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Article submission

## A strong colonizer rules the trematode guild in an intertidal snail host

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## Abstract

We examined the extent to which supply-side, niche, and competition theories and concepts help explain a trematode community in which one species comprises 87% of the trematode individuals, and the remaining 15 species each have < 3%. We collected and dissected the common and wide-ranging snail host *Heleobia australis* over four seasons from three distinct habitats from the intertidal area of the Bahía Blanca estuary, Argentina. Inside a snail, trematodes interact with each other with outcomes that depend on facilitation, competition and preemption, suggesting that dominant species should be common. The abundant trematode species, *Microphallus simillimus*, is a weak competitor, but has life-history traits and strategies associated with higher colonization ability that could increase its probability of invading the host first, allowing it to preempt the rare species. Rather than segregate by habitat, trematode species aggregated in pans during the summer where dominant trematode species often excluded subordinate ones. Despite losses to competition, and a lack of niche partitioning, *M. simillimus*, ruled this species-rich trematode guild through strong recruitment and (potentially) preemption. Therefore, extremely skewed species abundance distributions, like this one, can derive from extremely skewed colonization abilities.

**Key words:** competition; preemption; spatio-temporal heterogeneity; parasitic castrators; *Heleobia australis*; Cochliopidae; Bahía Blanca estuary, Argentina.

## Introduction

Community ecologists have long pondered why a few species are common whereas many are rare (Tilman 1982). An obvious explanation is that species are adapted to specific sets of conditions and a skewed species abundance follows from skewed niche opportunities in the environment. Competitive differences can further shape relative abundances to favor

dominant species where species niches overlap. On the other hand, if recruitment rates help determine carrying capacity, then relative recruitment rates could shape relative abundances through a variable input of new individuals that determines the local adult density, a process linked to supply-side ecology (Lewin 1986). Furthermore, a strong competition-colonization tradeoff might lead to subordinate species being more abundant than dominant species (Tilman 1994). But species differences are not needed to drive abundance differences. Skewed species abundance can result among identical interacting species if recruitment is stochastic, space is limited, and colonists can hold their space through preemption (Warner and Chesson 1985, Hubbell 2001). Hypotheses for explaining species abundance distributions can be tested using parasite communities, because hosts and host populations are natural replicates that define a community (Esch et al. 1990). For example, as for most free-living communities, parasite component communities in fish hosts have a few common species and many rare species, with the ratio of the two most common species ranging from 1 to 18 (Poulin et al. 2008). Because parasite communities violate important neutral model assumptions (Poulin 2004), parasitologists have focused on explanations involving species differences. Here, we estimate the extent to which niche differences, species interactions and recruitment variability structure a highly skewed trematode component community in a snail host.

Species interactions often structure trematode communities within a snail, because trematodes sharing the same snail host interact intensely through intraguild predation (Kuris and Lafferty 1994). Here, dominant trematodes (*e. g.*, species with mouthparts) exclude subordinate ones (*e. g.*, species without mouthparts; Lie et al. 1968, Lie 1969, 1973, Lim and Heyneman 1972, Combes 1982) within a snail host, yet diverse trematode component communities are not uncommon within a local snail population, despite competitive

displacement. Given that trematode infracommunities within a snail are species poor, one hypothesis for how species-rich trematode component communities develop in snail host populations, is niche differentiation. Specifically, trematode distributions are driven by definitive host distributions and abundances, which might differ by habitat and season (Smith 2001, Hechinger and Lafferty 2005), so that competing trematode species might be isolated in space or time (Fernandez and Esch 1991), which can be interpreted as a form of species sorting. Another hypothesis (mutually non-exclusive) is that subordinates can also persist in the snail population if they recruit in periods that are unfavorable for dominant species, the so-called Storage Effect (Warner and Chesson 1985, Chesson 2000). For instance, seasonal increases in recruitment at other life stages (e.g. increased input of trematode eggs due to the arrival infected migratory birds) can increase the prevalence of trematode species within the snail host (Hechinger and Lafferty 2005).

Alternatively, it could be that inferior competitors have high recruitment rates due to a colonization-competition tradeoff. A tradeoff between competitive ability and colonization, where the most subordinate species colonize faster uninfected snails than dominant species do, has been hypothesized for many systems (Munday et al. 2001, Levine and Rees 2002, Coomes and Grubb 2003, Cadotte et al. 2006, Cadotte 2007) and demonstrated in trematode communities (Mordecai et al. 2016). Subordinate trematode species could be favored by a higher transmission rate from birds to snails, compared to the other trematodes. Indeed, some subordinate species (*e. g.*, the most common genus in our study, *Microphallus*) have life-history traits that enhance transmission success in highly fluctuating environments: (1) low specificity for snail-eating birds, (2) abbreviated life cycle (the same snail host can serve as the first and second-intermediate host; metacercariae encyst within the sporocyst in the infected snail), (3) rapid adult worm maturation with extensive first-intermediate host

exploitation (Skirnisson et al. 2004, Galaktionov and Skirnisson 2007, Galaktionov et al. 2012). The large exploitation of the snail host enables these subordinate species to produce thousands of small-bodied infective larvae that occupy the entire gonad and most of digestive gland of the snail host compared to (co)dominant species—that, in contrast, have larger infective larvae concentrated in the gonadal tissue (K. Galaktionov *personal communication*; May 17, 2015). This pattern is consistent with the competition-colonization tradeoff; dominant competitors use resources more conservatively than do weak competitors that are strong colonizers (Cadotte et al. 2006). For instance, dominant competitor parasites have strategies that should reduce host death to keep producing large-bodied infective stages (*i.e.* they invest less in fecundity) and also morphs that can outcompete smaller-bodied species by ingestion (*i.e.* the formation of a non-reproductive soldier caste that is specialized for encountering, recognizing, and killing invaders; Hechinger et al. 2011). By contrast, subordinate species might invest more in reproduction within the snail (as an adaptive response for those species with a greater chance of being killed by dominants) and have longer-lived eggs (as an adaptive response to increase arrival and survival) (Mordecai et al. 2016).

A final way that subordinates might persist is through preemption, in which a seemingly subordinate species can somehow hold its own against invading trematode species. Specifically, preemption should reduce the prevalence of other species by roughly half the prevalence of the preempting species (Lafferty et al. 1994). For instance, a preempting species that reaches 30% prevalence at a site should reduce the prevalence of other species to 0.85 times their recruitment rate at that site. Even if strong recruitment heterogeneity intensifies interactions among trematode species, preemption would reduce the prevalence of other species to a minimum of half their recruitment rates (Lafferty et al. 1994).

For our study, we collected and dissected the snail *Heleobia australis* (Cochliopidae) over four seasons from three distinct habitats from the intertidal area of the Bahía Blanca estuary, Argentina. *Heleobia australis* has a wide geographic range (from Brazil: 22° 54' S, to Argentina: 40° 84' S; De Francesco and Isla 2003) and is common in the estuaries and coastal lagoons where it hosts 18 larval trematode species. Alda and Martorelli (2014) reported 15 of these from the Bahía Blanca estuary (Argentina), and found that all but one are parasitic castrators, with an individual worm eventually filling up the digestive gland and gonad of the snail host (increasing the potential for competition). The overall infection prevalence in this host population is 28% but a seemingly subordinate species, *Microphallus simillimus* (Microphallidae), makes up 86% of the infections—with the rest of the species presumably (co)dominant to *M. simillimus* being less than 1% of the infections (Alda and Martorelli 2014). As a result, with a first to second species ratio of 30, this community is far more skewed than any parasite community studied (*e.g.* Poulin et al. 2008). We first considered the extent to which competition between species within snails could explain this skewed distribution. Finding little evidence for a competition effect on community structure, we investigated the hypothesis that the high skewness results from niche differences that isolate competitors in time or space. Given that niche differences had the opposite effect, we then evaluated whether preemption might explain the high *Microphallus simillimus* prevalence. With little evidence for competition or niche differences, we conclude that frequent colonization by *Microphallus simillimus* drives the highly skewed species abundance distribution in this community, especially if this subordinate is able to fend off dominant species through preemption.

## Material and Methods

### Study area

This study was conducted in the Villa del Mar saltmarsh-mudflat located in the middle reaches of the Bahía Blanca estuary, Argentina (38° 51' S – 62° 07' W). The tidal flats are affected by strong semidiurnal tides and high seasonal variation (Perillo et al. 2001). In general, the substrate is composed of a mixture of 87% mud and 13% sand and is partly covered by cordgrass (*Spartina alterniflora*; Pratolongo et al. 2010). We sampled three distinct habitats: (i) marshes, (ii) flats, and (iii) pans. Marshes are covered by cordgrass and the sediment is silt-sand with little organic content. Flats are free of vegetation, drain at low tide, and have clay sediment that is rich in organics. Pans are like flats, but remain covered by water during low tide. These distinct habitats create the potential for niche differences in this system.

### Field sampling and laboratory procedure

We sampled individuals of the intertidal mud snail *H. australis* in Summer (March 6); Autumn (July 15); Winter (September 20), and Spring (December 7) of 2012 in a one-hectare plot. We took nine samples from each habitat (marshes, flats, and pans) with 10 cm diameter and 2 cm deep circular samplers (Area = 78.5 cm<sup>2</sup>). Snails were sieved from the sediment through a 1 mm-mesh, then transported alive to the lab, kept in aquaria, and fed *ad libitum* with flake fish food. All 10,367 snails were photographed using a camera attached to a dissecting microscope. We measured the total shell length (apex to the base of the aperture) from each photograph using ImageJ software.

A random subset of snails (n = 6,250) was used to identify trematode species. Snails were



crushed using a mortar and a pestle, tissue was searched under a dissecting microscope, and trematodes were identified under a compound microscope following Alda and Martorelli (2014). We only considered those parasites that compete for the gonad and digestive gland. The remaining uncrushed snails ( $n = 4,117$ ) were used to estimate parasite and host biomass (Bonel and Alda, in prep.).

Older hosts have greater cumulative risk of infection than do young hosts (Lafferty et al. 1994). Thus, in order to analyze spatio-temporal heterogeneity in parasite recruitment, each sample should be standardized by age, collected at the same time from an area in which hosts are likely to mingle and where they have experienced relatively uniform risks of infection. We identified age cohorts by means of the length-frequency distributions in each sampling date and habitat. The size-class interval was calculated using Sturges's method (Bonel et al. 2013). We then applied Bhattacharya's method available in FISAT II software (Version 1.2.0, FAO-ICLARM Fish Assessment Tools; Gayanilo et al. 2002). To confirm each modal progression, we used the NORMSEP method also available in the FISAT II software (Pauly and Caddy 1985). Individuals outside the lower 95% confidence limit of the cohort with larger individuals were considered juveniles and were then removed from the dataset because their immature gonads make them less likely to be infected by parasitic castrators and/or because they have had less time to be exposed to infection (see '*Snail size-frequency distribution and cohort identification*' and Fig. S1 in Appendix S1).

Because we sampled in different habitats and seasons, we expected to find spatial and temporal differences in snail density and in overall prevalence (prevalence is the fraction of snails infected by a given trematode species). We therefore performed two independent two-way ANOVAs and *post-hoc* Tukey HSD tests, including habitats and seasons as explanatory

variables and snail density and overall prevalence as response variables. As snail density and parasite prevalence varied across habitats and seasons, trematodes from habitats with low prevalence and low density would be disproportionately overrepresented in terms of their contribution to the total trematode guild. To prevent this, we corrected the data by weighting observed values by sample size (which corresponds with density). Results for the ANOVA tests and data correction are described in ‘*Spatial and temporal variability of snail density and overall prevalence*’ in Appendix S1.

Once juvenile snails were removed and data weighted by sample size, the final dataset comprised 3,413 snails (2,189 uninfected and 1,224 infected) and was used to (i) describe the larval trematode guild in *Heleobia australis*, (ii) estimate prevalences, (iii) estimate species richness and diversity, and (iv) analyze if this guild departs from a random assemblage using null models that predict the frequency of double infections.

### **Null models**

To assess the frequency of interactions and their outcomes, we used null models to estimate recruitment rates. From this, we could also estimate competitive interactions as the expected number of double infections—*i.e.* where two parasite species co-occur in their host, expected (i) by chance, (ii) when competition and facilitation occur, and (iii) when competition, facilitation, and preemption occur. We then compared the observed double infections with the expected number of infections in each scenario using a chi-square test to establish which mechanism led to the best match between predictions and observations.

Community structure can be revealed by comparing observed patterns with null models.

Lafferty et al. (1994) proposed a null model that quantitatively measures the degree to which a larval trematode guild departs from a random assemblage due to the combined effects of habitat and seasonal heterogeneity and competition or facilitation. For instance, certain species combinations (*i.e.* double infections) may occur more frequently than expected by chance because space and time aggregate species and/or because the presence of a given species facilitates the entrance of a second one (facilitation). On the other hand, double infections may occur less frequently because space and time isolate parasite species and/or a dominant competitor species excludes a subordinate competitor parasite (competition). We used the null model proposed by Lafferty et al. (1994) which accounts for competition and facilitation (hereafter model 1) and an extended version of that model which accounts for a mix of species interactions: competition, preemption, and facilitation (hereafter model 2). These models do not assume that competition or preemption occur (observed double infections are counted in the model and, if species do not compete, these will be equal the expected double infections), only that if they occur, it is possible to predict the probability of winners and losers. We applied both models to partition the effects of habitat, season, and species interactions and to test if this trematode guild departs from a random assemblage.

Both null models require a putative dominance hierarchy (where dominance does not need to be absolute or fully resolved) to calculate an expected prevalence ( $e$ )—that is, a prevalence free of species interaction, or the expected prevalence of each species in the absence of competitive interactions. For the most dominant species, the expected prevalence and the observed prevalence are the same. For a subordinate species, the expected prevalence might be much higher than the observed prevalence due to losses from

competition with dominant species. Here, the goal is to estimate the expected prevalence of each species and, from this, generate an expected frequency of double infections (which can then be compared to observed double infections).

Estimating the expected prevalence requires making assumptions about which species are dominant to others. We first built a putative dominance hierarchy among trematode species (*e.g.* Kuris 1990, Soldánová et al. 2012), based on assumptions supported by the experimental work of Lie and others (Lie et al. 1968, Lie 1969, 1973, Lim and Heyneman 1972, Combes 1982): (1) rediae species dominate sporocyst species (redia have a muscular pharynx used to consume host tissue and also attack and feed on other invading trematodes), (2) rediae species with large pharynges dominate rediae species with small pharynges. We also analyzed the snail-tissue occupancy area of dominant and subordinate trematodes using longitudinal histological sections of uninfected and infected tissue of the intertidal snail *Heleobia australis* that were previously obtained by Alda and Martorelli (2014). Next, we accounted for the expected prevalence of each species ( $e$ ) for each model.

#### *Model 1*

Model 1 assumes a linear hierarchy (no preemption among species). The expected prevalence for each species (where prevalence is the proportion of snails with a particular trematode species) was estimated as:

$$e_i = \frac{p_i - p_{id}}{1 - p_d}$$

where  $p_i$  is the prevalence of species  $i$ ,  $p_{id}$  is the prevalence of double infections observed between  $i$  and the species dominant to species  $i$ , and  $p_d$  is the prevalence of species dominant to species  $i$  (Lafferty et al. 1994).

## Model 2

Model 2 derives from Model 1, but it is complicated by the assumption that a species can prevent the recruitment of other trematode species by preemption if it reaches the snail first (Lafferty et al. 1994). Because the subordinate trematode *Microphallus simillimus* may fully and rapidly colonize the snail body (and due to its high prevalence), we assumed that is the only species causing preemption. Given this context, the observed prevalence of any trematode species not causing preemption ( $p_i$ ; in our system, any trematode species except for *M. simillimus*) is equal to:

$$p_i = e_i + p_{id} - e_i p_d - \frac{e_h e_i}{2} + \frac{p_{ih}}{2}$$

where  $e_i$  is the expected prevalence of species  $i$ ,  $p_{id}$  is the observed prevalence of double infections observed between  $i$  and the species dominant to species  $i$ ,  $p_d$  is the observed prevalence of dominant species to species  $i$ ,  $e_h$  is the expected prevalence of species causing preemption (in our system, *M. simillimus*), and  $p_{ih}$  is the observed prevalence of double infections observed between  $i$  and *M. simillimus*. Solving for  $e_i$ , we get that the expected prevalence of species  $i$  is equal to:

$$\left\{ e_i \rightarrow \frac{2 p_{id} + p_{ih} - 2 p_i}{e_h + 2 p_d - 2} \right\}$$

whereas the observed prevalence of *M. simillimus* ( $p_h$ ) is equal to:

$$p_h = e_h + \frac{p_{th}}{2} - \frac{e_h e_t}{2}$$

where  $p_{th}$  is the observed prevalence of double infections *M. simillimus* and all other species and  $e_t$  is the expected prevalence of all the species combined except for *M. simillimus*. Solving for  $e_h$ , we get the expected prevalence of species  $h$  equal to:

$$\left\{ e_h \rightarrow \frac{p_{th} - 2 p_h}{e_t - 2} \right\}$$

The prevalence of all trematode species combined except for *M. simillimus* ( $p_t$ ) is equal to:

$$p_t = e_t + \frac{p_{th}}{2} - \frac{e_h e_t}{2}$$

Solving for  $e_t$ , the expected prevalence of all trematode species combined except for *M. simillimus* is equal to:

$$\left\{ e_t \rightarrow \frac{p_{th} - 2 p_t}{e_h - 2} \right\}$$

Substituting for  $e_t$  in the previous equation and isolating  $e_h$  leads to one rational root solution for  $e_h$ , we then obtain the expected prevalence of species  $h$  as:

$$\left\{ e_h \rightarrow \frac{1}{2} \left( -\sqrt{4 p_{th} + p_h^2 - 2 p_h p_t - 4 p_h + p_t^2 - 4 p_t + 4} + p_h - p_t + 2 \right) \right\}$$

Based on the putative dominance hierarchy, we calculated the expected prevalence of each species.

Finally, from the expected prevalences, we calculated the expected number of double infections using both models. We estimated the expected prevalence of double infections for each species pair  $i, j$ —in model 2, excluding *M. simillimus*—by multiplying the expected prevalence of trematode species  $i$  ( $e_i$ ) and the expected prevalence of trematode species  $j$  ( $e_j$ ). For instance, if there are two species, A and B, and A is dominant to B, if the observed prevalence of A is .4 and the observed prevalence of B is 0.3, (and no double infections are observed) then B has recruited to 1/2 of the safe space available to it. This means the expected prevalence of A is 0.4, the expected prevalence of B is 0.5, and the expected number of double infections between species A and B is 0.2. If there are 100 snails, we would expect to see 20 with double infections in the null model. Also, in model 2 we calculated the expected prevalence of double infections for each species pair  $i, h$  by

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multiplying the sample size (N) by the expected prevalence of trematode species  $i$  ( $e_i$ ) and the expected prevalence of trematode species  $h$  ( $e_h$ ). Hence, we calculated the prevalence expected for each species, in each combination of habitat and season, expected under two scenarios: model 1, which assumes a dominance hierarchy among trematodes and accounts for competition and facilitation, and model 2, which assumes a dominance hierarchy among trematodes and preemption caused by *M. simillimus* and accounts for competition, preemption, and facilitation.

#### *Comparing the expected and observed number of infections*

For each model, we summed expected numbers of double infections over all three habitats and four seasons and calculated the expected number of double infections for pooled data (hereafter Expected Pooled). The Expected Pooled estimate gives a measure of a guild that assumes neither habitat nor seasonal heterogeneity (it also assumes no species interactions given the expected null prevalences used in the models). We summarized in Table 1 the possible effects of habitat and seasonal heterogeneity and trematode interaction on the guild structure along with the interpretation for each assumption and comparison between expected values and between expected and observed number of infections.

To determine the effect of habitat (independent of seasons and species interaction), we compared the Expected Pooled with the sum of the expected number of double infections calculated separately for each habitat grouped across seasons (hereafter Expected Summed-Habitat). When Expected Pooled-Habitat is higher than Expected Summed-Habitat, habitat heterogeneity isolates trematode species. In contrast, when Expected Pooled-Habitat is lower than Expected Summed-Habitat, habitat heterogeneity aggregates parasites.

To determine the effect of season (independent of habitats and species interactions), we summed the expected number of double infections calculated separately for each season at a given habitat (Expected Summed-Season) and compared this figure to the expected number of double infections calculated from the values combined over all four seasons (Expected Pooled-Season). Here, if Expected Pooled-Season is significantly higher than Expected Summed-Season, seasonal heterogeneity isolates species; but if Expected Pooled-Season is lower than Expected Summed-Season, then seasonal heterogeneity aggregates species.

Finally, to determine the effect of species interactions, we plotted the expected prevalences due to recruitment against the observed prevalences (which show the combined effect of recruitment and competition). The coefficient of determination

in this relationship indicates the proportion of the species abundance distribution that can be explained by recruitment alone. To quantify how interactions affected each species, we also compared the observed number of double infections (hereafter Observed) with the sum of the expected double infections calculated separately for each sample (Expected Summed). If Expected Summed is lower than Observed, facilitation increases double infections; but if Expected Summed is higher than Observed, competition (Model 1) or competition and preemption (Model 2) reduces double infections.

To determine whether habitat, season, and species interactions significantly affected the number of double infections, we statistically compared observed and expected numbers of double infections by a chi-square test at the significance level of 0.05. When the expected values (Expected Pooled and Expected Summed) were compared, we used the arithmetic mean of the two theoretical values to define the 'expected' figure, that is:  $X^2_{(d.f. = k-1)} = \frac{(\text{Expected Summed} - \text{Expected Pooled})^2}{((\text{Expected Summed} + \text{Expected Pooled}) / 2)}$ .



## Results

We found 16 species of larval trematodes parasitizing *H. australis* in the Bahía Blanca estuary (Table 2), five of which were not reported by Alda and Martorelli (2014). The overall prevalence of infected snails from the final dataset was 36% (1,224 infected out of 3,413 snails). However, there was a skewed distribution in the trematode guild, with one common species and many rare species. Indeed, the distribution was so skewed that no particular model fits this distribution well (Fig. 4). All the trematode species were present at prevalences equal to or lower than 1%, except for the microphallid *Microphallus simillimus*, which infected 32% of the snails (Table 2). The observed numbers of single and double infections are presented in Appendix S1: Table S1. Only 45 of 3,413 snails (0.76%) were parasitized by two trematode species (Appendix S1: Table S1). Most double infections involved the microphallid *M. simillimus* with either *Renicola* sp. or the other microphallid *Levinseniella cruzi* (Appendix S1: Table S1).

Heterogeneity was notable in space and time due to habitat and seasonal effects. Overall species richness was more than 2.3 times higher in snails from pans than in snails from marshes or flats ( $F_{(2, 104)} = 35.785, P < 0.001$ ; Fig. 2). In addition, the number of species was more than 1.8 times higher in summer than in autumn ( $F_{(3, 104)} = 6.228, P < 0.001$ ; Fig. 2), but species richness in summer was not significantly different from winter and spring. We found a marginally significant interaction between habitats and seasons ( $F_{(6, 104)} = 2.247, P = 0.045$ ). As for richness, pans showed a 1.6 times higher species diversity than marshes or flats ( $F_{(2, 96)} = 4.458, P = 0.014$ ; Fig. 2). Also, diversity was significantly higher in summer than in autumn ( $F_{(3, 96)} = 3.482, P = 0.019$ ) but it was not different from winter or spring. We found no significant interaction between habitats and seasons ( $F_{(6, 96)} = 0.715, P = 0.638$ ).

The putative dominance hierarchy contained three groups of codominant species, with *M. simillimus* within the group of the most subordinate trematode species. From the most dominant species group to the less dominant species group: Group 1 had large rediae with large pharynges, Group 2 had small rediae with small pharynges, and Group 3 had sporocysts (Fig. 3). The histological sections showed that *M. simillimus* occupied a greater fraction of the host biomass (both gonadal and digestive gland tissue), whereas (co)dominant species to *M. simillimus* parasitized the gonadal tissue but left much of the digestive gland unaffected (Appendix S1: Fig. S2).

We found that in pans, double infections were less common than expected, presumably due to species interactions. Specifically, expected Summed-Habitat interactions were twice the Observed interactions for model 1 (*i.e.* assuming only dominance hierarchy among species; 51.8 vs. 26.6; Appendix S1: Table S2; Fig. 4B) and more than twice for model 2 (*i.e.* assuming dominance hierarchy among species and preemption caused by *M. simillimus*; 69.2 vs. 26.6; Appendix S1: Table S2; Fig. 4D), which is consistent with our expectation that competition (model 1) and competition and preemption (model 2) eliminated some trematodes from the community. However, the total number of trematode infections lost to species interaction in pans was small: 6.5 (model 1) and 26.8 (model 2; Table 3). Although we cannot determine whether the competition (Model 1) or the preemption (Model 2) model is more accurate, the higher estimated loss rates in Model 2 suggest that many more trematodes might recruit to the system (as we would expect given that such species are abundant elsewhere), but are lost to preemption at this site, and, therefore, are not observed by us.

Double infections in the other habitats were also less common than expected, but lower sample sizes made it difficult to statistically separate observed from expected (Appendix S1: Table S2; Fig. 4B, D), flats (Appendix S1: Table S2; Fig. 4B, D), and combined habitats and seasons (Appendix S1: Table S2; Fig. 4A, C). The same qualitative pattern was observed for habitat and seasonal heterogeneity—that is, habitat and season tended to aggregate trematodes—but, again, these were not significantly different (Appendix S1: Table S2, Fig. 4C,D). Expected infections and expected double infections for both null models are indicated in Appendix S1: Table S3 and S4.

Even though niche differences did not reduce interactions, and despite the observation that interactions did reduce some trematode individuals, at the community level, interactions were so infrequent that recruitment rates among the 15 rare species determined 99.9% of their species abundance distribution without preemption and 99.4% with preemption. Clearly, recruitment, not species interactions or niche differences, drives this particular community despite strong potential for dominant species to displace subordinate species if they were to occupy the same host.

## **Discussion**

Overall, trematode recruitment to *H. australis* is low, with one exception, the subordinate species *M. simillimus*, which infects about one third of the snails. The numerical dominance of *M. simillimus*, is all the more remarkable because spatial and temporal heterogeneity aggregate the trematode infections, increasing potential interactions. Most of these interactions are eliminated by competition or preemption. But interactions are too rare to structure the community in a meaningful way.

Species richness and diversity varied across space and time: both measures were higher in habitats covered by water at low tide (pans) and in warmer seasons (summer). The seasonal variation in species richness and diversity could result from an increase in abundance of migratory birds in the Bahía Blanca estuary in warmer seasons (Delhey and Petracci 2004). Birds are the main definitive hosts in this estuary (Alda and Martorelli 2014); however, other intermediate and definitive hosts (invertebrates, fish and mammals) could also affect this seasonal variation in species richness and diversity. This was observed in a similar parasite-snail host system from a different ecosystem, where habitat variation was associated with the abundance of the second-intermediate hosts, because parasitic trematodes are transmitted to snails only after final hosts consume the second-intermediate host (Parietti et al. 2013). However, the habitat differences in species richness and diversity observed in our study could arise if snail infection risk differs in various habitats. Snails in habitats that are covered by water at low tide (pans) are parasitized more often because the longer submersion time allows snails to increase time spent foraging and thus ingesting parasite eggs or by being penetrated by miracidia (Fredensborg et al. 2006).

The increased parasite prevalence in pans versus in other habitats supports our prediction that similarities among species niches aggregate parasites in pans during the summer increasing species interactions, which is in line with results found in other studies (Kuris and Lafferty 1994, Lafferty et al. 1994, Soldánová et al. 2012). Accordingly, considering the putative dominance hierarchy hypothesis, we found that in pans, competition eliminated 1% (Table 3) of all trematode infections, a proportion much lower than the percentages of infections lost to competition estimated for other trematode guilds: 13%, (Kuris and Lafferty 1994), 16% (Lafferty et al. 1994), and 11% (Soldánová et al. 2012). This was due to the surprisingly low prevalences of putatively (co)dominant species to *M. simillimus*. It is puzzling that *M.*

*simillimus* dominates the trematode assemblage even though it is a subordinate species and conditions seem just as suitable (in terms of habitats and required hosts) for the other trematode species. One possible explanation for the high prevalence of *M. simillimus* and the low prevalence of other species is if *M. simillimus* arrives early in the season before the competitive dominants and preempts their establishment. Once *M. simillimus* has colonized the snail's tissue, parthenogenetic generations produce metacercariae that occupy the entire gonad and most of digestive gland of the host (Alda and Martorelli 2014). These metacercariae are most likely invulnerable to the attack by rediae and thus potentially resistant to removal by (co)dominant species, which could explain the high prevalence of *M. simillimus*.

Assuming preemption caused by *M. simillimus*, we found that competition plus preemption (model 2) eliminated 4% of infections from the system (Table 3). The structure of model 2 prevented disentangling the particular effects of competition or preemption. However, the percentage of infections lost to competition plus preemption for the species (co)dominant to *M. simillimus* was twelve times higher than the percentage of infections lost only to competition (14.6% vs. 1.2%, respectively; Table 3). Such a priority effect has been shown in other systems. For instance, Lie (1969) showed that if the dominant species *Hypoderaeum dingeri* first infects the snail host, the codominant species *Echinostoma audyi* could not be established, and *vice versa*. Likewise, our preemption hypothesis could be empirically tested by seeing whether *M. simillimus* in sentinel snails persisted while uninfected sentinel snails became infected with other trematode species. Regardless of whether preemption occurs, interactions among trematodes are still lower than in other systems, suggesting that other factors, such as low recruitment rates, short snail life spans, and high species unevenness

reduce expected interactions even while spatial and temporal heterogeneity aggregate species together to increase interactions.

If the common subordinate trematode *M. simillimus* is the first to colonize an uninfected snail and become well established, it might prevent the recruitment of (co)dominant species.

Preemption, however, would not impede coexistence if trematode species were not limited in their colonization ability and the competitive tradeoff was not intense (Calcagno et al. 2006).

For instance, in our case, subordinate species (*e.g.* species from Group 3) might exhibit higher colonization ability than dominant competitors (*e.g.* species from groups 1 and 2).

This, in turn, would allow them to coexist with a strong colonizer such as *M. simillimus*.

Accordingly, we observed that most double infections ( $n = 45$ ) involved *M. simillimus* with other species from the Group 3 (92% of double infections; Appendix S1: Table S1). This pattern is in line with results obtained by Mordecai et al. (2016) in a similar trematode guild where the incidence of infection is negatively correlated with position in the dominance hierarchy at levels sufficient to promote coexistence of subordinates.

The prevalence of (co)dominant species to *M. simillimus*, however, would still be low without the effect of preemption. The prevalence of these species decreased from 8.5% to 7.3% (see Table 3). This change (1.2%) represents a decrease of 14.1% in the overall prevalence of the (co)dominant species to *M. simillimus* (Table 3), indicating that preemption reduced the prevalence of these species to 85.9% of their recruitment rate in pans as predicted by Lafferty et al. (1994). Note that even after accounting for preemption and spatial heterogeneity, dominant species simply recruited infrequently to this habitat. As predicted by supply-side ecology, an ‘external recruitment source’ hypothesis can explain why (co)dominant species are rare and hence a competitively subordinate species remains

prevalent in the local system. At small spatial scales, such as in our study, recruitment of dominant species is low perhaps because their sources are external to the local system and their numbers are therefore decoupled from the outcome of local interactions. Supporting this, Alda et al. (2011) reported a White-Backed Stilt—the definitive bird host of *M. simillimus* (Martorelli 1991)—infected with (co)dominant species but without *M. simillimus* in a lagoon located close to the study area. With open recruitment, (co)dominant species become proportionately more abundant only as the habitat (host snails) saturates (with infections), such as in older age classes. However, if the habitat (host snails) remains unsaturated due to low recruitment (*i.e.* an overall low prevalence in the snail population), then the community will be similar in composition to the recruited assemblage as seen in our study.

In conclusion, niche overlap led to parasite aggregation in habitats covered by water at low tide (pans) and in warmer seasons (summer), intensifying potential species interactions.

Though competition theory would predict that the subordinate should be excluded from the system, this was not the case in our study—*M. simillimus*, a competitively inferior species, was, by far, the most abundant in the system. The abundance of the subordinate species *M. simillimus* was notably high, perhaps due to life-history traits that enhance its reproductive potential, its transmission success, and fosters relatively closed recruitment at sites where (co)dominant species were rare. When birds feed on snails, they acquire thousands of *M. simillimus* cysts while releasing parasite eggs into the snail host population. Taking these factors together, this subordinate's abundance is less puzzling. The common subordinate *M. simillimus* could have limited the recruitment of other trematode species by causing preemption due to its higher colonization ability and, if so, the infections lost by preemption effect were substantially greater than those lost only to competition. Even so, preemption had

minor effects on the species abundance distribution. A strong tradeoff between competitive ability and colonization rate combined with high transmission success increased the probability of a competitively inferior species to persist in and rule in this species-rich trematode guild.

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## Tables

**Table 1.** Possible effects of habitat and seasonal heterogeneity and trematode interaction on the guild structure.

Effects	Null models	Comparison between expected values and between expected and observed number of double infections	Interpretation
Habitats combined (no effect of season but effect of habitat)	Model 1 and 2	Pooled-Habitat > Summed-Habitat	Habitat heterogeneity isolates parasites
		Pooled-Habitat < Summed-Habitat	Habitat heterogeneity aggregates parasites
	Model 1	Summed-Habitat < Observed	Facilitation increases double infections
		Summed-Habitat > Observed	Competition reduces double infections
	Model 2	Summed-Habitat < Observed	Facilitation increases double infections
		Summed-Habitat > Observed	Competition and preemption reduce double infections
Within habitats (no effect of habitat but effect of season)	Model 1 and 2	Pooled Season > Summed-Season	Seasonal heterogeneity isolates species
		Pooled Season < Summed-Season	Seasonal heterogeneity aggregates species
	Model 1	Summed-Season < Observed	Facilitation increases double infections
		Summed-Season > Observed	Competition reduces double infections
	Model 2	Summed-Season < Observed	Facilitation increases double infections
		Summed-Season > Observed	Competition and preemption reduce double infections

**Table 2.** Prevalence of larval trematodes of intertidal mud snail *Heleobia australis* in the Bahía Blanca estuary, Argentina. Species are shown in order of dominance hierarchy. Prevalence figures (%) were estimated from the final dataset. Citation alludes to the references where the larval trematodes were described and revised except for those larval trematodes that were not previously described elsewhere and are first mentioned in this study.

Family	Trematode species	Trematode abbreviation	Prevalence	Citation
Echinostomatidae	<i>Himasthla</i> sp.	HIMA	0.04	Alda and Martorelli 2014
Notocotylidae	Notocotylidae gen. sp.	NOTO	0.04	Alda and Martorelli 2014
Haploporidae	Haploporidae gen. sp. 1	HAPLO 1	0.17	Alda and Martorelli 2014
	Haploporidae gen. sp. 2	HAPLO 2	0.01	This study
Heterophyidae	<i>Ascocotyle (Phagicola) longa</i>	ASCO	0.45	Simões et al. 2010, Alda and Martorelli 2014
	Pleurolophocercaria	PLEURO	0.07	This study
Cryptogonimidae <sup>1</sup>	Cryptogonimidae gen. sp.	CRYPTO	0.37	Alda and Martorelli 2014
Aporocotylidae	Aporocotylidae gen. sp. 1	APORO 1	0.07	Alda and Martorelli 2014
	Aporocotylidae gen. sp. 2	APORO 2	0.15	This study
Cyathocotylidae	Furcocercaria	FURCO	0.03	This study



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Renicolidae	<i>Renicola</i> sp.	RENI	0.97	Alda and Martorelli 2014
Microphallidae	<i>Maritrema orensense</i>	MARO	0.79	Alda et al. 2013, Alda and Martorelli 2014
	<i>Maritrema bonaerense</i>	MARB	1.06	Etchegoin and Martorelli 1997, Alda et al. 2013, Alda and Martorelli 2014
	<i>Levinseniella cruzi</i>	LEVI	0.59	Martorelli 1988, Alda and Martorelli 2014
	<i>Odhneria</i> sp.	OD	0.12	This study
	<i>Microphallus simillimus</i>	MICRO	32.33	Martorelli 1991, Alda and Martorelli 2014

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**Table 3.** Effect of species interaction on the relative abundance of trematode species in pans.

The expected number of infections (single and double infections combined) was calculated from null prevalences from model 1 ( $Ne_{i,j}$ , assuming dominance hierarchy among species) and from model 2 ( $Ne_{i,h}$ , assuming dominance hierarchy among species and preemption caused by *Microphallus similimus*). The observed figures correspond to the abundance after species interaction. The number of infections lost to species interactions was obtained by subtracting the number of infections between ‘before’ and ‘after’. The percentage of trematode infections lost to species interactions was estimated as:  $(\sum \text{observed infections of dominant species } ij \times 100 / \text{expected infections of species } i) - 100$ . Prevalences were estimated as:  $(\text{number of snails infected} / \text{total number of snails sampled in pans}) \times 100$ . N total = 1,138 snails.

Trematode species are coded as in Table 1 and listed in order of dominance.

Groups	Trematodes species	Before (Expected)			Number of infection lost to	
		competition	competition / preemption	After species interaction (Observed)	competition	competition / preemption
1	HIMA	0	0	0	0	0
	NOTO	0.5	0.2	0.5	0	0.3
	HAPLO 1	2.3	2.3	2.3	0	0
	HAPLO 2	0.4	0.6	0.4	0	-0.2
2	ASCO	9.2	11.4	9.1	-0.1	-2.3
	CRYPTO	3.7	4.7	3.7	0	-1
	PLEURO	1.4	1.9	1.4	0	-0.5
3	APORO 1	0.9	1.3	0.9	0	-0.4
	APORO 2	0	0	0	0	0
	FURCO	1	1.3	0.9	-0.1	-0.4
	RENI	20.9	22.7	20.6	-0.3	-2.1

MARO	18	21.2	17.7	-0.3	-3.5
MARB	20.2	24.7	19.9	-0.3	-4.8
LEVI	5	4.4	4.9	-0.1	0.5
OD	0.5	0.2	0.5	0	0.3
MICRO	624.6	631.8	619.1	-5.5	-12.7
Sum of infections excluding MICRO	83.8	96.9	82.8	-1 (-1.2%)	-14.1 (-14.6%)
Infections only by MICRO	624.6	631.8	619.1	-5.5 (-0.9%)	-12.7 (-2.0%)
Total of infections	708.4	728.7	701.9	-6.5 (-0.9%)	-26.8 (-3.7%)
Prevalence excluding MICRO (%)	7.4	8.5	7.3	-0.1	-1.2
Prevalence of MICRO (%)	54.9	55.5	54.4	-0.5	-1.1
Total prevalence (%)	62.3	64	61.7	-0.6	-2.3

## Figure captions

**Figure 1.** Species abundance distribution (Log abundance axes in order from most to least abundant species), including best fits to four common distributions: log-normal, log-series, Broken stick, and Zipf distribution. Trematode species are coded as in Table 1: MICRO (1), MARB (2), RENI (3), MARO (4), LEVI (5), ASCO (6), CRYPTO (7), HAPLO 1 (8), APORO 2 (9), OD (10), PLEURO (11), APORO 1 (12), HIMA (13), NOTO (14), FURCO (15), and HAPLO 2 (16).

**Figure 2.** Mean species richness (S) and mean diversity (H') values of trematodes parasitizing the snail *Heleobia australis* collected from the Bahía Blanca estuary, Argentina. Figures were back transformed and are indicated for each habitat and season. Error bars represent 95% confidence limits. Different letters (a, b) indicate significant differences.

**Figure 3.** Putative dominance hierarchy for the larval trematodes in *Heleobia australis*. Equal sign means that larval trematodes are in the same range of dominance. Species are coded as in Table 1.

**Figure 4.** Effect of habitat and seasonal heterogeneity and trematode interaction on the guild structure. The expected numbers of double infections (Pooled and Summed) were calculated by means of the model 1,  $Ne_{i,ej}$  (A, B); model 2,  $Ne_{i,hej}$  (C, D). Here, qualitative results show that Pooled is lower than Summed, which indicates that habitat and season aggregated trematodes. Also, Summed is higher than Observed, which indicates that competition (A, B), or competition and preemption (C, D) eliminated trematodes from the system. (We found that

only in pans Summed was significantly higher than Observed.) Proportion of double infections was calculated as the number of (observed or expected) double infections divided by the total number of individuals (habitats combined:  $n = 3,413$ ; within habitats:  $n = 1,138$ ) and multiplied by 100. Error bars represent 95% confidence limits.









