How invader traits interact with resident communities and resource availability to determine invasion success

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Competition for limited resources is considered a key factor controlling invasion success. Resource availability can be viewed in either the long or short-term. Long-term availability depends on the baseline nutrient availability in the ecosystem and how those conditions shape the ecological community. Short-term resource availability fluctuates with disturbances that alter nutrient availability and/or the density and composition of the ecological community.

We investigated how species' traits interact with short and long-term resource availability to determine the outcome of invasions. We manipulated long-term baseline resource availability, disturbance intensity, disturbance frequency, and propagule pressure in a fully factorial design using protist microcosms. Our results show that short and long-term resource availability and the direct mortality from disturbance interact with the traits of resident community members and traits of invaders to determine community invasibility. While competitively dominant invaders with slow growth rates may suffer rather than benefit from short-term resource fluctuations, quickly growing but competitively inferior invaders can benefit from both the resource fluctuations and the heterogeneity in community composition created by disturbance. Our findings empirically synthesize two explanations for invasion success, namely short-term resource fluctuations and long-term resource availability, and highlight the importance of considering traits of invaders and residents, such as growth rate and competitive ability, in the context of productivity and disturbance gradients. This species' traits approach could resolve idiosyncratic results from natural systems undergoing disturbance and invasion that do not follow patterns predicted by traditional invasion frameworks.

Understanding which community and invader characteristics facilitate establishment of invasive species has been the subject of intense study for decades (Elton 1958, Lonsdale 1999, Mack et al. 2000, Sakai et al. 2001). Elton (1958) hypothesized that invasibility is determined by overall resource availability, which in turn relates negatively to community diversity and density. More recently, Davis et al. (2000) and Tilman (2004) emphasized the importance of resource fluctuations, rather than overall resource availability, in determining invasibility. Disturbances are the most commonly cited cause of resource fluctuations, and they can increase resource availability by decreasing resident uptake or moving resources within a system. The magnitude of those fluctuations, however, depends on long-term nutrient availability, disturbance severity, and the interaction of those factors with species' traits to influence community density and composition. In this paper, we manipulated disturbance character to test how disturbance-mediated short-term resource fluctuations, disturbance-mediated mortality, and long-term resource availability influence the resident community and the invasion success of two species with disparate competitive and reproductive abilities.

Although we present our study in an invasion context, and the supporting literature draws heavily from theoretical and empirical support developed in the context of invasive species, our study is also highly relevant to more general considerations of community assembly.

Long-term resource availability and short-term resource fluctuations

A successful invader must be able to capitalize on resources that are unused by resident competitors and avoid stochastic extinction due to small population size (Tilman 2004). Resources may become available over long or short time periods. Long-term resource availability is determined by baseline nutrient supply rate and the rate of resident resource uptake. Partitioning of these long-term resources among species is a stabilizing mechanism of diversity maintenance, increasing the impact of intraspecifc interactions relative to interspecific interactions (Chesson 2000). Elton (1958) hypothesized that higher resident diversity would lead to lower invasibility because resources would be more efficiently partitioned, lowering long-term resource

availability. Though there are examples of a negative relationship between diversity and invasibility (Tilman 1997, Knops et al. 1999, Levine and D'Antonio 1999, Stachowicz et al. 1999, Naeem et al. 2000, Kennedy et al. 2002), there are also a number of examples of diversity having a neutral or positive relationship with invasibility (Lonsdale 1999, Stohlgren et al. 1999, Levine 2000). Many observational studies find a positive relationship between diversity and invasibility at larger scales, likely reflecting environmental heterogeneity that favors native and invasive diversity (Davies et al. 2005, 2007, Stohlgren et al. 2006). Modeling work using the classic Lotka–Volterra competition framework suggests that, as the scale of observation increases and includes more species and resources, the degree to which those species and resources impact the sum of interspecific interaction strengths will determine the diversity–invasibility relationship (Byers and Noonburg 2003). Adding species will increase interspecific competition and decrease invasibility, while adding resources will counteract that effect and increase invasibility.

More recently, Davis et al. (2000) and Tilman (2004) emphasized the importance of short-term resource fluctuations, rather than long-term resource availability, in determining community invasibility. Disturbance is one possible cause of resource fluctuations. Disturbance can decrease nutrient availability through leaching, increase nutrient availability by decreasing resident uptake or transporting nutrients spatially, or have no effect. When disturbance causes resource pulses, through resident mortality or a biochemical release of nutrients, it can create windows of greater invasibility (Hobbs and Huenneke 1992, Burke and Grime 1996, Davis et al. 2000, Davis and Pelsor 2001, Shea and Chesson 2002). The significance of those windows to invading species depends on the amplitude of the fluctuations, as determined by long-term nutrient availability and disturbance severity, and the propagule pressure of resident and invading species. Propagule pressure mediates the relationship between disturbance and invasibility by counteracting the negative effects of disturbance on both invasive and native species (Lockwood et al. 2005, Colautti et al. 2006). In this context, disturbance promotes invasion by serving as an equalizing mechanism of coexistence, minimizing the fitness differences between species (Chesson and Huntly 1997, Chesson 2000). As an equalizing mechanism, disturbance slows, but cannot stop, competitive exclusion in the long-term under constant environmental conditions. In the short term, however, disturbance can have profound effects on community composition and potentially allow inferior competitors to persist until conditions change in their favor.

Huston's (2004) dynamic equilibrium model (DEM) accounts for the impacts of short and long-term resource availability on invasibility by incorporating productivity, diversity, and disturbance into one theoretical framework. According to the DEM, in highly productive environments where species have rapid growth rates, frequent and/or severe disturbance is required to counterbalance competition-driven extinction. Alternatively, in unproductive environments where species have slow growth rates, infrequent and/or mild disturbances are adequate to slow competitive exclusion and promote invasion. The DEM, therefore, is a modified form of Connell's intermediate disturbance hypothesis (1978), which suggests that diversity peaks when disturbance levels are intermediate relative to species' growth rates and those growth rates are affected by productivity. Empirical support for the DEM is mixed. McCabe and Gotelli (2000) found some support for the importance of growth and competitive exclusion rates in determining the effect of disturbance on diversity, though they did not manipulate productivity. Others, however, have found interactions between productivity and disturbance in determining diversity that are variable through time and differ qualitatively from DEM predictions (Scholes et al. 2005), or have found no interaction at all (Svensson et al. 2007).

Invader and resident species' traits

Applying the DEM to real communities, however, it is important to consider how the traits of invading and resident species interact with disturbance-influenced resource availability and disturbance-driven mortality to not only impact the speed of interspecific interactions, but also community composition and the competitive environment. Grime (1977) outlined three life history strategies competitors may take within a community: the competitive, stress-tolerant, and ruderal strategies. The latter is often attributed to invasive species. Successful invaders often have plastic growth rates that respond readily to resource pulses (Daehler 2003, Gerlach and Rice 2003, Burns 2004), and greater resource use efficiency, growth rates, and/or reproductive output than congeneric species that are either native, or not native but not invasive (DeFalco et al. 2003, Grotkopp and Rejmanek 2007, Feng and Fu 2008, Muñoz and Ackerman 2010, Matzek 2011). Those differences, however, can diminish, disappear, or even be reversed along resource gradients, emphasizing the need for consideration of species' traits in frameworks of invasibility (Radford and Cousens 2000, Burns 2006, Richards et al. 2006).

Resident species' traits also play a prominent role in invader establishment. Deterministic factors, such as interspecific interactions and the abiotic environment, shape the available niches in an ecosystem. Environmental and demographic stochasticity interact with those deterministic factors and introduce an element of randomness in community composition. The magnitude of stochastic influence, however, depends on community density, defined as the total number of individuals in a community. As communities become smaller, such as through decreasing resources or increasing disturbance, the role of deterministic processes decreases relative to the role of stochasticity (MacArthur and Wilson 1967, Hubbell 2001, Orrock and Fletcher 2005, Orrock and Watling 2010). In big communities with large, stable populations of many species, competitive ability is of primary importance for invader establishment. As communities shrink, populations of resident species become smaller and more prone to stochastic extinction (Orrock and Fletcher 2005). Resident extinctions open niche opportunities for invaders, particularly if strong competitors become extinct (Orrock and Watling 2010). If disturbance is the cause of community shrinkage, and the community displays a competition–colonization hierarchy, strong competitors that reproduce slowly may be the first species to go extinct as community density decreases.

Hypotheses

Our study asks how disturbance-induced resource pulses interact with long-term nutrient availability and propagule pressure to determine the invasion of microcosm communities by two species with disparate traits. Rather than focusing on the subset of invasive species that are destructive, we address general questions about what allows novel species to invade established communities, making our results also applicable to community assembly processes involving native species. We conducted our experiment over multiple generations in laboratory communities consisting of naturally co-occurring freshwater protists. Microcosm studies allow replication and simplicity in studies of long-term dynamics that is nearly impossible in field systems (Warren et al. 2006).

We used two species that are novel to the system as invaders: *Tetrahymena pyriformis*, a competitively weak but rapidly reproducing species (termed the 'Reproducer'), and *Euplotes eurystomus*, a competitively strong but slowly reproducing species (the 'Competitor'). Table 1 summarizes our general predictions regarding how life-history strategies (focusing on reproduction versus competition) are tested in our treatments. We hypothesized that increasing disturbance intensity and frequency would increase invasibility by the Reproducer through resource pulses and shifts in community composition toward r-selected species. Conversely, for the Competitor we hypothesized that increasing disturbance would either have no effect, or a negative effect through disturbance-induced mortality. We expected nutrient availability to enhance the Competitor's establishment by providing additional resources and to suppress the Reproducer by creating a denser community dominated by species that were more effective at competition. The positive effect of propagule pressure on establishment is expected to increase establishment of both types of invader by decreasing the frequency of stochastic extinction. The positive effect of propagule pressure is expected to increase in communities with slower finite growth rates resulting from high disturbance severity and nutrient deprivation.

Methods

We conducted our experiment in aquatic microcosms. Experimental disturbance and nutrient treatments created a gradient of resident species richness and diversity, as well as community density. The resident bacterivore protist community originated in a single pond in New Jersey, USA (McGrady-Steed et al. 1997). Our general approach was as follows: 1) to establish a community of eight protozoan species known to naturally co-occur; 2) immediately subject that community to a sustained drop in available nutrients or allow it to remain the same; 3) implement disturbance for 31 days; 4) introduce two new species that did not occur in the pond and that differed in key traits of growth rate, carrying capacity, and competitive ability; and 5) continue the disturbance regime for 31 more days. Each 31-day period represents between approximately 39 and 218 generations (time from one division to the next) of the study species, based on finite growth rates given in Haddad

Table 1. Predictions for community characteristics and invader success under varying nutrient and disturbance conditions. The 'Competitor' refers to *Euplotes eurystomus* and the 'Reproducer' refers to *Tetrahymena pyriformis*.

		Short term resource availability	
		Less severe disturbance	More severe disturbance
Long-term resource availability	High nutrients	Community type: very dense, intermediate species richness – Competitor favored	Community type: somewhat dense, high species richness – Reproducer slightly favored
	Low nutrients	Community type: somewhat sparse, high species richness – Competitor slightly favored	Community type: very sparse, low species richness – Reproducer favored

et al. (2008). The response of individual protist species during growth trials outlined in our results and those of Haddad et al. (2008) suggests that abiotic resource levels were an adequate proxy for biological (bacteria) resource levels.

Establishing the native communities

Each replicate began as a 240-ml glass bottle filled with 100 ml of bacterized nutrient medium and inoculated with approximately 50 individuals of each protist species. Tinfoil covers excluded most airborne contaminants while allowing oxygen to reach the communities. To create the nutrient medium, we autoclaved 1.5 l of bottled spring water mixed with 2.4 g sterilized and sifted soil and 0.6875 g protozoa pellet. Approximately 12 h before using the medium, we added 2 ml of a stock bacteria culture containing *Bacillus cereus*, *B. subtilus* and *Serratia marcescens*. We then created a stock solution of the eight protozoan species native to the single pond, including *Coleps* sp., *Colpidium* sp., *Cyclidium* sp., *Euglena* sp., *Euplotes* sp., *Paramecium aurelia*, *P. bursaria* and *Spirostomum* sp., and added it to the bacterized medium (details in Haddad et al. 2008). These species represent a range of reproductive and competitive abilities. Throughout this paper, we define 'competitive ability' using species ranks based jointly on their ability to persist and their ability to cause extinctions in pair-wise comparisons with each of the other species in the community (Cadotte et al. 2006).

Establishing and maintaining the disturbance regime

Before disturbing our microcosm communities, we thoroughly mixed the liquid in each replicate (bottle) to spatially homogenize the communities. Because of the mixing, we assumed that the solution we removed in the following step contained an equal proportion of each species' population, thus inflicting equal mortality levels across species. We then removed a proportion of that solution (and the protozoa inhabiting it at rates equivalent to the amount of media removed) according to the nutrient, intensity, and disturbance treatments, and replacing the solution with the appropriate nutrient medium. We used two levels

of nutrient concentration, high and low, throughout the experiment. The nutrient concentrations were chosen arbitrarily to represent extremes. We started all communities under the same high nutrient conditions to establish self-sustaining populations and then inflicted low-nutrient conditions on half of the bottles during the first disturbance. This caused an initial drop in nutrients that was more severe with increasing disturbance intensity. To maintain the nutrient regimes, at each disturbance we either replaced the medium with standard soil water (high nutrient treatment) or with dilute soil water (low nutrient treatment). For 31 days before invasion, we varied the intensity and frequency of disturbance under high and low nutrient regimes in a fully factorial design. We define disturbance intensity as percent mortality per disturbance. We varied disturbance intensity by thoroughly mixing the contents of each bottle with a pipette and then removing 50, 89 or 98% of the medium and replacing it with protozoan-free, nutrient-enriched, bacterized media that kept nutrient levels constant over the course of the study despite varying disturbance levels. Those disturbance frequencies represent low, intermediate, and severe disturbance mortality, respectively. Our chosen levels of disturbance intensity are artificial in that they do not represent known disturbance intensities in nature, but reflect our perception of the abilities of the species in our communities to adapt to disturbance. We expected and then confirmed that most species could cope with 50% disturbance under the varying nutrient and disturbance frequency regimes, and that fewer could tolerate 98% disturbance, particularly when disturbance frequency was also high and nutrients were low. We predicted that removal of 89% of the medium would represent an intermediate disturbance intensity, in terms of species' richness and density, based on species' growth rates. Disturbance frequency describes the interval between disturbances. We varied disturbance frequency by disturbing communities either once every 3.5 or 14 days, which was also based on our perception of high and low frequencies of disturbance relative to our species' growth rates and generation times. Disturbances began one week after communities were assembled. Additionally, we maintained undisturbed control bottles that were not part of the factorial design. The controls began just as the treatment bottles, but never underwent disturbance. Each week starting the third week we replaced 10% of the medium in the control bottles with soil water to prevent a slow decline in nutrient availability and accumulation of waste products. We created 10 replicates of each treatment plus 10 controls for a total of 130 bottles.

After 31 days, we sampled the densities of each species, providing pre-invasion estimates of diversity and abundance of protozoan communities. To sample the communities prior to invasion, we thoroughly mixed the contents of each bottle using a pipette and then removed a 10 ml sample. Protists were counted in 10 1-ml drops from a pasteur pipette, or larger volumes until we reached a minimum of eight individuals of each species. We also diluted samples if populations were too dense to count in drops under a stereomicroscope. For most species, considerably more than eight individuals were counted in the 10 drops, but a minimum was required to reduce sampling error. After sampling, we replaced the medium according to the nutrient level of the treatment. After 31 days, the disturbance and nutrient regimes had significantly affected community richness and composition, creating very different biological and physical environments to which we introduced our invaders. The full analysis of the effects of disturbance and nutrients on these communities up to that point, prior to invasion, is presented in Haddad et al. (2008).

Introducing the invaders and measuring their r_0 and K

After sampling at 31 days, we let the communities establish for four more days and then introduced two new species: *Euplotes cf. eurystomus* (the Competitor) and *Tetrahymena pyriformis* (the Reproducer). We hereafter refer to these two species as 'invaders' and 'invading' species, although our use of that terminology lacks the connotation of negative impacts on the native community. These species came from stock cultures and did not originate from the same community as the other eight species. *Euplotes eurystomus* feeds primarily on bacteria but can also feed on small protozoa (Kloetzel 1974, Naeem and Li 1998). Other species of *Euplotes* demonstrate an intermediate competitive ability when compared to other species in our community (Cadotte 2007), and in this study we assume that *E. eurystomus* is similarly situated in the middle of the competitive hierarchy. *Tetrahymena pyriformis* is a much smaller bacterivore that is a poor competitor (Cadotte 2007). Using the 10 replicates per treatment combination (2 nutrient levels × 2 frequency levels × 3 intensity levels × 10 replicates = 120 communities total), we introduced both *E. eurystomus* and *T. pyriformis* to every bottle at two densities, 25 or 300 individuals per species, each in five replicates (see Fig. 1 for experimental diagram). We continued to disturb the communities as described above for an additional month, and sampled
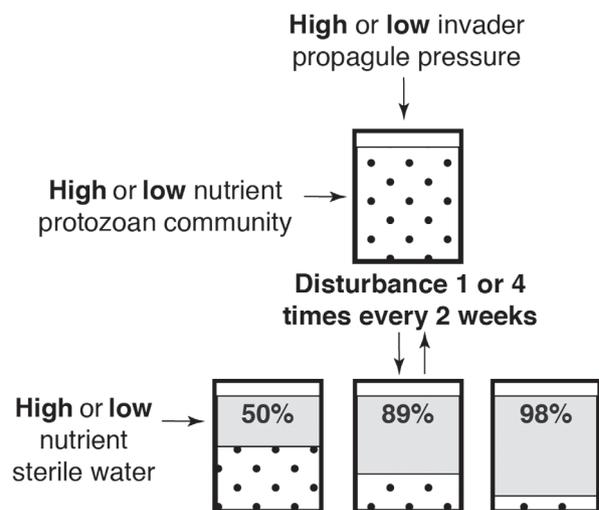

Figure 1. Experimental design. *Euplotes eurystomus* and *Tetrahymena pyriformis* were added to communities at high or low propagule pressure. Communities were disturbed once or four times every two weeks (disturbance frequency) by homogenizing and removing 50, 89 or 98% of the media (disturbance intensity) and replacing it with high or low nutrient media. Each treatment combination had 10 replicates, for a total of 120 replicates across the experiment.

on days 62 and 63 for species diversity and abundance as described above. Because of the large and very time-sensitive effort in sampling the communities, we chose to focus on the endpoint result of introduction rather than a time series study of temporal dynamics between the pre and post-invasion sampling. The rapidity of protozoan population dynamics, with these species going through as few as 57 (*E. eurystomus*, high nutrients) or as many as 598 (*T. pyriformis*, high nutrients) generations in 31 days, made it impossible to sample the invading species at the very early stages of establishment. We believe that sampling at 62 days is a reasonable representation of the invading species' probability of long-term establishment.

Separately, we grew *E. eurystomus* and *T. pyriformis* in monoculture in high and low bacterized nutrient solutions to estimate their finite growth rates and carrying capacities in the absence of interspecific competitors. We started our cultures at 0.24 individuals ml^{-1} and 0.17 individuals ml^{-1} for *T. pyriformis* and *E. eurystomus*, respectively. We sampled *E. eurystomus* density at 0, 30, 60, 75, 150, 300, 500, 700 and 800 h, and *T. pyriformis* density at 0, 25, 30, 50, 75, 150 and 300 h, which was sufficient time for population densities to approach asymptotes.

Analyses

We tested invader establishment as a presence/absence outcome using a generalized linear model with a logit link function, assuming a binomial distribution, and weighting for sample size. The model consisted of intensity, frequency, nutrient level, and propagule pressure as independent variables, and *E. eurystomus* and *T. pyriformis* presence as dependent variables in two separate analyses. Models for both species included all interactions up to three-way interactions. We excluded the four-way interaction term because it was not significant in either analysis. We treated disturbance intensity as a continuous variable because the odds of establishment for both introduced species showed a linear relationship with disturbance intensity. We treated disturbance frequency, propagule pressure, and nutrient level as categorical variables. We excluded control treatments from this analysis because they could not be part of the fully crossed design; a Dunnet's test confirmed that the controls were no different in species richness than the least disturbed treatment (50% intensity, once weekly frequency, high nutrients, alpha = 0.05). To remedy model convergence problems from treatment combinations with complete or quasi-complete separation of data points, we used the Firth's penalized likelihood method with 100 iterations. We analyzed effects using a type 3 analysis based on the Wald χ^2-test (alpha = 0.05). A type 3 analysis is similar to a type III sum of squares analysis, except that it is based on likelihood ratios. The models for both *E. eurystomus* and *T. pyriformis* met convergence criteria (1×10^{-8}) and satisfied the Hosmer and Lemeshow goodness-of-fit test for a binary logistic regression (alpha = 0.05).

We characterized community composition before and after invasion with general linear models and regression analysis in the SAS system (9.1.3, SAS Inst.) and with non-metric multi-dimensional scaling (NMDS) using PRIMER v6 (Clarke 1993, Clarke and Gorley 2006). We inspected

quantile plots visually to confirm normality. We tested the effect of nutrients, disturbance intensity, and disturbance frequency on species richness and community density ($\log_{10}$(community density $+1$)) using general linear models. We treated disturbance intensity as a continuous variable. To visualize the interactions, we then ran separate regression analyses to test the relationship between disturbance intensity and either species richness or community diversity, one analysis for each of the four possible treatment combinations of nutrients and frequency.

To better understand the community composition of the different treatment combinations, we used NMDS. First, we performed a $\log_{10}$(density $+ 1$) transformation on abundance of each resident species in each replicate community. Second, we generated a zero-adjusted Bray–Curtis similarity matrix of the communities using a correction of $\log_{10}(1 + 0.01) = 0.041$, which represents the lowest possible density in our experiment after the $\log_{10}$ transformation ($0.01 = 1$ individual 10 ml^{-1}). We applied the zero-adjusted Bray–Curtis technique to de-emphasize the dissimilarity between very depauperate communities caused by harsh disturbance (Clarke et al. 2006). Pre- and post-invasion communities were plotted on the same non-dimensional axes, such that distance between communities is a measure of dissimilarity.

To determine carrying capacities and maximum per capita growth rates (r_0) of invading species (i.e. the growth rates when resources are not limiting), we fit logistic models using Proc NLIN in SAS. We additionally tested exponential and theta-logistic models, but logistic models provided the best fit as determined by AIC.

Results

Invader establishment

Despite the lack of persistence of *Euplotes eurystomus* (the Competitor) when grown in low nutrient monoculture, disturbance intensity was the only factor that significantly affected establishment of *E. eurystomus* (p = 0.006; Table 2). As disturbance intensity increased from lowest to

Table 2. Type 3 analysis of effects for the binary logistic regression including all terms up to three-way interactions. Alpha = 0.05, n = 120. Only significant factors are shown. Because *T. pyriformis* establishment was influenced by a significant three-way interaction, all factors and two-way interactions within that three-way interaction are shown regardless of significance.

Species	Parameter	DF	Wald χ^2	p
E. eurystomus	intensity	1	7.6523	0.0057
T. pyriformis	nutrients	1	1.8775	0.1706
	intensity	1	8.0088	0.0047
	frequency	1	2.8878	0.0892
	propagule pressure	1	2.7730	0.0959
	intensity × propagule pressure	1	4.5805	0.0323
	nutrients × intensity	1	1.5740	0.2096
	nutrients × frequency	1	3.4904	0.0617
	intensity × frequency	1	3.4234	0.0643
	nutrients × intensity × frequency	1	4.4971	0.0340

highest levels, the probability of *E. eurystomus* establishing dropped from 84% to 38%. At a disturbance intensity of 89%, regardless of frequency, nutrients, or propagule pressure, *E. eurystomus* had about a 50% chance of establishing (Fig. 2a).

The establishment dynamics of *Tetrahymena pyriformis* (the Reproducer) were more complicated (Table 2). Disturbance intensity significantly interacted with propagule pressure (p = 0.03). As disturbance intensity increased, so did probability of establishment. The probability of establishment rose more sharply, however, when propagule pressure was low (Fig. 2b). There was also a significant three-way interaction between nutrient availability, disturbance intensity, and disturbance frequency (Fig. 2c–d). When nutrient levels were high and disturbance frequency was also high, disturbance intensity had a more positive influence on establishment (Fig. 2c). The effect of intensity was negligible when nutrients were high but disturbance frequency was low, with *T. pyriformis* having a uniformly low probability of establishing (Fig. 2c). When nutrient levels were low, the positive effect of disturbance intensity on

probability of establishment was not dependent on disturbance frequency (Fig. 2d).

Community composition and density

Disturbance affected species richness and community density similarly both before and after invasion (Fig. 3, 4, regression coefficients and r-square values in Supplementary material Appendix A1 Table A1). Prior to invasion, increasing intensity and frequency of disturbance, and decreasing nutrient levels reduced species richness (Fig. 3a, c) as described fully in Haddad et al. (2008). Conversely, prior to invasion, community density only decreased significantly with intensity when frequency was high and/or nutrients were low (Fig. 4a–b). After invasion, communities still showed a decrease in richness with increasing disturbance intensity (Fig. 3c–d), but high nutrient communities showed a lesser decline in richness when frequency was high (Fig. 3d). When nutrients were low, however, communities showed a steeper decline in richness with increasing disturbance intensity when disturbance frequency was high (Fig. 3d).
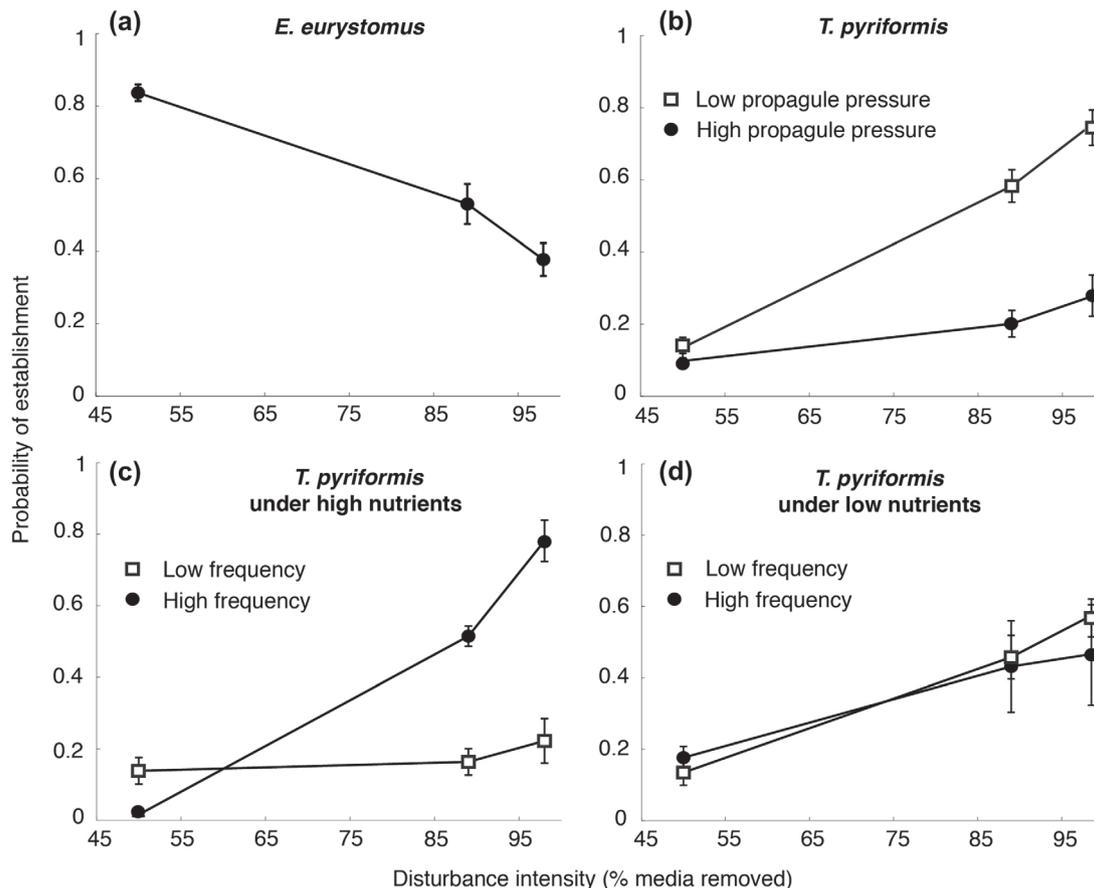

Figure 2. All significant interactions between nutrients, intensity, frequency and propagule pressure in affecting invader establishment. Mean probability of establishment and standard error bars shown for each treatment represented on the graph, though in some cases error bars are small and covered by the data point (n = 10 per treatment combination, 120 replicates total). (a) Intensity decreased establishment of *E. eurystomus*. (b) Intensity increased establishment of *T. pyriformis*, but more so when propagule pressure was also low. (c) and (d) demonstrate the three way interaction between nutrients, intensity, and frequency on *T. pyriformis* establishment. (c) Under high nutrients, probability of establishment increased with disturbance intensity when disturbance frequency was also high. When disturbance frequency was low but nutrients remained high, intensity had no effect on establishment. (d) Under low nutrients, establishment increased with disturbance intensity, but was not affected by disturbance frequency.
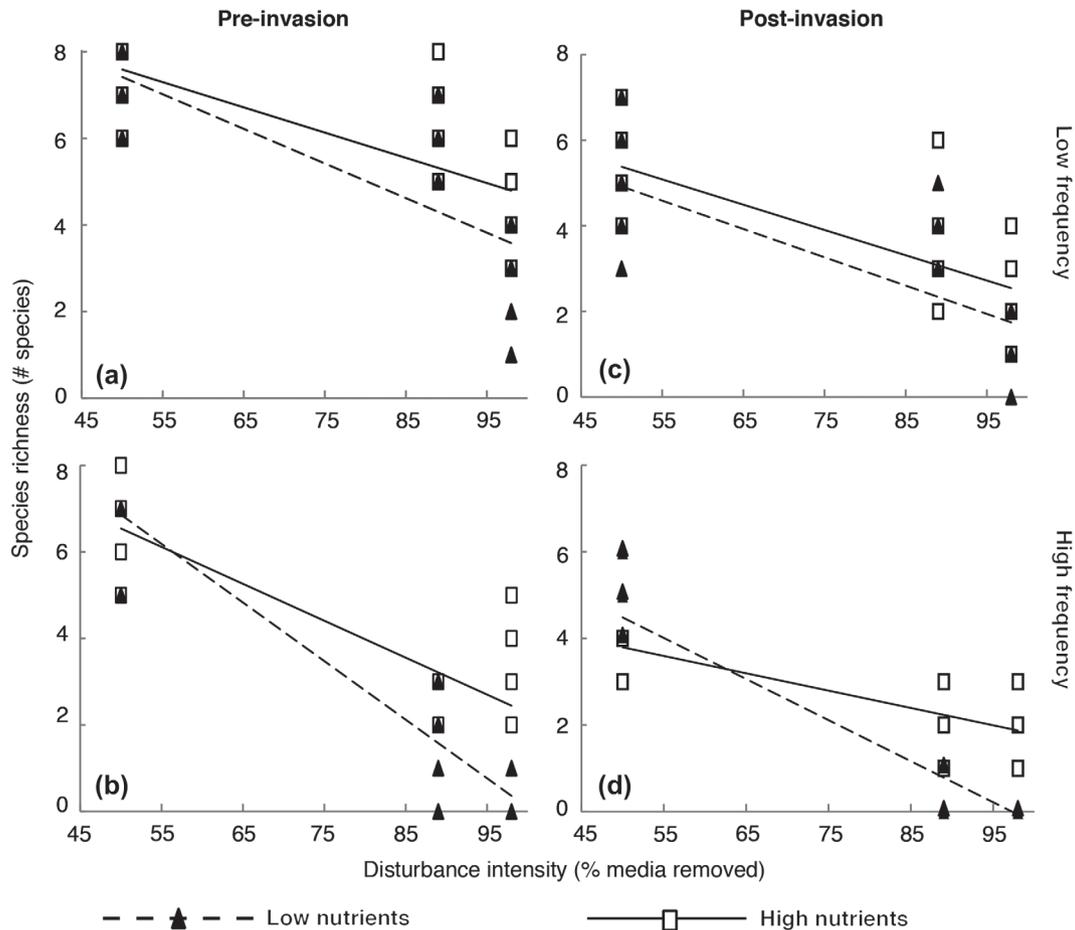
Pre-invasion **Post-invasion**

Figure 3. Linear regression results for effects of disturbance intensity on species richness under varying nutrient and disturbance frequency regimes (n = 10 for each treatment combination). Increasing disturbance intensity decreased species richness before and after invasion across treatments. Low nutrient availability exacerbated this decrease under high frequency conditions (b, d). Regression coefficients and model r-square values are available in Supplementary material Appendix A1 Table A1.

Post-invasion community density showed a slightly positive relationship with disturbance intensity in communities with high nutrients and high disturbance frequencies (Fig. 4d, p < 0.001), and no relationship under high nutrients and low disturbance frequencies (Fig. 4c, p = 0.69). When nutrients were low, disturbance intensity lowered community density, more so than under high disturbance frequency (Fig. 4d).

Pre and post-invasion resident communities generally separated along the y-axis of the NMDS plot, showing a shift in composition over time (Fig. 5). Low nutrient communities were more variable than high nutrient communities before and after invasion, both within treatments and between treatments (Fig. 5a). Frequency had little effect on community composition. Despite our predictions, high frequency communities were not more variable either within or between treatments (Fig. 5b). Lastly, higher levels of disturbance intensity (89% and 98%) promoted more variability in community composition both within and between treatments than 50% disturbance intensity (Fig. 5c). Nutrients levels and disturbance intensity, therefore, account for most of the abiotically-driven changes in community composition. Greater variability in composition

within treatments for low nutrient, high disturbance intensity communities suggests a larger role for stochasticity.

Abundances for each species in each of the 12 treatment combinations were variable but somewhat predictable based on treatment type (Table 3). Regardless of other treatment conditions, almost all species were more likely to be present and more abundant in higher nutrient communities, with the exception of *P. bursaria* and *Euglena* sp., the two resident mixotrophs (species that can both photosynthesize and consume bacteria). Mild disturbance treatments included the most species, though the two species of *Paramecium* were dominant. *Colpidium* sp. and *P. aurelia* best maintained abundances with severe disturbance, while *Spirostomum* sp. was completely intolerant of all but the mildest disturbances.

Growth rate and carrying capacity

As expected, *T. pyriformis* (the Reproducer) had a faster growth rate and higher carrying capacity than *E. eurystomus* (the Competitor) when grown in monoculture in bacterized nutrient medium. In high nutrient conditions, *T. pyriformis* populations grew at 2.53 (95% CL = 2.03–3.04) individuals
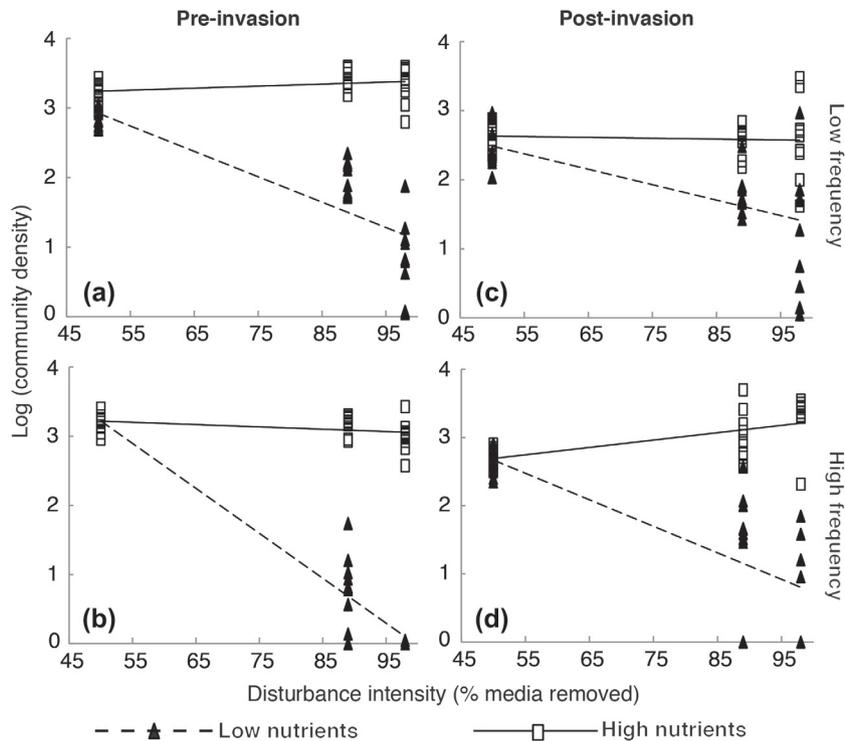
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Figure 4. Effects of disturbance intensity on community density under varying nutrient and disturbance frequency regimes (n = 10 for each treatment combination). Increasing disturbance intensity decreased community density under low nutrient conditions before and after invasion. Under high nutrient and low disturbance frequency, disturbance intensity had no effect on community density before and after invasion (a, c). Under high nutrient and high disturbance frequency, the effect of disturbance intensity changed before and after disturbance (b, d). Before disturbance, increasing intensity decreased community density (b). After disturbance, increasing intensity increased community density (d). Regression coefficients and model r-square values are available in Supplementary material Appendix A1 Table A1.

individual^{-1} per day and had a carrying capacity of 3892 individuals ml^{-1} (95% CL = 2899–4885). When nutrients were low, the finite growth rate and carrying capacity was 2.56 (95% CL = 1.89–2.23) and 986 (95% CL = 644–1327), respectively. Both the high and low nutrient finite growth rates for *T. pyriformis* are well above all other species in the community under both nutrient conditions (Haddad et al. 2008). However, *E. eurystomus* populations grew at 1.14 (95% CL = 0.81–1.48) individuals individual^{-1} per day and reached a carrying capacity of 60.6 (95% CL = 33.3–87.9) individuals ml^{-1} when nutrients were high, putting it exactly in the mid-range of high nutrient growth rates in the resident community, in which four of eight species had faster growth rates (Haddad et al. 2008). Under low nutrient conditions, *E. eurystomus* populations crashed in all replicates after 150–300 h, such that its growth rate was negative. On average, *E. eurystomus* reached maximum densities of 7.9 (SE = 1.67) individuals ml^{-1} in low nutrient treatments.

Discussion

Many studies in invasion biology have attempted to characterize traits that predict the ability of a species to invade a community and the environmental conditions that promote invasions (Rejmanek and Richardson 1996, Daehler 2003,

Richardson and Pyšek 2006, van Kleunen et al. 2010). Our study builds on this theoretical and empirical work, simultaneously manipulating both invader traits and environmental traits, and extends it to a fully factorial design over multiple generations. We found that the establishment success of invaders depended on the interaction between traits of species and characteristics of the environment, including resource fluctuations and mortality-impacts from disturbance, as well as productivity. In addition to the effect that these environmental variables had on the invaders themselves, they also created distinct resident communities that varied in density and composition. These community variables likely also influenced invasibility through competitive interactions. The two species we studied invaded environments that greatly differed in their levels of productivity and disturbance character, and hence their community characteristics. These environments and corresponding communities interacted with two key traits of the invaders, finite growth rate and competitive ability, to determine whether invasion was successful. Our findings synthesize two explanations for invasion success, short-term resource fluctuations and long-term resource availability, by looking at their contribution to invasions through the lens of resident and invading species' traits. These results suggest that our trait-based approach could be useful in resolving idiosyncratic results in natural systems undergoing invasion.
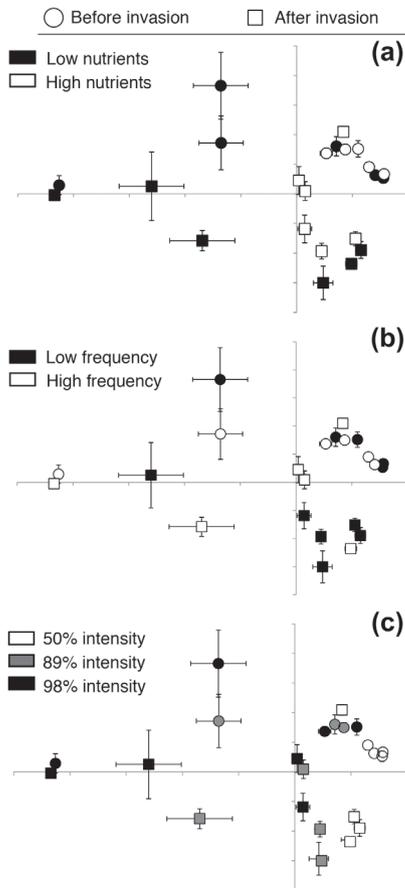
Figure 5. Disturbance effects on community composition. Data points represent the average 2-D NMDS (stress = 0.13) scores for each treatment combination, and bars show the standard error for x and y-axes (n = 10 per treatment combination, 120 replicates total). Where standard error bars are not visible, they are too small to extend beyond the data point. Circles indicate pre-invasion communities and squares represent post-invasion communities. Like in any NMDS analysis, axes are non-metrically scaled using ranked data. (a) High nutrient treatments show little variability within and between treatments relative to low nutrient treatments. (b) High and low frequency communities show similar levels of variability within and between treatments. (c) Variability within treatments increases from 50% intensity to 89% and 98% intensity, as does variability between treatments. Collectively, (a), (b) and (c) show that low nutrient, high intensity (89% and 98%) communities are the most variable communities within and between treatments.

Finite growth rate and stochastic mortality

An invader's finite growth rate played a prominent role in determining its response to increasing disturbance and short-term resource fluctuations. *Tetrahymena pyriformis* (the Reproducer) had a higher finite growth rate than all other species, including *Euplotes eurystomus* (the Competitor), under both high and low nutrient conditions. *T. pyriformis* establishment became more likely under increasing disturbance intensity, but likelihood of establishment was greatest when productivity was high and short-term fluctuations were enhanced by high disturbance frequency (Fig. 2c). As predicted by Huston's (1994) dynamic equilibrium model (DEM), increasing long-term resource

availability without increasing disturbance frequency and intensity suppressed *T. pyriformis* establishment. Conversely, *E. eurystomus*' growth rate lacked sufficient plasticity under our nutrient and disturbance regimes to avoid stochastic extinction under high levels of disturbance. This result is consistent with the findings of others, including Haddad et al. (2008), who demonstrated the importance of finite growth rate for persistence under disturbance for the wider suite of resident species considered in our study.

Competitive ability and interactions with community composition

An invader's competitive ability was also informative in predicting invasion success. Long-term resource availability had no discernable effect on *E. eurystomus* establishment, while short-term resource fluctuations could not outweigh the negative impacts of the disturbances that caused them. This suggests that nutrient availability is not limiting for this relatively strong competitor. Contrary to DEM predictions, nutrient increases were not sufficient to influence *E. eurystomus*' finite growth rate and hence establishment in highly disturbed environments. This result seems peculiar in light of *E. eurystomus*' tendency to go extinct under low nutrient conditions in monoculture. The key, however, may lie in *E. eurystomus*' omnivory. Though we maintain *E. eurystomus* cultures on bacteria as a food source, it can also feed on small protozoa (Naeem and Li 1998). The suite of species present in our communities, including heterotrophs, may have been able to exploit and transfer resources to *E. eurystomus* that were crucial for persistence under low nutrient conditions. This dynamic may have evened out the nutritional differences between high and low nutrient communities for *E. eurystomus*, and given it a competitive edge. Additionally, species with slower finite growth rates are also thought to better withstand periods of nutrient scarcity by being better at storing and competing for resources (Arendt 1997). *T. pyriformis*, on the other hand, was ranked as the worst competitor in our system (Cadotte et al. 2006) and was more dependent on disturbance-induced resource pulses for establishment (Fig. 2b–d). Even in its least hospitable environment (98% disturbance intensity treatments), *E. eurystomus* still had a probability of establishment that was comparable to *T. pyriformis* across many treatment combinations.

Tetrahymena pyriformis achieved its greatest invasion success in highly disturbed, nutrient-rich environments that harbored low diversity and were characterized by low community density. Our cyclical disturbances created a smaller effective community density over time (Orrock and Fletcher 2005), and a chronically depressed community size in low nutrient treatments. Orrock and Fletcher (2005) suggest that when total community density decreases, environmental and demographic stochasticity plays a larger role than deterministic competitive outcomes in structuring communities, and that the role of stochasticity increases as the rate of community shrinking increases. Indeed, we observed the greatest variability in community composition (Fig. 5) as disturbance increased, nutrients decreased, and community density shrank (Fig. 4). At the community level, nutrient rich and mildly disturbed communities were

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Table 3. Mean densities (individuals/bottle) ± SE of each species in each of the twelve treatment combinations after invasion (n = 10 per treatment combination). 'Extinct' refers to extinction by sampling time, though all species were present in the original communities. Species whose names are abbreviated: *E. eurystomus* = *Euplotes eurystomus*, *T. pyriformis* = *Tetrahymena pyriformis*, *P. aurelia* = *Paramecium aurelia*, *P. bursaria* = *Paramecium bursaria*.

Intensity	Nutrients	Frequency	Competitor *E. eurystomus*	Reproducer *T. pyriformis*	*Coleps* sp.	*Colpidium* sp.	*Cyclidium* sp.
50%	high	low	2.82 ± 0.732	0.354 ± 0.354	27.3 ± 13.8	14.2 ± 9.18	22.5 ± 11.1
		high	2.17 ± 0.691	extinct	63.6 ± 11.3	extinct	extinct
	low	low	1.14 ± 0.365	1.45 ± 1.45	18.3 ± 5.65	14.6 ± 14.6	106 ± 70.0
		high	2.06 ± 0.753	0.0105 ± 0.0105	16.8 ± 4.11	extinct	16.5 ± 11.6
89%	high	low	1.13 ± 0.361	extinct	1.29 ± 1.19	1.45 ± 1.38	8.17 ± 6.77
		high	5.67 ± 1.75	565 ± 291	0.431 ± 0.397	358 ± 273	extinct
	low	low	1.84 ± 0.535	6.58 ± 6.48	1.40 ± 0.475	extinct	30.4 ± 24.8
		high	extinct	56.7 ± 31.9	extinct	extinct	extinct
98%	high	low	1.16 ± 0.574	476 ± 297	0.0307 ± 0.0307	24.7 ± 16.5	56.1 ± 37.9
		high	1.00 ± 1.00	2100 ± 348	1.85 ± 1.85	283 ± 160	extinct
	low	low	0.289 ± 0.184	107 ± 91.5	0.0102 ± 0.0102	4.28 ± 3.06	extinct
		high	extinct	13.0 ± 7.33	extinct	extinct	extinct

Int.	Nutrients	Frequency	*Euglena* sp.	*Euplotes* sp.	*P. aurelia*	*P. bursaria*	*Spirostomum* sp.
50%	high	low	extinct	9.97 ± 3.16	315 ± 40.0	60.9 ± 20.9	0.0215 ± 0.0215
		high	extinct	10.6 ± 4.07	453 ± 42.5	8.64 ± 3.85	extinct
	low	low	43 ± 42.5	3.29 ± 2.18	92.0 ± 6.26	81.1 ± 12.1	0.0208 ± 0.0138
		high	1.02 ± 1.02	18.5 ± 5.53	362 ± 47.1	24.2 ± 9.91	extinct
89%	high	low	extinct	3.58 ± 2.26	391 ± 49.9	4.94 ± 2.08	extinct
		high	extinct	extinct	462 ± 108	extinct	extinct
	low	low	0.834 ± 0.729	0.0755 ± 0.0646	22.0 ± 5.07	14.9 ± 4.29	extinct
		high	extinct	extinct	20.6 ± 6.38	extinct	extinct
98%	high	low	extinct	0.674 ± 0.456	203 ± 52.2	0.0638 ± 0.0328	extinct
		high	extinct	extinct	5.87 ± 13.9	extinct	extinct
	low	low	2.47 ± 2.47	extinct	5.43 ± 5.25	0.0108 ± 0.0108	extinct
		high	extinct	extinct	extinct	extinct	extinct

more constrained in community composition before and after invasion pointing to a stronger role for deterministic forces. *T. pyriformis* established more often in the variable communities by capitalizing on niche opportunities provided by stochastic extinction in the resident community, while better withstanding stochasticity with its high growth rate. *E. eurystomus*, however, suffered from disturbance in the same way as resident species with similar low growth rates. Interestingly, increasing the initial community size of the invader populations themselves through higher propagule pressure had no effect on *E. eurystomus* and actually dampened the positive response of *T. pyriformis* establishment to increasing intensity. We had expected propagule pressure to increase establishment success by decreasing the chance of stochastic extinction (Lockwood et al. 2005, Pyšek et al. 2009). Perhaps high initial *T. pyriformis* densities rapidly depleted availability of limited bacteria resources in such a way that caused the population to crash, representing a down-side to exceedingly high growth rates.

The competition–colonization tradeoff under disturbance and productivity gradients

Competitive ability and growth rate are often considered as two ends of a spectrum. Most models of coexistence through disturbance assume a tradeoff between competitive ability and finite growth, yet our species do not exhibit a strict tradeoff. This makes it difficult to make generalizations about the competitive environment in our communities using the competition–colonization framework (Haddad

et al. 2008). Additionally, the traditional competition–colonization tradeoff considers only stable, long-term nutrient availability (Hastings 1980, Tilman 1994). The DEM builds on traditional models by considering how different levels of long-term availability interact with disturbance and the competition–colonization hierarchy, predicting that high nutrient environments require greater levels of disturbance for coexistence than low nutrient environments (Huston 1979, 1994). Contrary to DEM predictions, *T. pyriformis* generally failed to invade low-nutrient, low-disturbance treatments and *E. eurystomus* fared best in low disturbance environments regardless of nutrients. Additionally, we saw a steady decline in species richness with disturbance regardless of nutrient level. Discrepancies between our experiment and DEM predictions may have been caused by two factors. First, our chosen treatments may not be representative of disturbance and nutrient regimes encountered by these species in nature. Second, there are likely to be complicated interactions between environmental conditions and the community's life-history tradeoff structure. The DEM does not consider whether the competition-growth hierarchy is maintained across nutrient levels or changes with nutrients (i.e. are the best competitors always the best competitors regardless of nutrient level?). It is possible that shifts in the competitive hierarchy across nutrient environments can also affect diversity and invasibility by changing the competitive community. The low-nutrient, low-disturbance environments that the DEM and we incorrectly predicted would be highly invasible by *T. pyriformis* were very different in

community composition than the high nutrient, high disturbance environments that *T. pyriformis* invaded as predicted (Fig. 5). Studies of the impact of productivity on competition–colonization hierarchies in a framework like the DEM and experimental set up like ours would shed further light on the resident community dynamics that determine invasibility.

Conclusions

Though our study focused on the introduction of nonnative species to a system, our framework and results are relevant to any situation in which a species is establishing and growing from a small initial population size, including re-establishing native species. Our study is limited by the use of only two invaders and trait-combinations, and thus future work that looks at a range of invader traits under similar experimental conditions would further illuminate the interaction between invaders' traits, disturbance and productivity. Expanding the grain and range of the physical manipulations to more fully represent possibilities in nature could also resolve discrepancies between our predictions and results, and could indeed be useful in clarifying many experiments exploring the effect of disturbance on communities.

Predictions made from frameworks like the DEM can change dramatically based on the relationship between an invaders' competitive and reproductive abilities relative to those of resident community members. This suggests that explicit consideration of species' traits may resolve idiosyncratic results in systems undergoing invasion. We found that the role of short-term resource fluctuations and long-term resource availability in determining invasion success depended on species' traits. The positive effects of disturbance on fast-growing, poor competitors are unlikely to be solely based on resource fluctuations. Although we cannot separate the effects of disturbance from the effects of community composition in our study, it is clear that *E. eurystomus* invaded diverse communities and *T. pyriformis* invaded simple communities, and that this difference originated in their competitive differences. Disturbance can permanently alter the competitive community by decreasing or eliminating slow-growing species that are often the best competitors, thereby slowing down the process of exclusion until the next disturbance opens up new opportunities for rapid population growth. This effect of disturbance may be particularly crucial for invaders in highly productive, resource-rich environments. Oppositely, invaders and resident species with intermediate to low growth rates are more likely to suffer than benefit from disturbances, as was the case in our study. Competitive ability becomes relatively unimportant in these situations. Still, our contrasting results between species with very different traits demonstrate that ecological debates about the role of diversity and disturbance in controlling invasion success may be illuminated through understanding the interactions of these environmental characteristics with the traits of invading and resident species.

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