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Species Diversity and Invasion Resistance in a Marine Ecosystem

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Theory predicts that systems that are more diverse should be more resistant to exotic species, but experimental tests are needed to verify this. In experimental communities of sessile marine invertebrates, increased species richness significantly decreased invasion success, apparently because species-rich communities more completely and efficiently used available space, the limiting resource in this system. Declining biodiversity thus facilitates invasion in this system, potentially accelerating the loss of biodiversity and the homogenization of the world's biota.

Along with habitat modification, the intentional or accidental introduction of new species by humans is a leading cause of the global biodiversity crisis (1). Because biological invasions can dramatically alter community composition and ecosystem function (2–4) and cause considerable economic damage (5), there is substantial interest in understanding why and how successful invasions occur. Although all systems do not appear to be equally invulnerable (3, 6, 7), factors determining the susceptibility of a community to invasion remain unclear. Theory predicts that species-rich communities should be less susceptible to invasion because of a more complete utilization of resources (6, 8, 9),

but data in support of this prediction have been elusive (10). Some observational studies do support a positive relation between biodiversity and invasion resistance (7, 8), but others do not (11). However, the large number of uncontrolled factors in these studies makes interpreting these findings difficult; manipulative experiments are needed to assess the effect of species richness on invasion success more directly. Studies of terrestrial grasslands and aquatic microbial communities in laboratory microcosms have demonstrated that species-rich communities are more resistant to being invaded by additional species than are species-poor communities (12). However, no studies have investigated this relation by using exotic species that currently pose an invasion threat to natural systems, and few studies offer evidence for the mechanisms underlying these patterns.

A growing number of marine invertebrates have been introduced to the coastal waters of southern New England (13). In some habitats,

these species have invaded successfully and reduced the abundance of native species, whereas in others, they have been unsuccessful and the native community remains unchanged (14). Some of these invaders have become locally dominant space holders, including the colonial ascidian *Botrylloides diegensis*, native to the Pacific Ocean (13). By introducing invasive species recruits (<1 week old) into experimentally assembled epifaunal communities with varying numbers of native species, we tested the effects of native community species richness on the ability of *Botrylloides* to invade coastal habitats.

Experimental communities were composed of zero to four native species (Fig. 1). This range of diversity treatments was selected because most of the space in undisturbed areas that were equal in size to our communities (100 cm²) was occupied by three to four species. Each community consisted of 25 2-cm-by-2-cm tiles that fit on tracks bolted to a larger substrate (10 cm by 10 cm). Native sessile invertebrates were cultured on tiles in the field by allowing individuals to settle on tiles, then these tiles were "gardened" weekly to remove all other species except the target species. Once a single tile was covered by an individual or colony of a native species, a number of such tiles were arranged to produce communities with the desired species richness (Fig. 1). Five *Botrylloides* recruits were interspersed throughout each community so that there was only one individual in each row and column of the five-by-five grid of tiles that composed the community (Fig. 1). The remaining 20 tiles in each community were covered by native species. In multispecies communities, available space was divided equally among native species, and the

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spatial arrangement of individuals of different native species was determined with a random-number generator. Native species were drawn at random from among five of the most common species at the location where experiments were conducted: the blue mussel (*Mytilus edulis*), two solitary ascidians (*Molgula manhattanensis* and *Ciona intestinalis*), the colonial ascidian (*Botryllus schlosseri*), and the encrusting bryozoan (*Cryptosula pallasiana*). Each native species combination was replicated four times, and each level of species richness was replicated with different species combinations.

Experimental communities were deployed in the field in eastern Long Island Sound near Groton, Connecticut (15), and they were monitored until all invaders had either been eliminated or had successfully reproduced (indicating a successful invasion). Reproductive status was assessed by the presence of mature brooded larvae visible through the translucent orange tunic of *Botrylloides*. Communities were photographed weekly to evaluate the survival and reproductive status of invaders and to measure (using image analysis) the availability of primary space.

We found decreased survival of *Botrylloides* recruits in communities with higher species richness (Fig. 2A). Species richness manipulations explained 73% of the variance in the survival of invaders ($r = -0.855$ and $P < 0.0001$). This result was not attributable to dominant effects of any one species, because species that were best at resisting invasion in monospecific communities were not necessarily members of the most resistant multispecies

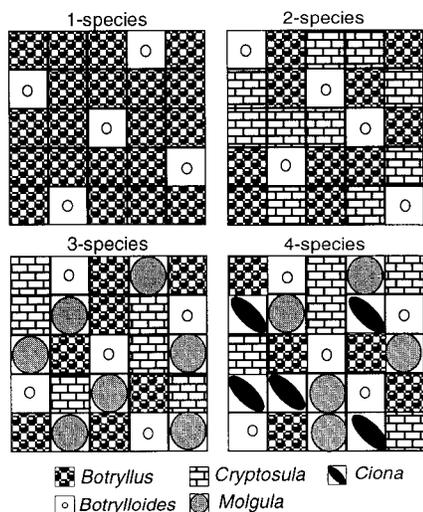


Fig. 1. Plan view of experimental communities showing random arrangement of native species and interspersions of invasive species recruits (zero-species treatments not shown). Four replicates of each species combination were assembled, and several different species combinations were assembled for each level of species richness. All communities (except those with zero species) begin with about the same initial cover of native species.

communities. Conversely, species that were more susceptible to being invaded when grown alone (for instance, the slow-growing bryozoan *Cryptosula pallasiana*) were often members of highly resistant multispecies communities. *Botrylloides* has no obvious unique attributes and seems likely to be representative of other invasive colonial marine invertebrates in its response to native community diversity.

Although we cannot be sure of the mechanism by which increased species diversity enhances the resistance of our experimental communities to invasion, our results support the hypothesis that reduced resource availability is responsible for the decreased success of invasions in communities with increased diversity (8, 9). Primary space is often the limiting resource in marine hard-substrate communities (16–18), and repeated measures analysis of variance indicated significant effects of species richness ($F = 86.9$ and $P < 0.0001$) and time

($F = 102.2$ and $P < 0.0001$) on the amount of open space in each community, as well as an interaction between these factors ($F = 22.0$ and $P < 0.0001$). These results are reflective of the fact that, although there was no initial difference in the availability of space among communities with species richnesses of one through four, as the communities developed, more space became available in communities with fewer native species (Figs. 2B and 3).

These differences arose because natural population cycles created large increases in open space in simple communities but did not create increases in those that were more complex (Figs. 2B and 3). For example, when the solitary ascidian *Molgula manhattanensis* was the only species in our experimental community, increasing community biomass caused by gregarious settlement of conspecifics on the tunics of adults caused the entire aggregation to slough off the substrate. This left considerable

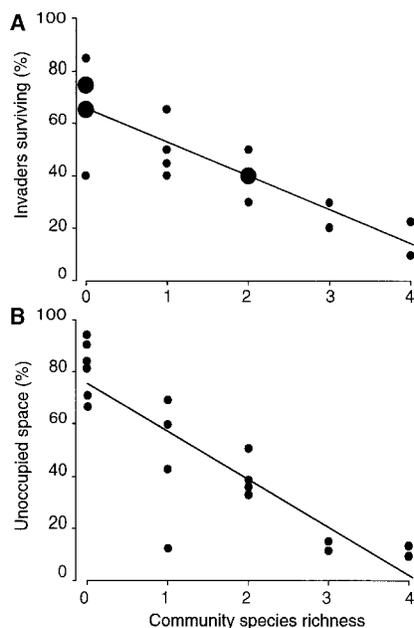
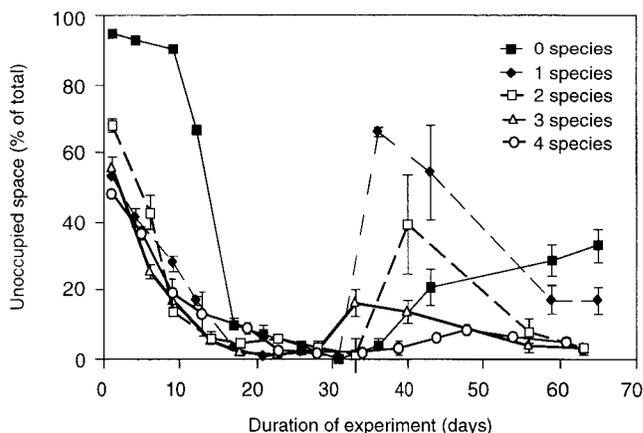


Fig. 2. (A) Survival of recruits of the exotic ascidian *Botrylloides diegensis* and (B) availability of free space, which are plotted versus native community species richness. Availability of free space is taken as the highest measured open space that occurred after communities were fully developed (after 14 days) (see Fig. 3) and thus represents the amount of resources (space) freed because of population cycles in each community. Each dot represents results (survival of recruits or availability of space) averaged over the four replicates of a given species combination, and larger dots indicate two coincident data points. Statistical analysis was by linear least squares regression (solid lines) [in (A), $r = -0.855$ and $P < 0.0001$; in (B), $r = -0.867$ and $P < 0.0001$]. Results are qualitatively unchanged when the zero-species treatment is deleted from the analysis [in (A), $r = -0.839$ and $P = 0.0003$; in (B), $r = -0.702$ and $P = 0.009$].

Fig. 3. Time series of the availability of open space (symbols represent the mean; error bars represent ± 1 SE) in representative communities of each species richness level (zero species; one species, *Molgula manhattanensis*; two species, *Molgula* and *Botryllus schlosseri*; three species, *Molgula*, *Botryllus*, and *Cryptosula pallasiana*; four species, *Molgula*, *Botryllus*, *Cryptosula*, and *Ciona intestinalis*). These five communities are displayed because they were deployed at the same time of year and the one-, two-, and three-species treatments are composed of a subset of the species used in the four-species experiment.



bare space (~70% of total) (Fig. 3), allowing *Botrylloides* recruits that had survived beneath the *Molgula* "canopy" to expand. A similar pattern was observed among communities initially composed of only the semelparous colonial ascidian *Botryllus schlosseri* (19) (not shown), which died after reproducing. "Boom and bust" population cycles are characteristic of many epifaunal marine invertebrates (17–20), and this feature may contribute substantially to the susceptibility of these simple communities to invasion.

Species-rich communities appear to be buffered from such fluctuations in space availability. Although the abundance of each species in multispecies communities varied, these variations were out of phase, and the amount of open space that became available was less than that in simpler communities. For example, communities that initially contained *Botryllus*, *Molgula*, *Cryptosula*, and *Ciona* showed little change in the availability of free space throughout the course of the experiment (Fig. 3). This resulted from the sequential replacement of species; when one species declined, others increased and thus maintained high total cover. Because little space became available in these experiments, *Botrylloides* recruits had little room to grow, and few survived (Fig. 2). The consistently high cover in more species-rich communities may also reduce new recruitment of exotic invaders into these communities because these organisms typically do not settle directly on resident adults (21). In theory, a single species that could effectively monopolize space for a long period of time could resist invasion at least as well as a multispecies assemblage. However, the existence of such species in shallow-water epifaunal communities such as these appears unlikely because of the short life-span of most species, the absence of a rigid competitive hierarchy, and the importance of "priority" effects (17). Differences in primary space availability appear to drive the relation between diversity and invisibility in this system, but this model should be applicable to any system in which the limiting resources (such as light or nutrients) are clearly identifiable.

All native species used in our experiments could be placed in the same trophic and functional groupings, as they are all sessile, suspension-feeding invertebrates. As has been proposed for other communities (22), functionally redundant species may represent a form of biological insurance against the inevitable loss of any one species as a consequence of natural population cycles or disturbances. Our results lend empirical support to this idea from the marine environment, strengthening the argument for efforts to preserve naturally occurring biodiversity, regardless of whether some species are functionally similar. Because biodiversity loss promotes invasion and successful invasion may further decrease biodiversity (2–4),

a negative feedback cycle may be initiated that ultimately results in severe impoverishment and homogenization of the global biota.

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Structural Analysis of the Mechanism of Adenovirus Binding to Its Human Cellular Receptor, CAR

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Binding of virus particles to specific host cell surface receptors is known to be an obligatory step in infection even though the molecular basis for these interactions is not well characterized. The crystal structure of the adenovirus fiber knob domain in complex with domain I of its human cellular receptor, coxsackie and adenovirus receptor (CAR), is presented here. Surface-exposed loops on knob contact one face of CAR, forming a high-affinity complex. Topology mismatches between interacting surfaces create interfacial solvent-filled cavities and channels that may be targets for antiviral drug therapy. The structure identifies key determinants of binding specificity, which may suggest ways to modify the tropism of adenovirus-based gene therapy vectors.

Many viral infections are initiated by the specific binding of specialized proteins or attachment factors on the virion's surface to glycoprotein receptors on the surface of host

cells. Enveloped viruses, such as human immunodeficiency virus (HIV), attach to host cells by means of spike-like membrane glycoproteins, whereas most nonenveloped viruses, such as poliovirus, attach by means of specialized domains integral to their capsids. Adenoviruses (Ad) are hybrids: They are nonenveloped but have trimeric fibers (320 to 587 residues) emanating from the vertices of their icosahedral capsid, which terminate in

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