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Friendly competition: evidence for a dilution effect among competitors in a planktonic host–parasite system

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Abstract. The “dilution effect” concept in disease ecology offers the intriguing possibility that clever manipulation of less competent hosts could reduce disease prevalence in populations of more competent hosts. The basic concept is straightforward: host species vary in suitability (competence) for parasites, and disease transmission decreases when there are more incompetent hosts interacting with vectors or removing free-living stages of a parasite. However, host species also often interact with each other in other ecological ways, e.g., as competitors for resources. The net result of these simultaneous, multiple interactions (disease dilution and resource competition) is challenging to predict. Nonetheless, we see the signature of both roles operating concurrently in a planktonic host–parasite system. We document pronounced spatiotemporal variation in the size of epidemics of a virulent fungus (*Metschnikowia bicuspidata*) in Midwestern U.S. lake populations of a dominant crustacean grazer (*Daphnia dentifera*). We show that some of this variation is captured by changes in structure of *Daphnia* assemblages. Lake-years with smaller epidemics were characterized by assemblages dominated by less suitable hosts (“diluters,” *D. pulicaria* and *D. retrocurva*, whose suitabilities were determined in lab experiments and field surveys) at the start of epidemics. Furthermore, within a season, less suitable hosts increased as epidemics declined. These observations are consistent with a dilution effect. However, more detailed time series analysis (using multivariate autoregressive models) of three intensively sampled epidemics show the signature of a likely interaction between dilution and resource competition between these *Daphnia* species. The net outcome of this interaction likely promoted termination of these fungal outbreaks. Should this outcome always arise in “friendly competition” systems where diluting hosts compete with more competent hosts? The answers to this question lie at a frontier of disease ecology.

Key words: *Daphnia*–*Metschnikowia*; dilution effect; disease transmission; host–parasite; lake plankton; multivariate autoregressive (MAR) time series models; resource competition

INTRODUCTION

Interactions of focal hosts with other host species can amplify or diminish (“dilute”) infection prevalence in host populations (Keesing et al. 2006, Hatcher et al. 2007). These outcomes in disease ecology depend critically on the relative competencies of hosts as carriers of parasites. When other host species serve as alternative sources of infection or support higher populations of vectors that transmit disease, disease prevalence can increase in the focal host (Norman et al. 1999, Gilbert et al. 2001, Power and Mitchell 2004, Keesing et al. 2006). For example, spread of the parapox virus among red squirrels was enhanced by the introduction of highly competent gray squirrels in the United Kingdom

(Tompkins et al. 2003). Conversely, the presence or higher relative abundance of less competent host species can diminish infections in the focal host. Dubbed “the dilution effect,” this phenomenon may operate in a variety of vector-borne diseases, such as malaria, tick-borne encephalitis, and West Nile virus—but it has received most attention in studies of Lyme disease (Norman et al. 1999, Dobson et al. 2006, Ostfeld et al. 2006). In the Lyme disease system, small-mammal hosts differ in their competency for the bacterial pathogen; variation in relative densities of these different host species translates into variation in disease prevalence (Ostfeld and Keesing 2000a,b, Schmidt and Ostfeld 2001, Allan et al. 2003, LoGuidice et al. 2003). Of course, this same dilution effect concept could also apply to diseases in which parasites spread via free-living infective propagules (Yahnke et al. 2001, Keesing et al. 2006). When such epidemiology operates, less-competent hosts can clear these propagules before they contact

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highly competent hosts. As a result, disease prevalence should diminish when less competent hosts become more abundant (Holt et al. 2003). In either vector-borne or free-living parasite systems, the dilution mechanism merits attention because it offers the tantalizing possibility that outbreaks in focal hosts could be inhibited with targeted manipulation of populations of less-competent hosts.

Although the dilution effect dangles these intriguing possibilities, disease management based on such assumptions could quickly go astray without accounting for other types of interactions among host species. For instance, less-competent hosts may compete with more-competent hosts; such competition for resources could influence densities of both host species (Grover 1997). This complication could prove quite important because it might enhance or diminish the dilution effect. Competition for resources might reduce density of the competent host below levels required to sustain epidemics (Keesing et al. 2006), thus indirectly helping to control disease. Alternatively, competition could undermine management strategies if parasitism catalyzes competitive displacement of focal hosts by less-competent hosts. Additionally, consumption of resources by competing hosts could modify the interaction of hosts with its parasite. Transmission and virulence of parasites can vary sensitively with the quantity and quality of resources consumed by hosts (Jokela et al. 1999, Bedhomme et al. 2004, Tseng 2004, 2006, Fels 2005, Hall et al. 2007a, b, Ryder et al. 2007; S. R. Hall, J. L. Simonis, R. M. Nisbet, A. J. Tessier, and C. E. Cáceres, *unpublished manuscript*). Since competition and epidemiology may hinge centrally on these resources, the net outcome of competition and dilution could influence disease dynamics in manners that defy a priori prediction.

We argue here that a dilution effect likely operates among different planktonic grazer species that vary in competence for a virulent fungal parasite. However, this system also shows the signature of (likely) competition between “diluters” and classes of the focal host (uninfected and infected). The microcrustacean grazer *Daphnia dentifera* serves as a highly competent (albeit genetically variable) host for the fungal parasite *Metschnikowia bicuspidata* in small freshwater lakes in Michigan, USA (Hall et al. 2005b, 2006, 2007b, Duffy and Sivars-Becker 2007, Duffy and Hall 2008, Duffy et al. 2008). This competent host becomes infected by consuming spores of the fungus that were previously released from dead, infected *Daphnia*; once *Daphnia* become infected, they produce massive numbers of spores that eventually kill the host (Codreanu and Codreanu-Balcescu 1981, Ebert 2005, Hall et al. 2007b). Other species of *Daphnia*, such as *D. pulicaria* and *D. retrocurva*, commonly co-occur and compete with *D. dentifera* for algal food resources (Leibold 1991, Leibold and Tessier 1997) but serve as much less competent hosts, if they become infected at all (as determined by

lab experiments and field observations). These other *Daphnia* species also consume spores while grazing. Therefore, they should act as a sink for the parasite, facilitating a dilution effect (Pulkkinen 2007). In an extensive survey, we found that, among lake-years, higher abundance of *D. pulicaria* and *D. retrocurva* diminished maximal prevalence of the fungal parasite in *D. dentifera* populations. Within a season, increases of these diluters correlated with the decline of epidemics. Both patterns signaled a dilution effect. However, detailed analysis of within-season disease dynamics using multivariate autoregressive models uncovered more to the story: diluters diminished disease but also likely benefited from declines of their competitors (i.e., the competent host) caused by the virulent fungus. Yet, the net result of this “friendly competition” still appeared to lower disease prevalence and to catalyze termination of epidemics.

METHODS

Study system

The various *Daphnia* species in this study typically dominate the planktonic grazing community of the small, thermally stratified kettle lakes common to the upper Midwestern United States (Peters and De Bernardi 1987, Tessier and Woodruff 2002). The focal host, *D. dentifera* (formerly named *D. galeata mendotae*) coexists with the two putative diluters (*D. pulicaria* and *D. retrocurva*). This coexistence is enabled via a variety of mechanisms, including variation in competitive abilities (which depend upon temperature and food quality), predation by fishes and invertebrate *Chaoborus*, and vertical habitat segregation (Threlkeld 1980, Leibold 1991, Hu and Tessier 1995, Gonzáles and Tessier 1997, Leibold and Tessier 1997, Cáceres 1998). All three species are generally nonselective foragers on small algae (1–60 μm). As a result, all can encounter and consume spores of the fungal parasite *Metschnikowia bicuspidata* (length, $47.4 \pm 5.0 \mu\text{m}$ [mean \pm SD]; width, $1.8 \pm 0.1 \mu\text{m}$; $N = 61$) that are dispersed in the water column (Green 1974, Codreanu and Codreanu-Balcescu 1981, Ebert et al. 2000, Hall et al. 2007b). This fungus infects *D. dentifera* by first piercing through the host's gut wall, then multiplying within its hemolymph (Ebert 2005). While reproducing within the host, the fungus virulently reduces host growth and fecundity and eventually kills its host 8–30 days following infection (depending on water temperature and food quantity/quality [Ebert et al. 2000, Hall et al. 2006, Duffy and Hall 2008; S. R. Hall, J. L. Simonis, R. M. Nisbet, A. J. Tessier, and C. E. Cáceres, *unpublished manuscript*]). Once hosts die, spores of the fungus are released into the water column where they can then infect new hosts.

Host competency

We classified competency of hosts using a series of observations and lab-based experiments. We established that *Daphnia dentifera* serves as a competent host for the

fungus with extensive field sampling in these lakes (this study; also Hall et al. 2005b, Cáceres et al. 2006, Duffy and Hall 2008) and laboratory work with clones collected from them (this study; also Duffy and Sivers-Becker 2007, Duffy et al. 2008). To compare this competency to that of other species, we conducted two separate laboratory assays using previously established methods (Hall et al. 2006, Duffy et al. 2008). Briefly, we examined infectivity of one or two clones from each of nine *Daphnia* species (*D. ambigua*, *D. dentifera*, *D. laevis*, *D. mendotae*, *D. parvula*, *D. pulex*, *D. pulicaria*, a *D. pulex-pulicaria* hybrid, *D. retrocurva*); various combinations of these competing species commonly co-occur in more shallow vs. more deep lakes (Tessier and Woodruff 2002). We exposed eight-day-old animals to either 100 or 500 spores/mL for 24 hours (while fed ~1.5 mg/L of algal food, *Ankistrodesmus falcatus*, and reared in 100 mL of filtered lake water at 20°C and a 16 h:8 h day:night cycle; five animals/150 mL glass beaker; eight replicates per individual species or clone). Following exposure, animals were incubated without spores but maintained at high food levels until infection diagnosis could be made (visually at 40× using a dissecting microscope), usually 8–15 days. Such an interval allows ample growth of the fungal parasite within the host; visual diagnosis is then readily made using a microscope because spores pack the hemolymph (see Plate 1 in Hall et al. 2006). We also compared infection prevalence of the fungus in *D. dentifera*, *D. pulicaria*, and *D. retrocurva* during several sampling visits in several lakes (see methods for diagnosis in *Field survey: among lake years and within-season dynamics*).

Then, we demonstrated that *D. pulicaria* removes spores from the water column, and this removal can reduce infection prevalence of the competent host, *D. dentifera*. In the first experiment, we exposed 250 spores/mL of the fungus to a gradient of *D. pulicaria* (0, 2, 4, 6, and 8 animals, each replicated five times; 1.5 mg/L of algae, 100 mL filtered lake water). Following a 24-hour incubation, we stained (with cotton blue) and filtered the remaining spores onto 25 mm diameter membrane filters (Millipore MF, 0.45 µm HA; Millipore, Billerica, Massachusetts, USA) and estimated densities at 400× using a compound microscope. In a separate, but similar, experiment, we first allowed a gradient of *D. pulicaria* (0, 2, 4, 8) to graze both algae (initially 1.5 mg/L) and spores (250 spores/mL) for 24 hours (eight replicates) at 20°C in 100 mL of filtered lake water. Then, we removed the *D. pulicaria*, thoroughly mixed each beaker and took a small subsample (3 mL) from each beaker to estimate remaining algal biomass (measured as chlorophyll *a* using a Phyto PAM fluorimeter; Heinz Walz GmbH, Effeltrich, Germany). This measure quantified consumption of algae by *D. pulicaria*. Then, to the remaining spores and algae in each beaker, we introduced five eight-day-old *D. dentifera*. After a 24-hour exposure, these *D. dentifera*

hosts were placed in fresh water (i.e., no spores, 1.5 mg/L food) and incubated for 10 days until diagnosis.

We tested for differences in host reservoir competence among *Daphnia* species, spore removal, infection prevalence, and chlorophyll *a* using standard ANOVA and regressions in Systat 12 (Systat Software, San Jose, California, USA).

*Field survey: among lake years
and within-season dynamics*

Here, we present data from a broader monitoring program estimating *Metschnikowia* prevalence in lake populations of *Daphnia dentifera* southwestern Michigan (Kalamazoo and Barry Counties, USA; see Cáceres et al. [2006] and Duffy and Hall [2008] for more details on the overall sampling regime). From 2003 to 2006, we sampled each lake every other week during August through October. During 2004, we also intensively sampled epidemics in three of the 18 lakes (Bassett, Bristol, and Warner) every three days, July through October. During each lake visit, we collected separate samples to estimate density of the different *Daphnia* species (preserved samples) and infection prevalence (live samples) using bottom-to-surface net tows (153 µm, 13 cm diameter Wisconsin net).

In the first set of analyses of this data set, we examined relationships between maximal prevalence of infection and composition of *Daphnia* assemblages in six lakes (Bassett, Bristol, Little Mill, Three Lakes II, Warner, Whitford) with both fungal epidemics and substantial populations of two or more of the focal *Daphnia* species. The response variable was the maximum prevalence of infection in *D. dentifera* (see Cáceres et al. 2006). One predictor variable was a “relative host index,” calculated using mean host densities at the start of these epidemics (i.e., the mean of sampling visits before the epidemic started and those before infection reached 5%; for years without epidemics, we used the mean sampling visits for the start of epidemics in other lakes in that year). More specifically, this index was the density of *D. dentifera* (the “good” host) divided by the summed densities of all three *Daphnia* species (*D. dentifera*, *D. pulicaria*, and *D. retrocurva*). Values near 100% corresponded to a *Daphnia* assemblage dominated by the highly competent host, while lower values indicated increasing relative densities of the “diluters.” Additionally, we used absolute densities of either the “diluters” (*D. pulicaria* and *D. retrocurva*) or the competent host as predictor variables. In all cases, we fit maximal prevalence of infection to relative and absolute densities of *Daphnia* using linear and nonlinear regressions; parameters were estimated by minimizing sums-of-squares (Hilborn and Mangel 1997). When using nonlinear models, we computed significance of the regressions with 9999 randomizations and confidence intervals around each parameter estimate using 10 000 bootstraps (Matlab R2007a; MathWorks, Natick, Massachusetts, USA).

In a second set of analyses, we explored in detail the within-season dynamics of disease in the three, intensively sampled lakes. More specifically, we fit multivariate autoregressive (MAR) models to the time series data collected from epidemics in each lake (Ives et al. 2003). The MAR fitting approach allows estimation of parameters that relate density of a host class (uninfected, U , or infected, I) or density of a diluting *Daphnia* competitor (D) at time $t - \tau$ to densities of a class at time t , where τ is a lag in sampling visits to each lake (here, approximately three days between visits). This statistical approach embraces the notion that species influence each other's densities indirectly but in a temporally lagged manner. To illustrate the structure of the model, we can write an equation for the density of (log-transformed) uninfected (U) hosts:

$$U(t) = \alpha_1 + \beta_{11}U(t - \tau) + \beta_{12}I(t - \tau) + \beta_{13}D(t - \tau) + \varepsilon_1(t) \quad (1)$$

where α_i is an intercept, the β_{ij} coefficients relate the effect of uninfected, infected (I), or diluting (D) *Daphnia* at time $t - \tau$ on uninfected hosts at time t , and $\varepsilon_1(t)$ corresponds to normally distributed process error (e.g., environmental variability). Notice that this model closely resembles multiple regression in structure. When equations for $U(t)$ (Eq. 1) and those for $I(t)$ and $D(t)$ are combined and put into matrix form, this model becomes

$$\begin{bmatrix} U(t) \\ I(t) \\ D(t) \end{bmatrix} = \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \end{bmatrix} + \begin{bmatrix} \beta_{11} & \beta_{12} & \beta_{13} \\ \beta_{21} & \beta_{22} & \beta_{23} \\ \beta_{31} & \beta_{32} & \beta_{33} \end{bmatrix} \begin{bmatrix} U(t - \tau) \\ I(t - \tau) \\ D(t - \tau) \end{bmatrix} + \begin{bmatrix} \varepsilon_1(t) \\ \varepsilon_2(t) \\ \varepsilon_3(t) \end{bmatrix} \quad (2)$$

or written even more compactly in matrix/vector form,

$$\mathbf{X}(t) = \mathbf{A} + \mathbf{B}\mathbf{X}(t - \tau) + \mathbf{E}(t) \quad (3)$$

where \mathbf{X} corresponds to a matrix of host densities at a given time, \mathbf{A} is a vector of intercepts, matrix \mathbf{B} contains the slope coefficients, and vector $\mathbf{E}(t)$ has the error terms, i.e., the variation in $\mathbf{X}(t)$ not predicted by the deterministic portion of the model, $\mathbf{A} + \mathbf{B}\mathbf{X}(t - \tau)$. For our purposes here, \mathbf{B} captures the most useful information, except the parameters on the main diagonal (β_{11} , β_{22} , β_{33}), which are autocorrelation coefficients of each species or infection class on itself. Coefficients β_{13} and β_{23} quantify the effect of diluters, at some lagged sampling visit in the past, on uninfected or infected hosts (respectively), β_{31} and β_{32} relate reciprocal effects of these host classes (in the past) on the diluters, β_{12} indicates the influence of past infected hosts on uninfected hosts, and β_{21} relates past uninfected hosts to infected ones. For presentation purposes, we fit these models to standardized data (each time series divided by its standard deviation) to allow comparison of parameters among lakes. In the Appendix, we detail proce-

dures for estimating confidence intervals around each of these beta parameters.

RESULTS

Host competency

The 11 clones of *Daphnia* differed in susceptibility to *Metschnikowia* infections (ANOVA; experiment 1, $F_{6,34} = 35.06$, $P < 0.001$, Fig. 1A; experiment 2, $F_{4,29} = 31.97$, $P < 0.001$, Fig. 1B). Among these, *D. dentifera* and *D. ambigua* were highly susceptible to fungal infection, *D. laevis*, *D. parvula* and *D. pulex* had low prevalence of infection, and the remaining clones were not infected by *Metschnikowia* (Fig. 1A, B). Of these different species, *D. dentifera*, *D. pulicaria*, and *D. retrocurva* together, on average, make up 85% of the cladoceran abundance in our study lakes during epidemics. Among these three species, *D. dentifera* was most susceptible, *D. retrocurva* could be infected but typically to a much lesser extent than *D. dentifera* in the field (Fig. 1C), and *D. pulicaria* was never infected (examination of over 37 000 animals, August through October of 2004–2006). Poor competence of *D. pulicaria* was not explained by avoidance of fungal spores. Spore density declined with increasing *D. pulicaria* densities following 24 hours of grazing (Fig. 1D; regression, $R^2 = 0.95$, $F_{1,23} = 401.67$, $P < 0.001$). Additionally, grazing by *D. pulicaria* also lowered algal food densities before *D. dentifera* were introduced (quadratic regression, $R^2 = 0.95$, $F_{2,29} = 340.2$, $P < 0.001$; Fig. 1E). This simultaneous removal of spores and food translated into lower infection prevalence in *D. dentifera* (linear regression, $R^2 = 0.18$, $F_{1,30} = 6.53$, $P = 0.016$; Fig. 1E). Thus, *D. pulicaria* decreased infection while consuming food resources.

Field survey: among-lake years

We found that maximum prevalence of infection of the fungus among lake-years was associated with variation in the "relative host index" (Fig. 2A; all lakes; nonlinear regression model; $Y = \exp(aX + b) + \varepsilon$; $a = 0.092$ [95% CI = 0.008, 0.21]; $b = -5.00$ [−15.22, 2.57]; $N = 24$; $P = 0.0413$). Epidemics in Little Mill Lake did not seem to follow this pattern closely (for reasons that currently remain unknown to us; Fig. 2A); not surprisingly, then, statistical significance was improved when this lake was omitted from the analyses (Fig. 2A; the same nonlinear regression model: $a = 0.11$ [0.06, 0.22], $b = -6.23$ [−16.06, −2.52]; $N = 20$; $P = 0.0084$). This relative host index declined with natural-log-transformed density of diluters ($R = -0.67$, $P = 0.0003$) but increased with $\ln(\text{density of } D. \text{ dentifera})$ ($R = 0.6508$, $P = 0.0002$). However, maximum prevalence of infection was only influenced by $\ln(\text{density of diluters})$ (linear regression; slope = -5.8 [−11.5, −4.1]; intercept = 65.6 [18.0, 121.3], $R^2 = 0.18$, $N = 24$, $P = 0.044$; without Little Mill, slope = -8.7 [−14.4, −4.1]; intercept = 90.3 [47.0, 145.3], $R^2 = 0.40$, $N = 20$, $P = 0.011$; Fig. 2B). In contrast, $\ln(\text{density of } D. \text{ dentifera})$, the competent host, did not show a significant relationship with maximum

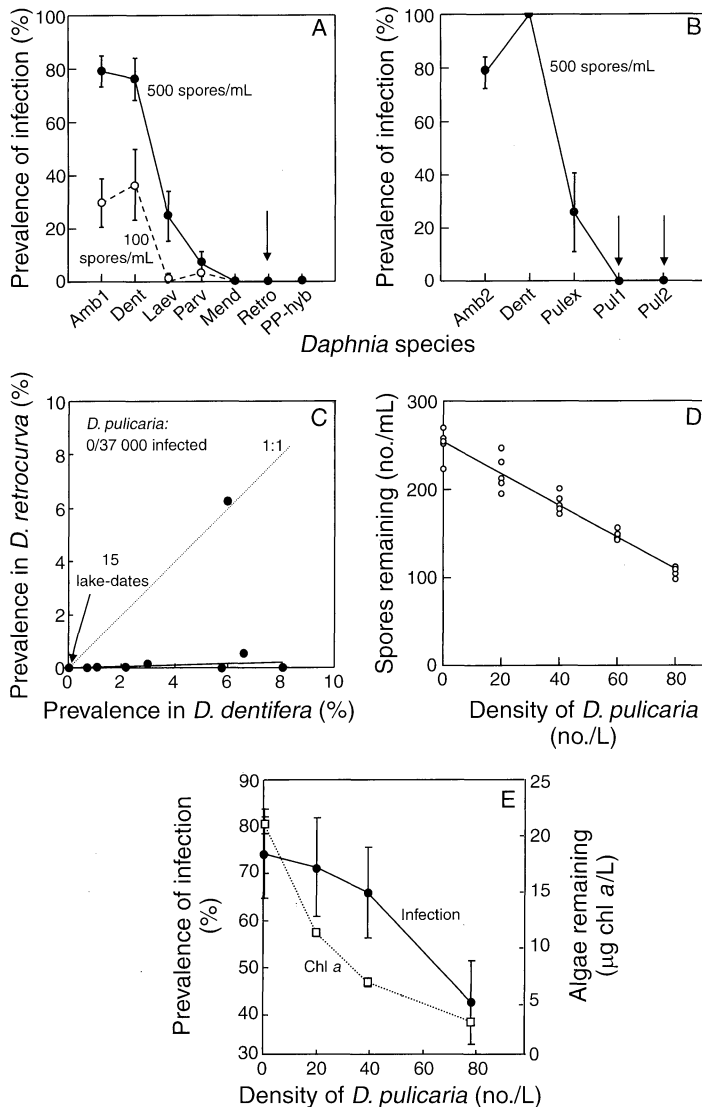


FIG. 1. Comparison of infectivity of various *Daphnia* species and establishment of *D. pulicaria* and *D. retrocurva* as "diluters." (A, B) Two experiments estimated infection prevalence (0–100%) of clones of different *Daphnia* species exposed to either 100 or 500 spores/mL of the fungal parasite *Metschnikowia bicuspidata*. Species codes: Amb1 and Amb2, two clones of *D. ambigua*; Dent, *D. dentifera*; Laev, *D. laevis*; Parv, *D. parvula*; Mend, *D. mendotae*; Retro, *D. retrocurva*; PP-hyb, *D. pulex-pulicaria* hybrid; Pulex, *D. pulex*; Pul1 and Pul2, two clones of *D. pulicaria*. Both *D. pulicaria* and *D. retrocurva* did not become infected (see vertical arrows pointing to these clones). (C). In the field, *D. retrocurva* can become infected, but typically at a much lower prevalence (%) than *D. dentifera*. The one exception involved the point falling along the 1:1 line; on that sampling visit, we had low sample size (two of 30 animals were infected; typically 80 or more animals were diagnosed). Other points fell along a line with regression slope of 0.0265 (i.e., infection prevalence in *D. retrocurva* is typically 2.65% that of *D. dentifera*). On 15 lake-dates, we found no infection in either species, and we do not see infection of *D. retrocurva* when *D. dentifera* remain uninfected. (D). In the lab, spore density declined with increasing density of *D. pulicaria* during a 24-hour grazing experiment. (E). In a separate experiment, prevalence of infection (%) of *D. dentifera* (the competent host) and algal biomass (indexed by chlorophyll *a*) declined with increased density of *D. pulicaria* following 24 hours of grazing/spore consumption by *D. pulicaria*. Thus, the chl *a* data captured grazing by *D. pulicaria*; the infection data involved infection of *D. dentifera* after grazing/spore clearance by *D. pulicaria*. In panels A, B, and E, points are means \pm SE (some small error bars in panel E are hidden by the symbol itself).

prevalence (Fig. 2C; all lakes, $P = 0.14$; without Little Mill Lake, $P = 0.32$). Thus, the nonlinear relationship between relative host density and maximum prevalence of infection among lake years was driven by variation in absolute density diluters, not variation in absolute density of the competent host.

Field survey: within-season dynamics

In each of the focal lakes in 2004, prevalence of the fungus *Metschnikowia* correlated negatively with density of diluting hosts following peak infection (Fig. 3). In Bassett Lake, the fungal epidemic peaked in mid-September; in Bristol Lake, a mid-September peak followed an earlier maximum in late August; and in Warner Lake, peaks occurred in mid September and early October (Fig. 3; see also Cáceres et al. 2006). The decline of prevalence of infection in each epidemic (i.e.,

post-peak or post-secondary peak) correlated negatively with simultaneous increases in densities of the dominant diluter (Fig. 3 shows lag-0 cross correlation coefficients during these periods). Of course, prevalence is a composite metric composed of both infected host density and overall (uninfected plus infected) host density. In Bassett and Bristol, declines in post-peak prevalence were driven by both decreased infected host density (Bassett, $R = 0.79$, $P = 0.001$; Bristol, $R = 0.91$, $P < 0.001$) and increased uninfected density (Bassett, $R = -0.92$, $P < 0.001$; Bristol, $R = -0.5$, $P = 0.05$). In Warner, infected host density did not decrease (Warner, $R = 0.61$, $P > 0.1$), but uninfected density increased (Warner, $R = -0.99$, $P < 0.001$).

Complimentary analyses focused on densities of infection classes and diluters, rather than prevalence of infection, further uncovered links between density of

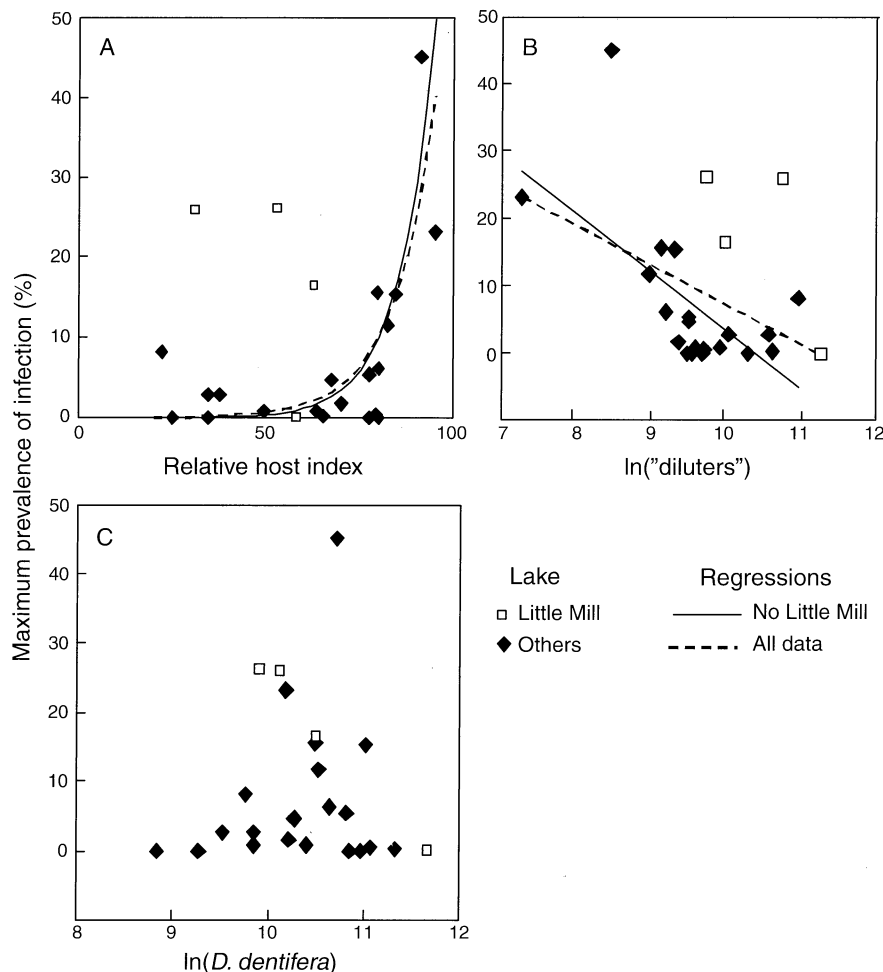


FIG. 2. Diluters as determinants of infection prevalence in six Midwestern U.S. lakes experiencing epidemics of *Metschnikowia bicuspidata*, 2003–2006. Maximum prevalence of infection of the fungus *Metschnikowia* increased in the competent host *D. dentifera* as (A) the *Daphnia* community became relatively more dominated by competent hosts (i.e., relatively more *D. dentifera*) and (B) absolute density of “diluters” (*D. pulicaria* and *D. retrocurva* combined) declined; (C) there was no relationship with absolute density of competent hosts. Each point is a lake-year; open squares denote Little Mill Lake, and closed symbols denote the other five lakes. Dashed lines are regressions using data from all six lakes, and solid lines are the same regressions after Little Mill was omitted.

diluters and that of infected and non-infected host classes. The results of these analyses become central to the “friendly competition” argument. Using the multivariate autoregressive models fit at a lag of four and five sampling visits, MAR(4) and MAR(5), we see first that infected hosts have a negative effect on later densities of uninfected hosts in all three lakes (Fig. 4; see Fig. A1 in the Appendix for time series with model fits at a lag of four visits and Fig. A2 for coefficients estimated at lags 1–5). Thus, the MAR(4) and MAR(5) models captured the virulent effects of this parasite on its host. The lag of four and five sampling visits likely reflects both an observation bias (animals become infected with the fungus before we can visually diagnose them, often 6–12 days depending on water temperature in the field) but also delayed, indirect effects of the resource-based interactions involved. These MAR models at the two lags also revealed a negative effect of diluters on infected

host density (Fig. 4), which is consistent with the results of our lab experiments (Fig. 1E): diluters should decrease density of infected hosts if they remove fungal spores that could otherwise infect the competent host. We also find a positive effect of diluters on uninfected host density (Bassett and Bristol, both lags 4 and 5); this most likely reflects an indirect effect, whereby diluters decrease infected host density, reducing negative virulent effects of infected host density on uninfected host density (via transmission of the parasite). However, the analysis reveals a strong negative effect of uninfected hosts on diluters in all of the lakes (both lags; see also Fig. A3), likely resulting from resource competition. Diluters may benefit from the decline of hosts infected by parasites (early during epidemics); rebounding host populations (as epidemics wane) may indirectly harm diluters. Both factors would produce the negative coefficients detected by the MAR models. A similar

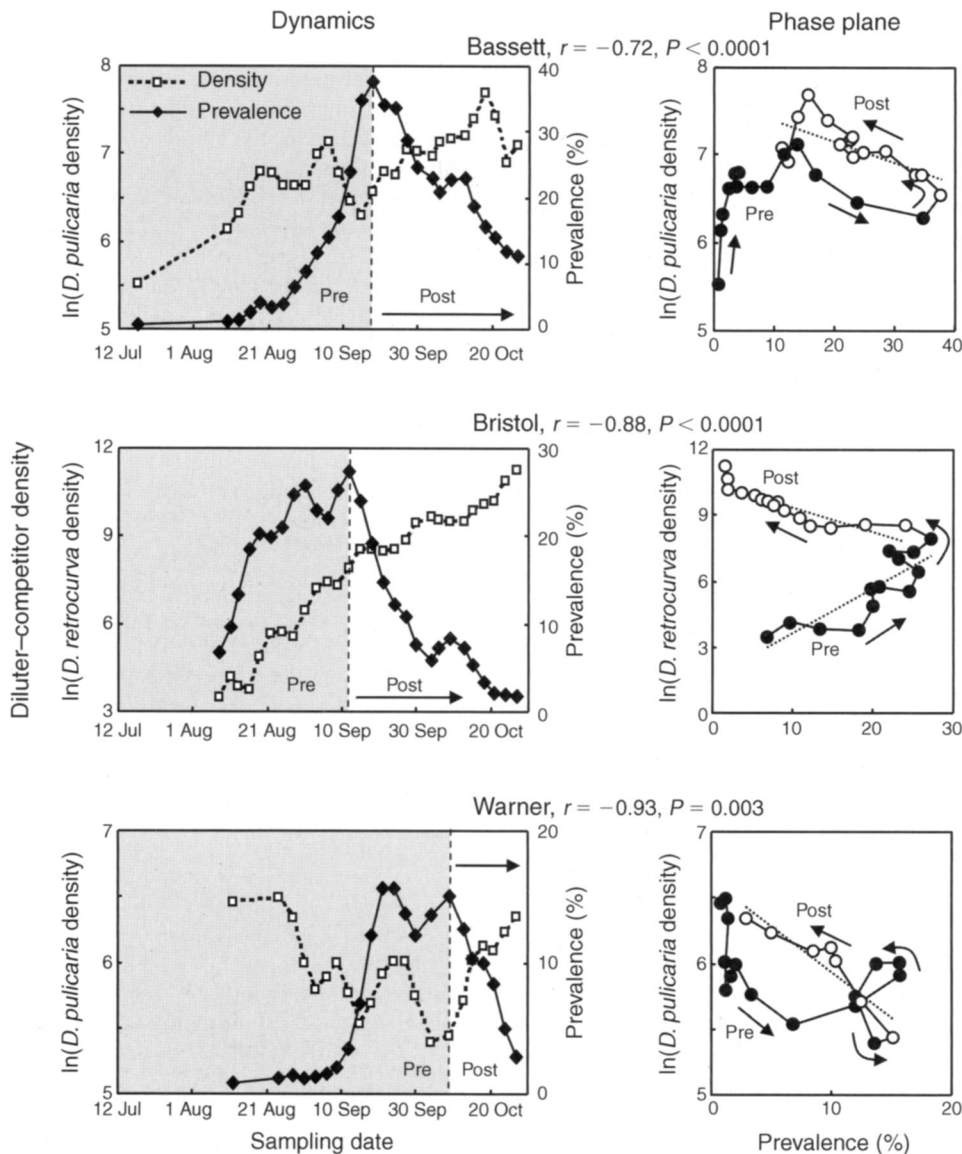


FIG. 3. Time series (dynamics) and phase plane views of large, intensively sampled epidemics of the fungus *Metschnikowia* in three lake populations (Bassett, Bristol, and Warner) of the zooplankton *Daphnia dentifera* in 2004. Data shown include prevalence (proportion) of infection and density (ln-transformed number/m²) of "diluting" *Daphnia*, either *D. pulex* or *D. retrocurva*. The gray section and dashed vertical line separate "pre-peak" dynamics from "post-peak" dynamics. In the "phase plane" plots, we illustrate negative relationships between density of diluters and infection prevalence as each epidemic wanes (relevant points in the "phase plane" plots in open symbols with dotted regression lines to illustrate the focal relationships). In the phase plane plots, arrows point in the direction of time, from earlier (pre-peak, solid symbols) to later dates (post-peak, open symbols).

negative relationship effect of infected hosts on diluters was detected at either lag 4 or 5 in each lake (Fig. 4).

DISCUSSION

The "dilution effect" concept in disease ecology offers a potentially potent option for management of epidemics in wildlife populations. The idea seems simple enough: manipulation of non-competent hosts could reduce prevalence of disease in focal wildlife populations. Disease prevalence should drop in the focal host when non-competent (or less-competent) hosts act as

sinks for the parasite, effectively reducing transmission rate (Van Buskirk and Ostfeld 1995, Norman et al. 1999, Ostfeld and Keesing 2000a, b). However, ecological interactions between various host species are likely not limited to this indirect, parasite-mediated link. For instance, hosts might compete for resources or share predators. These interactions might complicate the dilution effect if they change the density of the focal host (Keesing et al. 2006). It seems possible that resource competitors could diminish disease merely by reducing densities of focal hosts below thresholds required to

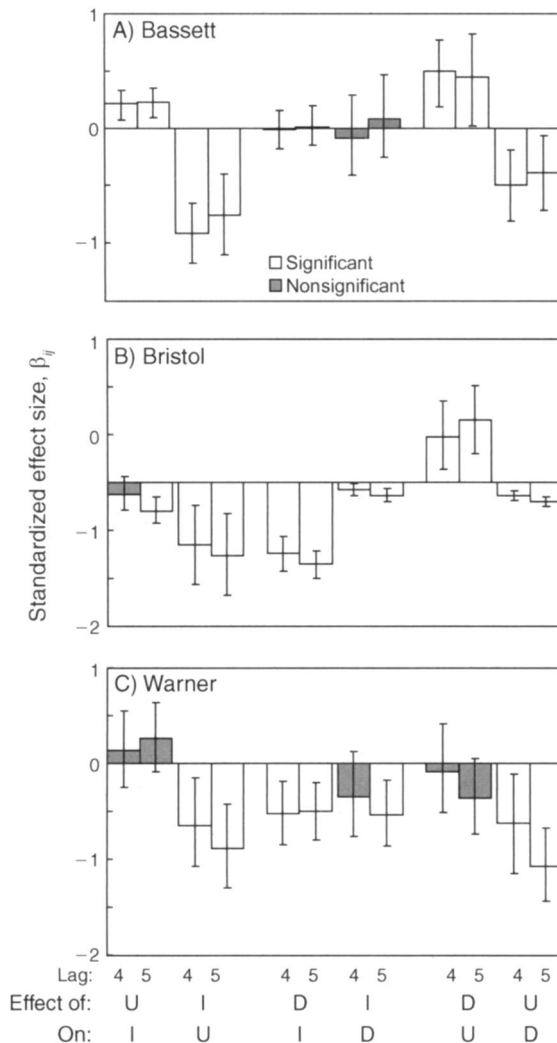


FIG. 4. Results from multivariate autoregressive models fit to time series data of uninfected (U) and infected (I) focal hosts (*Daphnia dentifera*) and diluters (D) (either *D. pulicaria* in Bassett and Warner Lakes or *D. retrocurva* in Bristol Lake) during intensively sampled epidemics of the fungus *Metschnikowia bicuspidata* in 2004. The standardized coefficients (β_{ij}) related current densities of a host class at four or five sampling visits in the past ($\tau = 4$ or $\tau = 5$) to densities of another host class in the present. Error bars represent 95% confidence intervals (10 000 bootstraps); coefficients with 95% confidence intervals that did not overlap zero were deemed "significant" (white), while those that did overlap zero were considered not significant (gray). See the Appendix (Fig. A1) for time series data with model fits.

sustain epidemics (Keesing et al. 2006). Conversely, focal hosts could depress populations of "diluters" and undermine effectiveness of disease management strategies. From our analysis of epidemics, we believe that dynamics of a fungal parasite–*Daphnia* host system is likely built on tension between both dilution and competition, but the net outcome seems to reduce disease prevalence and catalyze the end of epidemics.

Using lab experiments and field observations, we see that species of *Daphnia* can vary greatly in competency for a fungal parasite. Such variation in competency is central to the dilution effect (Ostfeld and Keesing 2000a, b, LoGiudice et al. 2003, Keesing et al. 2006). This variation, in turn, has implications for transmission of *Metschnikowia* to the focal, competent host, *Daphnia dentifera*. First, in the lab and field we see that several species rarely, if ever, become infected with the fungus. This finding complements evidence that susceptibility can vary qualitatively and quantitatively among genotypes of *D. dentifera* in this system (Duffy and Sivers-Becker 2007, Duffy et al. 2008) and in other *Daphnia*–parasite combinations (e.g., Carius et al. 2001, Decaestecker et al. 2003, Wolinska et al. 2004). Of the species tested here, *D. pulicaria* and *D. retrocurva* commonly co-occur with the competent host in the deeper lakes that we study (Gonzales and Tessier 1997, Tessier and Woodruff 2002); *D. pulicaria* in particular seems invulnerable to the fungus, while *D. retrocurva* is a less competent host than *D. dentifera*, a conclusion based most strongly on observations of epidemics in nature. These fairly incompetent hosts also remove infective stages of the parasite, thus providing another key component of the dilution effect (Holt et al. 2003, Keesing et al. 2006, Pulkkinen 2007). This fungus makes spores that closely resemble the hosts' algal food in size and shape (Green 1974) and these spores cannot move to select good hosts and avoid removal by unsuitable hosts (unlike, for instance, trematodes [Hass et al. 1995]). Since *Daphnia* feed nonselectively on particles in this size range (Bern 1990), this spore-clearance phenomenon should be quite general in filter-feeding plankton. Furthermore, as we see here, removal of spores during feeding decreases opportunities for transmission with competent hosts (Holt et al. 2003, Pulkkinen 2007). Thus, the *Daphnia* system contains the requisite components of a potential dilution effect: large variation in host competency and parasite removal by less competent/incompetent hosts.

This system broadly shows the spatiotemporal signature of a dilution effect. Pronounced year-to-year and among-lake variation in *Daphnia* assemblages at the start of epidemics correlated with epidemic size. Some lake-years were dominated by the competent host (*D. dentifera*) while others were more commonly dominated by diluters (*D. pulicaria* and *D. retrocurva*). In general, relative composition of planktonic grazer systems commonly differs among years, due to a variety of factors such as fluctuations in climate, food resources, and predation intensity (Sommer et al. 1986, Bengtsson 1987, DeMott 1989, Tessier and Welser 1991, Cáceres 1998, Tessier and Woodruff 2002). Furthermore, this variability of host composition resembles that in the Lyme disease system, where relative and absolute densities of hosts also vary spatiotemporally (Ostfeld et al. 1996, Jones et al. 1998, Allan et al. 2003). Back in the plankton, this variation in relative composition

helped to explain pronounced variation in epidemic size in these study lakes. More specifically, large fungal outbreaks occurred when “diluters” (*D. retrocurva* and *D. pulicaria*) remained relatively and absolutely rarer at the start of epidemics. More diluters at the beginning of the epidemic ultimately reduced the size of the resulting epidemic. Thus, on a broad spatiotemporal scale, we saw a community composition-epidemic size signature that remained consistent with a planktonic dilution effect.

Analysis of within-season dynamics also supported the dilution effect in this system, and it highlighted important roles for diluters once epidemics start and then ultimately stop. During epidemics, diluters negatively affected infected host density (by removing parasites); subsequently, they indirectly benefited uninfected host density. This positive signal arose because fewer *Daphnia* became infected and because infected hosts produced fewer offspring than healthy ones (Ebert 2005, Hall et al. 2006; S. R. Hall, J. L. Simonis, R. M. Nisbet, A. J. Tessier, and C. E. Cáceres, *unpublished manuscript*). However, our data also showed that the beneficial effects of diluters could be countered or at least influenced by negative interactions between diluters and competent hosts. Diluters increased after uninfected hosts decreased in the past (likely due in part to virulent effects of the parasite on the *D. dentifera* hosts); likewise, diluters decrease when uninfected hosts increased. This component of the story likely involves competition among hosts for shared algal resources, interactions which have been characterized for many years (Leibold 1991, Gonzales and Tessier 1997, Leibold and Tessier 1997). Thus, we have likely observed the net effect of simultaneous resource competition and dilution. What are the long-term, net effects of these interactions? Should they promote termination of epidemics, extinction of the competent host, coexistence of hosts and parasite via stable dynamics, or oscillations among hosts and parasite? Answers to these questions remain unknown without more controlled experiments and development of mathematical models. Such models would push the dilution effect past its current boundaries (Schmidt and Ostfeld 2001, Holt et al. 2003, Keesing et al. 2006) and promote stronger integration of it with more standard resource competition theory (Grover 1997).

The time series analysis suggests that increases in densities of “diluters” contributes to the termination of fungal outbreaks. This result makes intuitive sense, but other factors also operate during the transition from summer (start) to autumn (end) during these epidemics. It is possible that these other factors complicate interpretation of the results from fits of the MAR models. For instance, water temperature declines considerably, and this cooling itself depresses per capita transmission rate (Hall et al. 2006). In conjunction with selective predation from fishes (Duffy et al. 2005, Hall et al. 2005a, Johnson et al. 2006, Duffy and Hall 2008), colder temperatures could also inhibit epidemics (Hall et

al. 2006). Additionally, food conditions elevate considerably during seasonal transitions. Transmission rate diminishes when food resources are good (but spore production elevates [Hall et al. 2007a, b; S. R. Hall, J. L. Simonis, R. M. Nisbet, A. J. Tessier, and C. E. Cáceres, *unpublished manuscript*]; elsewhere, we hypothesize that seasonal changes in food quality/quantity could even squelch the outbreaks intensively documented here (in Bristol, Bassett, and Warner Lakes; Hall et al. 2009). Simultaneously, evolution of resistance to this virulent parasite proceeds rapidly, even within a season (Duffy and Sivars-Becker 2007, Duffy et al. 2008; M. A. Duffy, S. R. Hall, C. E. Cáceres, and A. R. Ives, *unpublished manuscript*). Rapid evolution of resistance (i.e., lower transmission rate) could terminate the epidemics, perhaps involving a within-species dilution effect as well (since less susceptible genotypes also clear spores from the water column). Indeed, all of these factors (thermal physiology, selective predation, rapid evolution, resource quality and transmission, dilution effect) proceed simultaneously and perhaps even interactively (Thomas and Blanford 2003, Mitchell et al. 2005, Duffy and Hall 2008). Thus, the dilution effect is likely only one of several processes contributing to the seasonal demise of epidemics in these systems.

Nevertheless, lab- and field-based evidence point towards a mixed resource competition–dilution effect (which we term “friendly competition”) operating during fungal epidemics in *Daphnia* populations. This system provides the relevant natural history for future experimental work and development of dynamical theory for “friendly competition” in host–parasite systems with free-living infective stages. This type of epidemiology commonly arises in commercially and medically important disease systems (e.g., plant disease, snail–trematode, insect defoliators, virus [Gubbins et al. 2000, Williams and Barker 2001, Fenton et al. 2002, Wobeser 2006]). Such theory, in our view, represents a next step forward in development of community-ecology-of-disease framework (Ostfeld et al. 2008). Arguably, enhancement of mechanistic theory remains essential for deeper and more predictive linkage between species diversity and disease outbreaks in wildlife populations (Holt et al. 2003, Dobson 2004, Keesing et al. 2006).

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APPENDIX

More methods and results (*Ecological Archives* E090-054-A1).