

How host diversity and abundance affect parasite infections: Results from a whole-ecosystem manipulation of bird activity

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ABSTRACT

As environmental change drives reductions in free-living species abundance and diversity, at least two alternative pathways are possible for parasitic species. On one hand, diversity losses could drive parasite population declines or extirpations, with potentially influential effects on ecosystem processes, given parasites' ecological importance. On the other hand, host species loss could reduce the abundance of non-competent hosts that interfere with pathogen transmission or facilitate increases in the abundance of "weedy", highly competent host species, intensifying transmission. While many experimental studies have investigated how changes in free-living species affect the fate of individual parasite species, comparatively little is known about the consequences across multiple parasite taxa within an ecosystem, limiting opportunities to assess the proportion of species that are likely to take each of the alternative pathways. Here, we present results of a before-after-control-impact (BACI) experiment conducted in central California, USA, in which we manipulated bird activity at the scale of wetland ecosystems and tracked the resulting effects on the identity and abundance of protozoan and metazoan parasites of amphibians. Of the eight common parasite taxa that constituted ~97% of parasite observations, four responded negatively to bird-augmentation treatments, two responded positively, and two exhibited no significant response. We conclude that it is possible, within a single ecosystem, for free-living species change to produce declines in some parasite species, increases in others, and no change in yet other species. Disease ecology urgently needs tools for forecasting when and where each of these effects should occur, which will facilitate management efforts focused on mitigating outbreaks of disease on one hand and preventing extinction of parasite species on the other.

1. Introduction

Parasites cannot exist without hosts, and the loss of host species diversity has therefore become the primary concern of parasite conservation efforts (Dunn et al., 2009; Colwell et al., 2012; Carlson et al., 2017). Parasite ecologists have warned about the threat of parasite co-extinction for decades (Windsor, 1990; Stork and Lyl, 1993; Windsor, 1995), even suggesting that co-extinction might be the most common form of biodiversity loss (Dunn et al., 2009; Dougherty et al., 2015). If a parasite species is obligately dependent upon – and specific to – a particular host species, it should go extinct as its host's population dwindles toward extirpation (Koh et al., 2004). If each host species has several host-specific parasites, this could result in a greater loss of diversity among parasites than in free-living species; in fact, Dunn et al. (2009) predict that the extinction of five North American carnivore species would lead to the co-extinction of 56 associated parasite

species. But hosts need not go completely extinct to influence the fate of their parasites. Because hosts constitute both habitat and resource for parasites, the population size of parasites is regulated by this resource and any decline in host density can negatively affect the occurrence of parasitic infections (e.g., Dobson and May, 1987; Arneberg et al., 1998; Hudson et al., 1998; Dhondt and Hochachka, 2000; Wood et al., 2014b; Wood et al., 2015; Wood and Lafferty, 2015), particularly in cases where parasites are host-specific.

Simultaneously, a separate literature has predicted that the loss of host species could lead to increases in the transmission of parasites through the "dilution effect" (Keesing et al., 2006; Civitello et al., 2015). The dilution effect hypothesis posits that increasing free-living diversity should dampen parasite transmission by limiting the availability of competent hosts (e.g., through species interactions such as predation and competition) or by interfering with the transmission of infectious stages (e.g., by diverting vector bites to less-competent host

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species; Keesing et al., 2006). For example, in ponds of central California, enhanced amphibian diversity leads to a reduction in transmission of the pathogenic trematode *Ribeiroia ondatrae*, both because more diverse communities contain lower densities of the most competent hosts and because low-competence hosts tend to divert infectious stages away from more competent species (Johnson et al., 2013a; Johnson et al., 2013b; Johnson et al., 2019). Although the dilution effect has received empirical support (reviewed in Civitello et al., 2015 and Halliday and Rohr, 2019), most tests have focused on only a single parasite species at a time, even in systems containing multiple parasites of zoonotic or conservation concern (Randolph and Dobson, 2012, Lafferty and Wood, 2013, Salkeld et al., 2013, Wood and Lafferty, 2013, Wood et al., 2014a, Johnson et al., 2015a, Johnson et al., 2015b, Wood et al., 2016, Wood et al., 2017, Buck and Perkins, 2018; but see Mitchell et al., 2002, Rottstock et al., 2014). This highlights the importance of studies examining the full range of responses in parasite communities, which could help to resolve uncertainty regarding the consequences of host biodiversity losses for infectious disease.

A key challenge in the study of the diversity–disease relationship is to conduct experimental manipulations of host biodiversity at realistic scales and across more than one parasite taxon. Thus far, most manipulations of host diversity have been performed at relatively small spatial scales (Civitello et al., 2015; Halliday and Rohr, 2019; Rohr et al., 2019), often without consideration of the potential for parasites with varying transmission modes or life histories to respond differently to identical manipulations. In part, continued controversy related to the effects of biodiversity loss on infectious diseases stems from the high likelihood that responses will vary as a function of the specific host–parasite interaction involved (Wood et al., 2014a; Wood et al., 2016; Halliday et al., 2017; Wood et al., 2017), as well as the difference between “randomized” versus “realistic” shifts in host community composition (e.g., Johnson et al., 2019).

One study that adopted this multi-parasite approach was conducted at the Kenya Long-Term Exclusion Experiment (KLEE), a large-mammal exclusion experiment located at the Mpala Research Center in central Kenya that has been used to test the effects of simulated wildlife species loss on the abundance of rodent-borne parasites (Young et al., 2014; Young et al., 2015; Titcomb et al., 2017; Weinstein et al., 2017; Young et al., 2017). Because rodents tend to increase in abundance in response to the removal of large wildlife, several rodent-borne parasites are more abundant in exclusion relative to control treatments (e.g., *Bartonella*, Young et al., 2014; *Borrelia*, *Theileria*, *Hepatozoon*, Young et al., 2017; three intestinal nematode parasites, Weinstein et al., 2017; *Coxiella* and *Rickettsia*, Titcomb et al., 2017). One parasite did not respond to the wildlife-exclusion treatment (*Anaplasma*, Young et al., 2017). These examples demonstrate increasing parasite abundance in response to reductions in diversity due to a loss of susceptible host regulation, consistent with the broader definition of dilution (see Box 2 in Keesing et al., 2006). The approach taken in these studies improves on the preceding, single-parasite-taxon experiments, providing a broader perspective on how multiple parasite species are likely to respond to host diversity loss. However, because the spatial scale of the KLEE manipulation is relatively small (1 ha), it does not accurately simulate the effects of geographically extensive large-wildlife loss; dilution effects detected at the scale of 1 ha could become amplification effects at larger spatial scales for those parasites that are detected in treatments infecting one host species but that at other points in the life cycle use host species that are removed by processes of diversity loss (Perkins et al., 2006; Buck and Perkins, 2018; Halliday and Rohr, 2018). Experiments that fully encompass the spatial and temporal scale of parasite transmission are needed to address this possibility (Rohr et al., 2019).

We conducted a field experiment in which our manipulation spanned the spatial scale of entire wetland ecosystems across two years, and where no a priori judgment was made about which parasite taxa to track among the metazoan and protozoan parasites of amphibians. We worked at freshwater ponds in central California, USA to create

treatments with differing levels of bird activity, where each pond was a single replicate (Wood et al., 2019). We manipulated the environment to either enhance (i.e., bird-augmentation treatment) or leave unchanged (i.e., control treatment) bird activity across 16 randomly assigned ponds. Birds were almost twice as abundant in the bird-augmentation treatment relative to the control (Wood et al., 2019). Bird-augmentation treatments also mitigated the negative effects of a major drought on bird species richness, and resulted in the addition of 0.90 raw species and 1.23 jackknife-estimated species between the before and after time points, relative to the control (Wood et al., 2019).

We expected that there would be several pathways by which bird-augmentation treatments could influence parasite abundance. First, birds function as definitive hosts for several of the trematode parasites present in this system, so we hypothesized that these parasites would benefit from enhanced abundance of their definitive hosts (i.e., amplification). However, increasing bird activity could also induce susceptible host regulation, whereby increasing competition among bird species limits the abundance of competent bird hosts (i.e., dilution). Similarly, increasing bird activity could induce transmission interference, whereby increasing bird diversity increases the proportion of amphibians being consumed by non-competent definitive hosts (i.e., dilution). Finally, increasing bird activity might have downstream impacts on other key hosts in parasite life cycles through predation, competition, or other species interactions, with either positive (i.e., amplification) or negative (i.e., dilution) effects on parasite transmission.

With the bird-augmentation manipulation in place, we tracked the response of metazoan and protozoan parasites of four common amphibian hosts to our treatments. Our experiment was designed to provide perspective on which parasite species are expected to increase, decrease, or remain unchanged in abundance as free-living diversity change proceeds.

2. Materials and methods

2.1. Sites and study design

We selected 16 small (area range = 31–2588 m², area average = 628 m²) ponds located on two adjoining properties in the Bay Area of central California (37.340491°, –121.690558°; Fig. 1). This area is located on the Pacific flyway, which serves as one of four major migration routes for birds in North America and provides naturally high levels of bird activity (Migratory Bird Program 2012). We selected eight ponds at Joseph D. Grant County Park and another eight at San Felipe Ranch (all in Santa Clara County), based on accessibility, feasibility of manipulation, and existence of prior data. All ponds were then randomly assigned to one of two treatments: bird-augmentation or unmanipulated control (eight ponds per treatment, four on each property). The ponds were all at least ~1 km apart and occurred in oak woodland habitat typical of the California Floristic Province. The greatest distance between ponds (i.e., the spatial extent of the study) was 11.8 km, and the ponds were distributed across an area of 29.4 km².

To attract birds to bird-augmentation-treatment sites, we added perching habitat, nesting habitat, two mallard duck decoys (one male, one female), and one floating platform to each pond (Wood et al., 2019). All manipulations were installed in June and early July 2015. We assessed bird abundance by monitoring ponds with DLC Covert MP6 trail cameras (Covert Scouting Cameras, Inc., Lewisburg, KY). We set cameras to capture photographs in one sampling bout one year prior to installation of treatments (3–9 July 2014; hereafter, “before”) and a second sampling bout two years after installation of treatments (1–8 July 2017; hereafter, “after”). The species richness of birds was significantly higher in the bird-augmentation treatments compared to control treatments (see details in Wood et al., 2019). Specifically, bird-augmentation treatments mitigated the negative effects of a major

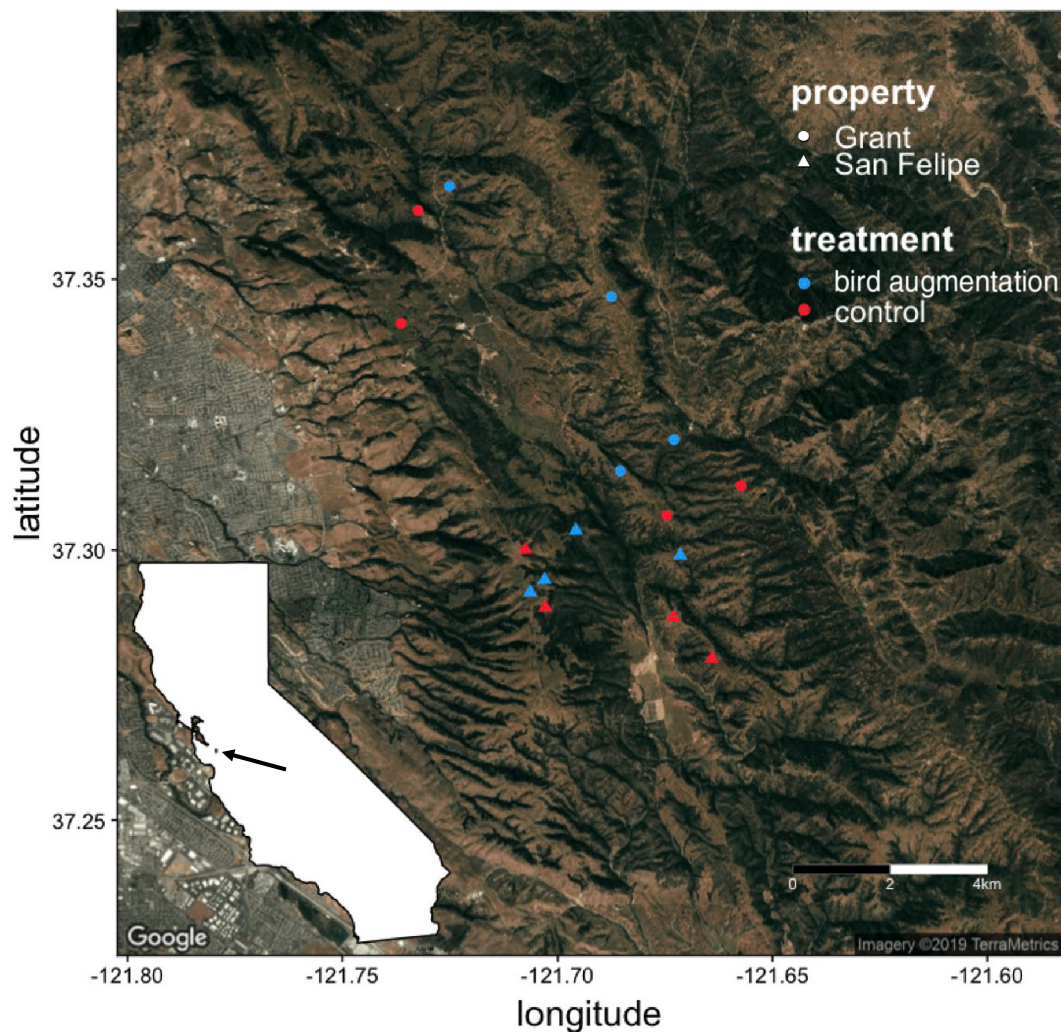


Fig. 1. Map of study sites in the East Bay region of central California. Eight experimental ponds were located in Joseph D. Grant County Park (circles) and eight were located on San Felipe Ranch (triangles). Of these, eight were randomly assigned to the bird-augmentation treatment (blue) and eight were randomly assigned to the control treatment (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

drought on bird species richness; while the control treatment declined from $\sim 3.30 \pm 0.87$ (mean $\pm$ SE) to $\sim 1.52 \pm 0.55$ bird species per site-day over the course of the experiment, the bird-augmentation treatment remained relatively steady, increasing slightly from 2.18 ± 0.81 to 2.42 ± 0.61 species per site-day (see Fig. 4a in Wood et al., 2019). Losses in richness among the control ponds primarily involved American Robins, Black Phoebe, California Quail, Western Kingbirds, unidentified passerines, raptors, and waterbirds. Simultaneously, the bird-augmentation treatment generated a near-doubling of bird abundance in the presence of attractants, with bird abundance increasing in the bird-augmentation treatment and declining in the control treatment (Wood et al., 2019). The same bird species that drove the richness changes (see above) also drove the abundance changes (i.e., American Robins, Black Phoebe, California Quail, Western Kingbirds, unidentified passerines, raptors, and waterbirds).

2.2. Assessment of infection in amphibians

For each of our eight bird-augmentation and eight control ponds, we assessed amphibian infection status before manipulation (i.e., in 2014) and in each of the four years following manipulation (2015–2018). During peak metamorphosis ($\sim$ July of each year), we collected 10 to 15 recently emerged individuals of up to four amphibian species (Western toad [*Anaxyrus boreas*], Pacific chorus frog [*Pseudacris regilla*],

American bullfrog [*Rana catesbeiana*], and California newt [*Taricha torosa*]) from each pond to quantify the richness, identity, prevalence, and abundance of parasitic infections. Each host was measured (snout-vent length) and systematically necropsied to record helminth and protozoan infections in the skin, digestive system, major organs, and body cavity. For helminth infections, which were dominated by larval trematodes, we quantified the number and position of infectious stages (e.g., metacercariae and mesocercariae), and used a combination of morphological features as well as genetic analysis for identification to the lowest taxonomic level. For protozoan infections, we visually identified any protozoan taxa in the gastrointestinal tract using microscopy and recorded their presence or absence for each frog (after Johnson et al. 2018). Because metamorphosing amphibians have only recently emerged from an aquatic (larval) existence, their parasite fauna primarily reflects aquatically derived infections, rather than those obtained through terrestrial soils (e.g., some nematodes) or through a carnivorous diet (e.g., adult stages of trophically transmitted parasites). This makes them an appropriate host for assessing changes in infection mediated through shifts in the abundance, identity, or overall richness of bird definitive hosts. Amphibian care and use protocols were approved by the Institutional Animal Care and Use Committee of the Office of Research Integrity at the University of Colorado Boulder (Protocol 1302.01).

2.3. Statistical analysis

We used a before–after–control–impact (BACI) framework to assess the influence of treatments on parasite abundance. We chose to investigate only those parasites where we detected > 200 parasite individuals (for the helminth macroparasites where infection burdens were quantified) or where we detected infection in > 200 host individuals (for protozoan microparasites where we could only assess infection status as a binary response variable: infected or uninfected). This cut-off represented a natural breakpoint in the data (Supplementary Fig. S1), and power to detect differences among treatments for parasites detected fewer times was low. In the two generalized linear mixed-effects models, the response variable was parasite abundance (i.e., in the macroparasite model, response = number of parasite individuals per frog, in the microparasite model, response = presence/absence of parasite in each frog). The models each contained a fixed effect of treatment (i.e., control vs. bird augmentation), a fixed effect of time (i.e., before vs. after manipulation), a categorical fixed effect of parasite species, and interaction terms (treatment*time, time*parasite species, and treatment*time*parasite species), as well as random intercept terms for pond identity (to account for multiple observations at each pond), year (to account for multiple observations within each year [i.e., 2015, 2016, 2017, and 2018 are all within the “after” level of the “time” fixed effect]), and host species (i.e., Western toad [*Anaxyrus boreas*], Pacific chorus frog [*Pseudacris regilla*], American bullfrog [*Rana catesbeiana*], California newt [*Taricha torosa*]). For the macroparasites, the response variable was modeled as a negative binomial distribution with a log-link function to account for overdispersion using the `glmer.nb` function in the `lme4` package in R (Bates et al., 2015). For the microparasites, the response variable was modeled as a binomial distribution with a logit-link function using the `glmer` function in the `lme4` package in R (Bates et al., 2015). Because we were interested in the interaction treatment*time for each parasite species, we systematically switched each parasite species into the “baseline” or “reference” position (i.e., so that n identical models were run, each with a different one of n parasite species represented by the intercept), and recorded the coefficient for each parasite species in Table 1. Full model results are reported in Supplementary Table S2.

We assessed the response of parasite species richness to bird-augmentation treatments at two levels of ecological organization (i.e., individual host and site-year–host species combination) and using two metrics of diversity, for a total of four analyses. We performed analyses at both the individual and site-year–host species combination levels because we sought to test the effects of bird activity on the taxonomic richness of parasites both within individual hosts (i.e., host alpha diversity) and within host populations (i.e., population alpha diversity). Our two metrics for richness were raw richness (raw number of parasite taxa observed) and the non-parametric jackknife estimator of species richness. We included the jackknife estimate to project parasite species

richness at the saturation of the species accumulation curve for each year at each pond, calculated using the SPECIES package in R (Wang, 2011). This approach produces an estimate of richness that is independent of estimates of sampling effort (i.e., it corrects for the fact that the number of parasites observed or the number of hosts examined might influence the estimate of richness; Gotelli and Colwell, 2001). We excluded site-year combinations in which the jackknife estimate failed to converge (i.e., where there were too few parasite detections to calculate parasite species richness at the saturation of the species accumulation curve). Host individuals and site-year–host species combinations where zero parasites were observed were included in analyses.

To assess the impact of treatments on raw parasite species richness and the jackknife estimate of parasite species richness, we used a BACI framework dependent on generalized linear mixed-effects models (GLMM) with a fixed effect of treatment (i.e., control vs. bird augmentation), a fixed effect of time (i.e., before vs. after manipulation), and their interaction (treatment*time). Analyses of population alpha diversity (i.e., those conducted at the site-year–host species combination level) included random effects of site (to account for multiple observations at each pond), year (to account for multiple observations within each year), and host species (to account for multiple observations per host species). Analyses of host alpha diversity (i.e., those conducted at the individual level) used a nested random effect of site-year–host species combination instead of a random intercept for site (as above), to account for the multiple individual hosts evaluated within each site-year–host species combination. Analyses were conducted using the `glmer()` function in the `lme4` package in R (Bates et al., 2015). We chose an error structure for each model (i.e., Gaussian, Poisson, or negative binomial) based on model fit, which was evaluated by AIC.

3. Results

In total, we detected 20 parasite taxa in 1213 unique individual hosts across four amphibian species (Supplementary Table S1). The parasite detections were dominated by eight taxa: the larval trematodes *Alaria marcinae* ($n = 6897$ individuals detected, average for all hosts, infected or uninfected = 5.7 parasites / host), *Cephalogonimus americanus* ($n = 1306$, average = 1.1 parasites / host), *Clinostomum marginatum* ($n = 668$, average = 0.6 parasites / host; see Calhoun et al., 2019 for taxonomic identification), *Echinostoma* spp. ($n = 9872$, average = 8.1 parasites / host), and *Ribeiroia ondatrae* ($n = 1470$, average = 1.2 parasites / host), the adult trematode *Haematoleochus* spp. ($n = 994$, average = 0.8 parasites / host), and the protozoan parasites *Nyctotherus* spp. ($n = 208$ host individuals infected, 17% prevalence) and *Opalina* spp. ($n = 358$ host individuals infected, 30% prevalence). Together, the six trematode taxa constituted 96.7% of the total detections of macroparasites across the before and after time points, and the two protozoan taxa constituted 96.6% of the total

Table 1

Coefficients for the effect of treatment[control]*time[before] for each parasite species from generalized linear mixed models assessing correlates of parasite abundance for (a) macroparasites (i.e., model with negative binomial error) and (b) microparasites (i.e., model with binomial error). For (a), n observations = 7278, n unique amphibian hosts = 1213, n sites = 16, n years = 5, n host species = 4. For (b), n observations = 2266, n unique amphibian hosts = 1213, n sites = 16, n years = 5, n host species = 4. Each coefficient represents the effect of treatment[control]*time[before] when the indicated parasite species is in the reference position (i.e., when the indicated parasite species is represented by the model intercept). Full model results are reported in Supplementary Table S2.

Parasite group	Parasite species	Coefficient $\pm$ SE	z	p
(a) macroparasites	<i>Cephalogonimus americanus</i>	+2.32121 $\pm$ 0.26214	8.855	< 0.0001
	<i>Ribeiroia ondatrae</i>	+0.73087 $\pm$ 0.26228	2.787	0.0053
	<i>Clinostomum marginatum</i>	−0.59751 $\pm$ 0.30100	−1.985	0.0471
	<i>Echinostoma</i> spp.	−0.87100 $\pm$ 0.23240	−3.748	0.0002
	<i>Haematoleochus</i> spp.	−0.97713 $\pm$ 0.28058	−3.483	0.0005
	<i>Alaria marcinae</i>	+0.26060 $\pm$ 0.28339	0.920	0.3578
(b) microparasites	<i>Nyctotherus</i> spp.	+0.5833 $\pm$ 0.6192	0.942	0.3462
	<i>Opalina</i> spp.	−2.1675 $\pm$ 0.5646	−3.839	0.0001

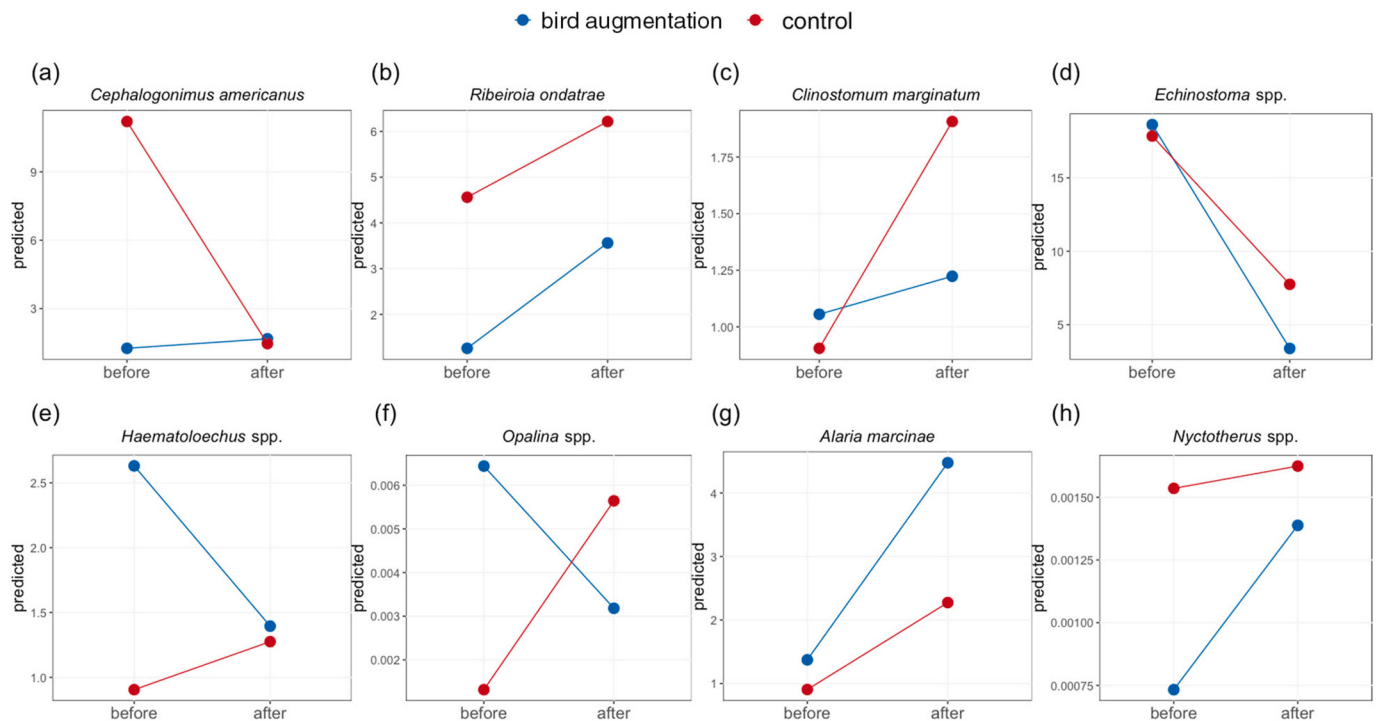


Fig. 2. Effect of treatment (bird augmentation versus control) and time (before versus after implementation of treatments) on parasite abundance in amphibians across the eight most abundant parasite species. Effects of treatment/time are shown for each individual parasite species: (a) *Cephalogonimus americanus*, (b) *Ribeiroia ondatrae*, (c) *Clinostomum marginatum*, (d) *Echinostoma* spp., (e) *Haematoleochus* spp., (f) *Alaria marcinae*, (g) *Nyctotherus* spp., and (h) *Opalina* spp. Data represent predicted (fitted) values for the response of parasite abundance to treatment, time, and parasite species, computed while keeping all other factors (including random effects) in the model constant, and were calculated with the `ggeffects()` function in the `ggeffects` package in R (Lüdtke, 2018). Red indicates control treatment and blue indicates bird-augmentation treatment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

detections of microparasites across the before and after time points.

The effect of treatment on total parasite abundance/prevalence per amphibian host diverged among the eight focal parasite species (Table 1, Supplementary Table S2). Of the eight, two responded positively to the bird-augmentation treatment (*Cephalogonimus americanus*, Fig. 2a; *Ribeiroia ondatrae*, Fig. 2b), four responded negatively (*Clinostomum marginatum*, Fig. 2c; *Echinostoma* spp., Fig. 2d; *Haematoleochus* spp., Fig. 2e; *Opalina* spp., Fig. 2f), and two did not have a significant response (*Alaria marcinae*, Fig. 2g; *Nyctotherus* spp., Fig. 2h; Table 1b). Together, the taxa that responded positively to the bird-augmentation treatment accounted for 31.0% of the total macroparasites counted before the experimental manipulation, and included the most pathogenic parasite in the system: the limb-deformity-inducing trematode *Ribeiroia ondatrae*. The taxa that responded negatively to the bird-augmentation treatment accounted for 60.1% of the total macroparasites counted before manipulation and 63.6% of the total microparasite detections before manipulation, and included a second pathogenic parasite, *Echinostoma* spp., which can decrease survival and growth in amphibian larvae (Holland et al., 2007; Johnson and McKenzie, 2008).

Parasite species richness did not respond to the bird-augmentation treatment. This was true for raw richness at the individual host level (Poisson GLMM: $\text{treatment}[\text{control}] \times \text{time}[\text{before}] = \text{coefficient} \pm 1 \text{ SE} = -0.2208 \pm 0.5652, t = -0.391, n \text{ observations} = 1133, n \text{ unique site-year-host species combinations nested in sites} = 56, n \text{ sites} = 16, n \text{ years} = 5, n \text{ host species} = 4, p = 0.6960$; Fig. 3a), for raw richness at the site-year-host species combination level (Poisson GLMM: $\text{treatment}[\text{control}] \times \text{time}[\text{before}] = \text{coefficient} \pm 1 \text{ SE} = 0.0698 \pm 0.3692, t = 0.189, n \text{ observations} = 112, p = 0.8501$; Fig. 3b), for the jackknife estimator of richness at the individual host level (negative binomial GLMM: $\text{treatment}[\text{control}] \times \text{time}[\text{before}] = \text{coefficient} \pm 1 \text{ SE} = 0.0475 \pm 0.3680, t = 0.129, n$

observations = 760, $p = 0.897$; Fig. 3c), and for the jackknife estimator of richness at the site-year-host species combination level (Poisson GLMM: $\text{treatment}[\text{control}] \times \text{time}[\text{before}] = \text{coefficient} \pm 1 \text{ SE} = 0.2266 \pm 0.5284, t = 0.429, n \text{ observations} = 77, p = 0.6680$; Fig. 3d; Supplementary Tables S3 and S4).

4. Discussion

We found that our experimental manipulations produced a gain in abundance (or prevalence) for some parasite species, a loss for others, and no effect for yet other species. This did not result in shifts in parasite species richness, but it did produce shifts in parasite community composition. Importantly, both the parasites displaying positive responses and those displaying negative responses included pathogenic species. This suggests that parasites might be both lost and gained in a changing world, but that it will be difficult to predict what this portends for host fitness.

The observed changes in parasite community composition were probably driven by the shifts in bird species richness, composition, and abundance produced by the bird-augmentation treatment. As reported previously (Wood et al., 2019), birds were almost twice as abundant in the bird-augmentation treatment relative to the control. Bird-augmentation treatments also mitigated the negative effects of a major drought on bird species richness, and resulted in the addition of 0.90 raw species and 1.23 jackknife-estimated species between the before and after time points, relative to the control (Wood et al., 2019). Because birds function as definitive hosts for several of the trematodes using amphibians as second intermediate hosts, we hypothesize that alterations in avian community structure are the most plausible mechanism underlying the observed changes in the parasite community. Importantly, the manipulation had few reported effects on other major definitive host groups, such as mammals (Wood et al., 2019).

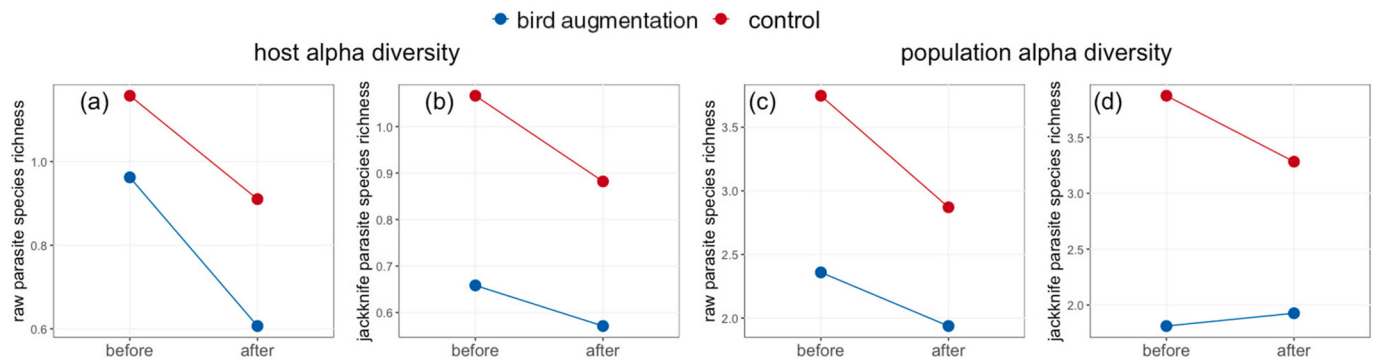


Fig. 3. Effect of treatment (bird augmentation versus control) and time (before versus after implementation of treatments) on parasite richness in amphibians across all parasite species detected. Effects of treatment/time are shown for: (a,c) raw parasite species richness and (b,d) jackknife estimate of parasite species richness at the (a,b) host alpha diversity (i.e., taxonomic richness of parasites within a host individual) and (c,d) population alpha diversity (i.e., taxonomic richness of parasites within the population, or site-year-host species combination) levels. Data represent predicted (fitted) values for the response of parasite abundance to treatment and time, computed while keeping all other factors (including random effects) in the model constant, and were calculated with the `ggeffects()` function in the `ggeffects` package in R (Lüdtke, 2018). Red indicates control treatment and blue indicates bird-augmentation treatment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

As we evaluate how environmental change affects the abundance of parasites, it can be informative to consider the details of each parasite's life history (Wood et al., 2014b; Wood et al., 2015; Weinstein et al., 2017; Halliday et al., 2017). Among the eight most abundant parasites detected (which together comprised ~97% of total detections), two parasites responded positively to the bird-augmentation treatment, four responded negatively, and two had no significant response. It is important to note that many parasites underwent an overall increase or decrease related to the passage of time (i.e., moving from the “before” to the “after” time point), and that treatment effects describe how this temporal trajectory diverged between control and bird-augmentation treatments. Therefore, it is possible for the bird-augmentation treatment to have, for example, a negative effect on parasite abundance, but for parasite abundance to still increase over time in the bird-augmentation treatment – as long as parasite abundance increases less in the bird-attractant treatment than it does in the control treatment (e.g., Fig. 2c).

Cephalogonimus americanus and *Ribeiroia ondatrae* both responded more positively to the implementation of the bird-augmentation treatment than to the control treatment. The primary definitive hosts of *R. ondatrae* are frog- and fish-eating birds (Johnson et al., 2004); that *R. ondatrae* responded positively to experimental bird augmentation suggests that its host might be one of the bird species facilitated by our treatments. In contrast, *Cephalogonimus americanus* trematodes typically inhabit the intestinal tract of amphibians or reptiles in their adult stages (Bray et al., 2008); although we found no evidence of increased reptile presence at bird-augmentation treatments (Wood et al., 2019), it is possible that addition of woody cover to the edges of ponds facilitated use of this habitat by predatory snakes, which could have increased the abundance of *Cephalogonimus americanus* metacercariae in amphibians at these sites.

Four other species responded negatively to the implementation of the bird-augmentation treatment. Interestingly, these parasites each exhibit different life cycles and definitive host use patterns. *Clinostomum marginatum* (Calhoun et al., 2019) uses piscivorous birds as definitive hosts, including egrets and herons – a fact that led us to expect an increase in infection following the manipulation, similar to that observed for *R. ondatrae*. There are several possible explanations for the negative relationship between bird activity and *C. marginatum* abundance: (1) increasing bird activity reduced the density of a specific definitive host favored by *C. marginatum* (susceptible host regulation), (2) increasing bird diversity increased the proportion of *C. marginatum*-infected amphibians consumed by non-competent definitive hosts (transmission interference), or (3) increasing bird activity had downstream effects on other hosts in the *C. marginatum* life cycle (e.g., the

abundance of amphibian or snail intermediate hosts). Hypothesis 1 is inconsistent with our data on egret and heron abundance (see Fig. 5b in Wood et al., 2019), but we do not yet have the data to test hypotheses 2 and 3. *Echinostoma* spp. is an extreme host-generalist in its adult stages, infecting birds, reptiles, fishes, and mammals (Bray et al., 2005) and it has been reported to respond positively to increasing suburban land use (VanAcker et al., 2019); if competence varies among the hosts that consume *Echinostoma* spp. metacercariae in amphibian prey, we would expect increasing host diversity to decrease transmission of this parasite through transmission interference or susceptible host regulation (see Appendix B in Wood et al., 2014a). *Haematoloechus* spp. use amphibians as definitive hosts, occurring as adults in the host's lungs after transmission from dragonfly intermediate hosts (Dronen, 1975). We surmise that bird augmentation might have had negative effects on the abundance of adult amphibian hosts (e.g., through enhanced bird predation), which in turn influenced the transmission of *Haematoloechus* spp.; a similar effect might have been responsible for the negative response of *Opalina* spp. prevalence (i.e., a directly transmitted protozoan parasite) in response to the bird augmentation treatment. However, we lack the data on adult amphibian abundance to test this hypothesis.

Two parasite species did not respond to the implementation of bird-augmentation treatments. These included larvae of the trematode *Alaria marcinae* and the protozoan *Nyctotherus* spp. *A. marcinae* uses mammals as its definitive host; since mammals were largely unaffected by our bird-augmentation treatments (Wood et al., 2019), we would not expect change in bird diversity to affect the abundance of *A. marcinae*. Interestingly, one protozoan parasite species (*Opalina* spp.) responded negatively to the bird augmentation treatment while the other (*Nyctotherus* spp.) had no significant response, despite the fact that both protozoans are transmitted through consumption of cysts passed in the feces of infected hosts. Perhaps the implementation of bird augmentation treatments limited (e.g., through predation) the abundance of the most competent hosts of *Opalina* spp., but not of *Nyctotherus* spp., but we lack the data (i.e., on [1] the relative competence of the four amphibian hosts for these protozoan parasites and [2] the change in the relative abundance of the four hosts caused by the implementation of the bird-augmentation treatment) to test this.

We found no effects of our bird-augmentation treatment on raw parasite taxon richness or on the jackknife estimator of parasite taxon richness; instead of changing the number of parasite taxa, treatments induced a turnover in the species represented among the parasite community. Kamiya et al. (2014) demonstrated that the “host-diversity-begets-parasite-diversity” relationship (Hechinger and Lafferty, 2005) is widely reported in the literature, and we had previously found that parasite species richness is strongly dependent on amphibian host

richness in this system (Johnson et al., 2016), so we were surprised that our manipulation of bird host richness did not produce an increase in parasite richness. It is possible that our manipulation produced only modest differences in host diversity (Wood et al., 2019) relative to the natural variability in host diversity that is typically used in assessments of the host-diversity-begets-parasite-diversity relationship (Kamiya et al., 2014). It is also possible that these small ponds are saturated with parasite species, and no further increases in parasite richness are possible, producing only species turnover in response to increases in host diversity (Cornell and Lawton, 1992; but see Johnson et al., 2016). However, the finding that parasite community composition turns over in response to host activity manipulation suggests that there will be both winners and losers among parasites as host diversity changes.

Previous work in this system has provided an empirical foundation for our understanding of the dilution effect (Johnson et al., 2015a; Johnson et al., 2015b). Multiple studies – including geographically extensive field observations and carefully controlled mesocosm experiments – demonstrate that amphibian, snail, and parasite diversity are all negatively correlated with *Ribeiroia ondatrae* transmission (Johnson et al., 2012; Johnson et al., 2013a; Johnson et al., 2013b). Why should it be the case that increasing intermediate host diversity reduces *R. ondatrae* transmission, while increasing definitive host diversity increases it? In part, this could stem from the fact that the current manipulation increased both the richness as well as the abundance of definitive hosts, which often covary in many natural systems. We also suggest that biodiversity can exert different effects on parasite abundance at each stage of a complex life cycle; the effect of change in diversity across an ecosystem will depend on the competence of various hosts for each parasite life stage in combination with the effect of diversity change on the abundance of those hosts (Joseph et al., 2013; Mihaljevic et al., 2014), the effect of diversity change on any non-competent, “decoy” hosts (Johnson and Thielges, 2010), and whether each life stage is a “rate-limiting step” in that parasite’s life cycle (Lafferty, 2012). In light of this evidence that diversity can have divergent effects across parasite life stages, we encourage a more explicit focus on parasite life stages in diversity–disease research. For instance, in coral reef ecosystems, we suspect that the life cycles of trematode parasites are affected by fishing in complex ways; while fishing might remove fish definitive hosts, it could also cause compensatory increases in the abundance of snail intermediate hosts (Wood et al., 2014b; Wood and Lafferty, 2015); whether a parasite experiencing these opposing influences would increase or decrease in abundance depends upon which host is more limiting (Lafferty, 2012).

The results for parasite abundance suggest that, as biodiversity loss proceeds, some parasite taxa will decline in abundance, while others will increase; what implications will this have for host fitness in a changing world? In our study system, the parasite that is most detrimental to amphibian fitness is *Ribeiroia ondatrae*, which encysts in tadpole limb buds, causing deformities that increase mortality, impair mobility, and increase the risk of predation by birds (Johnson et al., 2004; Johnson and Hoverman, 2012). *Ribeiroia ondatrae* responded positively to the bird-augmentation treatment, suggesting that increasing the abundance or diversity of birds could increase parasite-induced fitness loss for hosts. On the other hand, *Echinostoma* spp. displayed the opposite effect, responding negatively to the bird-augmentation treatment; the negative fitness effects of this parasite depend on infection intensity and host tolerance, but can include edema, reduced growth, and mortality (Johnson and McKenzie, 2008; Orlofske et al., 2009; Johnson and Hoverman, 2012). The other common parasites found in this study do not reduce host fitness when they occur in single-species infections, but can do so in co-infections (Johnson and Hoverman, 2012). Together, these results suggest that we cannot make generalizations about how parasite abundance change mediated by biodiversity loss may influence host fitness; this will depend on the responses of the most pathogenic parasites.

An important caveat to recognize with respect to the current study is

that the manipulations we employed simultaneously affected both bird species richness and abundance (Wood et al., 2019). This mimics additive community assembly (Joseph et al., 2013; Mihaljevic et al., 2014), which often yields very different effects on parasite transmission relative to when communities assemble substitutively (such that total community or biomass is constant). We therefore cannot disentangle the influence of species diversity per se from the influence of host abundance, and it is possible that both factors were simultaneously affecting infection, even in opposing directions (e.g., Johnson et al., 2015b). While this may limit opportunities for mechanistic inference, we suggest that it is important to recognize that host richness and abundance are likely to covary in natural systems due to variation in resource availability, evolutionary history, and colonization opportunities, and that, by making use of existing pond ecosystems and manipulating them at a whole-ecosystem scale, this experiment is noteworthy in addressing disease dynamics at realistic spatial scales in realistic communities. We encourage future experimental studies to test the mechanisms underlying the patterns revealed here.

Ecologists concerned about parasites in a changing world – both those who focus on the potential for loss of parasite species (e.g., Dunn et al., 2009; Colwell et al., 2012) and those who foresee a “rising tide of disease” that threatens ecosystem integrity and human health (e.g., Harvell et al., 2004; Keesing et al., 2006) – have primarily addressed free-living species diversity loss as the lever driving change in parasite populations. In the experiment presented here, we instead augmented free-living species diversity and abundance. This was done because we found it impossible to effectively simulate whole-ecosystem, long-term bird diversity reductions through time without the use of physical barriers impenetrable to birds, which were prohibitively expensive, dangerous to wildlife, and unacceptable to land managers (Wood et al., unpublished data). In contrast, bird augmentation could be achieved effectively, inexpensively, safely, and using interventions that simultaneously advanced the environmental stewardship goals of land managers (Wood et al., 2019). The ideal test of how diversity reductions affect parasite abundance would simulate diversity reductions. Although bird augmentation does not simulate the bird community in this ecosystem in some future diversity-loss scenario, it nonetheless: (1) allows a valid contrast between high-diversity (treatment) and low-diversity (control) states and (2) might simulate the bird community in this ecosystem in some past, pre-degradation state. The ponds where we worked are located ~3–9 km from San Jose, the third-largest city in California and the tenth-largest in the United States; the land on which these ponds are situated has been used for ranching and other human land-uses. Therefore, although we were not able to successfully simulate diversity loss at our treatment sites, our control sites probably reflect the effect of diversity loss from some past, higher diversity state (Merenlender et al., 2009; Jongsomjit et al., 2013).

5. Conclusions

Our results suggest that there is plenty of consternation to go around: in a world where free-living biodiversity is in decline, parasite conservationists should continue to worry about the potential for parasite species loss (e.g., Koh et al., 2004; Dunn et al., 2009; Colwell et al., 2012), while evidence of emerging infections in human and wildlife populations should continue to sound alarm bells about the potential for a “rising tide of disease” (Harvell et al., 2004; Keesing et al., 2006). However, both groups should bear in mind that these two opposing effects could occur simultaneously, side-by-side, in a single ecosystem. Our study included only eight common parasite species, and it was therefore impossible to assess the key attributes that divided taxa that experienced increases in response to ecosystem manipulation from those that experienced decreases. Disease ecology urgently needs tools for predicting when and where each of these effects should occur; only then will we be equipped to prevent unwanted outbreaks of disease on one hand and the extinction of parasite species on the other.

Conflict of interest

All authors certify the following:

- The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.
- No part of the research has been published in any form elsewhere, unless it is fully acknowledged in the manuscript.
- The research featured in the manuscript is not included in any other manuscript that we have published, in press, submitted or will soon submit to *Biological Conservation* or elsewhere.
- The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal.
- Any research in the paper not carried out by the authors is fully acknowledged in the manuscript.
- All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication.
- All appropriate ethics and other approvals were obtained for the research. Where appropriate, we have stated that research protocols have been approved by an authorized animal care or ethics committee, and included a reference to the code of practice adopted for the reported experimentation or methodology. The Editor will take account of animal welfare issues and reserves the right not to publish, especially if the research involves protocols that are inconsistent with commonly accepted norms of animal research.

CRediT authorship contribution statement

Chelsea L. Wood: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Margaret Summerside:** Investigation, Data curation, Writing - review & editing. **Pieter T.J. Johnson:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

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