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Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts

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An unappreciated facet of biodiversity is that rich communities and high abundance may foster parasitism. For parasites that sequentially use different host species throughout complex life cycles, parasite diversity and abundance in ‘downstream’ hosts should logically increase with the diversity and abundance of ‘upstream’ hosts (which carry the preceding stages of parasites). Surprisingly, this logical assumption has little empirical support, especially regarding metazoan parasites. Few studies have attempted direct tests of this idea and most have lacked the appropriate scale of investigation. In two different studies, we used time-lapse videography to quantify birds at fine spatial scales, and then related bird communities to larval trematode communities in snail populations sampled at the same small spatial scales. Species richness, species heterogeneity and abundance of final host birds were positively correlated with species richness, species heterogeneity and abundance of trematodes in host snails. Such community-level interactions have rarely been demonstrated and have implications for community theory, epidemiological theory and ecosystem management.

Keywords: diversity; community structure; spatial heterogeneity; recruitment; parasites; *Cerithidea californica*

1. INTRODUCTION

A rafting trip down the Congo will expose you to more parasitic diseases than a float down the Colorado. Although many factors contribute to such regional differences, this is partly an example of how parasitism, the most popular lifestyle on Earth (Price 1980; Thompson 1994; Poulin & Morand 2004), should be fostered by high host diversity and abundance. This makes sense, considering that hosts serve as both habitat and dispersal agents for parasites. For example, when transmission is density dependent, an abundance of hosts should lead to an abundance of parasites. Further, because parasites tend to be host specific, increased species heterogeneity of host communities can facilitate increased species heterogeneity of parasite communities. Species richness, perhaps the key measure of biodiversity, is a function of individual abundance and species heterogeneity, and a high richness of hosts should contribute to a high richness of parasites.

These predictions may be specifically applied to parasites with complex life cycles that sequentially use different host species. The diversity and abundance of infection in ‘downstream’ host species should logically increase with the diversity and abundance of ‘upstream’ host species (upstream hosts carry stages of parasites that subsequently infect downstream hosts; Combes 1991). A good example of this concerns trematode flatworm parasites and their hosts. Because various adult trematodes use different vertebrates as final hosts and trematode offspring infect snails as first intermediate hosts, snails should be at higher risk of infection by more species of trematode where vertebrate hosts are more abundant and

more diverse. Although perfectly logical, these assumptions have little empirical support. Are linkages between hosts so diffuse that spatial patterns break down? Alternatively, have studies lacked the power or the appropriate scale of investigation to reveal existing trends? If patterns are found, then are they general for the link between host diversity and parasitism?

It is a commonly held view that final host distribution governs larval trematode recruitment to snails, particularly regarding systems where the final hosts are birds (e.g. Hoff 1941; Cable 1956; Cort *et al.* 1960; Robson & Williams 1970; Sousa 1993; Keas & Blankespoor 1997; Bustnes & Galaktionov 1999; Marcogliese *et al.* 2001; Skirnisson *et al.* 2004). This is because highly motile, upstream host birds obviously vary in spatial distribution and, consequently, so should infections of larval trematodes in downstream host snails. However, most authors have based these logical assertions on circumstantial information with no data analysis. This is probably because it is difficult to relate the results of bird surveys to data on trematode parasites in snails. Because birds are highly vagile, typical bird surveys are usually performed at large spatial scales, such as several square kilometres (e.g. Ramer *et al.* 1991). On the other hand, since snail hosts are relatively dense and move little, larval trematode communities are usually sampled at much smaller scales (e.g. between 1 and 10 m²). However, as noted by Robson & Williams (1970), fine-scale heterogeneity of birds may be important for the distribution of trematode infections in snails, but the bird community observed over several square kilometres may not reflect the bird community’s use of any single small site within that area. Thus, sampling upstream hosts and parasites in downstream

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hosts at different spatial scales may obscure associations between the two communities.

Here, we report results from two independent observational studies conducted over 2 years in a California coastal wetland. We circumvented the problem of assessing highly vagile birds by using time-lapse videography to document bird use simultaneously at numerous sites at small spatial scales. We then examined the relationship between communities of birds and communities of larval trematodes in snail populations collected at the same spatial scales. This allowed effective tests, with results supporting the hypothesis that host diversity begets parasite diversity.

2. METHODS

(a) *Host-parasite system*

In Californian tidal wetlands, various species of final host birds transmit more than 18 species of larval trematode to their first intermediate host, the California horn snail, *Cerithidea californica* (Haldeman 1840); (Martin 1972). Infections in these abundant snails are long-lived (Kuris 1990; Sousa 1993) and the trematodes continuously asexually produce swimming stages that infect various second intermediate hosts. The trematodes infect and then mature in birds that prey upon infected second intermediate hosts (for a list of known hosts, see Huspeni & Lafferty 2004). Adult trematodes produce eggs and larvae (miracidia) that reach the outside environment with the bird excreta. These eggs and larvae are the trematode stages infective to snails.

(b) *Field sites*

Fieldwork took place in two types of habitat in Carpinteria Salt Marsh (34°24' N, 119°32' W), California, USA. This 93 hectare coastal wetland (1 hectare = 10⁴ m²) has a plain of vegetated salt marsh that is broken up by numerous tidal channels and pans (unvegetated shallow depressions). Birds often forage in channels and pans, and these habitats commonly support populations of first intermediate host snails. We chose six channel sites that have been the subjects of continuing long-term ecological monitoring projects. Channel sites were interspersed throughout the entire wetland; they were situated in different tidal channels and ranged in width from 2.8 to 7.7 m. We selected seven pan sites to ensure interspersed throughout the wetland. The pans varied in area from 34 to 195 m².

Certain environmental factors may affect rates of parasitism in snails and potentially need to be controlled for in analyses. Benthic communities vary with environmental factors such as sediment grain size, sediment organic content and tidal flushing (e.g. Bloom *et al.* 1972; Zedler *et al.* 1992). For channel sites, we measured channel width as a proxy for tidal flushing (which also correlates with sediment grain size; Zedler *et al.* 1992). For pan sites, we determined the sediments' percentage of mass of sand and organic matter. We collected sediment samples by taking 10 regularly interspersed 2.5 cm-wide × 6.5 cm-deep cores, which were frozen until analysis. In the laboratory, the percentage of sand was determined by washing sediments through a 63 µm mesh sieve and the percentage of organic content was quantified by combusting samples at 475 °C for 12 h.

(c) *Birds and time-lapse videography*

Accurately assessing bird communities at small spatial scales is difficult because birds are extremely patchy in space

and time. We therefore used time-lapse videography to quantify birds, using one camouflaged video camera at each plot simultaneously. Each camera was oriented so that a 3 m stretch of habitat filled the top of the field of view. We determined the actual area of the plot visible to the camera using field measurements inputted into IMAGEJ v.1.27 software (W. S. Rasband, US/NIH 2002). Plot areas ranged between 13.2 and 19.6 m² for channels and between 12.2 and 34.4 m² for pans. To capture seasonal variation, we sampled each habitat type throughout one winter month and one spring month (channels in November 2001 and May 2002, and pans from January to February and from April to May 2003). Video cameras sampled during all tidal levels by running 5 s min⁻¹ every minute for up to 12 h d⁻¹. Thus, channel sites were sampled for 346.9 ± 13.4 (± s.d.) h and pans for 268.8 ± 21.8 h. An analysis of this videography technique, including a comparison to typical bird surveys, will be published elsewhere (R. F. Hechinger and K. D. Lafferty, unpublished work). We recorded the presence and species identity of birds by inspecting the video tapes in the laboratory. The bird community at a site was thereby characterized using 20 813 ± 801 (± s.d.) video clips for channels and 16 128 ± 1306 video clips for pans.

(d) *Trematodes in snail populations*

We assessed the trematode communities in snails at the same 13 sites in which we assessed the bird communities. We sampled snail populations from channels during March and April 2002 and from pans in July 2003 using three parallel belt transects composed of adjacent 10 × 50 cm quadrats. We measured, to the nearest 0.1 mm, the length of each snail found in the transects to generate size-frequency distributions. To assess the trematode community at each site, we randomly sampled 100 snails of the most common size class of each habitat type: 20–25 mm snails from channels and 25–30 mm snails from pans. We sampled a narrow size-range from each habitat because trematode species richness and infection abundance increase with snail size (Sousa 1983). We dissected the 1300 snails in the laboratory to quantify trematode infections. We identified trematodes to species following Martin (1972) and T. C. Huspeni & R. F. Hechinger (unpublished work).

(e) *Community measures*

(i) *Abundance*

For each site, we calculated bird abundance as the number of birds observed per square metre per hour. We measured parasite abundance as the mean number of trematode infections per snail (terminology following Bush *et al.* 1997). However, post-recruitment competitive loss can influence larval trematode communities in snails (Kuris 1990; Kuris & Lafferty 1994; Lafferty *et al.* 1994). Thus, the observed abundance of trematode infections will underestimate actual trematode recruitment to snail populations. Therefore, to more accurately estimate recruitment of trematodes, we also calculated 'pre-interactive' abundances of trematodes using the techniques outlined in Lafferty *et al.* (1994).

(ii) *Heterogeneity*

As a measure of local species heterogeneity of birds and trematodes, we used estimates of the 'fundamental biodiversity number' (Hubbell 2001). Hubbell (2001) derived the relationship $S = (1 + \theta) \ln(1 + (J - 1)/\theta)$, where S is species

richness, \mathcal{J} is the number of individuals sampled and θ is the fundamental biodiversity number. Although not universally used as a measure of local species heterogeneity, estimates of θ should serve well in this capacity, since, like Fisher's α and Simpson's index, it increases with the slope of species-individual accumulation curves.

To calculate θ , we used the same general procedure for both bird and trematode communities. First, we generated randomized species accumulation curves (Gotelli & Colwell 2001) for each site by plotting the average number of species observed for various numbers of individual birds or trematodes observed (from one individual up to the maximum sampled for each site). The averages for number of species observed per number of individuals sampled were determined by permuting the data and resampling 100 times for each site. We then generated predicted species accumulation curves using Hubbell's equation. We iteratively solved the value of θ that resulted in the best fit of the curve to the data (the best fit was determined by minimizing the sum of the squared deviations on log-transformed abundance data). One pan site was excluded from the heterogeneity analysis because it had so few birds (five individuals) that it was not possible to obtain a precise estimate for θ .

(iii) Species richness

Species richness may be measured using either observed values or some sort of parametric or non-parametric estimator (Colwell & Coddington 1994; Magurran 2004). Species-richness estimators are based on various assumptions. Even non-parametric estimators assume the existence of relationships between the number of observed rare species and the number of unobserved species. These assumptions may not apply in the same way to bird communities and larval trematode communities in snails. Thus, we decided to use observed species richness rather than a species-richness estimator. However, because observed species richness increases with sampling effort, we standardized our effort when calculating the number of bird and trematode species seen at a site. For birds, since there was variation in the amount of time sites were video sampled, we used the average bird species richness observed in 1000 standard-sized random subsamples of the data for each site. The size of the subsamples was standardized for each habitat type as the amount of time that characterized the site with the smallest amount of sampling (19 983 min for channels and 13 854 min for pans). For trematodes, observed species richness at each site was standardized by counting the number of trematode species found in the standard-sized sample of 100 snails.

(f) Analyses

We investigated all associations using product-moment correlation coefficients (r). We examined the relationships between bird abundance and trematode abundance in snails (using both observed and pre-interactive trematode abundances), between bird species heterogeneity and trematode species heterogeneity, and between bird species richness and trematode species richness in snails.

To determine whether the environmental factors, channel width and sediment character were important variables affecting parasite abundance, we assessed whether there were relationships between trematode abundance and channel width, and between trematode abundance and the percentage of sand and the percentage of organics at pan

sites. In addition, to ensure that our measurements of bird species richness were not confounded by varying sample plot size, we examined the effects of video plot size on observed species richness.

Although we ensured high interspersed sites, spatial autocorrelation could still have resulted in non-independence of the data. Thus, we calculated the exact probability of a site being more similar to its nearest neighbour in the value of a variable than expected by chance (based upon complete enumeration of the similarities between all non-nearest neighbours for the appropriate habitat and measured variable).

We obtained one-tailed p -values for correlations by generating the null distribution of r by randomly permuting the data 100 000 times (Edgington 1995), using the Resampling Stats EXCEL Add-in 2.0 (2001 Resampling Stats, Inc.). When we could not specify the direction of a test *a priori*, two-tailed p -values were similarly generated using $|r|$. Because sampling timing, bird sampling effort and snail size varied between channels and pans, we did not pool channel and pan data. Instead, we analysed each habitat separately and, to assess the overall statistical support for the observed trends, we combined p -values (weighted by sample size) using the 'z-transform' procedure (Strube & Miller 1986; Rice 1990).

3. RESULTS

Bird and trematode abundance varied among sites within both channels and pans and, overall, were significantly positively correlated with each other (respectively, $r=0.69$, $n=6$, $p=0.15$ and $r=0.62$, $n=7$, $p=0.076$; combined $p=0.039$; figure 1). Similar results were obtained when we used estimated pre-interactive trematode abundances ($r=0.72$, $n=6$, $p=0.15$ and $r=0.64$, $n=7$, $p=0.064$, respectively; combined $p=0.034$). These results were not confounded by width of channels or variation in pan sediment character, as there was no relationship between trematode abundance and channel width ($|r|=0.15$, $n=6$, $p=0.81$) or between trematode abundance and the percentage of sand or percentage of organics (respectively, $|r|=0.036$, $n=7$, $p=0.97$ and $|r|=0.050$, $n=7$, $p=0.88$). Moreover, spatial non-independence was not problematic because sites were not more similar to nearest neighbours than non-nearest neighbours in either habitat for bird or trematode abundance measures (all $p>0.05$, mean $p=0.44\pm 0.32$ s.d.).

The species heterogeneity of bird and trematode communities also varied among sites in both studies. Bird species heterogeneity was strongly positively correlated with trematode species heterogeneity in both channels and pans (respectively, $r=0.95$, $n=6$, $p=0.012$ and $r=0.81$, $n=6$, $p=0.029$; combined $p=0.0017$; figure 2). Spatial autocorrelation was not problematic because sites were not more similar to nearest neighbours than non-nearest neighbours for bird or trematode heterogeneity in either habitat (all $p>0.11$, mean $p=0.49\pm 0.31$ s.d.).

The species richness of bird and trematode communities varied among sites in both studies. Bird species richness was strongly positively correlated with trematode species richness in both channels and pans (respectively, $r=0.88$, $n=6$, $p=0.017$ and $r=0.79$, $n=7$, $p=0.021$;

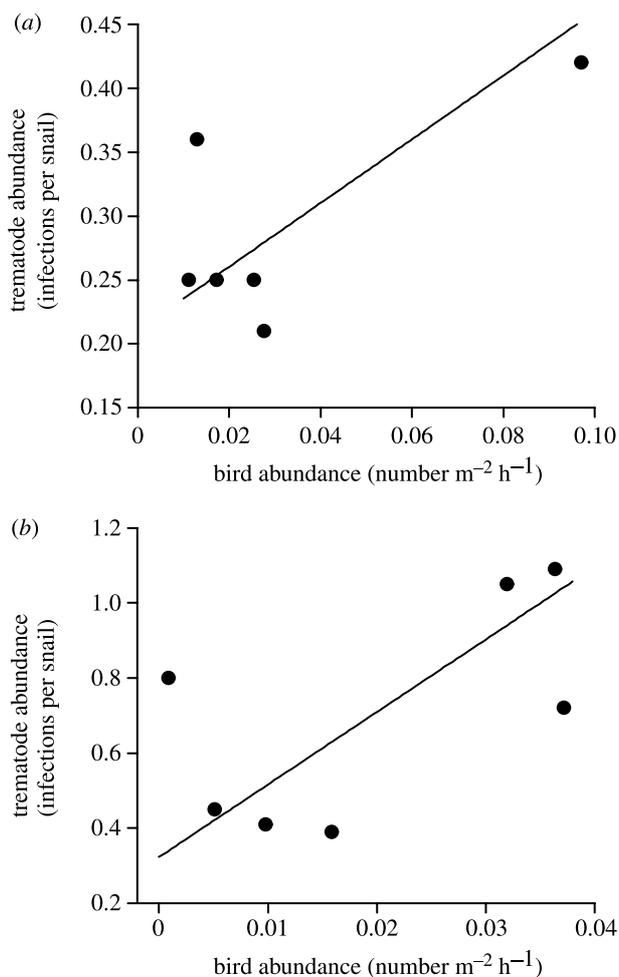


Figure 1. Positive correlations between abundance of trematodes in snail populations (mean number of individual infections per snail) and abundance of birds (number $m^{-2} h^{-1}$) across sites in (a) channels, with 20–25 mm snails and (b) pans, with 25–30 mm snails ($r=0.69$ and $r=0.62$, respectively; combined $p=0.039$). Trend lines are the standard major axes, reflecting the bivariate nature of the data (see Sokal & Rohlf 1981).

combined $p=0.0017$; figure 3). Bird species richness was not confounded by variation in the area of plot sampled in channels or pans (respectively, $|r|=0.45$, $n=6$, $p=0.20$ and $|r|=0.02$, $n=7$, $p=0.52$; combined $p=0.31$). Spatial autocorrelation was not problematic since there was no suggestion that sites were more similar to nearest neighbours than non-nearest neighbours in both habitats regarding observed species richness (all $p>0.16$, mean $p=0.56 \pm 0.23$ s.d.).

4. DISCUSSION

Findings from our two studies support the assumption that the spatial distribution of upstream hosts drives patterns of parasitism in downstream hosts. Host abundance influences parasite abundance, host heterogeneity facilitates parasite heterogeneity, and therefore host species richness begets parasite species richness. To the best of our knowledge, this is the first time that the diversity of an upstream host community has been shown to be associated with the diversity of parasites in a downstream host population.

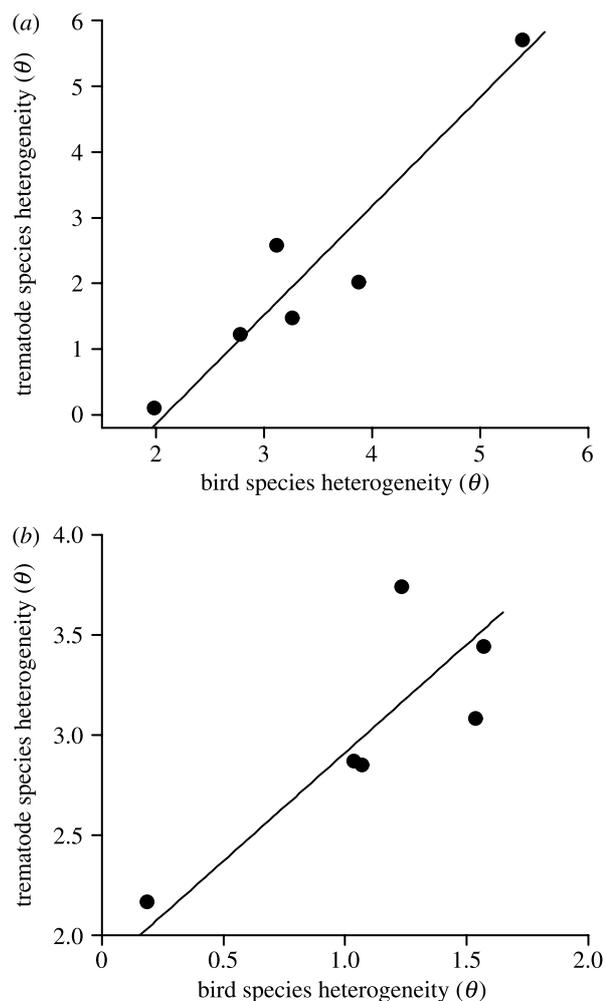


Figure 2. Positive correlations between species heterogeneity (θ) of trematodes in snail populations and species heterogeneity of birds, across sites in (a) channels, with 20–25 mm snails, and (b) pans, with 25–30 mm snails ($r=0.95$ and $r=0.81$, respectively; combined $p=0.0017$). Trend lines are the standard major axes, reflecting the bivariate nature of the data (see Sokal & Rohlf 1981).

Only two previous studies have explicitly examined the relationship between bird communities and larval trematode communities in snails, yielding mixed results. Kube *et al.* (2002) characterized the bird use of an area by surveying birds over 5–10 km², while characterizing the snail trematode community in a restricted area by using 'a few sweeps of a dip net'. The disparity between the scale of sampling for birds and snail hosts may explain why they found no association between bird abundance and trematodes in snails. Disparity in sampling scale may also explain why Latham & Poulin (2003) found only weak evidence for an association between final host birds and larval parasites in crabs (studying operationally similar acanthocephalan parasites). In the other previous study explicitly examining the relationship between birds and trematodes in snails, Smith (2001) sampled birds and larval trematodes in snails at the same spatial scale. She tackled the problem of quantifying vagile birds at small spatial scales by sampling replicated sites of varying numbers of naturally occurring bird perches. She found a positive association between bird abundance and trematode

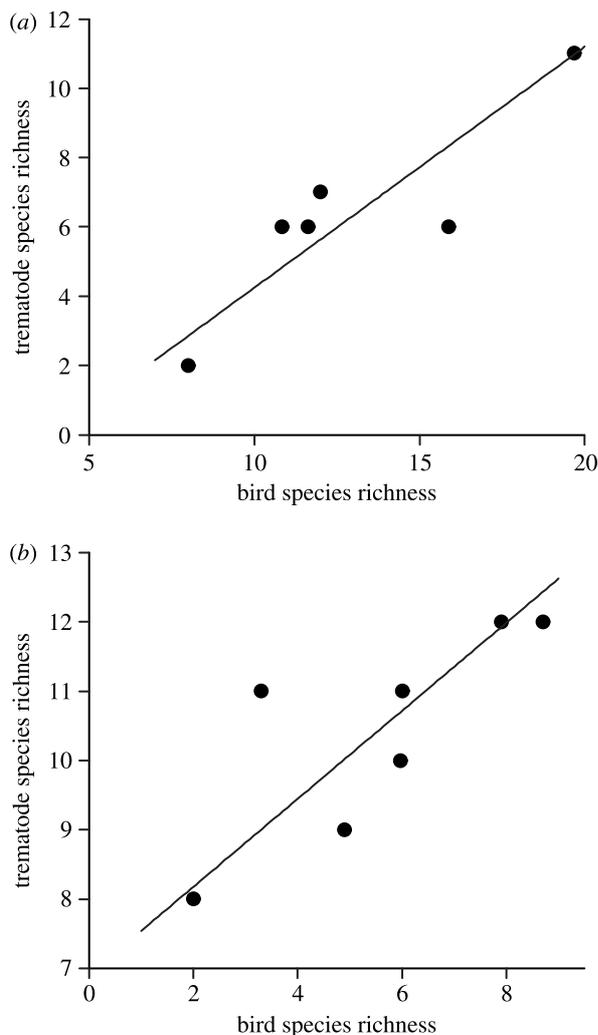


Figure 3. Positive correlations between species richness of trematodes in snail populations and species richness of birds, across sites in (a) channels, with 20–25 mm snails, and (b) pans, with 25–30 mm snails ($r=0.88$ and $r=0.79$, respectively; combined $p=0.0017$). Trend lines are the standard major axes, reflecting the bivariate nature of the data (see Sokal & Rohlf 1981).

prevalence in snails. However, she did not investigate associations between bird diversity and trematode diversity.

We were able to uncover relationships between the diversity and abundance of upstream host birds and larval parasites in downstream host snails by using time-lapse videography to sample the two communities at the same spatial scale. The associations between bird communities and parasite communities in snails were consistently in the same direction in both habitats sampled. The interesting outlier data point driving the positive correlation between channel bird abundance and trematode abundance in snails (figure 1a) occurs exactly where predicted. That is, the channel site that had by far the greatest bird abundance also had the greatest trematode abundance in snails. When such outliers occur, the best solution is to gather more data or do another study. This is what we did by studying pans, yielding results that further bolstered the hypothesis of a positive association between bird abundance and trematode abundance in snails (figure 1b).

Although we assessed the potential influence of some environmental conditions, some unmeasured factors may

have affected spatial variation of parasitism in our systems. For example, temperature stress, ultraviolet radiation and pollution may affect trematode survival and ability to infect snails (reviewed by Pietrock & Marcogliese 2003). It is possible that these stresses varied between sites. However, our analysis demonstrated that nearest-neighbour sites were not more similar to one another than expected by chance. Thus, we feel that it is problematic to assume that birds—the known sources of trematode stages infectious to snails—were truly unrelated to trematode communities in snails, and that some potential unknown environmental effect on parasitism spuriously covaried with bird abundance, heterogeneity and species richness.

Another possible explanation for residual variation in our results could be nocturnal final hosts, which were not adequately sampled with our videography technique. However, in our study system, there are primarily only two potential nocturnal final hosts: black-crowned night herons (*Nycticorax nycticorax*) and racoons (*Procyon lotor*). Racoons are almost certainly not important for our study because they defecate in only a few localized latrine areas (see Lafferty & Dunham in press) and none of these was present at our study sites.

The flip side of the relationships we studied should also occur. That is, birds as downstream hosts should be more frequently infected by more types of trematodes in areas where prey are more abundant and diverse. This is because many prey are upstream hosts for trematodes that are trophically transmitted to birds. Transmission to birds will often be more efficient in areas with greater prey (second intermediate host) density. Furthermore, since trematode parasites differ in what host species they use, areas with more types of prey should support a greater diversity of trematodes. Indeed, there is some evidence that hosts with a more diverse diet are parasitized by more species of parasite (see review in Combes 2001). This may explain why communities of trematodes in gulls appear to be more similar in wetlands that share certain physical and biological characteristics (Simkova *et al.* 2003).

Further consideration of our findings illustrates that the distribution of an upstream host community can not only drive parasite community structure in downstream hosts, but can also be indirectly responsible for the distribution of varied and profound impacts of parasitism on several downstream host communities. It is generally recognized that species may significantly affect one another via indirect interactions, such as ‘apparent competition’ (Holt 1977) and ‘parasite mediation’ (Price *et al.* 1986). Our work demonstrates that bird communities indirectly impact apparently unassociated snail populations by driving levels of trematode parasitism in snails. Trematode parasitism can strongly affect the ecological and evolutionary dynamics of snail populations since trematodes castrate and can increase mortality in snail first intermediate hosts (Kuris 1973; Sousa 1983; Lively 1987; Sousa & Gleason 1989; Lafferty 1993a,b). Moreover, birds may also indirectly affect fishes and benthic invertebrates because trematodes may also strongly impact these second intermediate hosts; for example, by greatly increasing the rate of predation on infected individuals (e.g. Lafferty & Morris 1996).

Spatial variation in infection caused by the distribution of upstream hosts may also be extremely important for post-recruitment dynamics in parasite communities.

For instance, spatial heterogeneity of trematode infection often increases competitive interactions between trematode species in snails (Kuris & Lafferty 1994). Lafferty *et al.* (1994) demonstrated that such intensification of interspecific competition is an important factor affecting parasite community structure in Carpinteria Salt Marsh. Our findings indicate that uneven use of the wetland ecosystem by birds drives the spatial heterogeneity in infection that causes this intensification of interspecific competition. Indeed, at our study sites, bird abundance and species richness both positively and significantly correlated with the proportion of trematodes lost to interspecific competition in snail populations (R. F. Hechinger and K. D. Lafferty, unpublished data).

Our results also strongly support exploring the use of trematode parasites as biomonitoring tools. Trematode communities in snails are common throughout the world (Yamaguti 1975; Kuris & Lafferty 1994; Poulin & Mouritsen 2003), and are easy to assess (Huspeni *et al.* 2005). If trematodes reflect the diversity and dynamics of surrounding free-living communities, then they may be extremely useful indicators of ecological condition. Huspeni & Lafferty (2004) recently used trematode communities in California horn snails to evaluate the ecological effects of a wetland restoration project. They found that trematode abundance and species richness increased after the restoration and suggested that this occurred because greater numbers of bird individuals and species used the wetland following the restoration. Our findings support this assertion. Further, we recently found correlations between the diversity and abundance of benthic invertebrates and trematodes in snail populations (R. F. Hechinger, K. D. Lafferty, T. C. Huspeni, A. J. Brooks and A. M. Kuris, unpublished work). We expected this primarily because birds prey upon benthic invertebrates, and areas with greater diversity and abundance of benthos should attract a greater diversity and abundance of birds, which subsequently bring a greater diversity and abundance of trematode stages infectious to snails (as documented in this paper). As an indication of their value as biomonitoring tools, in our study, trematode communities were much less time-consuming to assess than were birds; collecting and processing trematode data averaged 4.6 person h site⁻¹, whereas collecting and processing bird data averaged 53.2 person h site⁻¹. We are currently performing a full quantitative analysis of the cost-effectiveness of using trematodes as bioindicators compared with alternative methods of assessing ecosystem diversity.

At first sight, our finding that host diversity begets parasite diversity might seem to contradict results from research on a tick-transmitted disease. In the eastern United States, the risk of human exposure to Lyme disease decreases with increasing species richness of small mammals (e.g. see Ostfeld & Keesing 2000). Ixodid ticks vector Lyme disease (a spirochaete bacterium) to humans only after first becoming infected by feeding on a competent reservoir host. Since the bacterium thrives in only a few host species, greater mammal richness increases the proportion of incompetent hosts that ticks feed on. This lowers the prevalence of the bacterium in ticks, which decreases the abundance of Lyme disease in humans. However, increasing the diversity of competent hosts (e.g. ground-nesting birds) apparently increases the abundance

of Lyme disease (Ostfeld & Keesing 2000). Of course, increasing the diversity of any type of host will increase the diversity of parasites in general (although the abundance of a particular pathogen may decrease). In other words, there is no contradiction between what might superficially appear to be opposite findings.

5. CONCLUSION

Our work demonstrates consistent, positive and significant associations between final host bird communities and trematode communities in intermediate host snail populations. Such a link is expected because upstream host birds are the source of trematode eggs and larvae, which infect downstream host snails. Our work, along with that of Smith (2001), shows that abundant host bird communities drive recruitment of abundant larval trematode communities in host snails. We further demonstrate that species heterogeneity of bird communities leads to heterogeneity of parasite communities in snails. High abundance and heterogeneity increase species richness, and this explains our findings that species-rich bird communities are associated with species-rich trematode communities. Thus, our work demonstrates, for the first time to our knowledge, that diverse upstream host communities can drive the development of diverse parasite communities in downstream host populations.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.