteus*	$F = 0.0006$	0.012	5	0.70710678	Not plotted	n/a	Sampling not area-based	2,419	2,409.28	N
Merino et al., 2008	*Plasmodium*	$F = 0.34$	0.280	5	0.70710678	Not plotted	n/a	Sampling not area-based	2,419	2,409.28	N
Merino et al., 2008	*Leucocytozoon*	$F = 18.60$	0.928	5	0.70710678	Not plotted	n/a	Sampling not area-based	2,419	2,409.28	N
Vaughn and Taylor, 2000		$R = 0.31$	0.310	36	0.17407766	0.5351	0.2034	Sampling not area-based	257	194.93	N
Watters, 1992		$R^2 = 0.92$	0.959	37	0.17149859	0.43849	0.02567	Replicates not independent (nested watersheds)	439	224.35	N

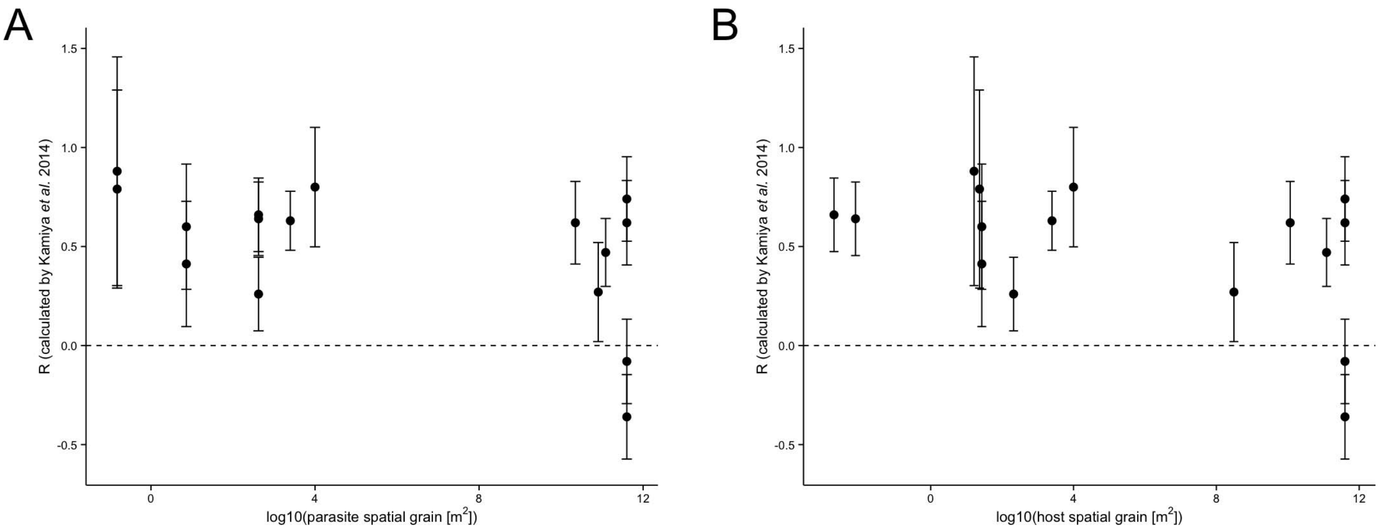

FIGURE 4. Relationship between spatial grain at which parasite species richness was measured (**A**), or spatial grain at which host species richness was measured (**B**), on the strength of the correlation between host and parasite species richness (R) as measured by Kamiya et al. (2014).

unbiased estimate is obtained by finding the value for cumulative parasite species richness at the saturation of this curve (Gotelli and Colwell, 2001). If the curve does not saturate, further sampling should be performed, or species richness estimators can be extrapolated from the species–effort curve. Alternately, effort may be accounted for by including a measure of effort as a predictor in statistical models, where it can compete with host diversity for variance. Several papers included in our meta-regression corrected parasite species richness for sampling effort (Krasnov et al., 2004, 2007), but many did not. If these uncorrected studies under-count parasite species richness (relative to host species richness), this might result in shallowing of the slope of the host diversity–parasite diversity relationship and a reduction in the strength of correlation. This is especially problematic for studies that rely on museum records (e.g., Watters, 1992) or species distribution datasets (e.g., Thieltges et al., 2011), where sampling effort may be difficult or impossible to quantify.

Finally, the host diversity–parasite diversity relationship may be unaffected by spatial scale if species–area relationships are less strong and general than expected. Many of the hypotheses posed above rest on the assumption that the number of host and parasite species will increase with increasing spatial grain (i.e., area) of the sample. But although the species–area relationship is a broadly recognized ecological pattern (e.g., Rosenzweig 1995; Drakare et al., 2006; Watling and Donnelly, 2006), it can break down in the presence of anthropogenic disturbance. For example, in a synthesis of data on animals in terrestrial habitat patches, Prough et al. (2008) found that patch area accounted for only 13% of variance in patch occupancy and posited that, if data on occupancy were collected after human disturbance had already extirpated the most-vulnerable

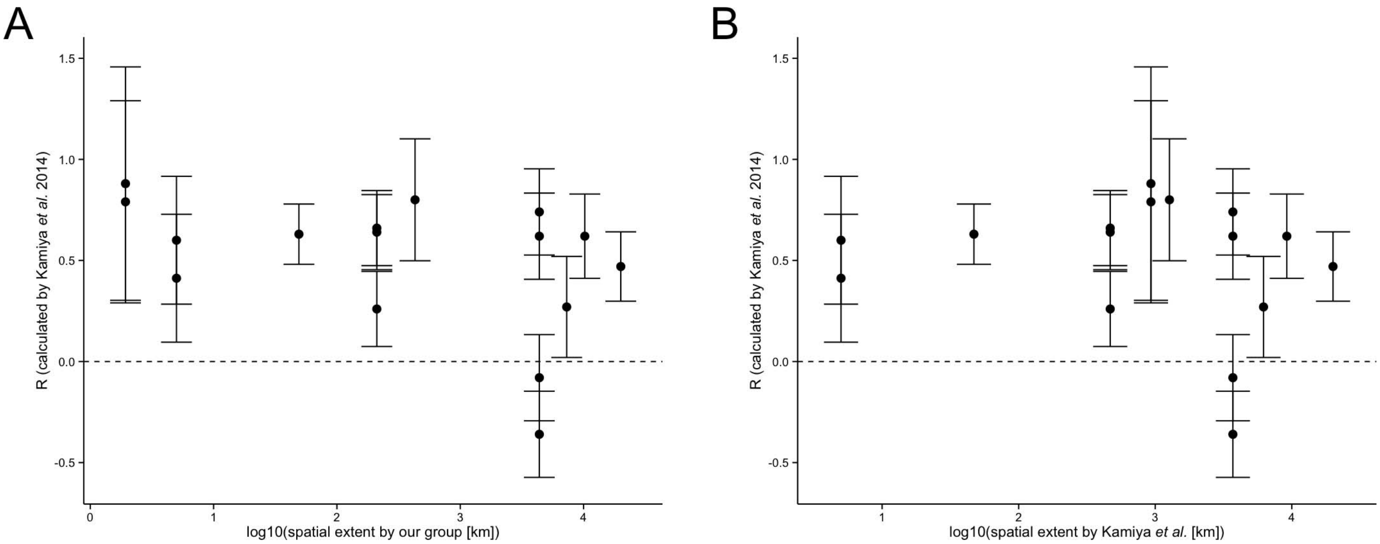

FIGURE 5. Relationship between spatial extent as measured by our group (**A**) or spatial extent as assessed by Kamiya et al., 2014 (**B**) on the strength of the correlation between host and parasite species richness (R) as measured by Kamiya et al. (2014).

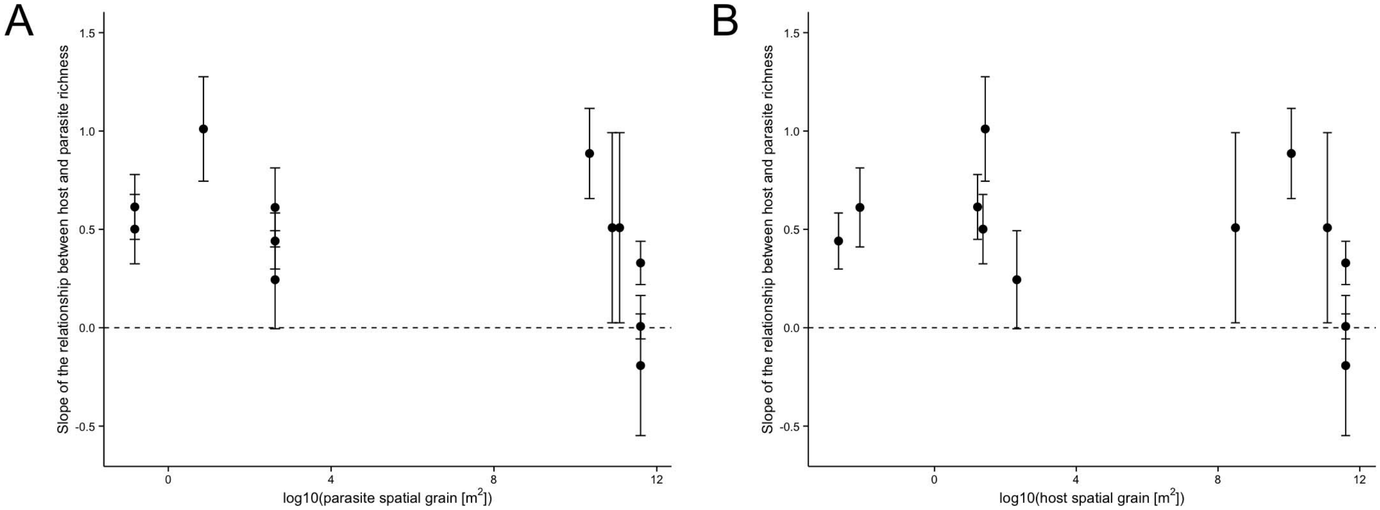

FIGURE 6. Relationship between spatial grain at which parasite species richness was measured (**A**) or spatial grain at which host species richness was measured (**B**) on the slope of the relationship between host and parasite species richness.

species, the leftover "survivors" might be relatively insensitive to further changes in patch area. The same effect might be at work for hosts and parasites: anthropogenic change may have left only those parasite species that are resilient to reductions in both host diversity and habitat area, decoupling the host diversity–parasite diversity relationship and reducing its sensitivity to changes in spatial scale. Similarly, the species–area relationship assumes that habitats are contiguous, and it does not account for the fact that anthropogenic disturbance often results in habitat fragmentation. If fragmentation creates patches that are too small to sustain populations, species–area relationships may overestimate the number of persisting species (Hanski et al., 2013). Differential effects of fragmentation on hosts and parasites could also decouple the host diversity–parasite diversity relationship and erode its sensitivity to spatial scale. Thus, anthropogenic disturbances have the potential to weaken the scale-dependence of the host diversity–parasite diversity relationship, and it may be worthwhile to compare the strength of this relationship in systems experiencing human disturbance against its strength in systems where disturbance is negligible.

Our meta-analysis raises more questions than it answers. While we have sound reasoning to expect scale-dependence in the host diversity–parasite diversity relationship, this was not observed in our meta-regression dataset. Several factors probably compromise our ability to detect such scale-dependence including mismatches between absolute spatial scale and spatial scale of ecological processes, variability in spatial grain size, taxonomic resolution, definitions of "hosts" and "parasites," sampling effort, and the effects of anthropogenic disturbance on the species–area relationship. What is now needed is a purpose-built study that contrasts the host diversity–parasite diversity relationship across spatial scales within a single host–parasite system. Our analysis does reinforce and add a quantitative dimension to an emerging paradigm in parasite ecology (Poulin, 2014): that host diversity begets parasite diversity.

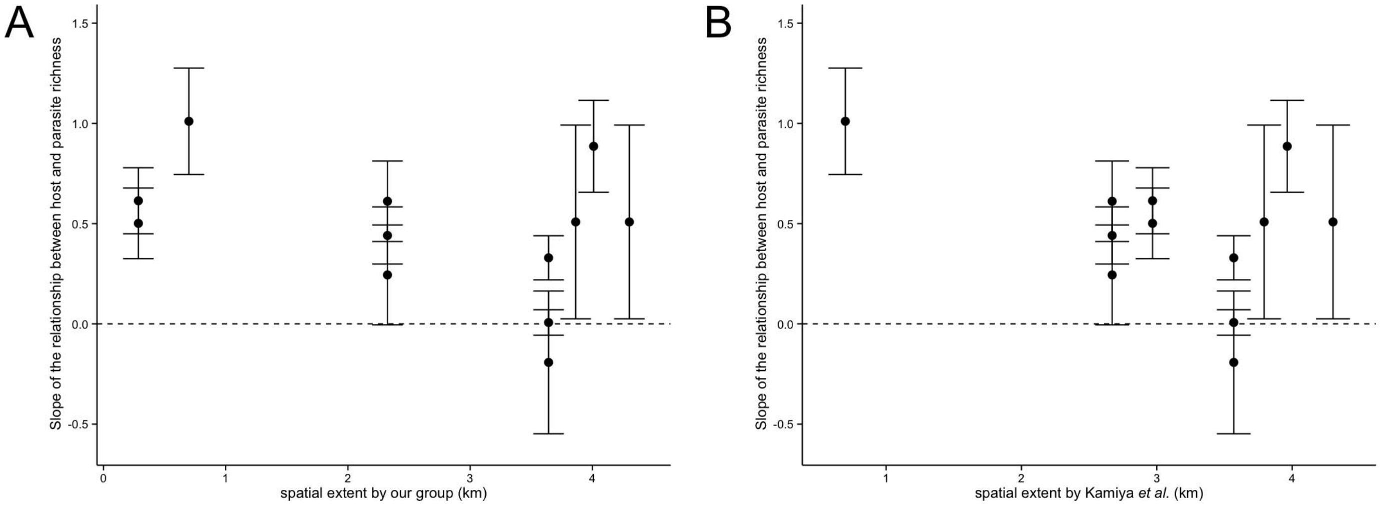

FIGURE 7. Relationship between spatial extent as measured by our group (**A**), or spatial extent as assessed by Kamiya et al., 2014 (**B**), on the slope of the relationship between host and parasite species richness.

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