

Prevalence of avian haemosporidian parasites is positively related to the abundance of host species at multiple sites within a region

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Abstract Parasite prevalence is thought to be positively related to host population density owing to enhanced contagion.

ranges (Murray and Lepschi 2004). Furthermore, phylogenetically informed analyses show that abundance (i.e., the number of individuals of a particular species) is an evolutionarily labile trait, meaning that closely related species often differ greatly in abundance (Webb and Gaston 2003; McGill 2008; Ricklefs 2011; Ricklefs 2012) despite their presumably similar ecological requirements. These observations suggest that localized, species-specific factors, rather than evolutionarily conserved species traits, may act independently across regions to influence population abundance. One hypothesis proposes that coevolution between specialized parasites and their hosts might generate these abundance patterns (Ricklefs 2011; Ricklefs 2012). Indeed, specialized soil pathogens limit the local abundance of temperate (Packer and Clay 2000; Packer and Clay 2003) and tropical tree species (Mangan et al. 2010), and parasites, including viruses, can depress population densities of their vertebrate hosts (Hudson et al. 1998; LaDeau et al. 2007), although few studies have investigated geographic variation in these effects (but see Ricklefs et al. 2016). Additional support for the influence of pathogens on populations comes from nonnative host species, which are often more common in their introduced ranges than in their native ranges, possibly because they have left their parasites behind (the “enemy release hypothesis,” Torchin et al. 2003; Marzal et al. 2011).

Individuals of rare forest tree species may survive less well in the presence of conspecifics than do individuals of abundant species (Comita et al. 2010)

study. The absence of an effect of nonnative species in the models might have been related to small samples from most of the sites (Table S3). However, all three of these species were well sampled at the Chicago site, allowing for a test of their effect at that site alone (see following paragraph).

Although the mixed-effect models provide an estimate of the relationship between parasite prevalence and host abundance generalized across all sites, it was instructive to examine the results of separate models for each of those sites. To that end, generalized linear models with a quasi-binomial error structure (to account for overdispersion) were run for each of the seven best sampled sites individually (using the five individuals per species cutoff) and those results are reported in Table 1. In the Chicago site, where the three nonnative species were well sampled, a categorical variable coding host species as native or nonnative was included in the model.

Generalized linear binomial mixed-effect models were also used to test whether parasite prevalence was related to the abundances of individual host species among the sites where

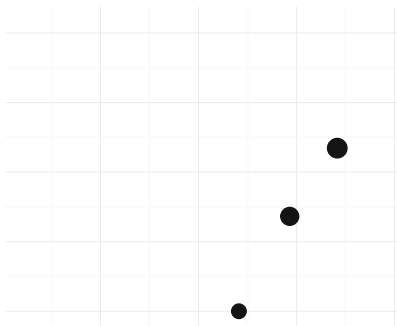
they were sampled. For this analysis, the data were restricted to host species sampled in at least four sites, with at least five ($n = 19$ species), ten ($n = 8$), or 15 ($n = 2$) individuals sampled per site. Since this analysis did not involve comparing multiple host species within the same site, all sites were included, even those with few species sampled. For example, the site

and all graphics were created with the ggplot2 package in R (Wickham 2009). R v.3.2.1 (R Core Team 2015) was used for all analyses.

Results

Parasite prevalence and host abundance of multiple host species within sites

Binomial mixed-effect models revealed a positive effect of host abundance on total prevalence of haemosporidian infection ($\beta = 0.47$, 95 % confidence interval (CI) = 0.27, 0.67; Fig. 2a, Table S2) and on the prevalence of *Plasmodium* ($\beta = 0.47$, 95 % CI = 0.26, 0.68). That is, the most common host species in an assemblage were the most likely to be infected by haemosporidian parasites. The effect of host abundance on *Haemaphysalis* prevalence was smaller, and the 95 %



CI of the coefficient approached zero ($\beta = 0.36$, 95 % CI = 0.03, 0.70). Separate models for each site of the effect of host abundance on parasite prevalence showed some variation among sites (Table 1), but *Plasmodium* prevalence was still more often positively related to host abundance than was *Haemaphysalis* prevalence. In Chicago, the three nonnative species were less infected than native species (total prevalence, $\beta = -1.34$, 95 % CI = -1.88, -0.83, $P < 0.001$; *Plasmodium* prevalence, $\beta = -0.87$, 95 % CI = -1.47, -0.30, $P = 0.007$). Interestingly, none of the nonnative species in Chicago were infected with *Haemaphysalis* parasites. However, *P. domeica* was infected with *Haemaphysalis* parasites in St. Louis and in Tennessee (Ellis et al. 2015).

Parasite prevalence and host abundance of individual host species among sites

The within-host species analysis (i.e., the binomial mixed-effect model with host species as a random effect) revealed no significant relationship between haemosporidian prevalence and the abundances of individual host species among sites at which they were sampled ($\beta = 0.29$, 95 % CI = -0.05, 0.64, Fig. 2b, Table S4). When modeled separately, *Plasmodium* ($\beta = 0.07$, 95 % CI = -0.29, 0.43) and *Haemaphysalis* ($\beta = 0.26$, 95 % CI = -0.16, 0.69) prevalence also was not related to the abundances of individual host species among the sites where those host species were sampled.

Discussion

Within the sites surveyed here, parasite prevalence was generally positively related to host abundance (Fig. 2a, Table 1, Fig. S2), a phenomenon that is likely mediated by higher vector-host encounter rates in denser host populations. This relationship was stronger for *Plasmodium* parasites than for *Haemaphysalis* parasites. Parasites of these two genera have different dipteran vectors: culicid mosquitos [Culicidae] vector *Plasmodium*, while biting midges [Ceratopogonidae] vector *Haemaphysalis* (Valkiūnas 2005). These vectors may respond differently to variation in host abundance. In an analysis of avian host utilization by mosquitos at one site investigated here (Chicago), Medeiros et al. (2015) found that abundant hosts were more often bitten by mosquito vectors and were also more likely to be infected by *Plasmodium* parasites compared with less abundant hosts. Their results are consistent with the idea that vector-host encounter rates contribute to the positive relationships between host abundance and parasite prevalence documented here at multiple sites.

Vector exposure might, however, be related to factors in addition to host abundance. This is consistent with the relationships between prevalence and host abundance within sites being statistically noisy (Fig. S2). Many avian hosts are bitten by mosquitos at different rates than expected based on their relative abundances in an assemblage (Kilpatrick et al. 2006; Hamer et al. 2009). Over- and under-utilization of hosts by vectors may, at least in part, be related to host traits (e.g.,

