

## The effects of odonate species abundance and diversity on parasitism by water mites (*Arrenurus* spp.): testing the dilution effect

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Water mites (*Arrenurus* spp.) parasitize adult dragonflies. We collected dragonflies weekly at 11 waterbodies in Greenville Co. and Pickens Co., SC, USA, to: (1) compare parasitism prevalence across species, sites, and sampling periods; (2) test the hypothesis that prevalence correlates with host abundance; (3) test the hypothesis that prevalence is inversely related to host diversity (the “dilution effect”); and (4) test the hypothesis that prevalence and intensity vary with ecological conditions. Parasitism prevalence varied among well-sampled ( $N > 30$ ) hosts; *Perithemis tenera*, *Plathemis lydia*, and *Celithemis ornata* had no mites, whereas prevalence exceeded 20% for *Argia fumipennis*, *Celithemis elisa*, and *C. fasciata*. Differences among species, however, varied across sites and through time, suggesting patchy or species-specific relationships not captured by our diffuse analysis at the generic level. Prevalence was positively correlated with species abundance and host site occupancy, as expected for generalist parasites. There was no evidence of a dilution effect: there were no significant negative relationships between prevalence and three measures of species richness (observed richness, extrapolated  $S_{est}$ , or CHAO2 estimated richness), considering all odonate species, parasitized species, or only species in the parasitized families Libellulidae or Coenagrionidae. Odonate communities in more pristine sites had higher mean prevalence ( $18.4 \pm 6.0$ ) and median intensity (4.5) than those in disturbed sites ( $13.1 \pm 7.0$ ; 3.0), but only intensities were marginally significantly different. Parasitism by *Arrenurus* spp. met the criteria for a dilution effect, but did not exhibit this effect as a diffuse community-level response.

**Keywords:** Odonata; dragonfly; *Arrenurus*; parasitism; host diversity; community ecology; dilution effect

### Introduction

Parasitism is the most common form of energy harvest by living things, exploited by 30–50% of known animal species (Price, 1980). Although the population dynamics of parasites and hosts have been central to ecology since the 1970s (Anderson & May, 1978) and usually commands an entire chapter in introductory ecology textbooks, the interplay between parasite and host communities is often underappreciated and absent from introductory texts (e.g. Ricklefs, 2008). However, parasites can act as “keystone species” and promote diversity in host communities by limiting the effects of dominant competitors or predators (Hatcher, Dick, & Dunn, 2006, 2014; Holt & Dobson, 2006; Kiesecker & Blaustein, 1999; Schall, 1992) or altering the behavior of ecosystem engineers in ways that benefit other species (Mouritsen & Poulin, 2010). On the

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other hand, parasites can reduce host diversity by facilitating competitive exclusion among hosts (Price, Westoby, & Rice, 1988; Whitlaw & Lankester, 1994), or eliminating species in communities already destabilized by extinctions, invasive species, habitat loss, or climate change (Brooks & Holberg, 2007; Lafferty & Kuris, 1999). In some ways, parasites are the “dark matter” of ecology – directing system dynamics while going largely unseen themselves.

The structure of host communities can also affect parasites. Increased host diversity can decrease parasitism through a “dilution effect” (Dizney & Ruedas, 2009; Hall et al., 2009; Johnson & Thielges, 2010; Ostfeld & Keesing, 2000; Schmidt & Ostfeld, 2001; Venesky, Liu, Sauer, & Rohr, 2014; but see Randolph & Dobson, 2012), where an increase in the relative or absolute abundance of unsusceptible host species reduces the rates of parasite encounter and transmission in susceptible species. Of course, species composition of the host community is critical; a low-diversity host community lacking a susceptible (“competent”) host will have a lower parasitism rate than a species-rich host community that contains a competent host. Likewise, the addition of an incompetent species to a host community might reduce parasitism rates, but the addition of a competent species, acting as a reservoir for parasite populations, might amplify parasitism rates among other species (Keesing, Holt, & Ostfeld, 2006; Venesky et al., 2014). Even when a dilution effect occurs, several mechanisms could be responsible. Dilution might be a direct, additive effect of adding less susceptible species to progressively more diverse communities (LoGiudice, Ostfeld, Schmidt, & Keesing, 2003), or it could be a non-additive effect of changing interactions among species, such as greater niche partitioning in more diverse communities leading to lower parasite encounter and transmission rates between species (Becker et al., 2014).

Although these complexities make the dilution effect appear intractable and anecdotal, there are some general conditions that should increase its likelihood (Ostfeld & Keesing, 2000). Dilution effects should occur when: (1) a generalist parasite exploits differentially competent host species; (2) common host species are the most competent; and (3) the host community exhibits some degree of nested-subset structure, in which the species found in low diversity sites are also found in progressively more diverse communities. These conditions are fairly specific, but they should also be fairly common. Widespread hosts should be locally abundant (Brown, 1984), and selection should favor generalist parasites that exploit abundant, widespread hosts (Dobson, 1990; Ostfeld & Keesing, 2000; but see Mlynarek, Knee, & Forbes, 2013). If the host community exhibits nested-subset structure (Worthen, 2003), then depauperate host communities will be dominated by common competent species and parasitism rates will be high; more diverse communities will include rare, less competent species, diluting the parasitism rate. For closely related generalist parasite species, parallel evolution for using the most common, widespread hosts could reinforce the dilution pattern at a diffuse community level.

Water mites (Arachnida: Arrenuridae: *Arrenurus* spp.) that parasitize dragonflies (Insecta: Odonata) provide an attractive model system for describing relationships between parasite and host communities and testing the dilution effect. Mites hatch in water, and swimming instars climb aboard late instar dragonfly larvae as phoretic, non-feeding parasites. When these dragonflies emerge from their exuviae, the water mites attach – feeding on hemolymph and digested tissue through a secreted stylostome (Smith, 1988). Mites can also attach to mature, previously unparasitized adults (Hassell, Lowe, Harvey, Watts, & Thompson, 2010), probably through transfers during mating or combat. When dragonflies return to water bodies to mate, the mites drop off and complete their larval development – leaving scars that can be used as indicators of parasitism (as in Rolff, Antvogel, & Schrimpf, 2000). The cues for leaving the host are complex; *Arrenurus cuspidator* only detaches when *Coenagrion puella* hosts are in tandem and within 10 mm of the water (Rolff & Martens, 1997). Mites may need to feed for at least 10 days, and can increase 80–90 × in volume (Smith, 1988). The mite load on a single dragonfly can exceed 400 mites (Mitchell, 1967) and the combined effect of their synchronous feeding can be

acute; parasitism can reduce dragonfly flight distances (Reinhardt 1996), survival, and fecundity (Forbes & Robb, 2008; Nagel et al., 2009; Rolff, 2000, 2001; but see Rolff et al., 2000). Some dragonflies, however, can mount an immunological response – melanotic encapsulation – that clogs the mite’s feeding stylostome, stops feeding, and causes the mite to shrivel or “deflate” (Forbes, Muma, & Smith, 1999). This is useful, as competent and incompetent “dead-end” hosts can be distinguished by the presence of these “resisted” mites (Forbes et al., 1999). The host range of particular *Arrenurus* species is poorly described, but many are generalists that exploit both competent and resistant host species (Forbes, Muma, & Smith, 2002) across several dragonfly families (Andrew, Thaokar, & Verma, 2012; Conroy & Kuhn, 1977). Single dragonflies can be parasitized by as many as six species of *Arrenurus* mites (Mitchell, 1969).

Many mite species are generalists that exploit competent and incompetent hosts, and many larval dragonfly assemblages exhibit nested-subset structure (Worthen, 2003); so two of the three conditions for a dilution effect are met. In this context, our study had three goals. The first goal was to describe the frequency and intensity of mite parasitism across odonate species, sites, and time, and test the remaining condition of the dilution effect: that parasitism rate correlates with species abundance. The second goal was to test for a dilution effect, and determine whether the prevalence of mite parasitism is negatively correlated with dragonfly diversity. Finally, because communities in pristine habitats often have higher parasite diversity than disturbed systems (Hudson, Dobson, & Lafferty, 2006; Lafferty, Shaw, & Kuris, 2008), the third goal was to determine whether prevalence and intensity are related to differences in habitat quality or host community similarity. In addition to testing these hypotheses, this study also provides one of the few surveys on this system in the southern USA (but see Lajeunesse, 2007).

## Materials and methods

### Study sites

We surveyed adult odonates at 11 sites in Greenville and Pickens Counties, SC, USA, in summer 2014 (Table 1). The waterbodies are man-made impoundments that vary dramatically in size and ecology. The most pristine sites are the shallow ponds at Blue Wall and Buckhorn (90% less than 3 m), and the deeper Wattacoo Lake and Lake Oolenoy (maximum depth > 10 m); all are surrounded by forest and fed by mountain streams draining intact, protected, forested watersheds. Lake Oolenoy, however, is spanned by a highway that contributed runoff and has moderate use by anglers and kayakers. Pleasant Ridge is also fed by mountain streams from an intact, protected watershed, but approximately 25% of its border is turf grass and it receives runoff from two adjacent parking lots. Lake Placid and Swan Lake are shallow (90% less than 3 m), and fed

Table 1. The location and size of sampling sites in Greenville Co. and Pickens Co., SC, USA.

Site	County	Latitude (N)	Longitude (W)	Elev (m)	Area (ha)
Ashmore Preserve, Lake Wattacoo	Greenville	35° 5' 6.83"	82° 34' 43.64"	347	2.2
Blue Wall Preserve, Lower Pond	Greenville	35° 10' 52.57"	82° 15' 34.19"	365	1.3
Blue Wall Preserve, Upper Pond	Greenville	35° 10' 51.81"	82° 15' 55.82"	389	0.9
Bunched Arrowhead Preserve	Greenville	34° 59' 32.18"	82° 24' 26.68"	300	0.1
Furman University, Scott's Pond	Greenville	34° 56' 10.67"	82° 26' 29.31"	316	0.4
Furman University, Swan Lake	Greenville	34° 55' 35.99"	82° 26' 27.75"	302	11.3
Paris Mountain State Park, Buckhorn Lake	Greenville	34° 56' 43.34"	82° 23' 1.63"	350	0.5
Paris Mountain State Park, Lake Placid	Greenville	34° 55' 41.88"	82° 22' 4.27"	301	3.2
Pleasant Ridge County Park	Greenville	35° 5' 23.62"	82° 28' 54.14"	352	1.3
Snyder Pond	Greenville	34° 55' 0.42"	82° 25' 10.81"	310	1.0
Table Rock State Park, Lake Oolenoy	Pickens	35° 1' 12.89"	82° 41' 38.77"	327	27.1

by streams that receive significant runoff from roads and parking lots. Swan Lake at Furman University is surrounded by campus lawns; Lake Placid is surrounded by forest but is heavily used for swimming and paddleboats, and has an encircling hiking trail that causes significant bank erosion. Snyder and Scott's ponds are heavily impacted by human activity; Snyder is surrounded by a residential development and receives runoff from lawns mown to the waterline; Scott's is a former industrial retention pond of the W. R. Grace Zonolite Facility, which closed in 2010. All of these waterbodies have populations of largemouth bass and bluegill sunfish. The smallest pond, at Bunched Arrowhead Heritage Trust Preserve, is a shallow basin (maximum depth < 2 m) that occasionally dries completely during severe drought; it is the only sampling site without predatory fish.

### *Sampling methods*

We sampled each site 10 times from late May through early August 2014, at approximately weekly intervals. During each sampling event, we captured 15–30 dragonflies by aerial net and identified their species and sex. We counted the number of engorged and resisted (“deflated”) *Arrenurus* mites on each dragonfly with a 20 × loupe, and numbered a wing with permanent marker to avoid double-counting by recapture. Because mites drop off hosts to complete development, the number of dragonflies with mites will underestimate total number of dragonflies parasitized. We assessed this “underestimation rate” by calculating the percentage of dragonflies with scars in particular surveys taken across all sites and sampling periods.

We also recorded the presence of all other odonate species that could be unambiguously identified with binoculars. Several sites are close to one another; the two Blue Wall sites are only 450 m apart, Scott's Pond is 600 m from Swan Lake, Snyder Pond is 2.1 km from Swan Lake, and Lakes Buckhorn and Placid are 2.25 km apart.

### *Analyses*

We computed the parasitism rate – or “prevalence” (the fraction of captured odonates with at least one water mite) – for each species, site, and sampling period. Given the large number of rare species, a chi-square test was inappropriate for comparing prevalence between species (with many expected values < 5). We used chi-square tests, however, for describing differences in prevalence between sites and sampling periods. The large number of rare species also precluded examinations of interactive effects of species, site, and time on parasitism rate using hierarchical loglinear analyses; the number of empty cells (where a rare species only occurred at one site during one week) was too large. Therefore, we described the direct and interactive effects of “species”, “site”, and “sampling period” with a hierarchical loglinear analysis that included only the eight most abundant species (each with  $n > 100$ ). Although parasitism rates can vary between sexes (Nagel et al., 2009), we did not include this variable in any of our analyses as it would have created multiple empty cells when crossed with the other three variables. Rather, we described the difference in sex ratios and parasitism rates between sexes with separate chi-square tests.

To test the hypothesis that common species are parasitized at a higher rate than rare species, we used Spearman rank correlations to describe the relationship between prevalence and species abundance (total number of individuals captured). However, because sampling by aerial netting is biased in favor of the most easily captured species, we also correlated prevalence with site occupancy (number of sites at which the species was recorded). Geographic range should correlate with local abundance (Brown, 1984), so site occupancy should be a reasonable proxy

for abundance. Also, because prevalence is highly variable in small samples (rare species), we repeated these analyses on the sub-set of species captured at least 10 times.

We tested for dilution effects by describing the relationship between parasitism prevalence and species richness across the 11 sites using Pearson one-tailed correlations. A dilution effect would be indicated by a significant negative correlation between prevalence and richness. We used three indices of species richness: observed richness, estimated richness extrapolated to 20 samples ( $S_{est}$ ; Colwell, 2013), and the CHAO2 richness estimate (Colwell, 2013). The CHAO2 estimate uses incidence rather than abundance. This was most appropriate because sampling by aerial netting was biased in favor of the most easily captured species, and many species on a given sampling event were only recorded by sight, as “present”. The CHAO2 bias-corrected estimator was used. Where the coefficient of variation was  $> 0.5$ , the larger of the incidence-based coverage estimator (ICE) and CHAO2 classic estimator was used, per the instructions in Colwell (2013).

Because the actual host range of water mites is unknown, we described these relationships at several taxonomic scales. For the first series of analyses, we included all 58 odonate species captured. Mites were only found on 22 species of the families Libellulidae and Coenagrionidae. Appreciating that mites might ignore some species entirely that should not be considered potential hosts, or that there might be subsets of mite species that might specialize on dragonflies in a particular family (Forbes & Mlynarek, 2014), we repeated the correlation analyses for the subset of 22 dragonfly species that were confirmed hosts (parasitized at least once), and for species in the families Libellulidae and Coenagrionidae separately. Finally, because common host species should be most susceptible to parasitism and may be the most responsive to the diluting effects of additional incompetent host species in more diverse communities, we correlated the parasitism rates on the eight most abundant species (each with  $n > 100$ ) with total odonate richness indices (observed, extrapolated, and CHAO2 estimated species richness values; Colwell, 2013). Under the hypothesis of a dilution effect, prevalence on these species should decline with increasing community richness.

Finally, we examined possible effects of habitat or geographic proximity on parasite prevalence and dragonfly community structure by describing community similarity among sites with a hierarchical cluster analysis using a within-group clustering method and chi-square measurements appropriate for count data (SPSS, 2010). Rather than using abundance data that was skewed by differential capture probabilities, we used summed incidence values for each species at each site, summed across the 10 sampling periods (Chao, Chazdon, Colwell, & Shen, 2005). We ranked communities based on their similarity (which we used as a proxy for habitat), and correlated this index with parasitism prevalence using a Spearman rank correlation.

## Results

### *Variation in parasitism among species, sites, and sampling periods*

A total of 2384 adult dragonflies in 58 species and eight families were caught by net and examined for mites (Table 2). Two other taxa, *Epitheca princeps* Hagen and a *Macromia* sp., were seen and recorded but never collected. We made only two recaptures between weekly surveys; both at the same site where the individuals had been marked. Of the 2384 individuals collected, 386 (16.2%) in 22 species in two families had at least one mite (“Prevalence”, Table 2). In particular surveys where scars were recorded, only 18 of 1078 dragonflies (1.67%) had scars and no mites. Rather than conflating two sampling methodologies, we chose to use only “dragonflies with mites” as our index of prevalence (as in Mlynarek, Knee, & Forbes, 2013, 2014), recognizing that this slightly underestimates the true prevalence rate. The “intensity” of parasitism, measured

Table 2. The prevalence and intensity of parasitism by water mites (*Arrenurus* spp.) on species of Odonata collected at 11 sites in Greenville Co. and Pickens Co., SC, USA.

Family/species	N	With mites	Prevalence	Mean intensity	Median intensity	% of mites
<b>Calopterygidae</b>						
<i>Calopteryx dimidiata</i> Burmeister	4	0	0.0			
<i>Calopteryx maculata</i> (Beauvois)	25	0	0.0			
<b>Lestidae</b>						
<i>Lestes australis</i> Walker	7	0	0.0			
<i>Lestes inaequalis</i> Walsh	2	0	0.0			
<i>Lestes vigilax</i> Hagen in Selys	12	0	0.0			
<b>Coenagrionidae</b>						
<i>Argia apicalis</i> (Say)	4	1	25.0	4.00	4	0.05
<i>Argia fumipennis</i> (Burmeister)*	272	55	20.2	3.35	2	2.07
<i>Argia moesta</i> (Hagen)	32	0	0.0			
<i>Argia tibialis</i> (Rambur)	6	0	0.0			
<i>Chromagrion conditum</i> (Selys)	5	0	0.0			
<i>Enallagma aspersum</i> (Hagen)	47	12	25.5	16.75	12	2.26
<i>Enallagma basidens</i> Calvert	1	0	0.0			
<i>Enallagma civile</i> (Hagen)	2	1	50.0	17.00	17	0.19
<i>Enallagma daeckii</i> (Calvert)	16	3	18.8	1.67	1	0.06
<i>Enallagma divagans</i> Selys	56	11	19.6	44.45	8	5.5
<i>Enallagma doubledayi</i> (Selys)	1	0	0.0			
<i>Enallagma exsulans</i> (Hagen)	6	1	16.7	2.00	2	0.02
<i>Enallagma geminatum</i> Kellicott	34	5	14.7	2.00	1	0.11
<i>Enallagma signatum</i> (Hagen)	38	10	26.3	18.67	12	1.89
<i>Enallagma traviatum</i> (Selys)*	119	14	11.8	3.85	2	0.56
<i>Ischnura hastata</i> (Say)	10	1	10.0	2.00	2	0.02
<i>Ischnura posita</i> (Hagen)*	167	22	13.2	4.19	3	0.99
<i>Ischnura ramburii</i> (Selys)	3	0	0.0			
<i>Nehalennia integricollis</i> Calvert	21	0	0.0			
<b>Petaluridae</b>						
<i>Tachopteryx thoreyi</i> (Hagen in Selys)	10	0	0.0			
<b>Aeshnidae</b>						
<i>Anax junius</i> (Drury)	2	0	0.0			
<i>Anax longipes</i> Hagen	4	0	0.0			
<i>Epiaeschna heros</i> (Fabricius)	1	0	0.0			
<i>Nasiaeschna pentacantha</i> (Rambur)	1	0	0.0			
<b>Gomphidae</b>						
<i>Dromogomphus spinosus</i> Selys	1	0	0.0			
<i>Gomphus exilis</i> Selys	55	0	0.0			
<i>Gomphus lividus</i> Selys	2	0	0.0			
<i>Hagenius brevistylus</i> Selys	5	0	0.0			
<b>Corduliidae</b>						
<i>Epitheca cynosure</i> (Say)	12	0	0.0			
<b>Libellulidae</b>						
<i>Celithemis bertha</i> Williamson	2	0	0.0			
<i>Celithemis elisa</i> (Hagen)*	177	46	26.0	20.26	9.5	10.49
<i>Celithemis eponina</i> (Drury)	6	0	0.0			
<i>Celithemis fasciata</i> Kirby*	113	43	38.1	15.84	6	7.66
<i>Celithemis ornate</i> (Rambur)	33	0	0.0			
<i>Celithemis verna</i> Pritchard	15	2	13.3	1.00	1	0.02
<i>Dythemis velox</i> Hagen	7	0	0.0			
<i>Erythemis simplicicollis</i> (Say)*	133	35	26.3	39.71	4	15.64
<i>Erythrodiplox minuscula</i> (Rambur)	9	0	0.0			
<i>Ladona deplanata</i> (Rambur)	21	3	14.3	16.33	3	0.55
<i>Libellula auripennis</i> Burmeister	16	0	0.0			
<i>Libellula axilena</i> Westwood	7	0	0.0			
<i>Libellula cyanea</i> Fabricius	51	3	5.9	2.67	2	0.09
<i>Libellula flavida</i> Rambur	4	0	0.0			
<i>Libellula incesta</i> Hagen*	198	29	14.6	16.29	2	5.13

(Continued).



Table 2. Continued

Family/species	<i>N</i>	With mites	Prevalence	Mean intensity	Median intensity	% of mites
<i>Libellula luctuosa</i> Burmeister	31	9	29.0	9.22	3	0.93
<i>Libellula semifasciata</i> Burmeister	2	0	0.0			
<i>Libellula vibrans</i> Fabricius	13	0	0.0			
<i>Pachydiplax longipennis</i> (Burmeister)*	433	76	17.6	53.92	5	44.91
<i>Perithemis tenera</i> (Say)	37	0	0.0			
<i>Plathemis lydia</i> (Drury)	35	0	0.0			
<i>Sympetrum vicinum</i> (Hagen)	4	0	0.0			
<i>Tramea carolina</i> L.	44	4	9.1	18.5	4	0.83
<i>Tramea lacerata</i> Hagen	10	0	0.0			

Notes: *N* = number of individual dragonflies in each species examined; Prevalence = % of parasitized individuals; intensity = mean/median number of mites on parasitized individuals; “% mites” = % of all mites found on each species.

\*The eight most abundant species (*N* > 100) used in hierarchical loglinear analyses.

as the mean or median number of mites on parasitized dragonflies (Table 2), was strongly right-skewed. Mean ( $\pm 1$  SD) intensity =  $23.5 \pm 64.76$ , median intensity = 2.0, but 14 individuals had > 200 mites each and eight individuals had > 400 mites each. Across the 22 parasitized species, prevalence was positively correlated with both mean intensity (Spearman  $\rho = 0.419$ ,  $n = 22$ ,  $p = 0.05$ ) and median intensity (Spearman  $\rho = 0.612$ ,  $n = 22$ ,  $p = 0.002$ ).

Parasitism prevalence varied dramatically among dragonfly species, with a range of 0–38.1% (Table 2). There were also differences in prevalence across sites, with a range of 8.3–25.9% ( $\chi^2 = 61.735$ ,  $df = 10$ ,  $p < 0.0001$ ; Table 3a). In contrast, prevalence did not differ significantly across sampling periods, only ranging from 13.2 to 19.7% ( $\chi^2 = 7.417$ ,  $df = 9$ ,  $p > 0.05$ ; Table 3b).

We conducted a hierarchical loglinear analysis on the subset containing the eight most abundant dragonfly species (each with  $n > 100$ ); these species accounted for 67.6% of individual dragonflies collected, 82.9% of parasitized dragonflies, and 87.4% of individual mites tallied. There were statistically significant direct and interactive effects of species, sites, and sampling period on parasitism prevalence (Table 4). Prevalence varied from 11.8% for *Enallagma traviatum* to 38.1% for *Celithemis elisa* (among species with asterisks, Table 2). However, species differences in prevalence varied across sites (“species  $\times$  site  $\times$  mite” effect,  $p = 0.0001$ , Table 4). There was a significant difference in sex ratio among these species ( $\chi^2 = 185.23$ ,  $df = 7$ ,  $p < 0.0001$ ) with the percentage of females ranging from 4.1% in *P. longipennis* to 39.5% in *E. traviatum*. However, prevalence did not differ significantly between males (19.6%,  $N = 1343$ ) and females (21.2%,  $N = 269$ ;  $\chi^2 = 0.63$ ,  $df = 1$ ,  $p > 0.05$ ) when species were pooled, and *C. elisa* was the only species that exhibited a significant difference in parasitism rates between the sexes when species were examined individually (females = 52.0% prevalence, males = 21.7% prevalence;  $\chi^2 = 10.24$ ,  $df = 1$ ,  $p < 0.001$ ).

When species with at least 10 captures are compared at each site (Figure 1), *A. fumipennis* had the highest prevalence among the eight most abundant species at Oolenoy (32.7) and Snyder (15.0), *C. fasciata* had the highest prevalence of these species at Ashmore (40.0), Buckhorn (64.4), and Pleasant Ridge (47.1), *E. simplicicollis* had the highest prevalence of these species at Blue Wall Upper (58.3) and Swan (10.0), *L. incesta* had the highest prevalence at Placid (20.0), and *P. longipennis* had the highest prevalence among these species at Blue Wall Lower (21.4), Bunched Arrowhead (41.6), and Scott’s (31.4). Although *A. fumipennis*, *C. elisa*, and *P. longipennis* showed significant variation in prevalence across sites, the other species did not (Figure 1).

Differences in prevalence among species also varied across the sampling periods (“species  $\times$  week  $\times$  mite” effect,  $p = 0.002$ , Table 3); *A. fumipennis* and *E. traviatum* showed significant

Table 3. The number of dragonflies collected and parasitism prevalence (% with mites) compared across (a) 11 sites in the Upstate of South Carolina and (b) the 10 sampling periods, for all dragonflies and the eight most abundant species. When all species were included, there is significant variation in the parasitism rate between sites ( $\chi^2 = 61.735$ ,  $df = 10$ ,  $p < 0.0001$ ), but not between weeks ( $\chi^2 = 7.417$ ,  $df = 9$ ,  $p > 0.05$ ). When only the eight most common species are included, there are significant differences among sites and sampling periods (hierarchical loglinear analyses, Table 4).

Site	All dragonflies			Eight most abundant species		
	N	% with mites		N	% with mites	
a) Site comparison						
Swan	229	8.3	a	173	9.2	a
Placid	208	7.7	ab	124	12.9	ab
Ashmore	233	9.0	ab	140	13.6	ab
Blue Wall Lower	204	14.2	bc	120	17.5	abc
Bunched Arrowhead	219	15.1	bc	102	17.6	abc
Snyders	223	14.8	bc	169	17.8	abc
Blue Wall Upper	211	19.9	cd	133	23.3	cd
Buckhorn	215	21.4	cd	172	23.3	cd
Pleasant Ridge	215	20.5	cd	172	24.4	cd
Scotts	207	22.2	cd	148	25.0	cd
Oolenoy	220	25.9	d	159	31.4	d
b) Sampling period comparison						
Sampling period	All dragonflies			Eight most abundant species		
	N	% with mites		N	% with mites	
1 (14–23 May)	211	15.3	a	109	21.1	ab
2 (26 May–3 June)	217	16.9	a	160	20.6	ab
3 (2–8 June)	200	13.8	a	145	14.5	a
4 (9–15 June)	197	18.6	a	164	23.2	ab
5 (16–22 June)	209	18.4	a	173	23.7	b
6 (24–29 June)	188	19.7	a	177	24.3	b
7 (1–9 July)	199	14.6	a	187	15.5	a
8 (7–20 July)	200	14.9	a	163	20.2	ab
9 (15–25 July)	186	16.2	a	155	20.6	ab
10 (23 July–4 August)	191	13.2	a	179	15.1	a

Note: Values followed by the same letter are not significantly different ( $\chi^2$  tests,  $p = 0.05$ ).

Table 4. Partial  $\chi^2$  values from a hierarchical log-linear analysis, examining how the frequency of mite parasitism varies across species, sites, and sampling periods (“week”). Only the eight most abundant dragonfly species were included ( $n > 100$ ).

Factor	DF	$\chi^2$	p
SPECIES*MITE	7	53.388	0.0001
SITE*MITE	10	46.097	0.0001
WEEK*MITE	9	17.022	0.048
SPECIES*SITE*MITE	70	144.471	0.0001
SPECIES*WEEK*MITE	63	99.465	0.002
SITE*WEEK*MITE	90	155.223	0.0001
SPECIES*SITE*WEEK*MITE	630	211.628	ns

Abbreviation: ns = not significant ( $p > 0.05$ ).

variation in prevalence among weeks, while there were no significant relationships for any of the other species (Figure 2). When weeks with at least 10 captures are compared within each species (Figure 2), *Celithemis elisa* had its greatest prevalence in week 1 (47.6%), *Argia fumipennis* prevalence peaked in week 2 (36.4%), *C. fasciata* peaked in week 4 (62.5%), *I. posita* peaked in week 5 (22.2%), and *L. incesta* and *E. traviatum* peaked in week 6 (31.0% each). Finally, *P. longipennis* experienced its greatest prevalence in week 8 (26.0%).



Table 5. Pearson correlations between parasitism prevalence (the percentage of dragonflies parasitized by water mites) and several measures of species richness, at several taxonomic levels, across 11 water bodies in the Upstate of South Carolina. (N = 11 for all tests unless otherwise noted.)

Taxon	Correlation coefficients		
	Observed richness	S <sub>est</sub>	Chao estimate
Odonata (all species)	0.140 ns	-0.138 ns	-0.208 ns
Parasitized species	-0.029 ns	-0.261 ns	-0.226 ns
Libellulidae	0.160 ns	0.047 ns	0.003 ns
Coenagrionidae	-0.179 ns	-0.024 ns	0.280 ns
<i>Argia fumipennis</i> (n = 9)	-0.352 ns	-0.526 ns	-0.479 ns
<i>Celithemis elisa</i> (n = 10)	-0.027 ns	0.016 ns	0.154 ns
<i>Celithemis fasciata</i> (n = 10)	0.067 ns	-0.067 ns	-0.136 ns
<i>Enallagma traviatum</i> (n = 10)	0.329 ns	0.544 ns	0.698 ns
<i>Erythemis simplicicollis</i>	0.175 ns	-0.070 ns	-0.262 ns
<i>Ischnura posita</i>	0.373 ns	0.204 ns	-0.086 ns
<i>Libellula incesta</i>	0.252 ns	0.308 ns	-0.040 ns
<i>Pachydiplax longipennis</i>	0.439 ns	0.530 ns	0.113 ns

Notes: S<sub>est</sub> = extrapolated richness at 20 samples; Chao estimate = Chao2 bias-corrected estimate of richness (but see Methods for details). One-tailed tests were used to test for negative correlations (dilution effects) between prevalence and richness; ns =  $p > 0.05$ , or a positive relationship).

These eight abundant species were also the only dragonfly hosts that carried resisted mites, indicating some physiological response to parasitism. A significantly higher percentage of *C. fasciata* (26.7%) and *A. fumipennis* (18.4%) individuals carried resisted mites compared to the other six species (all < 6.0%;  $\chi^2 = 136.07$ , df = 7,  $p < 0.001$ ).

### ***Relationships between parasitism, host abundance and host site occupancy***

When all dragonfly species are included, parasite prevalence was strongly positively correlated with host species abundance (number captured; Spearman  $\rho = 0.567$ ,  $n = 58$ ,  $p < 0.0001$ ), and number of sites occupied by a host species (Spearman  $\rho = 0.526$ ,  $n = 58$ ,  $p < 0.0001$ ). When species with at least 10 captures are considered, there were again strong positive relationships with host abundance (Spearman  $\rho = 0.554$ ,  $n = 32$ ,  $p < 0.001$ ) and number of sites occupied by a host species (Spearman  $\rho = 0.449$ ,  $n = 32$ ,  $p < 0.01$ ). However, if only parasitized species are included, there was no relationship between prevalence and either host abundance (Spearman  $\rho = -0.030$ ,  $n = 22$ ,  $p = 0.893$ ) or sites occupied (Spearman  $\rho = -0.082$ ,  $n = 32$ ,  $p = 0.718$ ).

### ***Testing dilution effects***

We tested for negative relationships between parasitism prevalence and host species richness using one-way Pearson correlations (Table 5). There were no significant negative relationships between prevalence and any measure of species richness (observed richness, extrapolated S<sub>est</sub>, or CHAO2 estimated richness) whether we considered all odonate species, parasitized species, or only species in the families Libellulidae or Coenagrionidae (Table 5). Finally, there were no significant negative correlations between parasitism prevalence and any measure of community richness for any of the eight most abundant species (Table 5).

### ***Community similarity and habitat effects***

Dragonfly community structure mapped well onto habitat differences (Figure 3). The odonate community at Bunched Arrowhead – the only site without predatory fish – was different from

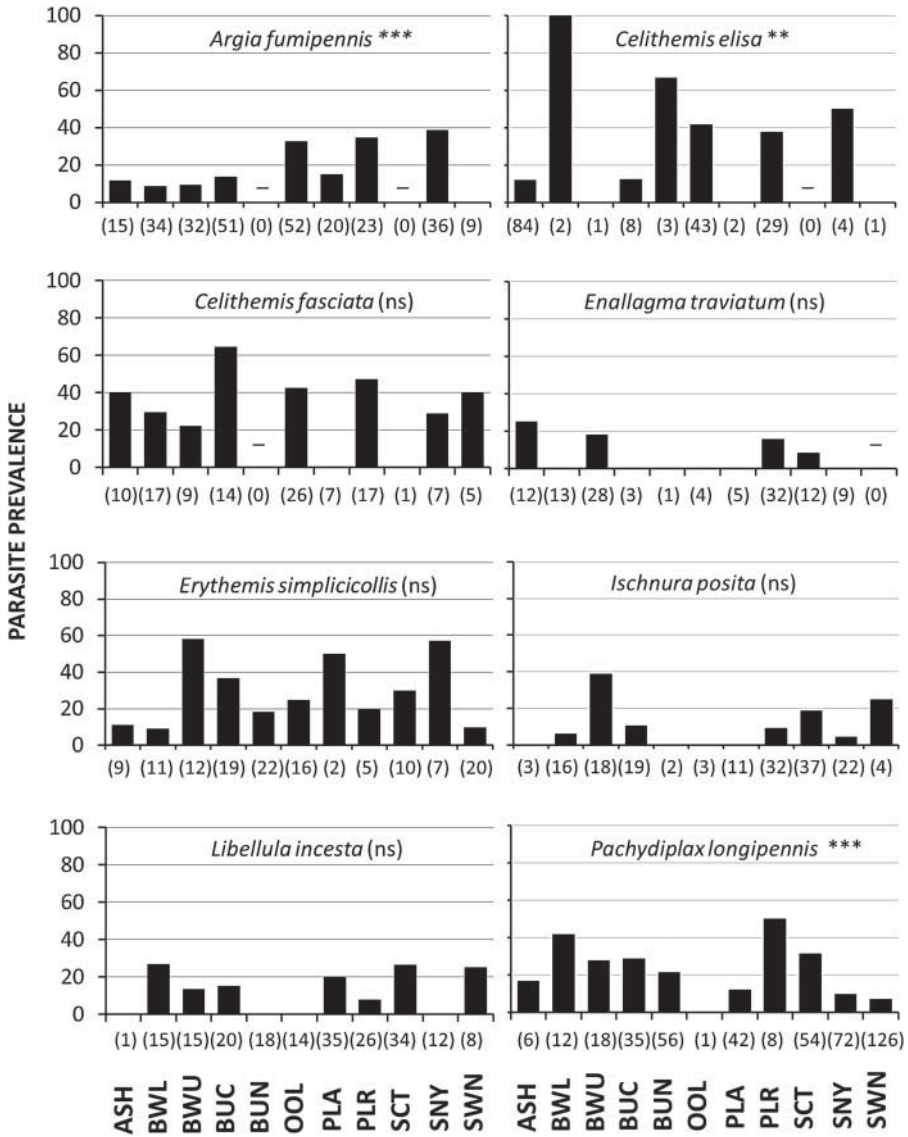


Figure 1. Prevalence of *Arrenurus* spp. parasitism of the eight most abundant odonate species across the 11 sampling sites (ASH = Ashmore, BWL = Blue Wall Lower, BWU = Blue Wall Upper, BUC = Buckhorn, BUN = Bunched Arrowhead, OOL = Oolenoy, PLA = Placid, PLR = Pleasant Ridge, SCT = Scot’s, SNY = Snyder’s, SWN = Swan; number of individuals captured in parentheses; results from  $\chi^2$  tests comparing prevalence rates across sites for each species: \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; ns =  $p > 0.05$ ).

the other 10 assemblages. The remaining communities divided into two clusters corresponding to more pristine sites (Blue Wall, Buckhorn, Pleasant Ridge, Oolenoy, and Ashmore) and more disturbed sites (Snyder, Scott’s, Placid, and Swan). The two Blue Wall sites, which were only 450 m apart, harbored the most similar communities (Figure 3). Swan Lake and Scott’s Pond are only 600 m apart, and with Snyder’s Pond (2.1 km from Swan Lake) form a cluster of similar communities. However, other neighboring sites, such as Lake Buckhorn and Lake Placid (2.25 km apart at Paris Mountain State Park) harbored very different communities (Figure 3). We assessed the relationship between parasite prevalence and intensity and “habitat” by using

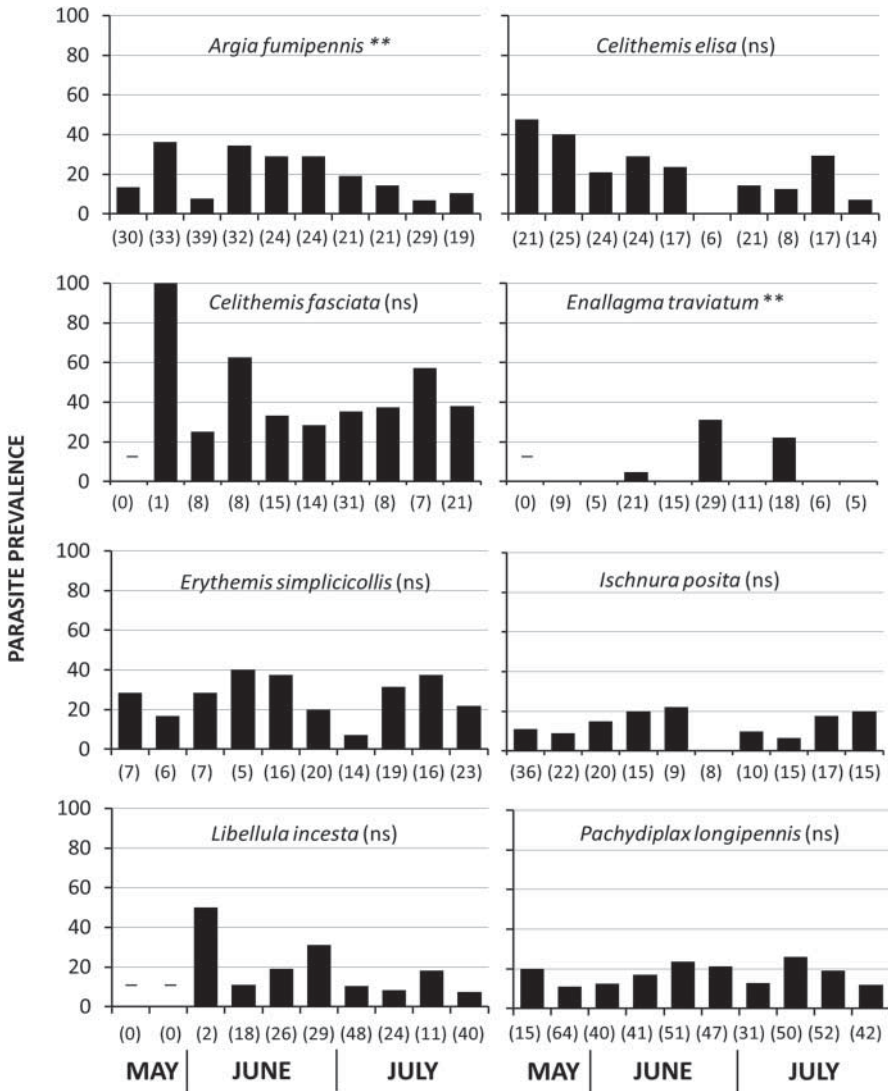


Figure 2. Prevalence of *Arrenurus* spp. parasitism of the eight most abundant odonate species across the 10 sampling periods (number of individuals captured in parentheses; results from  $\chi^2$  tests comparing prevalence rates across periods for each species: \*\* $p < 0.01$ ; ns =  $p > 0.05$ ).

community similarity as a proxy for habitat similarity. We excluded the fishless Bunched Arrowhead site from analyses, as it was the out-group to the other two clusters. When all dragonfly species were included, mean prevalence/site was greater at “pristine sites” ( $18.4 \pm 6.0$ ,  $n = 6$ ) than “disturbed” sites ( $13.1 \pm 7.0$ ,  $n = 4$ ), but not to a statistically significant degree (Student’s  $t = 1.29$ ,  $p = 0.233$ ,  $df = 8$ ). This pattern also held when only parasitized species were included (“pristine” =  $21.7 \pm 5.4$ ,  $n = 6$ ; “disturbed” =  $16.1 \pm 7.3$ ,  $n = 4$ ; Student’s  $t = 1.42$ ,  $p = 0.193$ ,  $df = 8$ ). When sites are pooled within categories and total prevalence is compared among all dragonflies collected, there was a significantly greater prevalence in “pristine” sites (18.4%) than “disturbed” sites (13.1%;  $\chi^2 = 10.555$ ,  $p = 0.001$ ,  $df = 1$ ). This was also true for the subset of parasitized species (“pristine” = 22.1%; “disturbed” = 16.1%;  $\chi^2 = 9.66$ ,  $p = 0.002$ ,  $df = 1$ ). Median parasitism intensity/site was also greater in “pristine” sites (4.5,  $n = 6$ )

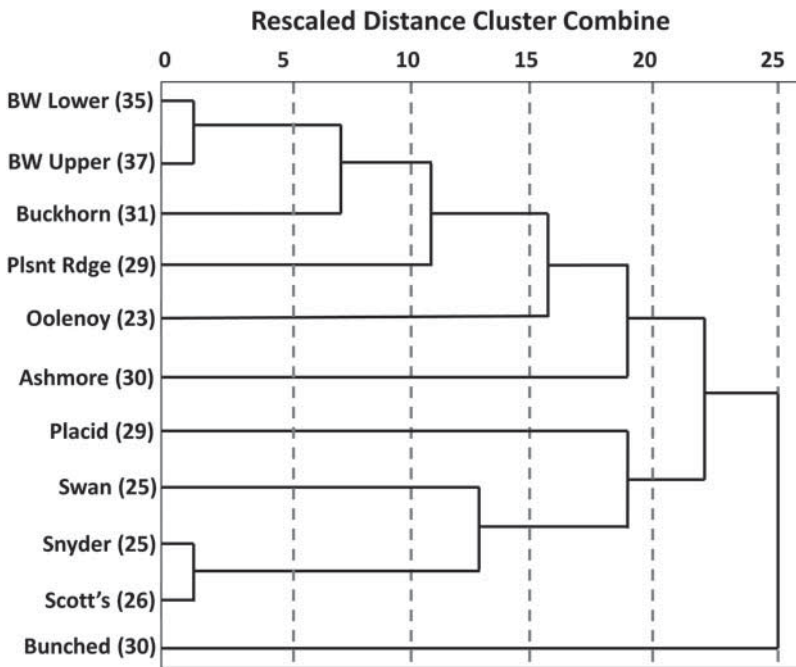


Figure 3. Dendrogram depicting the similarity among odonate communities at 11 sites in Greenville Co. and Pickens Co., SC, USA, produced by a hierarchical clustering analysis using species incidence at each site (species richness in parentheses).

than “disturbed” sites (3.0,  $n = 4$ ), though only to a marginally significant degree (Fisher’s exact test,  $p = 0.076$ ).

### Discussion

The first goal of this survey was to describe the variation in *Arrenurus* parasitism across odonate host species, sites, and time, and test the hypothesis that prevalence correlates with host abundance. Odonate species differed in susceptibility. Even within parasitized families, some species that were well sampled ( $n > 30$ ), like *Perithemis tenera*, *Platthemis lydia*, *Celithemis ornata*, and *Argia moesta* were never found with a mite, while several other well-sampled species such as *Argia fumipennis*, *Celithemis elisa*, *C. fasciata*, and *Erythemis simplicicollis* experienced prevalence rates over 20%. Except for *C. elisa*, males and females were parasitized at similar rates both within species and across the entire sample. So, the significant difference in sex ratios among species is unlikely to be responsible for differences in prevalence among species. And, while not the focus of this study, there were also differences in the frequency of resisted mites among susceptible species, suggesting differential adaptation to parasitism (Forbes et al., 1999). These results confirm that *Arrenurus* mites parasitize dragonflies in the families Coenagrionidae and Libellulidae, and that species have differential susceptibilities to *Arrenurus* parasitism (Forbes et al., 1999, 2002). That is the first condition for a dilution effect.

These patterns among species, however, were not consistent across space and time; species differences in prevalence varied across sites and across time at these scales, as has been shown for *Arrenurus* mites on coenagrionid damselflies (Mlynarek et al., 2014) and gregarine parasites of dragonflies (Locklin & Vodopich, 2010). It is possible that susceptible species are equally sensitive to these generalist mites, and variation is a random function of patchily distributed

mites haphazardly encountering patchily distributed hosts at smaller scales. However, it is also likely that our analysis was too coarse, taxonomically. Although most *Arrenurus* species are generalists, they might not be ecologically equivalent. We assumed that mite species might respond in a diffuse manner, as a community of generalists adapting in parallel to the same range of host species. It is far more likely that mite species have different arrays of suitable hosts, which would complicate and confound patterns pooled across the community. Nevertheless, there was some evidence for a diffuse response by the mite community to a set of shared hosts: parasitism prevalence was significantly correlated with host species abundance, confirming previous studies (Dobson, 1990; Mlynarek et al., 2014; Ostfeld & Keesing, 2000). This relationship held when abundance was measured by number of dragonflies captured (which is biased by ease of capture) or by sites occupied (consistent with Mlynarek et al., 2014). This confirms the second condition for a dilution effect.

The second goal of this study was to test for a dilution effect, in which parasite prevalence declines as host diversity increases (Ostfeld & Keesing, 2000). The three conditions for a dilution effect are met: prevalence varies among hosts, prevalence correlates with host abundance, and host communities have a nested subset structure (Worthen, 2003). However, there was no evidence for a dilution effect; this hypothesis was falsified at several scales of taxonomic and ecological resolution. There were no significant negative relationships between parasitism prevalence and observed species richness, extrapolated species richness (Colwell, 2013), or richness calculated by the CHAO2 estimator (Colwell, 2013), using all dragonfly species or those in the families Libellulidae or Coenagrionidae. Also, because host range is largely undescribed in *Arrenurus* mites, we repeated the analyses with the subset of confirmed hosts – those host species that were parasitized at least once in this survey. Again, there were no significant relationships between parasitism prevalence and any measure of species richness.

Because common species are more likely to be hosts of generalist parasites and thus might be most sensitive to a dilution effect when unsusceptible host species are added to the community, we analyzed relationships between the prevalence on the eight most abundant species and community-level species richness. Again, there were no significant negative relationships between parasitism prevalence and any metric of richness for any of these eight abundant species. None of these common species exhibited a consistent decline in prevalence as other species were added in more diverse communities.

There are several aspects of this study, however, that might obscure a dilution effect. First, species richness is a coarse measure of community diversity. A dilution effect is typically caused by a decline in the relative abundance of preferred hosts; their abundance is diluted by a pool of unsusceptible organisms, making it more difficult for parasites to find them. Richness is completely insensitive to potentially dramatic differences in the relative abundances of common species that occur at all sites. Second, richness is affected by the presence of rare species that, because they are rare, have little effect on the relative abundance of susceptible hosts (whether or not they were susceptible themselves). So, although host species richness is a good predictor of parasitism prevalence in other communities (Swaddle, Calos, & Buckling, 2008), this system might require a more sensitive measure of diversity to discern a pattern.

Another shortcoming of this study is the dearth of knowledge on the actual host range and host-seeking behavior of the water mites themselves. In order to unambiguously determine whether a dilution effect occurs, the analyses should be limited to confirmed hosts. This would include the “susceptible” hosts used by the parasite to complete the life cycle, as well as “unsusceptible” hosts that are parasitized erroneously (the parasite cannot complete development). We attempted to address this issue by testing for dilution effects at several scales of taxonomic resolution, but these may not correspond to the actual host range of the mites.

Finally, it is possible that the sites did not represent independent samples. Migration of adult dragonflies between ponds could skew our measurements in unpredictable ways. If migration

rates are low, we might tally the presence of these migrant adults (making species richness values between neighboring ponds more similar) that were unavailable to local mite populations. This could decouple any relationship between richness and parasitism rates. Or, if migration rates are historically high, two neighboring ponds might contain replicates of the same metacommunity and be parasitized at similar rates. However, the rate of recapture between weekly visits was very low ( $< 1\%$ ) and we never recaptured a marked individual at another site. While it is possible that unmarked teneral migrate between ponds, significant migration would make neighboring communities similar. Of the three pairs of neighboring sites, only the Blue Wall sites were most similar to one another in host communities, and all pairs were significantly different from one another in parasitism prevalence. So, it seems unlikely that neighboring ponds harbor the same communities of odonates and mites.

The third goal of the study was to determine whether parasitism was related to the ecological conditions of the site, using odonate community structure as a proxy. When sites were clustered by the relative incidence of odonate species (and not just total species richness), community similarity related more with ecological conditions than proximity. The fishless Bunched Arrowhead site was most different from the others. It was dominated by large and medium-sized species such as *L. incesta*, *L. cyanea*, *E. simplicicollis* and *P. longipennis*, and was the only site lacking the small libellulid, *P. tenera*. This pattern is typical of fishless ponds, where *P. tenera* abundances plummet as a function of intraguild predation or interspecific competition from larger larvae that are usually suppressed by predatory fish (Morin, 1984). Bunched Arrowhead had fish and *P. tenera* in 2006 (Worthen & Jones, 2007), but it dried completely during subsequent droughts. Without fish, larger species may have excluded *P. tenera* through competition or intraguild predation. The four most disturbed sites formed a distinct cluster, separate from the cluster of more pristine sites. When the prevalence and intensity of parasitism is compared between these clusters, there is suggestive evidence for more pristine sites having higher levels of parasitism than disturbed sites. This is consistent with Lafferty and Kuris (1999) who suggest that, although parasites can be facilitated by environmental stressors that weaken their hosts, they typically respond negatively as a consequence of their own tolerances to these stresses and the negative effect the stresses may have on the population dynamics of their hosts. This is also consistent with Mlynarek, Bert, Peralta-Vázquez, James, and Forbes (2011), who found the prevalence of gregarine parasitism of the damselfly *Ischnura verticalis* was higher in natural wetlands than man-made wetlands and correlated with the proportion of forest cover within 500 m and 1 km of the wetlands.

In conclusion, odonates were parasitized by *Arrenurus* mites to varying degrees, and several species within parasitized families showed either a partial response to parasitism (through melanotic encapsulation) or complete escape (with no individuals parasitized). Parasite prevalence correlated with host abundance, supporting a diffuse community-level response to shared hosts. However, there was no evidence for a dilution effect; there were no significant negative relationships between observed, estimated, or extrapolated odonate species richness and parasitism rate by water mites in the whole odonate community, in susceptible odonate families, among confirmed (parasitized) hosts, or in the most common species. Although a dilution effect may be exhibited by single parasite species on their particular set of hosts, it is not pervasive enough to be observed as a diffuse community response at these scales of community structure or taxonomic analysis.

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