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Disturbance-induced changes in community composition increase species invasion success

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Abstract: The process of biological invasions is necessary to understand to prevent future invasions and their negative impacts. Ecological theory and empirical work can provide a framework for approaching the process. Extrinsic factors, such as disturbances, can increase the probability of a successful invasion through several mechanisms. Disturbances may decrease native species' abundances, decrease species diversity, or change community composition. We conducted a microcosm experiment using a container protozoan and rotifer community to examine how disturbances and the timing of the invasion affected the probability of invasion success. Native species richness significantly decreased with disturbance presence, but total native abundance was not affected. Invader abundance and richness significantly increased with increasing disturbance. Invasion timing had no effect on invasion success, implying that changes in native abundance or biomass did not facilitate or prevent invasions. Several native species that dominated post-disturbance communities had lower abundance levels in no-disturbance and invasion treatments, indicating that species in this community may have exhibited trade-offs between competitive ability and disturbance tolerance. These results suggest that changes in species richness and composition are most important in facilitating invasions, and this may be the result of increased vulnerability to invasion in a post-disturbance community dominated by poor competitors. Understanding how species invasions are facilitated by community characteristics can provide further insight to identifying when communities are most vulnerable and how to prevent invasions.

Nomenclature: Pennak (1989).

Abbreviation: ANOVA – Analysis of Variance.

Introduction

Species invasions are one of the greatest threats to conservation efforts worldwide ([Vitousek et al. 1997](#), [Lonsdale 1999](#), [Mack et al. 2000](#)), while the mechanisms that can prevent or facilitate invasions continue to be a focal point of much research ([Williamson 1996](#), [Mooney and Hobbs 2000](#)). Ecological studies have provided a framework to understand the conditions that determine when a community is more likely to be invaded ([Elton 1958](#), [Lodge 1993](#), [Drake et al. 1996](#), [Levine and D'Antonio 1999](#)). One of the most common hypotheses is that more diverse communities are more resistant to invasion because they are better able to exploit all available resources ([Elton 1958](#), [Naeem et al. 2000](#), [Stachowicz et al.](#)

[1999](#)) or more likely to contain species that resist invasion ([McGrady-Steed et al. 1997](#), [Levine and D'Antonio 1999](#), [Wardle 2001](#), [Hodgson et al. 2002](#)). Local-community processes that directly affect species diversity (e.g., trophic structure, abiotic factors, and disturbances) can also indirectly facilitate the success of an invasion ([D'Antonio 1993](#), [Tilman 1997](#), [Kennedy et al. 2002](#), [Miller et al. 2002](#)).

Disturbances are a common feature of most communities ([Grime 1977](#), [Sousa 1984](#), [Shea et al. 2004](#)) and have been implicated in facilitating species invasions (e.g., [Hobbs and Huenneke 1992](#), [Burke and Grime 1996](#), [Davis et al. 2000](#)). Disturbances can provide a density mediated release from competition: directly by increasing re-

source supply rates or indirectly by reducing native species abundance and therefore resource consumption (Davis et al. 2000, Shea and Chesson 2002). If a community's invasibility fluctuates through time, the period immediately after a disturbance would be the most opportune time for a successful invasion, since it is at this time that native population densities are lowest and resource availability highest (Johnstone 1986, Davis et al. 2000).

A second explanation for disturbances increasing a community's susceptibility to invasion is that disturbances decrease species diversity, rather than a purely density-mediated effect (Hobbs and Huenneke 1992, Levine and D'Antonio 1999, Davis et al. 2000, Shea and Chesson 2002, Shea et al. 2004). Studies seldom address the traits (or identity) of the species occupying the available niches or those lost. A mechanism for species coexistence found in many systems requires a trade-off between species' abilities to compete and tolerate disturbances (Grime 1977, Sousa 1984, Petraitis et al. 1989, Chesson and Huntly 1997, Kneitel and Chase 2004a). In the absence of disturbances, the dominant resource competitors exclude weaker competitors, however, weaker competitors are more tolerant of disturbances which results in their dominance in the presence of disturbances (Shea et al. 2004, Kneitel and Chase 2004a). This provides the third explanation for increased invasion success: if this trade-off was present, a post-disturbance community would then be expected to be composed of species that are tolerant of disturbances (Grime 1977), but weak competitors; therefore, this community could be more vulnerable to invasion. This mechanism is also an example of the "sampling effect" (Wardle 2001).

While numerous field experiments have investigated disturbance-facilitated invasion, the majority of this work has been done in plant communities (e.g., Hobbs and Huenneke 1992, D'Antonio 1993, Burke and Grime 1996, Kotanen 1997). Many of these studies suggest that a reduction in native species abundance is sufficient to allow invasion (e.g., D'Antonio 1993), but abundance levels may also be tightly correlated with diversity levels (e.g., Johnstone 1986, Kennedy et al. 2002). In several studies, it has been suggested that the presence of certain species and not diversity per se can prevent species invasions (Hobbs and Huenneke 1992, Warren 1996, McGrady-Steed et al. 1997, Wardle 2001, Hodgson et al. 2002, Kennedy et al. 2002). Several studies have also found differential survival of species following a disturbance (e.g., Grime 1977, Hobbs and Huenneke 1992, Collins et al. 1995, Warren 1996) whose identity (traits) may also contribute to a community's vulnerability to inva-

sion. However, it remains unclear how changes in a community following a disturbance facilitate an invasion.

The purpose of this study was to test the two primary hypotheses for the successful invasion into disturbed communities: (1) the reduction in native community abundance, and alternatively (2) the absence of specific species which dominate in undisturbed communities. A microcosm experiment was conducted using the protozoa and rotifer community which inhabit container communities (artificial treeholes; Srivastava and Lawton 1998, Kneitel and Chase 2004b, Ostman et al. 2006). Microcosms have the potential to provide insight to general ecological phenomena and conservation issues (e.g., Gonzalez et al. 1998, Srivastava et al. 2004). Manipulative ecological experiments using microcosms can provide insight to the factors that prevent or facilitate a species invasion that are otherwise difficult to identify (Robinson and Dickerson 1987, Drake et al. 1996, McGrady-Steed and Morin 1996, Fukami 2001). The present experiment utilizes the bacterivore protozoan community which inhabit artificial treehole communities (Kneitel and Chase 2004b, Ostman et al. 2006). We manipulated disturbance presence and the invasion timing of novel protozoa in order to relate which components (composition and abundance) of a native community were altered in such a way to facilitate invasion.

Methods

Study system

This study used the protozoan and rotifer community that occurs in container communities (artificial treeholes; Srivastava and Lawton 1998, Kneitel and Chase 2004b). These communities are similar in composition to natural treeholes (J. M. Kneitel, *unpublished data*), but are typically found in abandoned tires, buckets, and other man-made sites where water collects (Juliano et al. 2002). The food web can be quite complex, but the present study included primarily resource competitors for bacteria (Table 1). Previous studies of container communities have identified drying (either partial or complete) as a natural disturbance that may alter survivorship of many species in this community (Bradshaw and Holzapfel 1988, Juliano et al. 2002, Kneitel and Chase 2004b).

The recipient (native) community for this experiment was established by combining media from 36 (500 ml) artificial treeholes, established and maintained at Washington University's Tyson Research Center for approximately 60 days before collection (Kneitel and Chase 2004b). A total of 16 native taxa (13 protozoa and 3 rotifers) were identified in the native regional pool of repli-

Table 1. List of container community taxa used in the present study and their feeding: B = Bacterivore, P = Predator of protozoans, PH = Photosynthetic.

Community	Species	Feeding
Native	<i>Actinopoda</i>	B, P
	<i>Aspidisca</i>	B
	<i>Bodo</i>	B
	<i>Chrysomonad</i>	B, PH
	<i>Colpidium</i>	B
	<i>Colpoda</i>	B
	<i>Cyclidium</i>	B
	<i>Entosiphon B</i>	B
	<i>Halteria A</i>	B
	<i>Litonotus</i>	B
	<i>Polytomella</i>	PH
	<i>Uroleptus</i>	B
	<i>Vorticella</i>	B
	Unknown Ciliate A	B
	Unknown Ciliate B	B
	Unknown Ciliate C	B
	Bdelloid Rotifer A	B
	Bdelloid Rotifer B	B
	Loricat Rotifer	B
Invader	<i>Coleps</i>	B
	<i>Mayorella</i>	B, P
	<i>Paramecium caudatum</i>	B

cate communities (Table 1). We used 3 protozoan invader species (*Paramecium bursaria*, *Mayorella* sp., *Coleps* sp.) from Snail Pond, also found at the Tyson Research Center. All three of the invader species have been found in container communities previously (J. M. Kneitel *unpublished data*) and were chosen haphazardly to be used in the present study.

Experimental design and analysis

The laboratory experiment consisted of a 3×2 factorial design with 3 levels of invasion timing (“no invasion”, “immediate invasion” and “delayed invasion”) and 2 levels of drying disturbance (“no disturbance” [no evaporation] and “high disturbance” [complete evaporation]). Five replicates of each treatment combination were established from 40 ml of the stock native (container) community in Petri dishes (100 mm \times 15 mm) and placed on laboratory countertop in a blocked design. Placement of blocks had no effect on experimental units (ANOVA: $F_{4, 29} = 0.715$, $P = 0.59$).

Disturbances were manipulated by altering the volume of deionized water added daily to replicates to maintain media volumes (Kneitel and Chase 2004b, Ostman et al. 2006). Media in replicates with no disturbance were maintained at 40 ml. Replicates subjected to disturbances were allowed to evaporate at natural rates until they were

completely dry (typically after 72 hours). Twenty-four hours after complete drying, disturbance replicates were rehydrated to 40 ml, minus 2 ml (the volume of invasion treatment). Timing treatments were implemented by altering the amount of time that each native community was allowed to recover from disturbance (after rehydration) before receiving its respective invasion treatment. Replicates with immediate invasion treatments were inoculated immediately following rehydration, and delayed invasion treatments were inoculated 48 hours after rehydration.

The invasion and disturbance treatments occurred twice through the course of the experiment. Invasions were conducted twice to increase our confidence of invasion success (or lack thereof) did not occur by chance. Five days after the final rehydration, all replicates were gently stirred, and 1 ml samples were extracted for species and abundance sampling in a Sedgewick rafter cell under a phase-contrast microscope. Rapid population growth rates of protozoa are sufficient for these treatments to approach equilibrium within this time frame (McGrady-Steed and Morin 1996, Kneitel and Miller 2002). Native and invader species richness (species number/ml), abundance (individuals/ml) were measured. In cases of high abundance levels for certain species, the abundance of those species were subsampled along cell transects. All abundance data were log transformed to control for non-normality. Native community biomass for each replicate was also estimated as each species length (μm) multiplied by its abundance. Native community biomass was not affected by any of the treatments (Disturbance: $F_{1,16} = 0.056$, $P = 0.816$; Invasion: $F_{1,16} = 0.137$, $P = 0.716$; $D \times I$: $F_{1,16} = 1.86$, $P = 0.192$) and therefore was not used in further analyses.

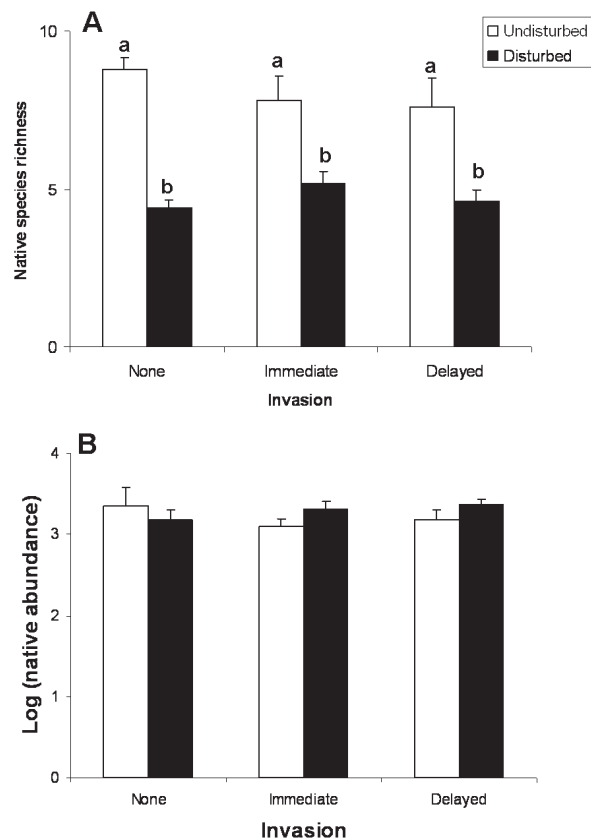
Two-way ANOVAs (using SPSS, version 12.0.1) were used to test disturbance (absence and presence) and timing of invasion (none, immediate, and delayed) treatment effects and interactions on invader and native species richness and abundance. Additionally, two-way ANOVA was used to test the effects of disturbance (absence and presence) and invasion (absence and presence) on the total abundance of three native species identified as possible disturbance tolerant, but weak competitors. Rank-order correlations were used as a measure of community similarity (Krebs 1999) in which native community composition in control-treatment replicates was compared with the disturbance-treatment replicates. Regression analyses were used to test whether there was a relationship between invader abundance and (1) total native abundance in disturbance treatments, (2) native species richness in disturbance treatments, and (3) weak competitor abundance across disturbance treatments.

Table 2. Results of 2-way ANOVA for native (A) species richness and (B) abundance and invader (C) species richness and (D) abundance testing the effects of disturbance, invasion timing, and their interaction.

Dependent variable	Source			
<i>A. Native species richness</i>		<i>df</i>	<i>F</i>	<i>P</i>
	Disturbance	1	50	<0.001
	Invasion	2	0.42	0.66
	Disturbance x Invasion	2	1.34	0.28
	Error	24		
<i>B. Native abundance</i>		<i>df</i>	<i>F</i>	<i>P</i>
	Disturbance	1	0.501	0.486
	Invasion	2	0.143	0.868
	Disturbance x Invasion	2	1.437	0.257
	Error	24		
<i>C. Invader species richness</i>		<i>df</i>	<i>F</i>	<i>P</i>
	Disturbance	1	16.94	<0.001
	Invasion	2	17.41	<0.001
	Disturbance x Invasion	2	4.24	0.027
	Error	24		
<i>D. Invader Abundance</i>		<i>df</i>	<i>F</i>	<i>P</i>
	Disturbance	1	35.92	<0.001
	Invasion	2	25.67	<0.001
	Disturbance x Invasion	2	11.00	<0.001
	Error	24		

Results and discussion

Disturbances can facilitate species invasions into communities by increasing resource availability (decreasing densities), opening niches (decreasing species diversity), and changing community composition (Hobbs and Huenneke 1992, Davis et al. 2000, Shea and Chesson 2002). This study examined whether successful invasions were related to changes in abundance and species composition of a native community following a disturbance. Disturbances had a significant effect on native species richness, decreasing richness by 53% (Table 2, Figure 1a). Similarly, community composition between the controls and disturbance treatments were approximately 15% similar. This response to disturbance was consistent with the results of previous work in this system (Kneitel and Chase 2004b, Ostman et al. 2006) and patterns seen in other systems (e.g., Sousa 1984, Hobbs and Huenneke 1992, Collins et al. 1995, Warren 1996). Invasion had no effect on species richness (Table 2, Figure 1A). Native species abundance at equilibrium was not affected by disturbance or invasion timing (Table 2, Figure 1B), but this does not necessarily reflect abundance immediately following a disturbance. In a previous study, it was shown that disturbances had decreased abundance after three days following the disturbance (Kneitel and Chase 2004b). Therefore, disturbances decrease abundance levels initially, but they appear to dissipate after 3-5 days. Nonetheless, abundance levels (immediately following

**Figure 1.** Mean (\pm SE) response of native (A) species richness and (B) abundance to disturbance and invasion timing treatments. Bars sharing letters are not significantly different from one another (Bonferroni-adjusted post-hoc tests).

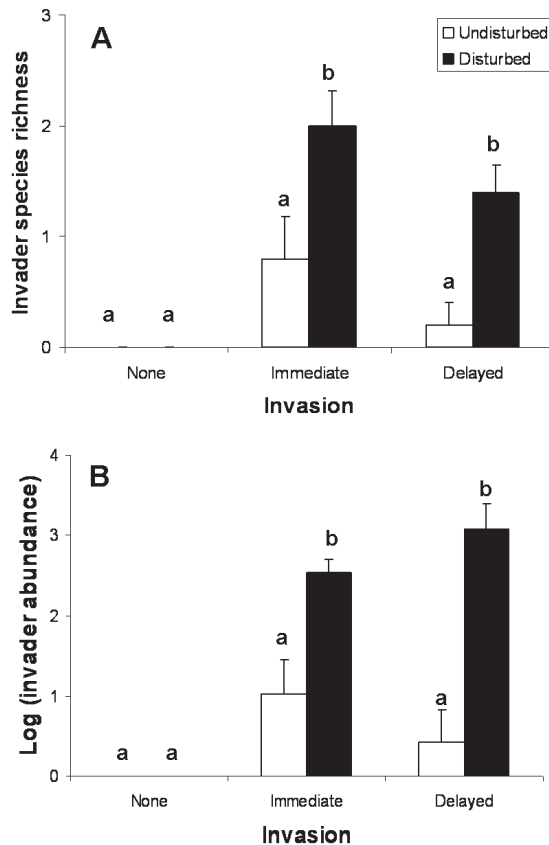


Figure 2. Mean (\pm SE) response of invader (A) species richness and (B) species abundance to disturbances and invasion timing treatments. Bars sharing letters are not significantly different from one another (Bonferroni-adjusted post-hoc tests).

disturbance or delayed) proved to have no effect on invasion success.

Invader species richness and abundance significantly increased with disturbance (Table 2, Figure 2). The period following a disturbance is expected to be the most vulnerable for invasion (Davis et al. 2000). However, invader richness and abundance did not significantly increase when the invasion was immediate, suggesting that native abundance levels alone were unlikely to facilitate or prevent species invasions. The success of invasion was dependent on the presence of disturbance as indicated by the interaction term (Table 2).

Disturbances have been associated with species invasions in numerous systems (e.g., Hobbs and Huenneke 1992, Burke and Grime 1996, McGrady-Steed et al. 1997) and related to decreased species diversity, abundance, or the absence of dominant competitors (e.g., Warren 1996, McGrady-Steed and Morin 1996, Kennedy et al. 2002).

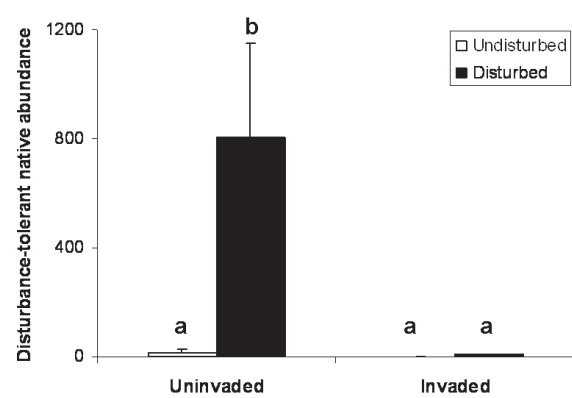


Figure 3. Mean (\pm SE) total response of three native species (*Colpoda*, *Polytomella*, and *Vorticella*) to disturbance and invasion treatments. Bars sharing letters are not significantly different from one another (Bonferroni-adjusted post-hoc tests).

The present study found no effect of invasion timing (native abundance levels), but did find that increased invasion success occurred following disturbances. To determine what may have allowed invasion under these conditions, we examined species-specific response patterns to disturbance in the native community.

Complete drying in the native community acted as a filter whereby a subset of species tolerated it through dormancy or resting cysts (Kneitel and Chase 2004b). Approximately half of the species in the native community survived the drying disturbance. Of these, only two of the five species (*Bodo* and an unidentified chrysomonad) that were found in the post-disturbance native community had similar abundance levels in the pre-disturbance community. In addition, the abundances of these species were similar with the addition of invaders (i.e., not affected by invasion). However, the other three species present following disturbances exhibited patterns that may shed insight to a possible mechanism for species invasion in this community.

Three of the five native taxa (*Colpoda*, *Polytomella*, and *Vorticella*) that survived the disturbance had greater abundance in the disturbance treatments than in the absence of disturbances (Disturbance: $F_{1,16} = 5.26$, $P = 0.036$; Invasion: $F_{1,16} = 5.43$, $P = 0.033$; $D \times I$: $F_{1,16} = 5.06$, $P = 0.039$). Their abundance increased with disturbance, as did invasion success (Figures 2, 3). These species' abundances decreased in the absence of disturbance and presence of an invasion (Figure 3), implying tolerance to disturbances with poor resistance to species invasions. While there was no relationship between invader abundance and native abundance ($P = 0.77$) or richness (P

= 0.484) following disturbance, there was a strong relationship with the presence of these weaker competitors (Figure 4). These results suggest that the protozoan species may exhibit trade-offs between competitive ability and disturbance tolerance, which may explain the increase in invasion success. This implies a novel mechanism facilitating species invasion in this system: when species exhibit this trade-off, a post-disturbance community will be composed of species that can tolerate the disturbance, but are poor competitors (Grime 1977, Petraitis et al. 1989), making it more vulnerable to invasion. This mechanism is related to previous explanations of the opening of niche space, however, specific species traits are specifically identified. Similar patterns likely occur in other systems (e.g., Hobbs and Huenneke 1992) and should be further tested.

We were not able to distinguish between several confounded mechanisms in this study. First, the changes in the native community and subsequent invasion can result from differential survival resulting from the direct effects of the disturbance (e.g., Hobbs and Huenneke 1992) or indirect effects resulting from changes in environmental variables (e.g., pH, dissolved oxygen) in response to the disturbance (e.g., Suding and Goldberg 2001). Second, the maintenance of species diversity in communities has been found to prevent the invasion of species in many communities (e.g., Stachowicz et al. 1999, Levine 2000, Kennedy et al. 2002). The most common mechanism for the prevention of species invasions is that more diverse

communities have fewer niches available (e.g., Elton 1958, Levine and D'Antonio 1999) and are more likely to contain dominant species that can exclude invaders. We could not separate the changes in species composition and diversity among our treatments, and hence, could not identify whether certain dominant species or niche availability was actually preventing invasion in the absence of disturbance.

A number of communities contain species that exhibit trade-offs between competitive ability and disturbance tolerance (Grime 1977, Sousa 1984, Kneitel and Chase 2004a). Consequently, disturbances may render a community more vulnerable to species invasions due to the increased presence of these weaker competitors. In addition, the presence of disturbances may also favor invasive species that are disturbance tolerant. Similar to the present study, Warren (1996) found that high-disturbance treatments (temperature increase) altered protozoan species diversity and composition, and it was these communities that were more likely to be affected by dispersal. Species abundance patterns appeared to have exhibited trade-offs in disturbance tolerance and competitive ability, a mechanism that maintains diversity in community (e.g., fire; Hobbs and Huenneke 1992, Kneitel and Chase 2004a). Future work needs to determine how widespread this mechanism is in facilitating species invasions.

Numerous factors can alter local community diversity and composition while indirectly facilitating species invasions (Hobbs and Huenneke 1992, Burke and Grime 1996, Mitchell et al. 2006). The present study focused on the invaded community, however, invader traits are certainly important to understanding the invasion process (e.g., Kolar and Lodge 2001, Daehler 2003, Thuiller et al. 2006). Indeed, the invasion process is a multifaceted problem (Mitchell et al. 2006, Thuiller et al. 2006) requiring increased experimental attention. The results of this study appeared to indicate that species invasions were more successful in the presence of disturbances when native species richness and composition were altered; there was little support for the hypothesis that decreased native abundance levels facilitated invasion. Further, the dominance of certain species in the community (weaker competitors) following a disturbance likely increased invasion success. Our study suggests that maintaining and restoring diversity in communities can prevent species invasions, but the factors (e.g., disturbance) that may facilitate species coexistence can also facilitate invasion. Future work should further explore how local and regional processes which alter species diversity, community composition, and species' traits (trade-offs; Kneitel and Chase

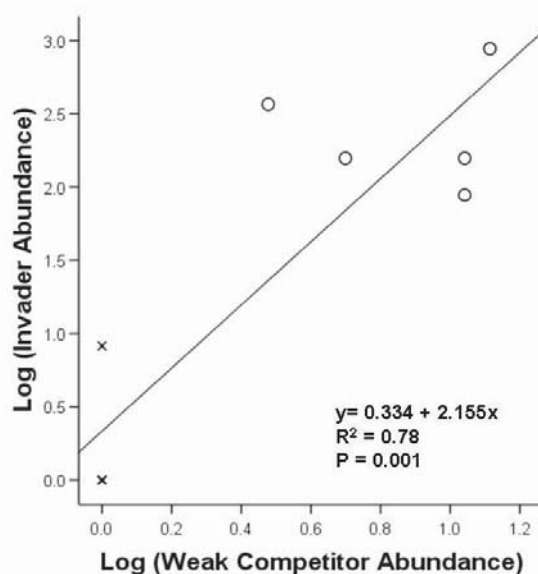


Figure 4. Scatterplot of log-transformed invader abundance on log-transformed weak competitor abundance. Results are from linear regression analysis, and (o) are disturbance treatments and (x) are undisturbed treatments.

2004a,b) also may change a community's vulnerability to invasion.

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