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 davidi (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 dramatically 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