The role of competition – colonization tradeoffs and spatial heterogeneity in promoting trematode coexistence

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Abstract. Competition – colonization tradeoffs occur in many systems, and theory predicts that they can strongly promote species coexistence. However, there is little empirical evidence that observed competition- colonization tradeoffs are strong enough to maintain diversity in natural systems. This is due in part to a mismatch between theoretical assumptions and biological reality in some systems. We tested whether a competition – colonization tradeoff explains how a diverse trematode guild coexists in California horn snail populations, a system that meets the requisite criteria for the tradeoff to promote coexistence. A field experiment showed that subordinate trematode species tended to have higher colonization rates than dominant species. This tradeoff promoted coexistence in parameterized models but did not fully explain trematode diversity and abundance, suggesting a role of additional diversity maintenance mechanisms. Spatial heterogeneity is an alternative way to promote coexistence if it isolates competing species. We used scale transition theory to expand the competition – colonization tradeoff model to include spatial variation. The parameterized model showed that spatial variation in trematode prevalence did not isolate most species sufficiently to explain the overall high diversity, but could benefit some rare species. Together, the results suggest that several mechanisms combine to maintain diversity, even when a competition – colonization tradeoff occurs.

Key words: Carpinteria Salt Marsh; Cerithideopsis californica; *coexistence; competition – colonization tradeoff; parasite; spatial heterogeneity; trematode.*

Introduction

The coexistence of competing species in nature requires that variation in competitive ability among species be offset by differences in resource use, impacts from natural enemies, or other niche differences (Levin 1970, Chesson 2000). Life-history tradeoffs can promote coexistence by increasing niche differences and reducing differences in competitive ability (Kneitel and Chase 2004, Edwards and Stachowicz 2010, Edwards et al. 2011). For example, a tradeoff between competitive ability and colonization rate can result in competitively inferior species colonizing open habitat and reproducing before being displaced by later-arriving superior competitors (Levins 1969, Hastings 1980, Nee and May 1992, Tilman 1994). This competition – colonization tradeoff has been proposed to explain coexistence in many taxa, including plants (Tilman 1994, Levine and Rees 2002), freshwater

microbes (Cadotte et al. 2006, Cadotte 2007), ants (Stanton et al. 2002, Adler et al. 2007), marine invertebrates and algae (Sebens 1986, Edwards and Stachowicz 2010, Castorani et al. 2014), and parasites (Harbison et al. 2008, reviewed by Bashey 2015). However, despite empirical documentation, whether or not the competition – colonization tradeoff is sufficient to permit coexistence remains poorly known in natural systems.

While competition – colonization tradeoffs occur in some systems (Sebens 1986, Stanton et al. 2002, Cadotte et al. 2006, Harbison et al. 2008, Edwards and Stachowicz 2010, Castorani et al. 2014), whether or not they are sufficient to maintain coexistence has rarely been tested (Clark et al. 2007), and in those rare cases the tradeoffs have been insufficient to explain coexistence (Levine and Rees 2002) or species abundance (Adler et al. 2007). There are several reasons that empirically demonstrated competition – colonization tradeoffs may not be solely responsible for the maintenance of coexistence as predicted by theory. First, the coexistence mechanism requires strong competitive asymmetry with clear dominance (Geritz et al. 1999, Adler and Mosquera 2000, Levine and Rees

2002, Amarasekare 2003, but see Calcagno et al. 2006). Yet many species, particularly plants, have reciprocal competitive effects, even if one species has a stronger effect (Tilman 1980). Second, the coexistence mechanism is strongest when superior competitors can displace inferior competitors from sites they occupy, precluding space preemption (Calcagno et al. 2006). By contrast, in nature, established adults (e.g., plants) often repel invasion by dominant species' propagules (Tilman 1994, Edwards and Stachowicz 2011). Although the competition – colonization tradeoff may occur in many systems, there is scarce evidence that it maintains coexistence in nature because these requisite conditions often are not met. Moreover, even when the above conditions are met, the colonization advantage of subordinate species may be insufficient to overcome their competitive disadvantages. For the tradeoff to sustain coexistence, it must allow all species to invade when rare in the presence of their competitors.

Spatial heterogeneity might interact with life-history tradeoffs to further promote coexistence. For example, spatial heterogeneity in recruitment, abundance, or performance among species can act as a niche difference, which can favor coexistence by isolating species and reducing interspecific competition relative to intraspecific competition (Ives 1991, Chesson et al. 2005, Melbourne et al. 2005, Edwards and Stachowicz 2011). However, spatial aggregation also increases the average effect of competition within species because the strength of competition increases nonlinearly with local density (Ives 1991, Chesson et al. 2005, Melbourne et al. 2005). Whether or not spatial variation promotes persistence of subordinate species therefore depends on whether species tend to segregate into different areas and, if so, whether the benefit of this segregation outweighs the negative effects of intraspecific aggregation (Chesson et al. 2005, Melbourne et al. 2005).

Here, we test the combined roles of competition – colonization tradeoffs and spatial variation in abundance and recruitment in maintaining coexistence in a salt marsh larval trematode guild. Trematode assemblages in populations of the California horn snail, *Cerithideopsis californica* (=*Cerithidea californica*), can contain up to 20 coexisting species. Despite this diversity, each trematode species requires the California horn snail to complete its life cycle (Kuris 1990, Sousa 1993, Lafferty et al. 1994). Moreover, niche partitioning within host snails is rare; when trematode species co-occur in the same snail, one species typically kills the other. This competition is asymmetric: superior competitors displace inferior competitors, while inferior competitors can only infect snails not already infected with competitive superiors (Kuris 1990, Sousa 1993). Moreover, the snails rarely, if ever, recover from infection (van der Knaap and Loker 1990, Kuris 1990, Sousa 1993). As a result, snails are discrete habitat patches that tend to harbor a single long-lived parasite infection (or transient displacements). Several lines of evidence support the importance of competition in

structuring trematode communities: (1) mixed infections are much less common than would be expected in the absence of competition; (2) larval trematodes have been observed consuming heterospecific trematodes; (3) some trematode species produce specialized defensive morphs; and (4) the prevalence of dominant species increases relative to subordinate species with snail age (Kuris 1990, Sousa 1993, Lafferty et al. 1994, Kuris and Lafferty 1994). Even though many snails remain uninfected, because subordinate infective stages cannot actively seek out uninfected hosts, competitive loss rates scale proportionally with the prevalence of competitive dominants (prevalence can increase with snail age to the point that nearly all snails are infected [Kuris 1990, Lafferty 1993*a*,*b*, Sousa 1993]). Furthermore, each competitive displacement event has a proportionally larger impact on the population growth of subordinate species as prevalence declines, so low prevalence does not alleviate the impact of competition on subordinate species (Chesson and Huntly 1997). In sum, trematode species compete strongly and asymmetrically for an obligate first-intermediate host in which there are no obvious niche differences, yet trematode diversity remains high in local snail populations. This suggests that a competition – colonization tradeoff could promote coexistence. Because the complex trematode life cycle can promote trematode dispersal within and among estuaries, spatial heterogeneity could also play a role in this system.

Previous research in this snail – trematode system suggests that spatial heterogeneity could influence species coexistence. Trematode recruitment to snails occurs via infectious trematode eggs or larvae that are distributed within and between estuaries by the birds that host the relatively short-lived adult worms, and trematode recruitment correlates with abundance and diversity of birds (Hechinger and Lafferty 2005). Bird species, which host varying, diet-dependent suites of trematode species, have different habitat preferences. The resulting spatial variation in trematode recruitment to snails could promote coexistence by spatially separating some competing trematode species (Sousa 1990, Edwards and Stachowicz 2011). However, in a previous study in a single estuary (Carpinteria Salt Marsh (CSM)), spatial heterogeneity in recruitment within salt marsh channels intensified competition between trematode species by aggregating infections, rather than isolating them (Lafferty et al. 1994). To test whether the competition-colonization tradeoff and spatial variation in recruitment could promote coexistence, we combined population growth models with field data on recruitment and prevalence. We first test the effect of each mechanism on invasion criteria derived from theory. In this way, we rigorously measure the strength of each mechanism. Then, we test whether the mechanisms can explain observed prevalence in the field, an additional test of model fit to empirical observations.

METHODS

Host – parasite study system

The California horn snail is common in salt marsh dominated estuarine habitats from Central California to halfway down the Baja California peninsula. DNA sequence evidence has recently revealed that the species extends further south, where it occurs in mangrove-dominated estuaries (Miura et al. 2010). The snails serve as the obligate first-intermediate host for up to 20 trematode species (Martin 1972, Hechinger and Miura 2014). Trematodes in a snail produce free-swimming cercariae that encyst in fishes or invertebrates, after which the cysts can infect predatory birds. In birds, sexual reproduction produces eggs or miracidia that leave the birds to infect snails. Within the snail, a trematode infection grows via asexual reproduction of worm-like parthenitae. In the most dominant species, parthenitae have large mouthparts and can kill other parthenitae, whereas species with smaller or no mouthparts are inferior competitors, even if they infect the snail first (Lie 1973, Kuris 1990). Due to strong competition for snail host tissue, which occurs through resource consumption and aggressive interactions between trematodes, most snail infections contain a single trematode species, and multi-species infections are much more rare and transient than they would be if interspecific competition did not occur (Lafferty et al. 1994). In essence, snails are habitat patches for inter-active trematode communities and are easy to measure in large quantities (Kuris and Lafferty 1994).

While the trematode life cycle requires three different hosts, we measured trematode population dynamics in the host snail population, the longest life stage and the only shared, obligate host for all the trematode species, for which competition is strong and asymmetric. The larval stage within the snail is the longest trematode life stage, and can last for years (Kuris 1990, Sousa 1993). Trematode recruitment into host snails integrates processes that occur in second-intermediate and final host life stages, but must at some spatial scale depend on the number of host snails infected. For a competition – colonization tradeoff to sustain coexistence, per-capita recruitment rates must decline with competitive rank (Hastings 1980, Tilman 1994). For this reason, we focus on how recruitment rate to host snails *per infected snail* (the source of recruits) differs across the competitive dominance hierarchy. For trematodes, these per-capita recruitment rates incorporate variation due to transmission, survival, and reproduction in other life stages as well as within the snail host. In Appendix S1 in Supporting Information, "*Full parasite life cycle model,*" we explore how the full parasite life cycle may contribute to the observed colonization rates. In this sense, we use the term "tradeoff" broadly to refer negative correlations between traits that permit coexistence, including differential usage of second-intermediate and final host communities as well as trait differences within host snails.

Because trematodes replicate asexually within the snail host (similar to pathogens such as bacteria and viruses (Anderson and May 1981)), we consider an infected snail to be an individual in the larval trematode population. For a given trematode species, we define *prevalence* as the fraction of snails it has infected, *recruitment rate* as the number of new successful snail infections per unit time, and *colonization rate* as per-capita recruitment rate (i.e., the number of new viable trematode infections produced from an infected snail per unit time). Calculating colonization rates from recruitment rates and background prevalence requires defining the snail "source" population from which future trematode recruits derive (i.e., the spatial scale of recruitment). The spatial scale of recruitment is not well understood, but likely falls somewhere between local (i.e., within the focal estuary) and global (i.e., well-mixed across all west coast estuaries). In the absence of direct data on trematode gene flow between estuaries, we fit models of these two opposing extremes (i.e., closed vs. open recruitment), with the goal of book-ending the spatial scale at which recruitment occurs in nature.

Study design

To estimate colonization rates in the field, we first measured recruitment to uninfected sentinel snails. We obtained sentinel snails from Carpinteria Salt Marsh (CSM), California, USA (34.40°N, 119.53°W) by placing 3300 snails from the 20–30 mm size class in individual containers of filtered seawater, heating with lamps to 25–30°C for 30 min, retaining only snails that did not shed cercariae, and repeating the process. From a sample of 129 dissected snails that did not release cercariae during shedding, we found that shedding was 88% accurate and that all but one of the false negatives contained an immature infection. We scrubbed and marked these 1800 uninfected sentinel snails with yellow enamel-based spray paint before dividing them into 12 cages (150 snails per cage) placed along four tidal channels in CSM in groups of three cages (15–20 m apart) on October 31, 2010. Channel sites were chosen because they support dense local snail populations; the four main sites were distributed throughout the estuary and represented two larger and two smaller channels (see Appendix S2 in Supporting Information for site map). Cages were black plastic mesh cylinders open on top and bottom, measuring 1-m in diameter and 1-m tall, staked to the ground using PVC pipe. To track trematode recruitment over time, we removed the sentinel snails (from 50 to all snails we could find in each cage) on twelve dates between November 2010 and May 2012 (approximately every 3 weeks), and individually shed them in 6-well boxes filled with filtered seawater, after which we identified shed cercariae using stereomicroscopes and keys by Martin (1972) and R. F. Hechinger and T. C. Huspeni *(unpublished manuscript)*. Shedding was repeated twice for all snails each sampling period. After shedding, infected

snails were labeled with nail polish and numbers glued to the shell, and all snails were returned to their original cages. These methods led to robust recruitment rate estimates.

Colonization rate is equal to the per-capita recruitment rate into uninfected snails, so measuring it requires both recruitment data (as above) and background prevalence data (to estimate recruits per infected snail per unit time). We calculated background prevalence at CSM using data from a large-scale bimonthly sampling effort from April 2012 to January 2014 at CSM that dissected 11 641 randomly selected snails from nine sites spanning the same area of marsh where sentinels were located (R. F. Hechinger et al., unpublished). Though the bulk of this sampling effort took place after the sentinel snail experiment, we used these prevalence data because they strongly correlated with the prevalence of each trematode species in an initial, coarser sample of 705 snails we conducted just prior to the sentinel experiment in 2010 ($r = 0.88$ for the prevalence of each species in the two surveys), but due to the large sample size, included data for twelve additional trematode species. (Models fit with the smaller 2010 prevalence dataset produced qualitatively similar results for the species present in both datasets.) The relative stability of trematode communities over time at this location (Huspeni and Lafferty 2004) further justifies using the larger "CSM prevalence dataset" to fit the models. This dataset also provided information about spatial variation in prevalence within CSM for each trematode species. We used this to estimate how spatial variation affected coexistence by parameterizing a spatial model as described below.

Models

To examine how the competition – colonization tradeoff and spatial variation in prevalence affect coexistence, we expanded a widely used competition – colonization tradeoff model (Hastings 1980, Tilman 1994) to include effects of spatial variation (Chesson et al. 2005).

Competition – colonization tradeoff model.—We described trematode population growth in snails using the model from Tilman (1994),

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j<i} p_j - p_i \right) - m_i p_i - p_i \sum_{j<i} c_j p_j, \qquad (1)$$

where p_i is the prevalence of species i in snails, m_i is the mortality rate for snails infected with species i (d^{-1}), and c_i is the colonization rate of species i (d^{-1}). In this model, the fraction of occupied patches (i.e., snails; p_i) is the unit of population growth (assuming a fixed snail density). The model assumes that recruitment (the first term in Eq. 1) is a function of the colonization rate per infected snail, current prevalence, and the fraction of snails available to the focal species for colonization. Colonization rates incorporate the effect of all processes in the life cycle from when cercariae leave snails to when eggs or miracidia infect

new snails (see Appendix S1 in Supporting Information, "*Full parasite life cycle model*" for details). Trematode mortality in infected snails occurs due to constant background snail mortality (the second term in Eq. 1) and due to competitive displacement by superior trematode species (the third term in Eq. 1). Species subscripts are ordered by competitive rank (one being strongest competitor), and the sum over subscript j represents all superior competitor species in the dominance hierarchy (as defined below). The model assumes that (1) the snail population size is constant (i.e., that new uninfected snails replace infected snails that die); (2) all snails are equally susceptible; (3) barring competitive displacement, infections only die when their host snail dies; and (4) unless otherwise specified, snail mortality rate is the same for all trematode species: hereafter, m (Hechinger et al. 2009, Sousa and Gleason 1989). We did not consider the rarer trematode species (those absent from the sentinel snails) in the competition – colonization tradeoff model because we are unable to estimate their colonization rates. However, because they did not recruit to the sentinels we know that their colonization rates must be low enough to preclude coexistence of these subordinate species via the competition – colonization tradeoff. We also excluded from analyses the few double infections that occurred in the sentinel snails (because most double infections are transient).

To estimate colonization rates using our experimental data, we could solve Eq. (1) (see in Supporting Information Appendix S1: Eq. S5). However, we derived a simpler and more intuitive solution by assuming that only primary infection, and not competition or mortality, occurred during the experiment (see Hall et al. 2006 for similar assumption). The experiment was designed to satisfy these assumptions and thereby allow straightforward estimation of colonization rates. With these assumptions, the prevalence of infection with species i in sentinels, s_i, becomes a linear function of time, t (in days), background prevalence, p_i, and colonization rates, c_i:

$$s_i(t) = c_i p_i t. \qquad (2)$$

Any competitive displacement that occurred in the experiment would lead to underestimates of colonization rates for subordinate species, making the estimated strength of the tradeoff conservative.

To estimate daily mortality rates of infected snails (m), we used data from Lafferty (1993b) in which 10 out of 428 infected snails died during a 92-d growth experiment (the mortality rate of uninfected snails does not affect the model). We measured time as the days since the sentinel snail experiment began, excluding the winter (assumed to be November 1 through February 15 each year), when snails are quiescent and new infections unlikely, resulting in 258 active days per year. However, if snail mortality is high during this inactive phase, this method might underestimate mortality and affect the magnitude of the predictions for equilibrium prevalence and the number of species coexisting. We tested the effect of different mortality rates using sensitivity analysis, as described below.

TABLE 1. Description of the trematode species used in the study. Prevalence values are weighted by snail density in each sampling location (sites in the CSM data and estuaries in the global data). Species that did not recruit into the sentinel snails (zeroes in the 6th column) were not included in the models. 95% highest posterior density (HPD) intervals for are shown in parentheses for the two prevalence surveys for the species included in the models. The sample size in the 6th column is the cumulative number of sentinel snails shed over the course of the experiment (individual snails were shed multiple times).

Species abbreviation	Species name	Competitive rank	CSM prevalence ($n = 11\,641$)	Global prevalence ($n = 38\,711$)	Cumulative number of sentinel infections ($n = 4518$)
PARO	*Parorchis acanthus*	1	0.012 (0.010, 0.014)	0.015 (0.009, 0.022)	4
HIMA	*Himasthla rhigedana*	2	0.048 (0.044, 0.052)	0.029 (0.021, 0.037)	44
HIMB	*Himasthla* sp. B†	3	0.106 (0.099, 0.112)	0.016 (0.010, 0.022)	22
ACAN	*Acanthoparyphium spinulosum*	4‡	0.005 (0.004, 0.007)	0.018 (0.013, 0.025)	1
CLOA	*Cloacitrema michaginensis*	5‡	0.012	0.011	0
EUHA	*Euhaplorchis californiensis*	6§	0.218 (0.210, 0.228)	0.044 (0.033, 0.054)	395
PYGI	*Pygidiopsoides spindalis*	7§	0.012 (0.009, 0.014)	0.007 (0.004, 0.011)	9
PHOC	*Phocitremoides ovale*	8§	0.005	0.015	0
STIC	*Stictodora hancocki*	9§	0.020	0.027	0
MESO	*Mesostephanus appendiculatus*	10¶	0.009 (0.007, 0.011)	0.004 (0.002, 0.008)	1
LGXI	Large xiphidiocercaria†	11¶	0.001 (0.0006, 0.002)	0.019 (0.012, 0.026)	2
SMCY	Small cyathocotylid†	12¶	0.018 (0.016, 0.021)	0.021 (0.015, 0.027)	16
CATA	*Catatropis johnstoni*	13#	0.006	0.022	0
RENB	*Renicola buchanani*	14#	0.026 (0.023, 0.029)	0.010 (0.005, 0.014)	62
RENC	*Renicola cerithidicola*	15#	6.0×10^{-5}	0.003	0
PROB	*Probolocoryphe uca*	16‖	0.012	0.042	0
SMMI	Small microphallid†	17‖	0.001	0.025	0

†Recognized as species, despite not being formally described. LGXI is currently known to represent two different, but very similar (i.e., same competitive rank) species (Hechinger and Miura 2014).
‡Relative competitive ability of ACAN and CLOA is unknown.
§Relative competitive ability of EUHA, PYGI, PHOC, and STIC is unknown.
¶Relative competitive ability of MESO, LGXI and SMCY is unknown.
#Relative competitive ability of CATA, RENB and RENC is unknown.
‖Relative competitive ability of PROB and SMMI is unknown.

To determine whether the trematode species exhibit a tradeoff between competitive rank and colonization rate, we used an updated version of the competitive dominance hierarchy (Kuris 1990, Sousa 1993), derived from Hechinger (2010), listed in Table 1. We also tested three variations within unresolved parts of the hierarchy listed in Table 1: (1) PYGI > EUHA, (2) LGXI > MESO > SMCY, and (3) SMCY > MESO > LGXI. Further study is needed to increase confidence in these parts of the dominance hierarchy.

Model parameterization.—From the empirical data, we used Bayesian models to estimate posterior distributions of the parameters p_i, m, and c_i. These posterior distributions describe the most likely parameter values given the data and the prior assumptions, and they allow us to estimate the uncertainty around parameter values.

The model first estimated the posterior distribution of prevalence for each species, p_i, using the CSM prevalence dataset and assuming infections are binomially distributed with probability p_i and sample size equal to the number of snails dissected from each site (total sample size = 11,641). Because snail density varies by site, we calculated overall average prevalence of each trematode species in CSM by weighting the site-level prevalence estimates by snail density at each site. Next, the model used Eq. (2), the parameter estimates for p_i, and the sentinel snail recruitment data to calculate a posterior distribution of c_i values, assuming that the number of sentinels infected is binomially distributed with probability $s_i(t)$ and sample size equal to the number of snails shed on that sampling date. Finally, the model used the Lafferty (1993b) snail mortality data to estimate the posterior distribution of daily mortality rate, assuming

a binomial distribution with a mean $m = 1 - (1 - q)^{(1/92)}$, where q is informed by the observation of 10 deaths out of 428 snails and 92 is the number of days in that experiment. Because colonization rates are non-negative, we used Gamma-distributed priors for c_i, with parameters $\alpha = 1$ and $\beta = 1000$ (mean = 1/1000, variance = 10^{-6}). Since m and p_i can range from zero to one, we used Beta-distributed priors with parameters $\alpha = 1$ and $\beta = 2$ (mean = 1/3, variance = 1/18). Priors were set to be uninformative except for restricting parameters to their biologically meaningful ranges, allowing the data to shape the posterior distributions. By estimating uncertainty in the parameter estimates, the Bayesian models also made it possible to propagate uncertainty through parameter estimates and model predictions.

We fit each model using MCMC sampling in the "rjags" package in R (R Development Core Team 2012) and JAGS (Plummer 2003), running two chains for 10 000 iterations and saving 1/5 of samples after a 5000-step burn-in. This generated 2000 samples from each posterior distribution, maintaining the correlation structure between p_i, m, and c_i values. We used these "parameter samples" to assess the posterior distribution of model predictions by performing model calculations (e.g., predicted equilibrium prevalence) for the 2000 parameter sets. We summarized the variation in parameters and model predictions by calculating 95% highest posterior density (HPD) intervals, a type of credible interval that represents the shortest central interval that contains 95% of the mass of the posterior distribution, using the "HPDinterval" function in "rjags."

Assessing the impact of the tradeoff on coexistence.—
Stable coexistence requires that each species be able to invade when it is rare and its competitors are at equilibrium. To assess whether each species could invade when rare given the measured parameters, we used the model to derive an invasion criterion, i.e., the minimum colonization rate, c_i^*, that would be required for species i to invade in the presence of all superior competitors at their equilibrium prevalence, $\hat{p}_j$, given the mortality rate m.

$$c_i^* = \frac{m + \sum_{j<i} c_j \hat{p}_j}{1 - \sum_{j<i} \hat{p}_j}. \tag{3}$$

However, because of the strong asymmetrical competition, errors in the model-predicted equilibrium prevalence of dominants strongly influence the invasion criteria of subordinates. To overcome these compounding errors, we instead calculated the invasion criterion using the empirically estimated posterior prevalence of dominants for $\hat{p}_j$. Other expressions for invasion criteria are also available (Hastings 1980, Tilman 1994, Gross 2007) and are equivalent to Eq. (3) when the resident species are at equilibrium. When posterior estimated colonization rates c_i exceed c_i^*, species i can stably coexist with dominant competitors. This criterion predicts whether or not a species can invade when rare even if the expected

prevalence of dominant species is inaccurate, because it relies upon the field estimated prevalence of dominants. We further evaluated the model fit to empirical observations by calculating the model-predicted equilibrium prevalence of each species, given the estimated colonization and mortality rates, by solving Eq. (1) for its nontrivial equilibrium. We compared the model-predicted prevalence with the posterior prevalence estimates from the field data to assess model fit.

We also examined the sensitivity of our results to deviations from the observed background mortality rate by calculating predicted equilibrium prevalence across a range of snail longevity between 1–50 yr. Mortality rate can have a hump-shaped impact on persistence of subordinate species because it directly shortens their lifespan, while potentially reducing the abundance of dominant competitors and thereby freeing more space for subordinate species colonization. Because the invasion criterion (Eq. 3) assumes a fixed prevalence of dominant competitors (set by the observed field prevalence), it does not capture the hump-shaped effect of mortality rate on trematode persistence. Instead, we used the equilibrium prevalence calculation across a range of mortality rates to determine whether a different mortality rate would facilitate the coexistence of more species.

Spatial variation model.—We incorporated spatial heterogeneity in prevalence into the model using scale-transition theory (Chesson et al. 2005, Melbourne et al. 2005). In this theory, a Taylor expansion of Eq. (1) around the spatial average prevalence of each species yields the following equation for spatial average population growth (see Appendix S1 "*Using scale transition theory to estimate influence of spatial variation*" for full derivation):

$$\begin{aligned} \frac{d\bar{p}_i}{dt} = &c_i \bar{p}_i \left(1 - \sum_{j=1}^{i-1} \bar{p}_j - \bar{p}_i \right) - m\bar{p}_i - \sum_{j=1}^{i-1} c_j \bar{p}_j \bar{p}_i \\ &- c_i \text{Var}(p_i) - \frac{1}{2} \sum_{j=1}^{i-1} (c_j + c_i) \text{Cov}(p_j, p_i), \end{aligned} \tag{4}$$

where $\bar{p}_i$ represents the spatial average prevalence of species i, *Var* and *Cov* represent the spatial variance and covariance in prevalence, and all other terms are as defined for Eq. (1). The first three terms are the same as in Eq. (1) but using spatial mean prevalence. The fourth term describes how spatial aggregation increases intraspecific competition, and the fifth term reflects the intensifying (when negative) or ameliorating (when positive) effect of spatial variation on interspecific competition. Spatial variation in prevalence promotes population growth when reduced interspecific competition due to isolation outweighs increased intraspecific competition due to aggregation. Intraspecific competition arises because a single infection of a snail uses most or all of the available resources so that conspecific double-infections, if they occur, result in minimal increases in trematode reproductive output (Lagrue et al. 2007,
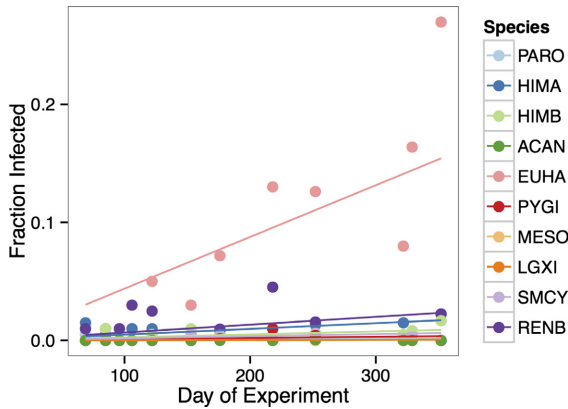
FIG. 1. Prevalence of each parasite species in the sentinel snails vs. time in field at Carpinteria Salt Marsh. The points are the data, and the lines are the fitted predictions. Points and lines are colored by trematode species, listed in the legend in order of descending competitive ability (Table 1 provides species abbreviations). Note that the x-axis does not go to zero, when all sentinels were uninfected.

Karvonen et al. 2011). Because the sum of the fourth and fifth terms in Eq. (4) can be positive or negative, spatial variation can either promote or undermine the persistence of subordinate species.

Similar to the competition – colonization tradeoff model above, for the spatial models we assessed the potential for coexistence by calculating both invasion criteria given the posterior prevalence estimates (using Appendix S1: Eq. S7). We also compared the model-predicted equilibrium prevalence (from Eq. 4) with observed prevalence to further assess model fit. To understand how spatial variation affects the invasion criteria, we made the simplifying assumption that spatial variation in prevalence is correlated with an environmental factor that determines habitat suitability for each trematode species (such as the abundance of host birds, fishes, or invertebrates). This assumption allowed us to calculate a spatial invasion criterion that inferred habitat suitability from variation in prevalence. Alternatively, assuming that spatial variation in prevalence is random with respect to underlying habitat quality would reduce how spatial variation impacts the invasion criterion by reducing the potential benefit of segregation to the invasion criterion (see Appendix S1 "*Invasion analysis in the spatial model*" for details).

Finally, because birds can move and deposit eggs and miracidia between estuaries, recruitment is not likely closed within CSM. In reality, recruitment likely incorporates a mix of local and regional dispersal between estuaries. Because we cannot measure the degree to which recruitment is closed vs. open, we explored an alternative scenario in which recruitment was globally well mixed across the geographic range of the trematodes, rather than closed within CSM. These local and global recruitment models represent opposing extremes between closed and open recruitment, and bracket model predictions around

the most likely recruitment scenarios. To model open recruitment, we refit the spatial model using background prevalence data from 40 estuaries in California and Baja California, hereafter the "global prevalence dataset". This dataset uses information on trematodes from three estuaries sampled in 2002 – 2004 (described in Kuris et al. 2008) plus 37 different estuaries over 2 months in 2005 (Hechinger et al., unpublished data). The latter effort involved sampling and dissecting snails from 40 quadrats randomly placed in each of 37 estuaries, resulting in ~26 000 dissected snails. Together, these surveys encompass over 90% of the horn snail populations occurring in West Coast salt marsh dominated estuaries and provide a good representation of trematode prevalence throughout this region. As with the CSM prevalence data set, we weighted average trematode prevalence across estuaries by the estimated snail density in each estuary.

Results

Over 19 months in CSM, the 1800 sentinel snails acquired 556 new infections by 10 trematode species (Table 1), plus 10 double infections. At the end of the study, prevalence in sentinel snails ranged across trematode species from 0.0007 (MESO) to 0.27 (EUHA) (Fig. 1). In the background snail population in CSM, the average prevalence from 11 461 snails was 0.46, representing all 10 trematode species that recruited to the sentinel snails; of those, ACAN and LGXI were lowest in prevalence and EUHA and HIMB were highest (Table 1). All focal species were detected in at least 50 snails in the CSM prevalence survey except LGXI, which was only detected in five.

Consistent with a competition – colonization tradeoff, subordinate species had higher colonization rates than dominant species on average (Fig. 2). Specifically, colonization rate declined with competitive ability, i.e., better competitors had lower colonization rates ($r = 0.50$). Two subordinate competitors, RENB and EUHA, had the highest colonization rates, while dominant species HIMB and subordinate species MESO had the lowest colonization rates (Fig. 2). Uncertainty in colonization rates (i.e., the width of the 95% credible interval shown in Fig. 2) was relatively large for some species, such as LGXI, PYGI, and RENB. These species tended to have low recruitment into the sentinels, low prevalence in CSM, or both. Resulting estimates of colonization rates were uncertain because of the imprecision of estimating the probability of rare events (i.e., recruitment in a sentinel given that colonization rate and/or background prevalence is low).

We used the invasion criteria to test whether the observed competition – colonization tradeoff was sufficiently strong to promote coexistence of all the trematode species. The invasion criteria predicted that five of the ten species could coexist, and the 95% credible interval spanned three to eight species coexisting (Fig. 3). All ten species could invade when rare for at least some portion
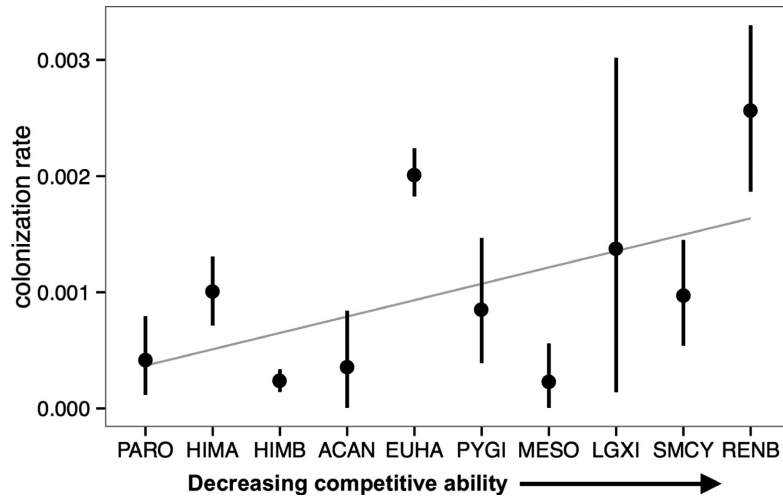
Fig. 2. Estimated colonization rates (d^{-1}) for the ten focal species in CSM (black), and a linear regression line showing the relationship between competitive rank and colonization rate (gray). Points are the mean values and error bars are the 95% highest posterior density (HPD) intervals of the posterior distributions. Species are listed from left to right in order of decreasing competitive ability (see Table 1 in the main text for abbreviations).

of the posterior distribution. Using alternative dominance hierarchies produced similar results, although six, rather than five, species coexisted on average in the PYGI > EUHA hierarchy. In sum, the competition–colonization tradeoff occurred and was strong enough to maintain coexistence of approximately half of the species.

Consistent with past work in this system (Lafferty et al. 1994), spatial variation did not promote coexistence overall, but slightly benefited some competitive subordinate species within CSM (Appendix S1: Fig. S1). Subordinate species MESO, LGXI, and RENB benefitted from spatial variation in CSM (Appendix S1: Fig. S1), as did RENC (a species that did not recruit into the sentinel snails). However, benefits of spatial variation in CSM were an order of magnitude smaller than the shortfall in colonization rates for subordinate species, so persistence of some species was not possible even with the benefits of spatial variation (Fig. 3). This shows that intraspecific aggregation tended to outweigh segregation of trematode species within CSM, except for some rare and subordinate species.

As a further test of model fit to field observations, we compared observed prevalence to the model-predicted equilibrium prevalence, given the estimated colonization rates and mortality rates. Measured colonization rates were higher than the model would predict for HIMA, EUHA, and RENB if the observed prevalence in the field represents a stable equilibrium. As a result of these differences and the strong asymmetric form of competition, the model-predicted equilibrium prevalence did not closely match the observed prevalence, whether or not spatial variation was included (Appendix S2: Fig. S1). This compounding error is a feature inherent to asymmetric competition models like this one (Hastings 1980, Tilman 1994, Calcagno et al. 2006).

The persistence of particular trematode species was sensitive to the background snail mortality rate. As

mortality rates increase, all trematodes suffered directly but subordinate species that follow the tradeoff (i.e., have sufficiently high colonization rates) could also benefit from a reprieve from competitive replacement, leading to species-specific hump-shaped relationships between prevalence and mortality (Appendix S1: Figs. S3 and S4). Regardless, the fit between expected and observed prevalence did not improve under different assumptions about background mortality rate (i.e., the observed background mortality rate promoted coexistence as well or better than higher or lower background mortality rates). Similarly, although a previous study suggested that some competitively dominant species cause elevated snail mortality under some stressful conditions (Sousa and Gleason 1989), including this differential mortality in our model did not explain the observed persistence of subordinate species (Fig. S5; see Appendix S1, "*Model with differential mortality across trematode species*" for details). Finally, we also tested a model in which trematodes could prevent subsequent infections through preemption, but the results did not fit observed prevalence (see Appendix S1 "*Model with space preemption*" for details).

Results of the open recruitment model were similar to the main (closed recruitment within CSM) model results but showed a weaker tradeoff. This model used the same sentinel snail recruitment data but refit colonization rates using prevalence data from 40 estuaries, assuming recruitment is open and well mixed. Although the competition–colonization tradeoff occurred, the average correlation between competitive rank and colonization rate was only 0.21, compared with 0.50 in the main model (Appendix S1: Fig. S6). Spatial variation did not promote coexistence for any species in the global recruitment model (Appendix S1: Fig. S7), but marginally benefitted the rare, subordinate species PHOC, STIC, CATA, and SMMI, which did not recruit into the sentinel snails.
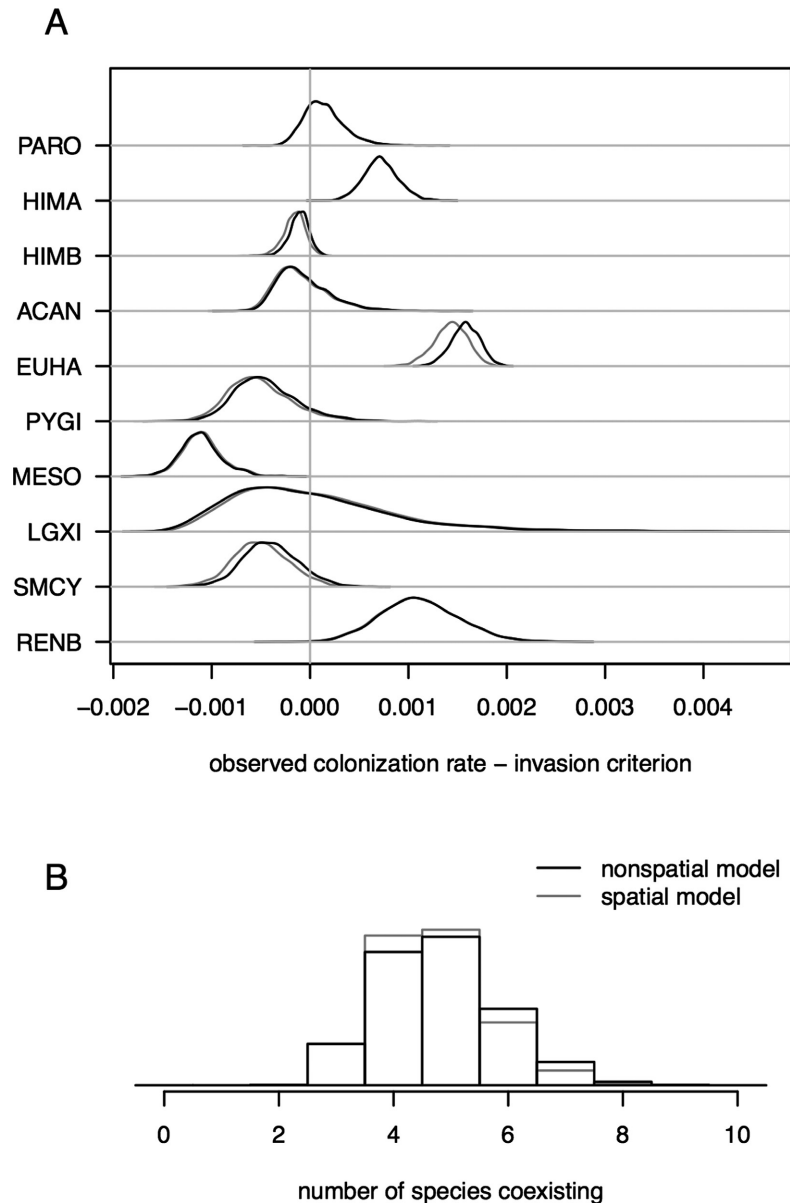
FIG. 3. Frequency distributions of the difference between the observed colonization rate and the invasion criterion (the colonization rate required for invasion when rare; both in d^{-1}) for each species (A), and histogram of the number of species predicted to coexist based on the invasion criterion (B). Predictions from the CSM nonspatial model are in black and for the CSM spatial variation model are in gray. Distributions represent the outcome across 2000 samples from the posterior distribution of estimated colonization rates, prevalence and mortality rates. In (A), positive values (to the right of the vertical line) indicate observed colonization rates large enough for invasion, given the observed prevalence of the competitively dominant species and the assumed mortality rate. Species are listed from top to bottom in order of decreasing competitive ability (Table 1 provides species abbreviations).

DISCUSSION

Although there is some empirical evidence for the existence of a competition-colonization tradeoff (Sebens 1986, Tilman 1994, Levine and Rees 2002, Stanton et al. 2002, Cadotte et al. 2006, Edwards et al. 2011), our study is one of the first to rigorously show the tradeoff is strong enough to maintain coexistence among competing species in nature. In our study, some subordinate species can coexist by recruiting more quickly than competitive dominant species. However, the tradeoff was only strong enough to sustain some species in the community (three to eight species, most likely five; Fig. 3), and the rest were competitively excluded. By contrast, spatial heterogeneity (another potential coexistence mechanism) had small effects that tended to intensify competition (Appendix S1: Fig. S4; Appendix S1: Fig. S6), although a few subordinate species weakly benefitted from

within- and among-estuary heterogeneity (Fig. 3; Appendix S1: Fig. S1).

Biological processes occurring throughout the trematode life cycle could underlie the competition – colonization tradeoff. Colonization rate in snails is a composite trait that integrates events occurring throughout the parasite life cycle, including cercariae that leave first intermediate host snails to infect second intermediate host fishes and invertebrates, metacercariae encysted in second-intermediate hosts, adult trematode interactions within birds, and eggs or miracidia that subsequently recruit to snails. Competitive dominance within the snail is largely determined by parthenita body size (e.g., large-bodied species can ingest smaller-bodied species), which is correlated with the size of individual dispersive offspring (cercariae). This may drive an offspring size vs. offspring number tradeoff, resulting in lower fecundity for the large-bodied dominants that could ultimately affect their recruitment into new snails. Similarly, the dominance of some species, including HIMA and HIMB, likely arises in part from their investment in an aggressive caste of soldier morphs within the snail (Hechinger et al. 2011, Garcia-Vedrenne et al. in press), with at least some cost to reproductive output. By contrast, some subordinate species appear to invest more in reproduction within the snail, probably an adaptive response for those species with a greater chance of being killed by dominants (Hechinger et al. 2009, Hechinger 2010). Adaptations that promote transmission to the second intermediate and final host stages also benefit species that are subordinate within the snail. For example, the relatively subordinate but most common species, EUHA, encysts on the brain and modifies the behavior of its second intermediate host, the California killifish, increasing trophic transmission to the final host (Lafferty and Morris 1996). Another common subordinate species, RENB, produces large, aggregating cercariae that attract second intermediate host fish to eat them and become infected (Martin 1971). Finally, and most immediately connected to recruitment into the snail, the first infective stage for dominants is more typically a short-lived miracidium (HIMA, HIMB, ACAN, PARO, MESO, SMCY, CATA), compared with the longer-lived egg of more subordinate species (EUHA, STIC, PHOC, PYGI, RENB, RENC, LGXI, PROB, SMMI), which may promote survival and ultimately transmission to the snail for subordinate trematodes. These and other life cycle differences probably contribute to the overall negative relationship (tradeoff) between competitive ability and colonization rates among species.

The competition – colonization tradeoff has strong empirical support in many systems (Sebens 1986, Tilman 1994, Levine and Rees 2002, Stanton et al. 2002, Cadotte et al. 2006, Adler et al. 2007, Cadotte 2007, Harbison et al. 2008, Edwards and Stachowicz 2010, Castorani et al. 2014, Bashey 2015), and the theoretical conditions under which it promotes coexistence are well established (Hastings 1980, Nee and May 1992, Tilman 1994, Adler and Mosquera

2000, Yu and Wilson 2001, Levine and Rees 2002, Amarasekare 2003, Calcagno et al. 2006). Yet few previous studies have directly applied a competition – colonization tradeoff model to empirical data to test whether observed tradeoffs are strong enough to maintain coexistence (Levine and Rees 2002, Adler et al. 2007). Such quantitative tests are important because requirements for the tradeoff to sustain coexistence can be strict, and may not match the biology of many systems (Geritz et al. 1999, Adler and Mosquera 2000, Levine and Rees 2002, Amarasekare 2003, Calcagno et al. 2006, Clark et al. 2007).

The tradeoff promotes coexistence in two ways: by reducing fitness differences between dominant and subordinate competitors, and by stabilizing coexistence (sensu Chesson 2000), thereby giving species advantages when rare. The tradeoff reduces the growth-rate (fitness) advantage of dominant competitors by disadvantaging them in colonization. The advantage when rare (stabilizing mechanism) arises for both dominant and subordinate competitors. For dominants, when they are rare they have all habitat patches available for colonization, regardless of occupancy by subordinates, whereas when they are common there is little remaining habitat for them to colonize. Subordinate competitors gain an advantage when rare under the tradeoff mechanism because dominants have lower colonization rates, and thereby leave more space available at equilibrium than the subordinate competitors. Despite this potential for stabilization, our empirically guided exploration of the competition – colonization tradeoff model suggests that it is unlikely to be the only, or even the main, stabilizing coexistence mechanism in most systems. First, the conditions required for the tradeoff to strongly stabilize coexistence—asymmetric, dominance competition with no space preemption—are unlikely to be met in many systems, without additional environmental variation to stabilize coexistence (Yu and Wilson 2001, Amarasekare 2003, Calcagno et al. 2006). Second, even in systems where the conditions for stabilization are met (such as the focal salt marsh trematode community), the tradeoff may be insufficiently strong to fully maintain coexistence. The tradeoff must be present not only on average but for every species in order to maintain the coexistence of all species. Departures from a strict tradeoff at the top of the hierarchy strongly limit the persistence of subordinate species. Moreover, the tradeoff must be finely tuned in order to promote coexistence and not result in competitive exclusion if a particular species' colonization rate is too low. The fact that the tradeoff can only sustain coexistence under a narrow range of fitness differences between species suggests that it provides a relatively weak stabilizing mechanism, consistent with previous theoretical work on single-axis tradeoffs (Clark et al. 2007). Instead, the competition – colonization tradeoff is more likely to operate as one of several coexistence mechanisms in most systems in which it occurs. This means that additional stabilizing mechanisms such as resource partitioning, fluctuation dependent mechanisms (Chesson 2000), or

tradeoffs between many different individual-level traits (i.e., high-dimensional tradeoffs, sensu Clark et al. 2007) are likely to be necessary in most systems where the competition – colonization tradeoff is present.

One class of fluctuation dependent coexistence mechanisms arises from variation in demographic performance over space. In this study, we applied nonlinear averaging across space to the competition – colonization tradeoff model and showed how the mechanisms combine in an empirical system. Our model results support previous findings that species must be negatively correlated in space in order for variation to promote coexistence, and that the benefits of spatial isolation between species must exceed the cost of aggregation within species (Chesson et al. 2005, Melbourne et al. 2005). More strikingly, we found that for this commonly used patch occupancy model (Hastings 1980, Tilman 1994), spatial variation is more likely to promote coexistence if the competition – colonization tradeoff does not occur (see Appendix S1 in Supplementary Information for details), similar to previous simulation results from a one-resource spatial competition – colonization tradeoff model (Gross 2007). This is because the colonization rates of dominant competitors determine the impact of interspecific competition, and therefore scale the potential benefits of spatial isolation, while the focal species colonization rate dictates the cost of intraspecific aggregation. As a result, for a subordinate competitor, a high colonization rate leads to a high cost of aggregation, while low colonization rates of competitive dominants lead to low benefits of isolation. Consistent with this theoretical result, the within- and among-estuary spatial analyses rule out this form of spatial segregation as a primary coexistence mechanism in the trematode system. Instead, increased intraspecific competition outweighs most of the potential benefits of spatial segregation within or among estuaries. These empirical results suggest that if spatial variation is important for coexistence it must interact with other factors such as variation in trematode demographic rates over time or across individuals (Clark et al. 2007).

Temporal variation in recruitment among species could also play an important role in the coexistence of salt marsh trematodes. The complex trematode life cycle creates many opportunities for temporal variation in recruitment to enhance species coexistence. Short-term stochastic or seasonal increases in recruitment at other life stages could benefit the longer-term population growth of trematodes, which can survive several years in this snail host. The resulting storage effect could benefit the persistence of rare species by offsetting their favorable periods for recruitment from periods favorable for competitively dominant species (Chesson and Grubb 1990, Chesson 2000). On the other hand, previous studies of temporal variation in trematode communities have found a high positive covariance among competing species that tends to increase competitive interactions rather than isolate species in time (Kuris and Lafferty 1994). Variation in lifespan in the adult stage could further promote storage effects. Temporal variation in our study system could lead to error in estimating

long-term mean colonization rates, making it more difficult to accurately capture observed patterns. Moreover, variation across time and individuals creates the opportunity for high-dimensional tradeoffs that are difficult to measure directly, but can strongly promote coexistence (Clark et al. 2007). Understanding how temporal variation in recruitment interacts with the competition – colonization tradeoff to affect coexistence is an important avenue for future empirical and theoretical work.

Given the multi-host trematode life cycle, the potential for movement within and between estuaries, and the many second-intermediate and final host species involved, it is remarkable that the study detected such a strong competition – colonization tradeoff, which could fully support the coexistence of half of the trematode species. Nonetheless, it is not surprising that this simple model does not completely capture the outcome of competition between trematodes. Gaps between predictions and field observations may arise from model assumptions or from unmeasured processes that contribute to trematode population growth. For example, recruitment into snails is linked indirectly to current snail prevalence, and variation over space and time could weaken the correlation between prevalence and recruitment. In addition, competitive displacement may not be strictly predictable based on the competitive hierarchy, and preemption could occasionally occur, particularly in the poorly resolved lower parts of the hierarchy (although this would not be sufficient to explain coexistence (Yu and Wilson 2001); see Appendix S1 "*Model with space preemption*"). Moreover, while our analysis of species-specific effects on host mortality showed no benefit of a tradeoff between dominance and longevity (see Appendix S1, "*Model with differential snail mortality across trematode species*"; Appendix S1: Fig. S5), better estimates of field mortality rates of infected snails could improve the model fit to field observations. Finally, our sentinel snail recruitment study was relatively short and geographically limited, and could have missed pulses or habitat variation in recruitment within and across estuaries. This opens the possibility that our field estimates of prevalence do not reflect a long-term stable equilibrium, as we assumed when comparing field prevalence to the model-predicted equilibrium. Future sentinel infection studies could measure variation in recruitment and prevalence across space and time, and models could incorporate the link between bird movement and recruitment more directly.

Competition – colonization tradeoffs occur in many systems (Sebens 1986, Tilman 1994, Levine and Rees 2002, Stanton et al. 2002, Cadotte et al. 2006, Adler et al. 2007, Cadotte 2007, Harbison et al. 2008, Edwards and Stachowicz 2010, Castorani et al. 2014, Bashey 2015), and are often invoked in maintaining coexistence, as well as in successional dynamics (Hastings 1980, Tilman 1990, 1994, Rees et al. 2001, Bergsten et al. 2013). Yet colonization and mortality rates have to be finely calibrated, and specific biological requirements met, for the tradeoff to fully support coexistence. Even for the focal salt marsh trematodes, which meet the biological requirements and

exhibit a strong tradeoff, the mechanism only sustained the coexistence of about half of the species. As a result, we argue that the competition – colonization tradeoff is unlikely to be the sole mechanism sustaining coexistence in most systems, and that its stabilizing effects are relatively weak. Instead, the tradeoff is more likely to operate in concert with other niche differences and temporal and spatial mechanisms. Multi-dimensional life history tradeoffs and demographic variation may combine with temporal and spatial variation to maintain coexistence of competing species in most natural systems (Clark et al. 2007, 2010, Edwards and Stachowicz 2010).

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