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Invited article

Lesser snow goose helminths show recurring and positive parasite infection-diversity relations

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ABSTRACT

The patterns and mechanisms by which biological diversity is associated with parasite infection risk are important to study because of their potential implications for wildlife population's conservation and management. Almost all research in this area has focused on host species diversity and has neglected parasite diversity, despite evidence that parasites are important drivers of community structure and ecosystem processes. Here, we assessed whether presence or abundance of each of nine helminth species parasitizing lesser snow geese (*Chen caerulescens*) was associated with indices of parasite diversity (i.e. species richness and Shannon's Diversity Index). We found repeated instances of focal parasite presence and abundance having significant positive co-variation with diversity measures of other parasites. These results occurred both within individual samples and for combinations of all samples. Whereas host condition and parasite facilitation could be drivers of the patterns we observed, other host- or parasite-level effects, such as age or sex class of host or taxon of parasite, were discounted as explanatory variables. Our findings of recurring and positive associations between focal parasite abundance and diversity underscore the importance of moving beyond pairwise species interactions and contexts, and of including the oft-neglected parasite species diversity in infection-diversity studies.

1. Introduction

Biodiversity has the potential to constrain or facilitate the spread of both micro- and macroparasites (Keesing et al., 2010; Ostfeld and Keesing, 2012). Therefore, understanding infection-diversity dynamics has important implications for human health, as well as conservation and management of wildlife and farmed animals (Keesing et al., 2010; Keesing and Ostfeld, 2015). Yet, the frequency of occurrence of infection-diversity relations and the particular mechanisms that result in the loss or spread of parasitic organisms in natural and human-affected ecosystems remain contentious issues (Johnson et al., 2015; Wood et al., 2016). Furthermore, research into infection-diversity patterns has focused almost exclusively on host diversity (see reviews on 'dilution effects' by Civitello et al., 2015; Johnson et al., 2015), and has neglected whether parasite diversity itself influences presence and abundance of focal parasite species. This is surprising given that concomitant infections are common (Behnke et al., 2001; Cox, 2001), infection patterns can be strongly influenced by interactions among parasites, and parasites are a diverse and abundant group. For example, co-infection research shows that parasite species pair-wise interactions can influence parasite infection probability and abundance (Lello et al., 2004), often more strongly than host traits and environmental factors (Telfer et al., 2010). Furthermore, parasites constitute a large portion of metazoan diversity that rivals or exceeds host species diversity in natural assemblages (Dobson et al., 2008; Kuris, 2012; Kuris et al., 2008), suggesting that parasite diversity-infection dynamics may not be any less frequent than host diversity-infection dynamics. Additionally, parasites can modify the strength of competitive and trophic interactions among free-living species, and stabilize communities (Hatcher et al., 2006; Hudson et al., 2006; Lafferty

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et al., 2008; Mouritsen and Poulin, 2005), which in turn might promote biodiversity at the host level and influence parasite infection-diversity dynamics.

Given that the primary goal of current infection-diversity studies is to clarify patterns and mechanisms linking changes in diversity to changes in infection (Johnson et al., 2015), a coherent framework for understanding these links ought to consider whether and how parasite diversity influences infection (e.g. Dobson and Auld, 2016). Such an approach is important to avoid erroneously ascribing patterns to particular attributes of host species assemblages when, in fact, those patterns might depend more on parasite species assemblages and the variable strengths of parasite interactions in their infracommunities. Despite this, only a handful of empirical papers addressing infection and host diversity relationships considered more than one parasite species and even fewer (Behnke et al., 2005, 2009; Johnson and Hoverman, 2012; Johnson et al., 2013; Rendón-Franco et al., 2014) have evaluated whether parasite abundance is potentially explained by some metric of parasite species diversity. Nonetheless, these few studies illustrate important ideas, but also limitations, of the current understanding of parasite diversity-infection dynamics. Whereas Johnson and Hoverman (2012) and Johnson et al. (2013) report negative correlations between abundance of trematode species and richness, Behnke et al. (2005, 2009) found positive correlations between parasite richness and the nematode *Heligmosomoides polygyrus* presence and abundance, suggesting that higher order patterns of infection and diversity do exist. In particular, Johnson and Hoverman (2012) and Johnson et al. (2013) considered whether the abundance of six species of directly transmitted trematodes was influenced by parasite richness among their amphibian hosts, but did not explore the potential effects of accounting for more nuanced diversity metrics that include species evenness (e.g. Shannon's Diversity Index), nor did they account for parasites with different modes of transmission and/or belonging to different taxonomic groups. Behnke et al. (2005, 2009) assessed whether presence and abundance of a single immunosuppressive nematode species (*Heligmosomoides polygyrus*) influenced intestinal helminth species richness; thus is unclear whether richness influenced other parasite species, and whether accounting for species evenness could influence outcomes. Finally, Rendón-Franco et al. (2014) assessed whether the presence of eggs/oocysts of four parasite species correlated with parasite species richness and Simpson's Diversity Index, yet samples sizes (53 samples among nine species of rodent hosts) and parasite prevalences (the nematodes *Syphacia* sp: 1.8%, *Trichuris* sp: 1.8%, and a genus from the Family Strongylidae: 1.8%; and an apicomplexan *Eimeria* sp: 13.2%) were low and precluded detection of significant relationships.

This broad issue of ignoring parasite diversity does not mean that there is a dearth of studies of parasite interactions, only that those studies are often limited to analyses of pair-wise relations (e.g. Forbes et al., 1999; Holmes, 1961, 1962; Lello et al., 2004; Morrill et al., 2013) which often lead to species-specific and context dependent outcomes (Behnke, 2008) with no apparent general patterns. These pair-wise interspecific interactions are often considered as indirect and mediated by host immune response, host health, or available resources for parasite growth (Behnke, 2008; Lello et al., 2004). More generally, presence or abundance of a given parasite species can facilitate, constrain or have no quantifiable effect on co-infecting heterospecific parasites (e.g. Cox, 2001; Forbes et al., 1999; Lello et al., 2004; Telfer et al., 2010). Therefore, given that co-occurring parasite species can influence each other's abundance, it seems plausible that such effects may become magnified with increasing parasite diversity. For example, if parasite interactions within infracommunities are on average negative, the abundance of particular parasite species could decrease as parasite diversity increases. Alternatively, if parasite interactions within infracommunities are positive on average, then abundance of particular species could increase as parasite diversity increases. Additionally, parasite interactions may also lead to emergent effects not captured by simply adding average outcomes of pair-wise interactions and abundances. By assessing directly how consistent relations are between parasite diversity and focal parasite presence and abundance, researchers can determine whether general infection-diversity patterns exist as a prelude to testing which factors might explain those recurring patterns.

Here, we assess whether two metrics of parasite diversity are associated with the presence and abundance of nine different species of helminths, representing three taxa, collected from >750 wild lesser snow geese (*Chen caerulescens*). That is, we focus on whether infection and parasite diversity in general present repeatable patterns, beyond the apparent species-specific and context-dependent outcomes of traditional pair-wise co-infection analyses. Our objectives were to identify the direction of presence- and abundance-diversity correlations, discuss potential mechanisms for the patterns we report, and examine their implications for our understanding of infection-diversity dynamics.

2. Materials and methods

2.1. Study system and data collection

Seven hundred and seventy-one wild lesser snow geese were collected between January and May 1983 as part of a wider project on nutritional ecology (Alisauskas and Ankney, 1992; Alisauskas et al., 1988). Geese were shot from undisturbed feeding flocks at 12 different sites across the USA and Canada, and sampling at some sites was repeated at later time-points, resulting in 27 date-site samples. On average, 28 geese were collected in each sample (25 of 27 samples had >20 geese, range 17–47). Across all samples, 85% of geese were adults, 15% were subadults; and 50% were females. Geese were dissected and their gastro-intestinal tracts, including contents, were searched for parasites. A detailed description of the collection and dissection methods is given elsewhere (Forbes et al., 1999). Nine species of gastro-intestinal helminths were identified and quantified by J.D.M.: the nematodes *Heterakis dispar* (Shrank, 1790), *Trichostrongylus tenuis* (Mehlis, 1846) and *Capillaria anatis* (Shrank, 1790); the cestodes *Drepanidotaenia lanceolata* (Bloch, 1782), *Drepanidotaenia barrowensis* (Schiller, 1952), *Sobolevicanthus gracilis* (Zeder, 1803), *Cladogyna longivaginata* (Furhmann, 1906) and *Platyscolex ciliata* (Fuhrmann, 1913); and the trematode *Echinostoma revolutum* (Cort, 1914).

These parasites are not only taxonomically diverse but also have different transmission modes and life-histories. Based on life cycle characteristics two distinct groups of parasites were present. The first group is composed by the nematode species encountered in this study, which have direct life cycles and do not require an intermediate host for transmission. Infection of geese occurs when larvated eggs (*H. dispar*, *C. anatis*) or hatched third stage larvae (*T. tenuis*) (McDonald, 1969) are ingested by geese when grazing in terrestrial habitats. The second group is composed by the four cestode species and the digenean trematode species which have indirect life cycles and are transmitted in freshwater environments including marshes, ponds and possibly seasonal or ephemeral wetlands. Three of the cestode species; *D. lanceolata*, *S.gracilis* and *P. ciliata* use freshwater microcrustaceans as intermediate hosts (McDonald, 1969). The intermediate hosts of *C. longivaginosus* are unknown, but this species belongs to the same family as *D. lanceolata* and *S. gracilis,* so it is likely that similar hosts are involved (McDonald, 1969). These cestode eggs are infective when shed from the host and, following ingestion by the crustacean hosts

(copepods, ostracods or cladocerans) each develops into a cysticercoid larva. Waterfowl acquire infections while foraging in shallow water. Several cysticercoids may occur in experimentally - infected crustaceans, however studies of infection levels in zooplankton from ponds in zoological gardens used by waterfowl have shown that most natural infection consist of one or two cysticercoids per host (Kotecki, 1970). *E. revolutum*, has an indirect life cycle that involves two intermediate hosts. The first intermediate host is a freshwater snail in North America, frequently a species of *Lymnaea*, although other species are susceptible. The parasite produces large numbers of dispersal stages (cercariae) asexually that emerge from the original snail. These infect other freshwater invertebrates primarily gastropods, but also bivalves, planarians and tadpoles. Each cercaria that establishes transforms into a metacercaria, the final larval stage. When eaten by a goose, each metacercaria will develop into an adult worm (McDonald, 1969).

Across all samples combined, prevalence of individual species ranged between 1.6% and 51.8%, with 7 helminth species having overall prevalence >5%; mean intensities ranged between 1.4 and 29.1 (Supplementary Fig. S1). As expected, those species with higher prevalence also had higher mean intensities (Supplementary Fig. S1). This dataset was appropriate for testing associations between parasite diversity and focal parasite presence or abundance because it has multiple parasite species present, with variable abundance and widespread representation among host samples, and because of variation in parasite species assemblages among samples.

2.2. Parasite presence- and abundance-diversity relationships

Our analytical approach was based on both parasite presence and abundance data. We first tested whether a parasite species' presence was related to the diversity of the remaining parasite species in their infracommunities. We used generalized mixed model logistic regressions with a binomial error distribution and a logit link because there was no evidence for significant over- or under-dispersion (sum of squared Pearson residuals divided by the residuals degrees of freedom always equals to 1.00 ± 0.035). We performed analyses with the lme4 package v.1.1–12 in R (Bates et al., 2015). Diversity (see below), host age (juvenile or adult), sex, and their interactions were included as fixed factors, and sample collection (hereafter sample) as a random factor in these analyses. Models were simplified through likelihood ratio tests. We tested at the infracommunity level (i.e. the assemblage of parasite populations found in individual hosts – Bush et al., 1997), that is, every host was treated as an independent community of parasites. Our principal reason for focusing on the infracommunity is that the arena in which parasites are expected to interact most strongly is within individual hosts. As diversity indices, we used parasite richness which is the number of parasite species present within a host, and Shannon's Diversity Index, which accounts for species richness and the relative abundance of each species present (Magurran, 2013). Importantly, we removed the parasite species for which presence was being assessed from the estimation of richness and Shannon's Diversity Index, because its inclusion could otherwise create a degree of autocorrelation between those measures. The strength of this autocorrelation was expected to be greater for those focal species with higher prevalence and intensity of infection.

We next extended our analyses to abundance of focal parasites because these data contained more information than presence/absence analyses. Abundance data were aggregated, as is typically the case for macroparasites (Poulin, 2007 pg. 134), and differed in their degree of aggregation by parasite species necessitating the use of non-parametric approaches. To test each parasite species, we used Kendall's Tau-b rank correlation (Abdi, 2007) approaches on combined samples, and included both hosts that were or were not infected with the focal parasite. We used Tau-b because it makes adjustments for ties among ranked data. We followed these analyses with a series of within-sample analyses, using the 27 individual samples independently, to test whether patterns observed for combined samples could be replicated with the same Kendall's statistic, within samples. Although this is one effective way to control for sample, such tests are necessarily underpowered because of reduced sample size. As with the presence data, we excluded the focal parasite species from each infracommunity before estimating diversity measures to avoid potential autocorrelation.

One reason for combining samples was to increase the likelihood of detecting associations by using the entire range of variation in focal parasite abundance and maximizing the range of species diversity measures, at an appropriate scale (i.e. the infracommunity level). However, this approach results in elevated degrees of freedom and could produce spurious relations. Spurious relations should not be consistently in one direction, nor should they be mirrored by within-sample outcomes. Claims of true positive or negative correlations between parasite diversity and focal species presence or abundance would be made stronger if there was consistency in patterns between combined- and within-sample correlations.

Finally, we tested whether patterns were consistent when particular sex and age classes of hosts were excluded, again using Kendall's analyses for combined samples. We did these analyses because males and females often differ in their exposure or ability to control parasites, leading to the widespread phenomenon of sex-biased parasitism (Forbes, 2007; Zuk, 2009; Zuk and McKean, 1996) which could, in turn, influence parasite infracommunity dynamics. Host age, by comparison, can also influence levels of parasitism, either because of a cumulative effect of ongoing exposure to parasites with host age, because juveniles have a less developed immune system than adults, or because of senescence (Anderson, 1993).

All analyses were conducted using the R Language and Environment for Statistical Computing V 3.2.3 (R development core team 2015). α was set at 0.05.

3. Results

Focal parasite species presence had a significant positive correlation with richness for six species (*H. dispar, T. tenuis, D. lanceolata, D. barrowensis, S. gracilis, C. longivaginata,* Table 1), and with Shannon's Diversity Index for three species (*T. tenuis*, *D. lanceolata*, *D. barrowensis*; correlations for *H. dispar* and *S. gracilis* were marginally non-significant, $P = 0.055$ and 0.065, respectively; Table 1). Including sex and age did not improve the model fit significantly, with two exceptions (*T. tenuis* and *S. gracilis*) which did not qualitatively change the effect of diversity on presence as reported in Table 1, in no case where interactions among fixed factors significant. *T. tenuis* presence was significantly affected by both sex and age of the host, subadults and males had higher infections than adults and females (when richness was the diversity metric-age: coef = 0.52, p = 0.02; sex: coef = 0.47, p < 0.01; richness: coef = 0.64, p < 0.001; when Shannon's Diversity Index was the diversity metric-age: coef = 0.54, p = 0.02; sex: coef = 0.46, p < 0.01; Shannon's: coef = 1.47, p < 0.001). *S. gracilis* presence was significantly affected by sex but not age, where males had higher infections than females (when richness was the diversity metric-sex: coef = 0.59, p = 0.03; richness: coef = 0.29, p = 0.02; when Shannon's Diversity Index was the diversity metric-sex: coef = 0.58, p = 0.03; Shannon's: coef = 0.78, p = 0.06).

Table 1
Generalized linear mixed models (GLMM; logistic regression with random sample effects) of parasite diversity measures fixed effects on focal parasite species[a] presence. Parasite diversity measures are calculated excluding the focal parasite. Regression coefficients of diversity measure fixed effect are shown with effect size in parenthesis for ease of interpretation, model estimates in bold indicate significant values[b] ($\alpha = 0.05$).

	Logistic GLMM estimate								
	Hd	Tt	Dl	Db	Ca	Sg	Er	Cl	Pc
Species richness	**0.45***** (1.57)	**0.64***** (1.90)	**0.54***** (1.71)	**0.69***** (2.00)	0.11 (1.12)	**0.28*** (1.33)	0.14 (1.15)	**0.71**** (2.04)	0.33 (1.39)
Shannon's diversity	0.64 (1.89)	**1.49***** (4.44)	**1.75***** (5.74)	**1.50***** (4.48)	0.20 (1.22)	0.74 (2.09)	0.09 (1.09)	0.77 (2.16)	1.18 (3.27)

[a] Hd = *Heterakis dispar*; Tt = *Trichostrongylus tenuis*; Dl = *Drepanidotaenia lanceolata*; Db = *Drepanidotaenia barrowensis*; Ca = *Capillaria anatis*; Sg = *Sobolevicanthus gracilis*; Er = *Echinostoma revolutum*; Cl = *Cladogyna longivaginata*; Pc = *Platyscolex ciliata*.
[b] Fixed effect p-values < 0.001 indicated by ***; p-values < 0.01 indicated by **; p-values < 0.05 indicated by *.

Parasites co-occurring in lesser snow geese had significant positive correlations between focal species abundances and both measures of heterospecific parasite diversity for six out of nine species (Table 2A). Five of the species that had a significant association with richness also had a significant association with Shannon's Diversity Index (*H. dispar, T. tenuis, D. lanceolata, D. barrowensis, S. gracilis*, Table 2A); *C. longivaginata* and *P. ciliata* only had significant abundance correlations with richness and Shannon's Diversity Index, respectively. Correlations between abundance of focal parasite species and heterospecific parasite diversity within samples led to significant results more often than would be expected by chance (i.e. >5% of times) in six species when diversity was measured as richness (averaging 10% significant relationships across the nine helminth species; Table 3), and in seven species when diversity was measured as Shannon's Diversity Index (averaging 11% across nine species; Table 3). All significant results were positive correlations between abundance and both diversity measures.

Parasites infecting both male and female lesser snow geese had positive correlations between abundance and heterospecific parasite diversity (Table 2B). This correlation was significant for both sexes and for both measures of diversity in five out of nine parasite species, with the exception of the Shannon's Diversity Index of *S. gracilis* infecting male geese (Table 2B). Abundance of *P. ciliata* infecting females also correlated positively with Shannon's Diversity Index. None had significant negative correlations.

Parasites infecting adult lesser snow geese had a significant positive correlation between abundance and both heterospecific parasite diversity measures in six out of nine species (Table 2B). Although they accounted for only 15% of geese sampled, subadults had significant correlations between abundance and richness in four out of nine species (Table 2B), and between abundance and Shannon's Diversity Index in two out of nine species (Table 2B). None had significant negative correlations.

As a means of confirming the recurrence of our above results, we randomized our abundance data and repeated Kendall's Tau-b estimations for each parasite 1000 times and subsequently assessed whether our Tau-b estimates from the original data fell below 2.5% (i.e. significant negative correlation) or above 97.5% (i.e. significant positive correlation) of the distribution of randomized values. Trends using this method have qualitatively the same results as in Table 2 (Supplementary Figs. 2–11).

4. Discussion

Recent debates on infection-diversity relations have neglected to investigate the effects of parasite diversity on infection dynamics (see supplementary materials in Civitello et al., 2015; Johnson et al., 2015), despite evidence for the role of parasites in modifying infection outcomes (e.g. Ezenwa et al., 2010; Lello et al., 2004; Telfer et al., 2010) and host community structure, stability and dynamics, all of which ultimately influence biodiversity (Minchella and Scott, 1991). We focused on parasite species diversity of hosts and report that parasite presence and abundance had recurring positive covariation with parasite diversity (richness and Shannon's Diversity Index). This pattern is reminiscent of the amplification effect hypothesis (i.e. that increasing host diversity correlates with higher infection) supported in some host species assemblages (Wood et al., 2014), and consistent with the notion that diversity begets diversity (e.g. Krasnov et al., 2005). Our results are robust when controlling statistically for sample, when considering the full dataset or individual samples, and when analysing datasets parsed by removing particular sex and age categories of hosts. Furthermore, our results indicate that a focus on diversity metrics of co-infections rather than on particular species' pair-wise interactions can lead to repeatable, broader patterns.

Positive correlations between parasite presence or abundance and parasite diversity could have been the result of statistical

Table 2
Kendall rank correlation tests (tau-b) of focal parasite species[a] abundance and parasite diversity measures for the entire data set as well as different subsets of data: males, females, adults, and subadults. Parasite diversity measures are calculated excluding the focal parasite. Tau coefficients in bold indicate significant tests[b] ($\alpha = 0.05$).

		Diversity measure	Kendall's tau-b								
			Hd	Tt	Dl	Db	Ca	Sg	Er	Cl	Pc
A) Full data set	(n = 771)	Species richness	**0.23*****	**0.26*****	**0.17*****	**0.15*****	0.04	**0.15*****	0.01	**0.07***	0.06
		Shannon diversity	**0.17*****	**0.22*****	**0.17*****	**0.13*****	0.03	**0.13*****	0.01	0.03	**0.07***
B) Parsed data sets	Males	Species richness	**0.24*****	**0.27*****	**0.15****	**0.13****	0.03	**0.12****	−0.01	0.06	0.05
	(n = 386)	Shannon diversity	**0.17*****	**0.22*****	**0.14****	**0.12****	0.02	0.09	−0.02	0.04	0.03
	Females	Species richness	**0.23*****	**0.25*****	**0.19*****	**0.18*****	0.05	**0.18*****	0.04	0.07	0.07
	(n = 385)	Shannon diversity	**0.18*****	**0.22*****	**0.2*****	**0.13****	0.05	**0.18*****	0.04	0.02	**0.11***
	Adults	Species richness	**0.23*****	**0.26*****	**0.16*****	**0.14*****	0.04	**0.15*****	0.02	0.05	**0.09***
	(n = 655)	Shannon diversity	**0.16*****	**0.21*****	**0.17*****	**0.12*****	0.04	**0.14*****	0.02	0.04	**0.09***
	Subadults	Species richness	**0.25****	**0.28*****	**0.21***	**0.2***	0.05	0.14	−0.06	0.11	−0.07
	(n = 116)	Shannon diversity	**0.21****	**0.29*****	0.15	0.14	0.03	0.05	−0.05	0.01	−0.05

[a] Parasite species abbreviations as in Table 1 legend.
[b] Kendall rank correlation test p-values < 0.001 indicated by***; p-values < 0.01 indicated by**; p-values < 0.05 indicated by*.

Table 3
Proportion of sites with focal parasites present within which Kendall rank correlation tests showed significant positive correlation between focal parasite species[a] abundance and parasite diversity measures ($\alpha = 0.05$). There were no significant negative correlations. Parasite diversity measures are calculated excluding the focal host. n refers to the number of sites in which the parasite species was infecting at least one host.

	Hd (n = 27)	Tt (n = 27)	Dl (n = 22)	Db (n = 19)	Ca (n = 24)	Sg (n = 18)	Er (n = 26)	Cl (n = 8)	Pc (n = 7)
Species richness	0.15	0.30	0.14	0.11	0.00	0.06	0.00	0.13	0.00
Shannon diversity	0.07	0.11	0.18	0.16	0.04	0.11	0.04	0.13	0.14

[a] Parasite species abbreviations as in Table 1 legend.

artifacts, host-level effects, or parasite species attributes. We first explore whether statistical artifacts might have influenced our findings. In presence/absence tests, the effects of sample were controlled statistically (i.e. sample sites were treated as a random effect) and did not influence the patterns we observed. For abundance data, a few samples with both high diversity and abundance could have caused the positive correlations we report when analysing the combined samples (i.e. Table 2A). Such a situation would indeed cause a spurious interpretation if parasite infracommunities at the within-sample level (i.e. collection of hosts at a given sample site) had negative correlations between abundance and diversity that were 'drowned out' by combining samples (i.e. hosts from all sample sites combined). Yet Kendall's tests for abundance-diversity correlations at the within-sample level for each parasite species led to no significant negative correlations between focal parasite abundance and diversity of other parasite species. Both combined- and within-sample analyses showed the same repeatable tendency towards positive associations between abundance and parasite diversity. Whereas significant positive relations were found for only a proportion of the within-sample results, those proportions were higher than expected by chance, a point that is particularly important given that such tests were underpowered. Therefore, we rule out that these consistent patterns were the outcomes of statistical artifacts.

Parasite infection-diversity correlations also were unrelated to inclusion of particular host sex or age categories. The effect of sex steroid hormones, in particular testosterone, and sexual size dimorphism can potentially cause different host susceptibilities to infection between males and females (Zuk, 2009; Zuk and McKean, 1996), which could then result in spurious correlations between abundances and parasite community diversity in the combined data. However, positive co-variations between parasite presence or abundance and diversity occurred regardless of host sex. Furthermore, both age groups had significant positive correlations between focal parasite presence or abundance and diversity when analysed independently. This occurred despite the fact that adult lesser snow geese were expected to eliminate helminth infections more effectively than subadult individuals, possibly due to a more mature immune system (Forbes et al., 1999; Hoeve and Scott, 1988). The fact that fewer abundance correlations were significant for subadults could be explained by their reduced sample size, accounting for only 15% of hosts.

Hosts may vary in attributes other than age or sex that could influence their parasite communities. One hypothesis is that host susceptibility to infection resulted in both the higher diversity and abundance of parasites; this seems a reasonable *a priori* explanation given that hosts can show considerable variation in health and ability to regulate infection (Sheldon and Verhulst, 1996). In our dataset, however, this possibility seems unlikely given that only weak positive correlations between parasite load and spleen mass were found (accounting for approximately 4% of variation in splenic size) (Shutler et al., 1999). Nonetheless variation in host susceptibility to infection cannot be completely discounted because host condition, a proxy for health, was negatively correlated with nematode abundance, and trematode abundance in four out of 27 samples and also inversely correlated with parasite species richness for two of 27 samples (Shutler et al., 2012). Alternatively, some parasite species could be recruited together through geese consumption of co-infected intermediate hosts, yet this would not explain positive infection-diversity associations between parasites species and communities with direct and indirect life-cycles.

A third possibility is that parasites with particular attributes are more prone to show positive infection-diversity relations than other parasite species or taxa. For example, parasites of a given species might co-occur more often with other parasite species simply by nature of having high prevalence and intensities. Beyond the fact that lower prevalence will mean that certain species are less often present within samples, which may affect detection of significant interactions, the above argument could hold true for species like *H. dispar* and *T. tenuis*, which have the highest levels of prevalence and intensity (Fig. S1). However, this argument falls short of explaining infection-diversity relations for species like *D. lanceolata, D. barrowensis, S. gracilis* or *P. ciliata*, which had recurrent significant positive correlations despite low prevalence and intensity of infections. Additionally, positive correlations do not seem restricted to a single taxon of parasites: we found it in cestodes (*D. lanceolata, D. barrowensis, S. gracilis*), and nematodes (*H. dispar, T. tenuis*), but not in the only species of trematode assessed (*E. revolutum*). Recurring positive co-variation between infection and diversity in this system may thus be driven by positive parasite interactions, whereby parasite species facilitate each other.

Facilitation among different parasite species can occur via parasite suppression of a host's immune system, as has been documented, for example, in cestodes (Good and Miller, 1976), nematodes (Behnke, 2008; Segura et al., 2007) and microparasites (Telfer et al., 2010) in mice, nematodes in African buffalo (Ezenwa et al., 2010), and trematodes in humans (Duvaux-Miret et al., 1992). Host immunosuppression and perhaps immunoredistribution (Braude et al., 1999) could, in turn, increase probabilities of establishment by other parasite species and lead to positive associations between infection and diversity, as reported here. Additionally, hosts activating an immune response against specific parasites may have reduced ability to control other parasites (Sadd and Schmid-Hempel, 2009), although such an effect would perhaps be stronger among parasites targeting different host tissues instead of parasites targeting the same tissue. Such processes would not require *all* parasite interactions to be positive, only that on average interactions tend towards facilitation rather than competition such that the magnitude of positive effects is greater than that of negative ones.

Definitive support for facilitation as a driver of positive parasite diversity-infection patterns in this and related systems will require experimentation. Such experiments should include estimation of parasite establishment or population growth rates, in artificially assembled parasite communities with varying degrees of diversity, as well as track changes in host immunity and condition (e.g. Johnson and Hoverman, 2012). Alternatively, hosts could be

experimentally infected with one species of parasite and then assessed for infracommunity assembly in natural settings (e.g. Benesh and Kalbe, 2016); although more representative of natural dynamics, this approach would be less informative about potential causal mechanisms. Irrespective of the ultimate explanation for positive co-variation between parasite presence or abundance and parasite diversity, we found these relations repeatedly for different parasite species and measures of diversity. That these findings were based on samples from natural settings, where multiple ecological variables could influence parasite dynamics, suggests that this is a strong and general pattern and not simply characteristic of particular parasite types or unique samples.

Our results are in agreement with those reported by Behnke et al. (2009, 2005) which showed that abundance of one nematode species (*Heligmosomoides polygyrus*) in wood mice (*Apodemus sylvaticus*) correlated positively with helminth richness across different years, divergent habitats, and geographically independent host populations. Saliently, our study considered nine species of parasites with different life-cycles and from different taxa (cestodes, nematodes, and trematodes) and found a recurrent positive correlation between parasite prevalence and abundance, and parasite richness, but also with Shannon's Diversity Index which accounts for variation in the relative abundance of each parasite infrapopulation (i.e. the parasite population within a given host - Bush et al., 1997). Our results do contrast with another study on parasite abundance-richness patterns (Johnson and Hoverman, 2012), which reported a negative correlation for six species of larval trematodes infecting the tree frog *Pseudacris regilla*. Interestingly, the tree frog study only assessed trematode species interactions, and in our study the trematode species present had no correlation between abundance and diversity of other parasites. Possibly, trematode species interactions are often negative, perhaps due to strong competitive interactions (Kuris and Lafferty, 1994) or cross-reactive immunity in hosts (Johnson and Hoverman, 2012), and this dynamic drives the discrepancy noted. We cannot exclude that the recurrent positive infection-diversity patterns are specific to our host-parasite study system or limited to homeotherms in general (Behnke et al., 2005, 2009). Additionally, they might be specific to within-guild interactions because we focused our exploration of these patterns on gastrointestinal parasites only. However, such overlap in space and resource use among species would not explain why recurrent positive correlations were so prevalent whereas negative ones were completely absent. Our study does underscore the need to simultaneously study multiple taxa when assessing infection-diversity correlations.

Understanding the drivers of infection-diversity dynamics has important implications for our ability to accurately assess and manage disease (Johnson et al., 2015; Keesing and Ostfeld, 2015; Wood et al., 2016). If facilitation is present, reductions or elimination of particular parasite species have the potential to reduce non-target parasite populations and the overall parasite burden of hosts. Such outcomes might be desirable for parasitic and disease organisms of immediate and direct interests of humans. However, parasites, like predators and competitors, play an important role in controlling host populations (Anderson and May 1978), promoting diversity (Karvonen and Seehausen, 2012) and regulating ecosystem functioning (Hatcher et al., 2012). Therefore, systems with depauperate parasite communities might face higher risks of species loss and instability (Hudson et al., 2006), and consequently could be undesirable for wildlife and even human welfare.

More generally, our findings contrast with the apparent recurrence of negative correlations between infection and host species diversity (i.e. 'dilution effects'- Civitello et al., 2015; but see Wood et al., 2016). The degree to which infection-parasite diversity interactions influence disease-diversity dynamics at the 'host-diversity level' deserves further consideration, especially for model systems cited often to support host dilution effects such as Lyme disease, West Nile virus, and Hantavirus (Keesing et al., 2010). Additionally, our results show variation among parasite species' responses to diversity and emphasize the importance of assessing these relationships in multiple species of parasites simultaneously. Studies at the host-diversity level would benefit from expanding their focus from single to multiple parasite species. Accounting for these kinds of complex interactions is crucial if we ultimately intend to use this knowledge to inform conservation strategies and policy-making (Wood et al., 2016).

Ethics statement

This study was performed under permit of various state and federal agencies in North America, and in accordance with the Canadian Council of Animal Care Guidelines at the time collections were done.

Data accessibility

All data are publicly available at DRYAD digital repository (http://dx.doi.org/10.5061/dryad.407c5).

Author contributions

FD conceived of the original ideas and wrote the first draft of the MS. RTA oversaw logistics of sampling and JDM identified and quantified helminths. DS provided context from earlier studies. AM, FD and MRF honed the ideas and provided insights into analyses and approaches. AM and FD analysed the data. All authors read and edited the MS and agree on its submission.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ijppaw.2017.01.003.

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