

Environmental productivity and biodiversity effects on invertebrate community invasibility

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Abstract

Productivity influences the availability of resources for colonizing species. Biodiversity may also influence invasibility of communities because of more complete use of resource types with increasing species richness. We hypothesized that communities with higher environmental productivity and lower species richness should be more invasible by a competitor than those where productivity is low or where richness is high. We experimentally examined the invasion resistance of herbivorous meiofauna of Jamaican rock pools by a competitor crustacean (Ostracoda: *Potamocypris* sp. (Brady)) by contrasting three levels of nutrient input and four levels of species richness. Although relative abundance (dominance) of the invasive was largely unaffected by resource availability, increasing resources did increase the success rate of establishment. Effects of species richness on dominance were more pronounced with a trend towards the lowest species richness treatment of 2 resident species being more invasible than those with 4, 6, or 7 species. These results can be attributed to a 'sampling effect' associated with the introduction of *Alona davidii* (Richard) into the higher biodiversity treatments. *Alona* dominated the communities where it established and precluded dominance by the introduced ostracod. Our experimental study supports the idea that niche availability and community interactions define community invasibility and does not support the application of a neutral community model for local food web management where predictions of exotic species impacts are needed.

Introduction

The question of what determines invertebrate community resistance to invasion by new species is especially relevant to aquatic communities worldwide. Plankton and meiofauna disperse between bodies of water through direct connections or via vectors, such as waterfowl or wind (Brendonck and Riddoch 1999). Humans have dra-

matically changed the rate of dispersal of these organisms by acting as efficient vectors for invasive species (Bollens et al. 2002). Among the slower dispersing aquatic invertebrates, hundreds of non-indigenous species of zooplankton have been introduced into new environments (Ruiz et al. 1997). While there is ample information on the occurrence of exotic invasions, few studies have attempted to determine the factors that

affect the ability of invaders to colonize new environments. Although colonization ability depends in part on characteristics of the species themselves, it may also be influenced by characteristics of the community or ecosystem (Stachowicz et al. 2002). The strength and nature of this influence requires further experimental exploration. Major factors that could influence the resistance of a community to colonization include the availability of resources such as nutrients, as well as extant species diversity. The mechanisms underlying the success or failure of species invasions, once dispersed, remain largely unexplored (Stachowicz et al. 2002). Whether biodiversity helps to stabilize community composition and thereby increase resistance to invasion is still an open question.

The study of assembly rules addresses the order in which species colonize a habitat and the identity of the species that persist in a particular community. Assembly rules can therefore guide understanding in the field of invasion ecology. Assembly rules imply that the history of a community is important in determining whether a new species can successfully colonize (Drake 1991). The outcome of that history is most immediately represented by the current community composition. Successful colonization by any additional species, or invader, is likely to be affected by the current community composition and other factors. In particular, it is potentially modulated by productivity and species richness levels for the following reasons. Because competitors share resources, the productivity of the common environment, as well as the identity and number of species present, have the potential to determine the niche space available to an invading population. In brief, community structure may play an important role in determining the success of invading species.

Elton (1958) first proposed that resistance to invasion increases with increasing species diversity – a topic that has since generated much discussion with regard to a possible link between biodiversity (richness) and community stability (Case 1990; Case 1996; Law and Morton 1996; Shea and Chesson 2002). The suggested mechanism underlying invasion resistance is that in the absence of new niche construction, competition for resources intensifies as species accumulate

and thus, fewer unused types of resources remain for new colonists. In addition, in order to avoid intense competition, species should increase their resource-use specialization as biodiversity increases (Hutchinson 1959). As a result, a reduction in the total unused pool of resources available for colonizing species is expected with increasing biodiversity. A few studies support a positive relationship between resistance to invasion and species richness in plant (e.g. Levine 2000; Naeem et al. 2000) and aquatic communities (e.g. Jenkins and Buikema 1998; Stachowicz et al. 2002). Further experimental manipulation of productivity and biodiversity will better address the question of whether niche space limitation inhibits invasion as a result of limited total resources or increasing local richness (i.e. limited relative resources).

Clearly linking species richness to invasibility in nature has proven to be difficult, as biodiversity effects do not operate in isolation. A recent meta-analysis by Herben et al. (2004) suggests that once dispersal has occurred, the only factor driving invasibility is total resource availability because it limits the number of individuals in the community. Herben et al. thus argue in favor of a neutral model for the relationship between invasive and native species richness. Neutral theory aside, large-scale observational studies suggest that more diverse communities are more susceptible to invasion (e.g. Knops et al. 1999; Levine 2000; Naeem et al. 2000; Symstad 2000), a result that contradicts those from manipulative studies which suggest the opposite (e.g. Wiser et al. 1998; Levine and D'Antonio 1999; Stohlgren et al. 1999; Levine 2000). The influences of uncontrolled environmental factors (predominantly resource levels that vary across landscapes) in observational studies have been proposed to explain the contradiction (Byers and Noonburg 2003). It is therefore important that manipulative studies examine simultaneously the role of biodiversity be embedded within a resource availability framework (Davis et al. 2000).

It is well established that nutrient availability strongly structures aquatic communities (Kalff 2002). Since the hypothesis that increasing species richness should buffer against invasion by competitors is predicated on the idea that resources become limiting as more species are

added to a community, we might expect that increased total resource availability could reduce the resistance afforded by biodiversity. A model by Byers and Noonburg (2003) demonstrates that it is the sum of community interaction strengths that matter and that by either adding resources or by reducing diversity, the sum is reduced, enabling invader success. Further, theories of dynamical stability, like the paradox of enrichment propose greater population fluctuations at higher productivity levels (Rosenzweig 1971). Heightened population fluctuations could generate periodic resource surpluses and thus open opportunities for invading populations to colonize. Extending the implications of these results to our experimental work, we would expect that an increase in native richness should decrease invasibility but that an increase in resource availability will counteract this effect.

The purpose of this study is to examine how environmental productivity and native community species richness affect the ability of a native crustacean species to colonize freshwater rock pools. We hypothesize that the invasibility of rock pool crustacean herbivore communities increases with increasing nutrients, but decreases with increasing species richness. In addition, we attempt to determine whether there are important interactions between environmental productivity and richness levels that influence the colonization success of a competitive invader. Such interaction effects are intimated by the common observation that richness itself peaks and then declines with productivity (reviews in Huston 1994) and may explain different conclusions from large-scale observational and experimental studies.

Materials and methods

The experiment was conducted in December 2002 to February 2003 at the Discovery Bay Marine Laboratory, University of West Indies in Jamaica (18°28' N 77°25' W). We used 120 identical 750 ml plastic containers to act as artificial rock pools. This site on the north coast of Jamaica has been described previously (Schuh and Diesel 1995; Kolasa et al. 1996; Therriault and Kolasa 1999). Water was collected from 10 natural

coastal rock pools. This water, filtered through a 63 μm mesh net, was mixed with tap water (non-chlorinated) at a 1:3 ratio and 500 ml of the mixed water was added to each plastic container. Experimental treatments consisted of two factors with three nutrient levels and four levels of biodiversity.

Forty artificial rock pools were assigned to each of three nutrient treatments: ambient, 10 \times ambient, and 100 \times ambient. Ambient nutrient levels for phosphorus (P) and nitrogen (N), determined from the average values of 50 naturally occurring rock pools sampled in 2001 (A. Greenaway, unpublished data), were estimated as 0.956 μM PO_4^{-3} and 36.923 μM NO_3^{-2} . Nutrients were added to 10 \times and 100 \times ambient nutrient treatments as solutions of KH_2PO_4 and NaNO_3 . The 10 \times ambient treatment falls within the natural upper range of observed PO_4^{-3} , while 100 \times ambient falls outside the natural range of nutrients and was used to test the system's response to greater than normally observed values of nutrients.

Crossed with the three levels of nutrient treatment were four levels of species richness with: 2, 4, 6, and 7 species. There were 10 replicate microcosms for each combination of treatments (total of 120 artificial rock pools). We collected organisms for the experiment from nearby rock pools. In order to determine which species to include in our experimental treatments, a cluster analysis was performed on a database consisting of ten years of continuous community censuses for 50 rock pools (J. Kolasa, unpublished data). We assigned species to treatments based on the frequency and high degrees of co-occurrence, but within the constraints of availability. Initial densities and species combinations are reported in Table 1.

The artificial rock pool communities were randomly distributed on an outdoor table. The containers were randomly re-distributed every 3 days in order to minimize site-specific effects, such as sunlight, shade, and wind. All containers were covered with a 63 μm mesh to prevent predation and colonization by unwanted species. A tarp roof, positioned 30 cm above the tops of the containers was erected overnight and during rainfall to prevent the containers from flooding. Water lost due to evaporation was replaced with

Table 1. Initial inoculation densities for each richness treatment in the artificial rock pool communities.

Species	$S = 2$	$S = 4$	$S = 6$	$S = 7$
Ostracoda: <i>Cypridopsis</i> cf. <i>mariae</i> (Rome)	5	5	5	5
Cladocera: <i>Ceriodaphnia rigaudi</i> (Sars)	5	5	5	5
Cladocera: <i>Leydigia leydigi</i> (Schoedler)	0	3	3	3
Ostracoda: <i>Candona</i> sp. (Baird)	0	3	3	3
Copepoda, Harpactacoida: <i>Nitocra spinipes</i> (Boeck)	0	0	3	3
Cladocera: <i>Alona davidii</i> (Richard)	0	0	2	2
Copepoda, Cyclopoida: <i>Orthocyclops modestus</i> (Herrick)	0	0	0	6
Total	10	16	21	27

non-chlorinated tap water as required. The artificial rock pools were left undisturbed for 16 days, to allow time for the community to develop. On day 16, 3 individuals of the invader *Potamocypis* sp., a native ostracod, were added to each rock pool to test the influence of nutrients and species richness on colonization resistance. Forty-two days after the start of the experiment, the entire container contents were filtered through a 63 μm mesh. Samples were preserved in 25% ethanol and completely censused under a dissecting microscope.

Several response variables were considered: final absolute invader abundance, relative invader abundance, relativized-to-expected invader abundance (calculated for a fully even community for the associated richness level using a D -value, as discussed in the next paragraph) and the proportion of all ten replicates successfully invaded to determine the probability of establishment. Log absolute density, arcsin transformed relative abundances and D -values in the various treatments were examined using a factorial ANOVA with an *a posteriori* Tukey test. A factorial ANOVA could not be executed for the proportion of replicates successfully invaded since there is no variation associated with a single measure of proportion of replicates. As a result, we performed a one-way ANOVA with either nutrient or richness level as the treatment level while aggregating the data over the untested treatment. We also examined the relationships between species and their abundances using a correspondence analysis on final population densities. In the analysis run in PC-ORD (MjM Software), densities were relativized by dividing by total community density and rare species were downweighted.

The analyses for the influence of species number on the relative abundances of community members are not as simple as those for nutrient effects because the quantitative definition of dominance shifts as more species are added. A null model of community organization would predict that as more species are added, the potential ecological space available for any one species should diminish proportionately. The definition of the threshold for dominance for a species in the community therefore will depend on what proportion of the total abundance any one species could maximally occupy if the community were completely even. Species that exceed these thresholds can be considered more dominant than expected with a neutral distribution of abundances across species. Thus, if there are two species in a community plus the invader, a species with a relative abundance greater than 33% (or proportion of 0.33) is the dominant one. For our treatment levels of species richness the threshold proportions are as follows: $S = 2$ (+invader), threshold = 0.33; $S = 4$, threshold = 0.2; $S = 6$, threshold = 0.143; $S = 7$, threshold = 0.125. In order to determine whether the invader was more or less dominant in different richness treatments, we calculated the difference (to be referred to as the D -value) between the observed proportion and the threshold proportion. The D -value will be positive when a species is more dominant than expected, negative when it is subdominant and equal to 0 where the species is at a value expected in a fully even community. We then compared the D -values across richness treatments for each species in the community to determine if dominance changed using an ANOVA.

Results

Invader density increased with nutrient input across species richness levels ($P = 0.0107$) (Figure 1), without any significant interaction between nutrients and richness ($P_{\text{interaction}} = 0.11$). The 100 \times ambient nutrient treatments had significantly higher total invader density than either the ambient or 10 \times treatments. There was no influence of nutrient addition at the 10 \times ambient level on final invader density. Species richness also had a significant effect on the density of invaders ($P = 0.0141$) but the relationship was complex. Invader density was significantly higher at the lowest native S treatment (i.e. $S = 2$) as compared with the more rich $S = 6$ treatment. Overall, the trend was towards highest invasion

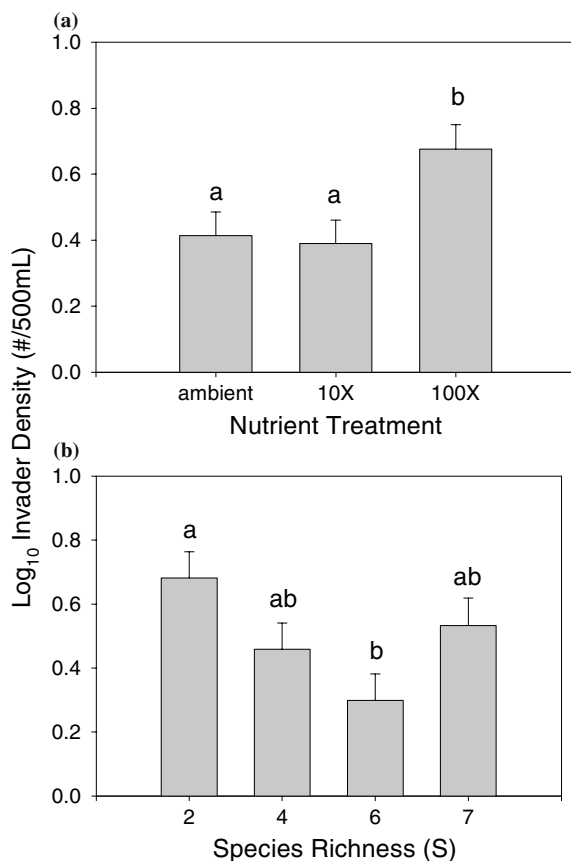


Figure 1. Mean final density with standard error of the invading ostracod by (a) nutrient treatment and (b) native community richness treatment. Bars with the same letters do not differ significantly at an $\alpha = 0.05$ level.

success, in terms of density, in the lowest community richness treatment.

The mean proportion of microcosms successfully invaded by *Potamocypris* declined significantly with species richness treatment ($P = 0.0091$) (Figure 2). By contrast, the proportion invaded increased significantly ($P = 0.00173$) with increasing nutrient levels. There were no significant effects of nutrient levels on the relative abundances of any species, including the invader (all P s < 0.05) (data not shown). The communities were similarly structured across nutrient levels.

For the invader (*Potamocypris*), there was no effect of richness treatment on D -values, which were consistently negative (mean = -0.087) indicating subdominance under all S conditions (Figure 3). The main species that showed strong dominance was *Alona* which increased significantly in D -value with increasing S

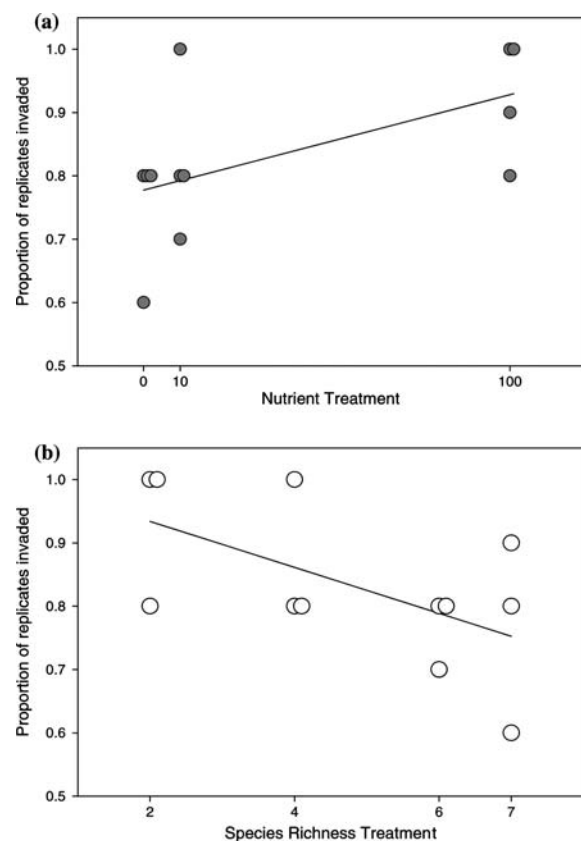


Figure 2. Invader dominance as a function of (a) nutrient treatment and (b) community richness treatment. The lines represent the best fit GLM model.

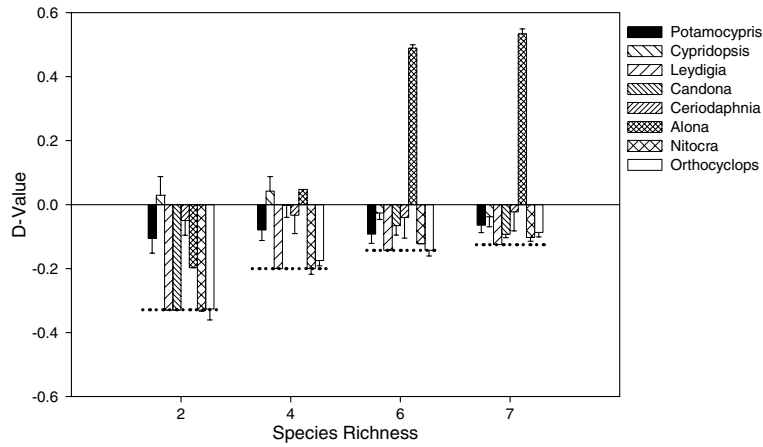


Figure 3. The mean difference (*D*-value) with standard error between observed relative abundance of each species in the containers at the end of the experimental period and the expected value for completely even communities containing the number of species (*S*) initially inoculated therein plus the invader. The expected values for fully even communities are indicated with the dotted line for each value of *S*. Positive bars indicate species that are more common than expected for an even community and that are therefore dominant. Species that were added together in each *S* treatment are indicated in bars with similar symbols (e.g. *S* = 4 treatment meant the addition of *Candona* and *Ceriodaphnia* which are both indicated with bars containing diagonal lines that are closely spaced).

($P < 0.0001$). The increase is due in part to the fact that *Alona* was only purposely inoculated in the *S* = 6 and 7 treatments. However, even in cases such as *S* = 4, *Alona* was able to show a greater dominance than that expected for an even community. Correspondence analysis showed a negative correlation between the com-

munities dominated by *Alona* and those where *Potamocypris* and most other species were successful (Figure 4). The species vectors (not drawn so the data points are more visible) show that the data across all treatments divides into groups dominated by *Alona* and those dominated by *Potamocypris*, and all other species further dem-

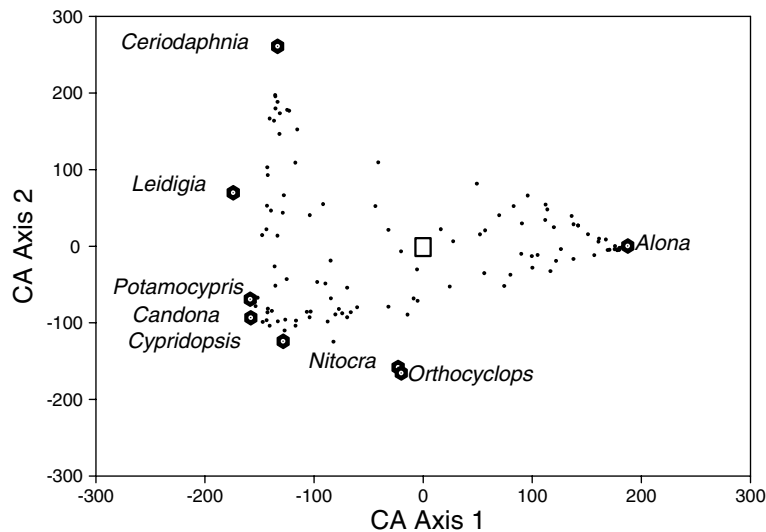


Figure 4. Results of the correspondence analysis (CA) showing the endpoints of the species vectors (hexagons) along axes 1 and 2 and the associated data (dots) for all replicate communities in all treatments. The square indicates the origin.

onstrating the dominance of *Alona* across the experiment.

Discussion

The ability of a competitive species to successfully colonize habitats depends on attributes of both the invader and the native community, including ecosystem aspects of the habitat being invaded (Lonsdale 1999). We have examined two habitat features that are highly variable across locations and that are likely to influence colonization success of new invaders: environmental productivity (represented by nutrient loading) and biodiversity (measured as species richness).

Previous studies have predicted and demonstrated an effect of resource availability on invasibility by a competitor, and have associated the effect with resource limitation in uninvaded communities (Elton 1958; Holland and Jenkins 1998; Brooks 1999). We found that more productive environments can favor a higher absolute abundance of an invading species. However, the roughly constant relative abundance of invader populations across nutrient treatments suggests that the invader is no more strongly represented in communities where more resources are available. Thus, at very high levels of resource availability (100 times ambient nutrient levels), increases in the abundance of the invading species correspond to general increases in population densities of the entire community. Although invader dominance (expressed as relative abundance) appears to be unrelated to resource availability (nutrient loading), our results do show a resource effect in terms of the habitat establishment success rate: the ability of an invading population to establish in a community increases with increased resource availability. That the main influence of resource availability in our study is its effect on establishment probability and not dominance suggests that the paradox of enrichment (Rosenzweig 1971) may play an important role in colonisation success, with the destabilization of resident populations at very high nutrient levels providing windows of opportunity for invasive establishment. However, this relationship and mechanism needs to be further

studied with detailed experiments monitoring population dynamics through time.

Our study also suggests an important but complex role of community structure and biodiversity on the invasibility of competitive communities. The clearest evidence is with regard to the proportion of habitats invaded, which declined significantly with initial community species richness. The richest communities had significantly lower successful invasion rates than the species-poor communities, which suggests that having more resident species prevents invaders from establishing a foothold in communities. A less clear pattern was found in terms of invader abundances. Although there was a trend toward a decline in invader density with increasing richness, this pattern was disrupted by larger invader abundances in the highest richness treatments. There are a couple of possible explanations for the observed pattern. First, there may be a threshold of invasibility with very low diversity communities ($S = 2$) having higher rates of invasion, but with further additions of species always leading to similar invader densities. Alternatively, it has been suggested that most studies that have detected effects of biodiversity on invasibility actually represent sampling effects whereby there is a greater chance of including a competitive dominant when species richness is increased (Huston 1994; Wardle 2001). Thus, it may be that in adding more species to achieve greater S in our native communities a species with a life history strategy that is highly competitive with the invading species was incorporated by chance. The prime candidate for this role in our study is *Alona*.

Resistance derived from richness in our artificial rock pools can be strongly linked to the role of *Alona* for a number of reasons. First, *Alona* was able to invade all treatments, *albeit* to a variable degree (Table 2), even some from which it had originally been excluded. All species showed declines in densities when *Alona* was abundant suggesting that at high densities *Alona* may strongly structure these rock pool communities. Even closely related cladoceran species, also with high reproductive rates (e.g. *Ceriodaphnia*), showed declines with high *Alona* abundances. Second, the only species to show an increase in dominance (D -value) with richness treatment was *Alona*.

Table 2. Proportion of 10 replicate microcosms wherein *Alona davidi* populations were detected at the end of the experimental period.

	$S = 2$	$S = 4$	$S = 6$	$S = 7$
Ambient nutrients	0.6	0.6	1	1
10× nutrients	0.7	0.2	1	1
100× nutrients	0.4	0.6	1	1

From long-term data on the 49 natural rock pools over the past 12 years, *Alona* is notably on average second in numerical dominance to only *Ceriodaphnia* (J. Kolasa, unpublished data). *Alona* is likely to be a close exploitative competitor of ostracods as they have similar feeding habits (Thorp and Covich 2001). Both groups feed preferentially on the sides of rock pools (and containers) on attached algae. In addition, *Alona* has a faster generation time because of parthenogenetic reproduction, giving it a head start on competition over the ostracods. Since our communities were unlikely at equilibrium after 46 days, these differential population growth rates would still be important for community composition. Compared to six other cladoceran genera, including *Ceriodaphnia*, *Alona* has the highest population growth rates, reaches the highest densities, and has one of the lowest threshold food level requirements (Nandini and Sarma 2003). It is therefore not surprising that *Alona* could come to dominate artificial rock pool systems, especially our small artificial pools with high surface area to volume ratios, where attached algae fed upon by *Alona* supplement pelagic phytoplankton upon which other species like *Ceriodaphnia* must rely more.

Wardle (2001) argued that no study had (up to that point) demonstrated a clear effect of plant species richness (on productivity) beyond very low levels of richness (2–3 species). Furthermore, Romanuk and Kolasa (2002) found increases in resource use to be unlikely except for very low richness values. Our study supports this argument in terms of community invasibility and the influence of species richness. We also found that the strongest effect of species richness on invader densities exists in the transition between two species and higher richness values (4, 6, and 7). In our case, we can attribute the presence of this

threshold most strongly to the presence of *Alona* in treatments with richness treatments higher than $S = 2$ (even though in the $S = 4$ treatment, its presence was inadvertent).

Our study provides further evidence to support the model results of Byers and Noonburg (2003) wherein a positive effect of resource levels, but a negative effect of biodiversity are expected on the probability of invader establishment. Under both of these conditions, according to their model, an elevated sum of interaction strengths favors low invasion success. Similar results with regard to the nutrient effect were found in a recent study by Jiang and Morin (2004) in a microcosm study with aquatic microbial communities, where they found that correlations between richness and resource supply favored invasibility. Our study does not support an extension of Herben et al.'s (2004) meta-analysis to rock pool meiofaunal communities. Rather, we find that species differences are important in our small-scale detailed study of community invasibility in rock pools. Although a neutral model may apply at large spatial scales, and with reference to species richness patterns of exotics and natives, it is still important to know the details of species interactions and resource availability at the local scale where resistance to invasion may need to be assessed. Species identity matters at the local scale - even if dispersal is the dominant feature at large scales or in cross-system comparisons - and must be considered by managers attempting to predict the invasibility of their food webs of concern.

It appears therefore, that speciose rock pool communities are more resistant to successful invader establishment (# habitats colonized) and invader dominance than species-poor communities. As proposed by Wardle (2001), our results can be mechanistically attributed to the strong influence of a highly competitive species (*Alona*), in the higher richness treatments. Resource availability enhances only the ability of an invading competitor to establish in a community but has no effect on invader dominance. Our study lends further experimental evidence to the roles of biodiversity and resource availability in mediating the establishment of new competitive invasive species.

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