

BIODIVERSITY, INVASION RESISTANCE, AND MARINE ECOSYSTEM FUNCTION: RECONCILING PATTERN AND PROCESS

JOHN J. STACHOWICZ,¹ HEATHER FRIED,² RICHARD W. OSMAN,³ AND ROBERT B. WHITLATCH²

¹Section of Evolution and Ecology, University of California, Davis, California 95616 USA

²Department of Marine Sciences, University of Connecticut, Groton, Connecticut 06340 USA

³Academy of Natural Sciences, Estuarine Research Center, St. Leonard, Maryland 20685 USA

Abstract. A venerable generalization about community resistance to invasions is that more diverse communities are more resistant to invasion. However, results of experimental and observational studies often conflict, leading to vigorous debate about the mechanistic importance of diversity in determining invasion success in the field, as well as other ecosystem properties, such as productivity and stability. In this study, we employed both field experiments and observational approaches to assess the effects of diversity on the invasion of a subtidal marine invertebrate community by three species of nonindigenous ascidians (sea squirts). In experimentally assembled communities, decreasing native diversity increased the survival and final percent cover of invaders, whereas the abundance of individual species had no effect on these measures of invasion success. Increasing native diversity also decreased the availability of open space, the limiting resource in this system, by buffering against fluctuations in the cover of individual species. This occurred because temporal patterns of abundance differed among species, so space was most consistently and completely occupied when more species were present. When we held diversity constant, but manipulated resource availability, we found that the settlement and recruitment of new invaders dramatically increased with increasing availability of open space. This suggests that the effect of diversity on invasion success is largely due to its effects on resource (space) availability. Apart from invasion resistance, the increased temporal stability found in more diverse communities may itself be considered an enhancement of ecosystem function.

In field surveys, we found a strong negative correlation between native-species richness and the number and frequency of nonnative invaders at the scale of both a single quadrat (25 × 25 cm), and an entire site (50 × 50 m). Such a pattern suggests that the means by which diversity affects invasion resistance in our experiments is important in determining the distribution of invasive species in the field. Further synthesis of mechanistic and observational approaches should be encouraged, as this will increase our understanding of the conditions under which diversity does (and does not) play an important role in determining the distribution of invaders in the field.

Key words: ascidians; biodiversity; bryozoans; ecosystem function; fouling community; invasion resistance; invasive species; invertebrates; marine ecology; species richness; temporal niche partitioning.

INTRODUCTION

Along with habitat modification, the intentional or accidental introduction of new species by humans is a leading cause of the global biodiversity crisis (Wilcove et al. 1998). Invasions directly and indirectly alter local community composition and diversity (e.g., Nichols et al. 1990, D'Antonio and Vitousek 1992, Travis 1993, Grosholz et al. 2000), dramatically altering ecosystem function and sometimes causing significant economic hardships (Office of Technology Assessment 1993). As a result, there is increasing interest in predicting why, how, and where successful invasions occur. However, there has been surprisingly little experimental work on the mechanisms underlying the success and failure of invasions (Kareiva 1996), and a focus on vascular

plants limits the generality of conclusions drawn from much of this work. In particular, despite a growing number of well-documented invasions in marine systems (Carlton 1996, Cohen and Carlton 1998), comparatively little is known about the mechanisms underlying the success or failure of invasions and their consequences for native communities (e.g., Byers 2000).

Just as some exotic species are more successful invaders than others (e.g., Rejmanek and Richardson 1996, Reichard and Hamilton 1997), some communities are more susceptible to invasion than others. Perhaps one of the oldest generalizations about community resistance to invasions is that more diverse communities should be more resistant to invasion (Elton 1958). Early support for this idea was derived from the observation that species-poor systems (e.g., islands) appeared to be more heavily invaded than species rich

systems (e.g., Elton 1958, Carlton 1979, Nichols and Pamatmat 1988, Usher 1988). There is also support for this idea over larger temporal and spatial scales, as communities with greater numbers of extinction events (i.e., reduced diversity) are also more prone to invasion (Vermeij 1991). The idea enjoys strong theoretical support (Robinson and Valentine 1979, Post and Pimm 1983, Case 1990, Drake 1990, Law and Morton 1996). The most commonly cited mechanism behind this phenomenon is that as species accumulate, competition intensifies and fewer resources remain available for new colonists (Elton 1958, Case 1990). However, there have been few rigorous tests of this prediction and its underlying mechanism (see Stachowicz et al. 1999, Naeem et al. 2000).

A review of the literature surrounding this debate highlights the lack of consensus on the strength and direction of the effects of diversity on community resistance to invasion (Levine and D'Antonio 1999). A similar debate characterizes our understanding of the effects of diversity on ecosystem function more broadly. Many studies of long-lived species, or those that occur over large spatial scales, employ an observational approach to compare the abundance or frequency of invasion with the diversity of the surrounding native community. Some of these studies show the expected negative relationship between diversity and invasion success (Case and Bolger 1991), but many more show that more diverse native communities actually support more invaders (Knops et al. 1995, Planty-Tabacchi et al. 1996, Rejmanek 1996, Wiser et al. 1998). Finally, some even suggest that the strength and direction of the relationship may change across spatial scales (Case 1996, Stohlgren et al. 1999). Interpreting these findings, however, is difficult, due to the large number of uncontrolled factors in these studies. Many other factors correlated with diversity can affect the establishment and spread of invasions; and, even if observational studies do support a negative relationship between diversity and invasion, it is unclear from these data whether low native diversity is a cause or a consequence of successful invasions (Woods 1993, Morgan 1998). Experimental manipulations of diversity are needed to assess directly the effect of diversity on invasions.

A recent surge in interest in the broader relationship between diversity and ecosystem function (e.g., review in Loreau et al. [2001]) has spawned several such tests (McGrady-Steed et al. 1997, Knops et al. 1999, Lavorel et al. 1999, Stachowicz et al. 1999, Levine 2000, Naeem et al. 2000, Symstad 2000), and most of these studies support the idea that species richness decreases invasion success. A rigorous experimental approach, while good at quantifying the direct effects of diversity, can only reveal the *potential* importance of diversity in determining invasion success in natural systems. Such experiments rarely assess whether diversity is important relative to other factors such as propagule sup-

ply, disturbance, or predation for generating patterns of invasion in the field. Conversely, observational studies can tell us whether the presence or success of non-native species is correlated with diversity, but not whether diversity itself has any effect on invasibility. A synthesis of observational and experimental approaches to the relationship between biodiversity and ecosystem function is urgently needed, but there has been frustratingly little crossover (but see Levine [2000]).

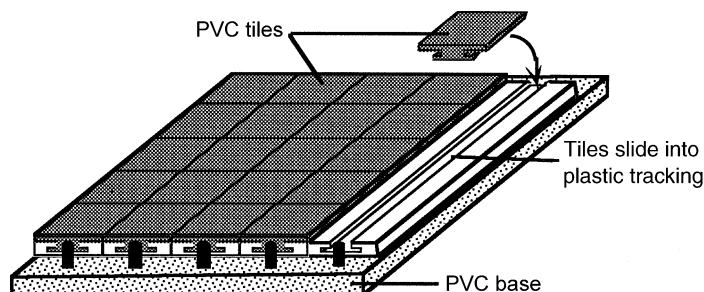
In contrast to the growing body of research on the effects of diversity on ecosystem function (including invasion resistance) in terrestrial plant communities (see reviews by Levine and D'Antonio [1999], Schlapper and Schmid [1999], Loreau et al. [2001]), studies in marine systems are still rare (Stachowicz et al. 1999, Duffy et al. 2001, Emmerson et al. 2001). Here we examine the effects of diversity on two measures of ecosystem performance, invasion resistance and space occupation, in a sessile marine invertebrate community. Our approach combines observational field surveys and field experiments in which we assemble communities of varying native diversity to assess the effects of diversity on the recruitment, survival, and growth of three species of recently introduced sea squirt. Previous work has demonstrated that these native communities are strongly space-limited and structured by a combination of biotic interactions and disturbance (e.g., Osman 1977, Sutherland 1978, Buss and Jackson 1979, Osman and Whitlatch 1996), so space may play an important role in the success and failure of invaders. We therefore examine how differentiation in the temporal patterns of abundance among native species contributes to a negative relationship between diversity and space availability over time. Finally, we compare the effect of our diversity manipulations on the success of native vs. nonnative "invaders" to assess whether the factors that govern natural vs. human-mediated invasions might differ.

METHODS

Study organisms

The sessile epibenthic invertebrate communities of eastern Long Island Sound (Connecticut–New York, USA) are typical of protected rocky coasts and bays throughout southern New England. They consist of solitary and colonial ascidians, encrusting and erect bryozoans, barnacles, mussels, hydroids, sea anemones, and some sponges. Many of these species have generation times on the order of one to two months and can be easily grown for use in manipulative field experiments. As representative native species, we selected the five most common species found on shallow subtidal pilings and boulders in eastern Long Island Sound: the colonial ascidian *Botryllus schlosseri*, the solitary ascidians *Molgula manhattensis* and *Ciona intestinalis*, the encrusting bryozoan *Cryptosula pallasiana*, and the blue

FIG. 1. Experimental substrate for diversity manipulations. See *Methods* for details.



mussel *Mytilus edulis*. These species will be hereafter referred to by genus. Although the true status of the New England sea squirts as natives or invaders is difficult to resolve due to the poor fossil record of these soft-bodied organisms, all of these species have been present in New England for as long as humans have been studying these animals (Couthouy 1838, *Ciona intestinalis* (as *Ascidia intestinalis*); DeKay 1843, *Molgula manhattensis* (as *Ascidia manhattensis*); Binney 1870 *Botryllus schlosseri*, cf. Van Name 1945). Thus, these species form the resident community that current invaders encounter upon arrival.

Five species of sessile marine invertebrates have been recently introduced (1970s–1980s) to New England and are common on hard substrates, including two colonial ascidians (*Botrylloides* sp., *Diplosoma listerianum*), two solitary ascidians (*Ascidella aspersa*, *Styela clava*), and one encrusting bryozoan (*Membranipora membranacea*). Although the *Botrylloides* sp. has long been thought to be *B. diegensis*, recent morphological evidence suggests that it may instead be *B. violaceus* (G. Lambert, *personal communication*). All of these invaders are similar in feeding mode and growth habit (they are all sessile suspension feeders), but they differ considerably in their ecology and life history (Berman et al. 1992, Osman and Whitlatch 1996). *Botrylloides* and *Diplosoma* brood very short-lived larvae (a few minutes to hours) that appear capable of settlement almost immediately upon release (Worcester 1994; J. Stachowicz, H. Fried, R. Osman, and R. Whitlatch, *personal observations*), whereas *Ascidella* and *Styela* are broadcast spawners whose larvae generally become competent to settle within 12–24 h after fertilization (Niermann-Kerkenberg and Hoffmann 1989). Thus, there may be differences in the scales over which populations of each species represent open vs. closed systems. *Botrylloides* can be semelparous (Whitlatch et al. 1995), with two cohorts per year. The second cohort of *Botrylloides* recruits in late summer or early autumn and overwinters as small colonies, a life history cycle remarkably similar to the native *Botryllus* (Grosberg 1988). Solitary species such as *Styela* and *Ascidella* overwinter as large juveniles and small adults. *Diplosoma* is a more recent invader and exhibits extreme year-to-year and site-to-site fluctuations in recruitment and abundance, often being ab-

sent from a site for several years and then becoming numerically dominant the following year. *Botrylloides* and *Diplosoma* are colonial and can rapidly propagate asexually, whereas *Styela* and *Ascidella* are solitary, and individual zooids can grow much larger than those of the colonial species, but must reproduce sexually. Thus these species, while taxonomically and ecologically similar enough to facilitate direct comparisons, also provide sufficient diversity in life history and ecological properties to allow an assessment of the generality of our results.

Field surveys

To assess whether native community species richness in the field was correlated with invasion success, we recorded the presence of native and introduced sessile species in 25 × 25 cm quadrats at 12 different sites (10 quadrats per site) in eastern Long Island Sound, including the Thames, Poquonnock, and Mystic river estuaries. Sites ranged within 1–10 m depth and included habitat provided by pilings, rocky outcrops, boulder fields, seagrass beds, and kelp forests. Sampling was initiated from a haphazardly chosen location within each site and individual plots were located at randomly selected distances and directions with a minimum of 5 m between samples. An inventory of all sessile organisms present in each plot was made and the data used to assess the correlation between the number of native and nonnative species in an individual quadrat. Data were later pooled within each site to assess the correlation between the number of invasive species and the number of native species at the scale of an entire site (~50 × 50 m). Plots of cumulative species totals vs. the number of quadrats sampled indicated that our sampling effort captured most macroscopic species present within a site (J. Stachowicz and R. Osman, *unpublished data*).

Manipulating species richness

We manipulated species richness and composition using a 10 × 10 cm polyvinyl chloride (PVC) substrate composed of a five-by-five grid of 2 × 2 cm PVC tiles (Fig. 1), each with a single individual or colony of a native species. One side of each tile was flat, and we transplanted juveniles or allowed larvae to settle onto this side. The other side of the tile had a T-shaped

TABLE 1. Species combinations used for experiments assessing the role of native-species richness on the survival and cover of invaders, and on the settlement and recruitment of invaders from the plankton.

No. species	<i>Ascidella</i> survival	<i>Botrylloides</i> survival	Settlement/Recruitment
0	Invader only (4)	Invader only (6)	Bare (3)
1	<i>Botryllus</i> , <i>Molgula</i> , <i>Cryptosula</i> , <i>Mytilus</i> , <i>Ciona</i>	<i>Botryllus</i> , <i>Molgula</i> , <i>Cryptosula</i> , <i>Mytilus</i> , <i>Ciona</i>	<i>Botryllus</i> , <i>Molgula</i> , <i>Mytilus</i>
2	<i>Mytilus</i> – <i>Botryllus</i> <i>Molgula</i> – <i>Ciona</i> <i>Mytilus</i> – <i>Molgula</i> <i>Ciona</i> – <i>Mytilus</i>	<i>Botryllus</i> – <i>Molgula</i> <i>Botryllus</i> – <i>Cryptosula</i> <i>Cryptosula</i> – <i>Molgula</i> <i>Mytilus</i> – <i>Botryllus</i>	<i>Botryllus</i> – <i>Ciona</i> <i>Cryptosula</i> – <i>Molgula</i> <i>Mytilus</i> – <i>Molgula</i>
3	<i>Molgula</i> – <i>Ciona</i> – <i>Botryllus</i> <i>Botryllus</i> – <i>Mytilus</i> – <i>Cryptosula</i> <i>Ciona</i> – <i>Molgula</i> – <i>Mytilus</i> <i>Molgula</i> – <i>Mytilus</i> – <i>Botryllus</i>	<i>Botryllus</i> – <i>Molgula</i> – <i>Cryptosula</i> <i>Mytilus</i> – <i>Molgula</i> – <i>Cryptosula</i> <i>Molgula</i> – <i>Ciona</i> – <i>Mytilus</i> <i>Molgula</i> – <i>Mytilus</i> – <i>Botryllus</i>	not done (see text)
4	<i>Cryptosula</i> – <i>Botryllus</i> – <i>Molgula</i> – <i>Mytilus</i> <i>Mytilus</i> – <i>Ciona</i> – <i>Botryllus</i> – <i>Molgula</i>	<i>Mytilus</i> – <i>Ciona</i> – <i>Botryllus</i> – <i>Molgula</i> <i>Cryptosula</i> – <i>Botryllus</i> – <i>Molgula</i> – <i>Ciona</i> <i>Ciona</i> – <i>Molgula</i> – <i>Mytilus</i> – <i>Crypto-</i> <i>sula</i>	<i>Mytilus</i> – <i>Ciona</i> – <i>Botryllus</i> – <i>Molgula</i> <i>Cryptosula</i> – <i>Botryllus</i> – <i>Mytilus</i> – <i>Ciona</i> <i>Ciona</i> – <i>Molgula</i> – <i>Mytilus</i> – <i>Crypto-</i> <i>sula</i>

Notes: Each combination listed was replicated four times. Numbers in parentheses for the zero-species treatments indicate the number of four-panel replicates of zero-species that were deployed over the course of the season (see *Methods: Effects of species richness on invader settlement and recruitment*).

projection that fit into a groove on preformed tracks bolted to a PVC plate. Each track held five tiles (Fig. 1). Five tracks were mounted side by side on a single PVC plate, such that the full experimental unit consisted of a continuous substrate with 25 interchangeable subunits. A single stainless steel screw at each end of the track held the tiles in place.

For all species except mussels, animals settled at the larval stage onto individual 2×2 cm PVC tiles, either as a result of exposure to natural recruitment in the field or to reproductive adults in the lab. In either case, individuals were raised from newly settled recruits to adults in the field on panels suspended face down beneath floating docks. The source of all native and introduced species was the location at which the field experiments (see *Methods: Effect of species richness on invader survival*) were deployed. Competing species were removed from individual tiles at least weekly to obtain tiles covered by only a single individual (or colony) of a native species. For mussels, juveniles were transplanted directly to the tiles by gluing them to the substrate. Within a few days the glue bond usually dissolved, but by then the mussels had attached themselves to the substratum via byssal threads. We observed no mortality as a result of the gluing process and these individuals continued to grow throughout the experiment.

Effect of species richness on invader survival

To test the hypothesis that communities with more native species are more resistant to invasion, we ran separate experiments designed to test the effect of species richness on (1) the survival of transplanted recruits, and (2) the recruitment of new individuals from the plankton. To address this first question we included

five tiles in each assemblage that each contained a single, newly settled (two to three days postsettlement), individual of a nonnative species, either *Ascidella* or *Botrylloides*. All invaders in a given assemblage were of the same species. The position of each was assigned randomly within the five-by-five grid, with the caveat that two adjacent tiles could not both have invaders. The remaining 20 tiles on these panels were divided equally among one, two, three, or four native species. Species used for various combinations were determined by random assignment, with the exception that each of the five species was used in one-species experiments for both invaders. There were at least four different species combinations at each level of species richness (except the four-species treatment in which, due to logistical constraints, there were three different combinations for *Botrylloides* and two for *Ascidella*). A list of species combinations employed for each invader is given in Table 1. All species combinations were replicated four times. Panels were interspersed and deployed in one meter of water, suspended facedown beneath a floating dock at Avery Point, Connecticut, USA. All species (natives and nonnatives) occur at the site where the experiments were conducted, and all of the native assemblage combinations occur naturally.

Because of the difficulty in culturing the large numbers of invertebrates used in these experiments and timing them so that they would all be ready for use within a narrow temporal window, we could not run all species combinations simultaneously. Experiments were initiated in July and August of each summer, and most ran for approximately two months. Each time experiments were deployed, we also ran four replicates of a “zero-species” assemblage in which we monitored the success of five invader recruits (two to three days

old at the start of the experiment) on an otherwise bare panel.

Approximately every five days, we photographed each panel with a digital camera; the photographs were later analyzed using NIH Image (image analysis software is available online from the National Institutes of Health)⁴ to calculate the amount of free space and the amount of space occupied by invaders in each assemblage. These data were analyzed using repeated-measures ANOVA, with percent cover variables arcsine-transformed to meet assumptions of normality where necessary. Each time panels were photographed, we manually checked the status of the recruits we had planted in these communities. Experiments continued until either all invaders had been eliminated or all surviving invaders successfully reproduced, indicating that the invasion was successful from the standpoint of the reproductive success of the initial propagule. For *Botrylloides*, reproduction could be observed directly by viewing tadpole larvae being brooded in the tunic. For *Ascidella*, a broadcast spawner, we examined in the lab the ability of various size classes of individuals to release mature gametes that could be fertilized, develop, and successfully settle onto benthic substrates. This allowed us to set an approximate size threshold at which first reproduction occurs (>18–20 mm length, unpublished data), and we used this as an indication of the size at which invasions could be declared successful. Experiments not terminated for one of these reasons were terminated at the end of the growth and recruitment season in late October.

In addition to obvious logistical constraints, we manipulated diversity at this local, neighborhood scale for biological reasons, as well. A propagule (marine invertebrate larva, terrestrial plant seed, algal spore) occupies a very small physical neighborhood (<1 mm² for our study animals) and the biotic and abiotic conditions in that neighborhood will likely determine the success of the individual propagule. The number of native individuals with which an individual invader will have contact is likely to be restricted to those that live in the immediate neighborhood, which is well approximated by our 10 × 10 cm experimental unit and 25 × 25 cm field sampling unit. A local “neighborhood” of this size is often dominated by only one to five resident species (Osman 1977; J. Stachowicz, H. Fried, R. Osman, and R. Whitlatch, *personal observations*), and the range of species richness treatments used in our experiments reflects this. Diversity at larger scales may be important in determining the size of the species pool from which individual neighborhoods are drawn, hence larger scale diversity may affect invasion success indirectly by determining local neighborhood diversity (Law and Morton 1996, Loreau 2000). However, assessment of this possibility is beyond the scope of this study.

Effect of species richness on invader settlement and recruitment

To test the short-term, direct effects of diversity on recruitment of larvae of nonnative species from the plankton, we again generated communities of varying species richness. In these communities all 25 tiles were occupied by a native species, and all had initially equivalent availability of open space (except the zero-species assemblage), as measured using image analysis on digital photographs of each assemblage prior to deployment. Because patterns of settlement can depend on the relative species composition of propagules in the plankton, and this can vary dramatically from week to week, we opted to reduce our replication of this experiment in order to run all experiments simultaneously. Thus, we performed only three different (randomly selected) species combinations at three levels of native-species richness (one, two, and four); although we still had four replicates of each species combination to allow us to distinguish the effects of richness and composition on invader recruitment.

To estimate the effects of native assemblages on larval settlement, panels were returned to the laboratory after one day in the field and examined under a dissecting microscope. All newly settled invertebrates were counted and identified to species. The same panels were redeployed and collected seven days later to estimate settlement integrated over a longer time period. Because this also incorporated some effects of postsettlement mortality, we call this measurement recruitment. Because settlement and recruitment vary seasonally, we ran this experiment once in July and a second time in September.

These experiments examine the effects of diversity on settlement and recruitment into assemblages with approximately equivalent availability of space. However, our longer term experiments show that available space decreases with increasing community species richness (see *Results: Effects of diversity on invader survival and growth*; Stachowicz et al. 1999), and from previous studies we know that the amount of available space can alter the magnitude of settlement and recruitment (Osman and Whitlatch 1995a, b). To test the potential of diversity to alter recruitment over longer time scales indirectly through occupation of space, we manipulated space availability independent of diversity within monocultures of *Ciona intestinalis*. We selected *Ciona* because (1) it is solitary and the total amount of free space available is unlikely to change much over a one-week experiment; and (2) its effects on settlement and recruitment of invaders (apart from space occupation) are neutral (see *Results*).

We created monocultures of *Ciona intestinalis* by first exposing bare panels to reproductive adults in the lab. After a few days the panels were covered with recruits and allowed to develop in the field until each had 100% cover of *Ciona*. Species other than *Ciona*

⁴ URL: (<http://rsb.info.nih.gov/nih-image>)

were periodically removed from the panels to maintain the monoculture. The assemblage on each panel was then thinned to ~0, 20, 60, or 90% cover, and some were left at 100% cover. These levels were chosen because they roughly corresponded to the availability of free space in our different diversity treatments (see *Results: Effects of diversity on invader survival and growth*; Stachowicz et al. 1999). These communities ($N = 8$ per cover treatment) were deployed in the field in mid-August and censused for newly settled invaders after one day and seven days. After the day-7 census, we returned the plates to the field to follow the development of these communities over two months, using weekly photographs to see if initial differences in space availability ultimately resulted in greater cover of invasive species.

RESULTS

Field survey

In individual 25×25 cm quadrats, the number of native species was strongly inversely correlated with the number of nonnative species (Fig. 2A; linear regression $R^2 = 0.42$, $P < 0.001$). Log-likelihood regression analysis of the same data showed that the number of resident species was a significant predictor of the likelihood that a plot contained a nonnative species ($r = 0.70$, $P < 0.001$, $N = 120$ plots). The curve produced by the log-likelihood model closely matches the observed frequency of invasion (Fig. 2B), suggesting a strong correlation between community species richness and the frequency of successful invasion. When the data are pooled within each site ($\sim 50 \times 50$ m), there is still a strong negative correlation between native and introduced species richness ($R^2 = 0.59$; $P < 0.001$), suggesting that the pattern is robust across spatial scales. Although we did not collect percent cover data in this field survey, invaders appeared to be of sufficiently low abundance within these plots that the negative correlation between diversity and invader presence is unlikely to be the result of the impact of invaders on native diversity.

Effects of diversity on invader survival and growth

Experimental manipulation of species richness demonstrated a strong negative effect of diversity on the survival of recruits of the nonnative *Botrylloides* ($R^2 = 0.79$, $P < 0.001$) and *Ascidella* ($R^2 = 0.63$, $P < 0.001$; Fig. 3A, B). In similar experiments with the native species *Botryllus schlosseri*, we saw a weaker correlation between species richness and survival of *Botryllus* recruits ($R^2 = 0.42$, $P = 0.03$, Fig. 3C). Particular native species (*Ciona* and *Molgula*) had a much stronger (positive) effect on invasion by this native than by either nonnative invader (Table 2). *Botryllus* recruits exhibited dramatically higher rates of mortality, so after 40 d few individuals remained and the experiment was terminated.

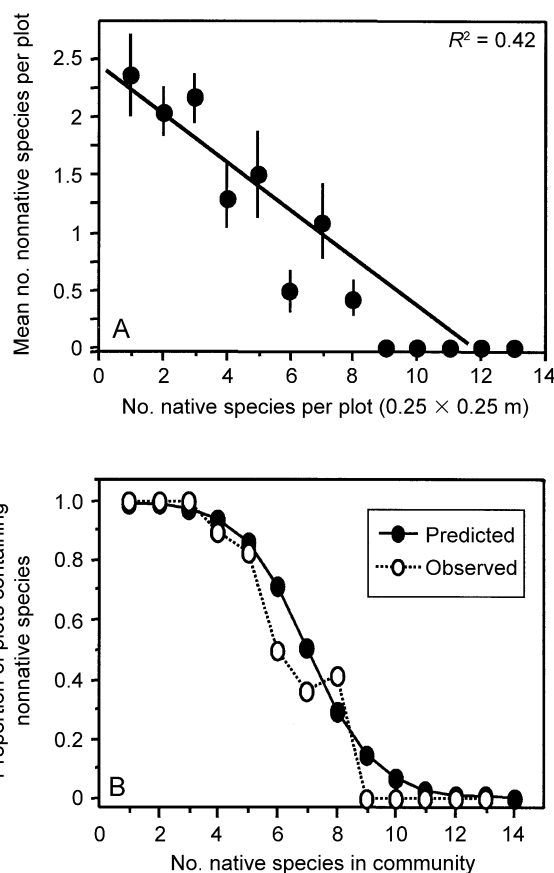


FIG. 2. Field surveys of (A) the total number and (B) the frequency of nonnative species as a function of native-species richness in 25×25 cm plots. Analysis in (A) is by linear regression ($R^2 = 0.42$, $P < 0.001$) and in (B) is by logistic regression ($r = 0.70$, $P < 0.001$). $N = 120$ quadrats. Error bars indicate ± 1 SE.

Stepwise multiple-regression analysis showed that species richness strongly decreased recruit survival for all invaders, whereas the abundance of any particular species explained only a minor portion of the variance in invader survival (Table 2). Species richness was the only significant variable in the multiple regression for *Ascidella* survival and explained 63% of the variance (all other variables $P > 0.10$). *Botrylloides* survival was also dominated by the effects of species richness ($R^2 = 0.79$), although the abundance of *Cryptosula* did explain an additional 5% of the variation. Species richness had a similar dominating effect on invader growth, as the total area covered by invaders decreased with increasing native species diversity at the end of the experiment (Fig. 3D, E; *Botrylloides*, $R^2 = 0.518$, $P < 0.001$; *Ascidella*, $R^2 = 0.521$, $P < 0.001$) and was not correlated with the abundance of any particular species. This suggests that species richness was more important than species identity in determining the postsettlement success of nonnative invaders in these assemblages.

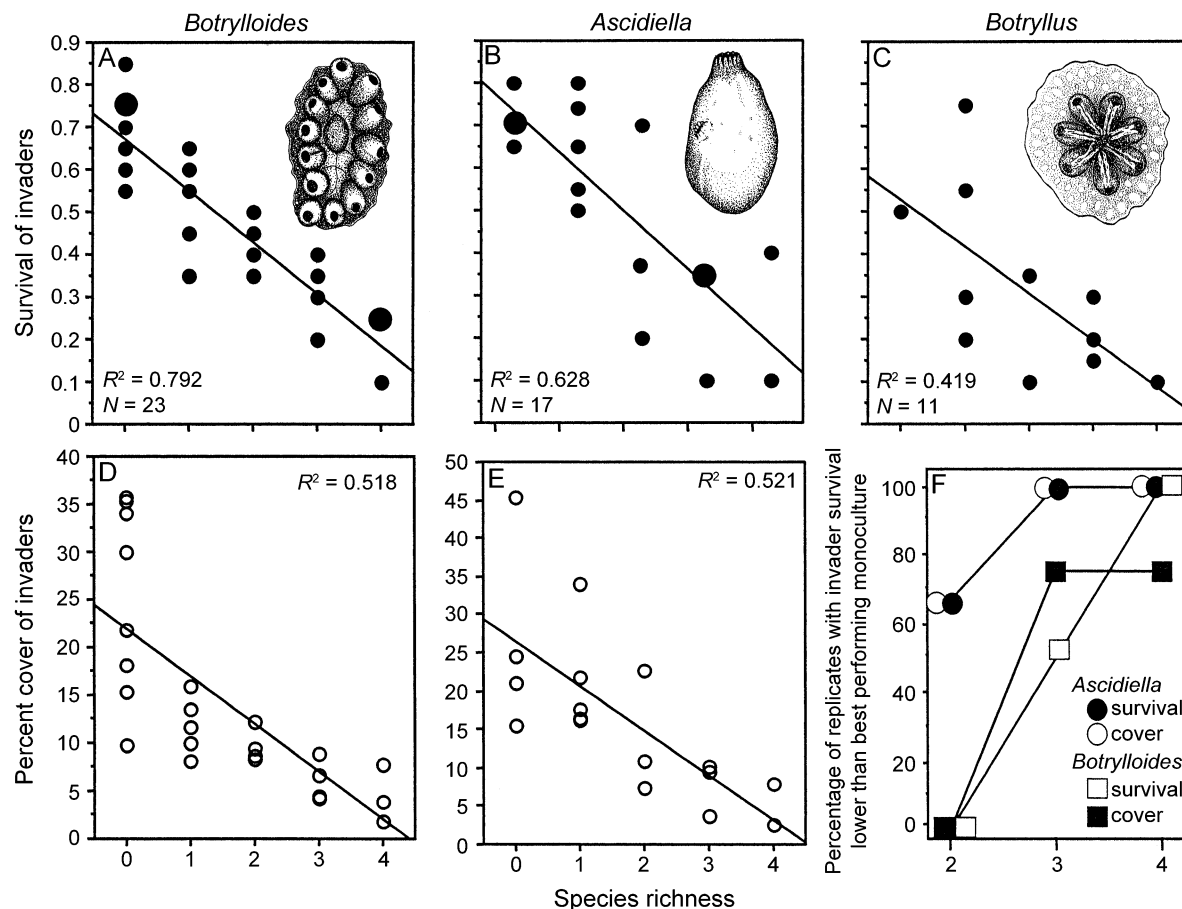


FIG. 3. Effects of native diversity manipulations on invasion success. Survival of transplanted recruits of the nonnative sea squirts (A) *Botrylloides* and (B) *Ascidiella* and (C) the native *Botryllus* decreases with increasing native-species richness. Increasing native-species richness also decreases the final percent cover of both (D) *Botrylloides* and (E) *Ascidiella*. Final cover of *Botryllus* is not presented due to low survivorship of transplanted recruits (see *Results: Effects of diversity on invader survival and growth* for details). Values of R^2 from simple linear regression are given on each panel. (F) Percentage of replicates of each level of species richness for which invader survival or percent cover is less than that in the monoculture with the lowest invader survival or percent cover ($D_{\min} < 0$; Loreau 1998). See *Results* for details.

A more direct test of whether the effect of diversity on invasion success is due to the strong effects of one species (i.e., the sampling effect; Huston 1997, Tilman et al. 1997) or true species complementarity is provided by the metrics of Loreau (1998). Among these, Loreau's D_{\max} , is the most stringent, because it compares whether the mixed-species treatment has significantly enhanced ecosystem function (in this case, invasion resistance) relative to the monoculture that is most able to resist invasion. For invader survival and percent cover, lower values indicate enhanced ecosystem function, so we calculated D_{\min} as the deviation of invader survival and percent cover in the multispecies experiments from the minimum observed in monoculture. This is essentially Loreau's (1998) formula: $D_{\min} = [O_i - \min(M_i)]/\min(M_i)$, where O_i is the observed invader survival or cover in a polyculture and $\min(M_i)$ is the minimum invader survival or cover in any of the monoculture treatments. For nearly all four-species com-

munities, and many three-species communities, the survival and percent cover of invaders is less than that of the most resistant single-species treatment (Fig. 3F), suggesting that species complementarity, and not the sampling effect, is responsible for the enhanced invasion resistance of more diverse communities.

Assemblages with more resident species also had lower availability of space, providing a potential explanation for the effect of species richness on invasion success. Repeated-measures ANOVA indicated significant effects of species richness and time on total available space, as well as a significant time \times species richness interaction. Similar results were obtained regardless of whether *Botrylloides* or *Ascidiella* were the invaders (Table 3). The significant interaction term in each analysis reflects the fact that all species richness treatments initially had similar availability of open space, but differences among treatments emerged over time (Fig. 4A, B). In all communities, space decreased

TABLE 2. Partial R^2 values from stepwise multiple-regression analysis with backward elimination, indicating the percentage of variation in invader survival explained by species richness or abundance of individual species.

Factor	<i>Botrylloides</i>	<i>Botryllus</i>	<i>Ascidella</i>
Species richness	(-)0.792*	(-)0.419*	(-)0.628*
<i>Botryllus</i>	0.008	...	0.004
<i>Ciona</i>	0.001	(+)0.211*	0.005
<i>Cryptosula</i>	(-)0.050*	0.013	0.018
<i>Molgula</i>	0.008	(+)0.164*	0.007
<i>Mytilus</i>	0.003	0.007	0.066

Notes: None of the independent variables were significantly correlated with each other ($P > 0.05$). A "+" or "-" in parentheses before each value indicates a positive or negative effect, respectively.

* $P < 0.05$.

TABLE 3. Results of repeated-measures analysis of variance of the availability of open space in *Botrylloides* and *Ascidella* survival experiments.

Source	df	MS	F	P
<i>Botrylloides</i> experiments				
Species richness	3	0.284	12.35	<0.001
Error (within panels)	38	0.023		
Time	7	1.081	56.44	<0.001
Species richness \times time	21	0.035	1.827	0.016
Error (between panels)	266	0.019		
<i>Ascidella</i> experiments				
Species richness	3	0.046	2.666	0.059
Error	44	0.017		
Time	12	1.142	91.70	<0.001
Species richness \times time	36	0.023	1.861	0.002
Error	528	0.012		

Note: Analysis does not include communities with zero native species, because initial free space in those communities was 100%.

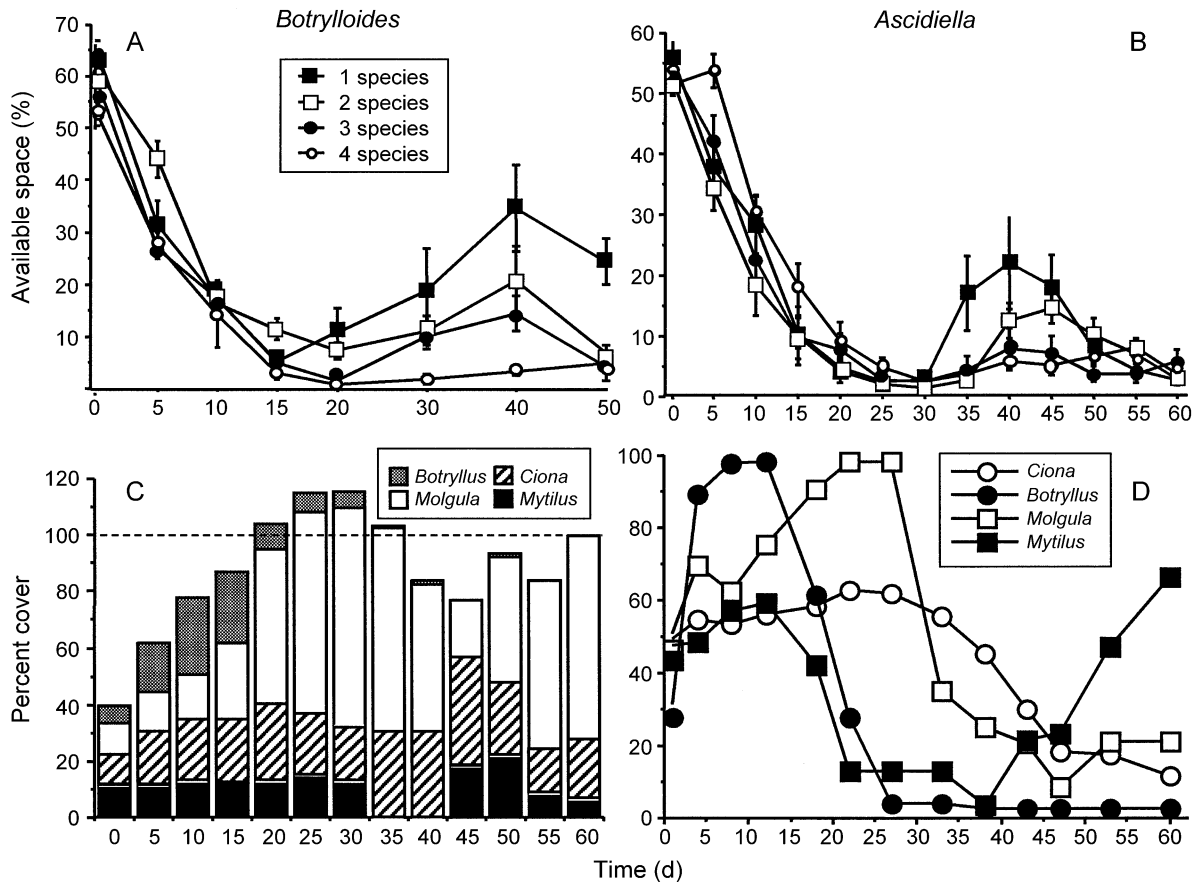


FIG. 4. Total amount of unoccupied primary space as a function of native-species richness for communities into which (A) *Botrylloides* and (B) *Ascidella* were transplanted. Repeated-measures ANOVA (Table 3) showed a significant time \times species richness interaction, reflecting the fact that all communities declined to near zero open space within the first few weeks, but more space subsequently became available in treatments with fewer native species. (C) Cover of species in a representative four-species assemblage. Note that although individual species fluctuate greatly in abundance, the total cover is always near 100%. (D) Cover of individual species in one-species experiments showing fluctuations in abundance of each species. Note that because there were initially no other species in these communities, a decline in the abundance of the native species resulted in a large increase in available space (panels A and B).

TABLE 4. Partial R^2 values, indicating the percentage of variation in settlement and recruitment, explained by species richness or abundance of individual species.

Factor	<i>Botrylloides</i>	<i>Diplosoma</i>	<i>Ascidella</i>	Natives
Settlement				
Species richness	0.004	(+)0.067*	...	0.048
<i>Botryllus</i>	0.008	0	...	(-)0.271*
<i>Ciona</i>	0	0	...	0.003
<i>Cryptosula</i>	(+)0.176*	0.014	...	0.001
<i>Molgula</i>	(+)0.102*	(+)0.598*	...	0.013
<i>Mytilus</i>	0.007	0.005	...	0.013
Recruitment				
Species richness	0.006	0.009	0.001	0
<i>Botryllus</i>	(-)0.114*	0.004	0.045	(-)0.136*
<i>Ciona</i>	0.027	0.045	(-)0.071†	(-)0.267*
<i>Cryptosula</i>	0.031	0	0.043	(-)0.050*
<i>Molgula</i>	0.071†	(+)0.221*	(-)0.075*	0.002
<i>Mytilus</i>	(-)0.129*	0.003	(-)0.142*	(-)0.276*

Notes: None of the independent variables were significantly correlated with each other ($P > 0.05$). Values were generated by stepwise multiple regression with backward elimination. A “+” or “-” in parentheses before each value indicates a positive or negative effect, respectively.

* $P < 0.05$.

† $P < 0.1$.

to near zero within the first few weeks of the experiment. After reaching zero, treatments subsequently differed in the extent to which free space became available, with more species-rich treatments having less space. Assemblages that initially contained zero native species (only transplanted invaders) were excluded a priori from this analysis, because they initially had 100% bare space, which would have produced a strong effect by itself. However, the inclusion of the zero-species data does not alter the qualitative conclusions or our statistical confidence in these conclusions.

Variation in the timing of each species' peak abundance buffered more diverse assemblages against fluctuations in the cover of individual species, leading to lower space availability in more diverse communities. To illustrate this, we describe and contrast patterns of abundance and free space for the four-species assemblage composed of *Botryllus*, *Molgula*, *Cryptosula*, and *Ciona* with the monocultures of each species (Fig. 4C and D, respectively), although similar results are obtained regardless of the particular species combinations examined. Single-species assemblages typically fluctuate in the abundance of the member species, and thus available space varies dramatically (Fig. 4D). For example, when *Molgula* was the only species in our experimental assemblage, gregarious settlement of conspecifics on the tunics of adults caused the entire aggregation to slough off the substrate (Fig. 4D), producing considerable open space for invaders. Similarly, assemblages composed solely of *Botryllus* rapidly occupied all available space, but died following reproduction. Although the abundance of individual species varies similarly in the four-species assemblage (Fig. 4C), these variations were out of phase, so the amount of open space that became available was less than in simpler communities (Fig. 4A–C). Because little space

became available in four-species communities, few *Ascidella* or *Botrylloides* recruits survived (Fig. 3A, B), and overall percent cover of invaders was low (Fig. 3D, E) relative to species-poor communities, which had more available space (Fig. 4A, B).

These experiments also provide evidence for a relationship between diversity and invader survival at spatial scales smaller than the 10×10 cm scale of an individual panel. Survival of invaders was greater among individuals that initially had two or fewer directly adjacent resident species (55%) than for those with three or four adjacent species (10–15%; analysis using a 3×2 contingency table [local species richness = 2, 3, or 4; invader success = yes or no], $G = 10.68$, $df = 2$, $P = 0.048$). These results were independent of the actual number of individuals surrounding a given invader, and suggest that the effects of diversity may be manifest at very small spatial scales.

Effect of diversity on invader settlement and recruitment

In contrast to the strong effects of species richness on invader survival, individual native species appeared to have a greater effect on settlement and recruitment of invading individuals (Table 4). Species richness only weakly enhanced the settlement of *Diplosoma* (simple $R^2 = 0.12$, partial $R^2 = 0.067$, $P < 0.05$; Table 4) and did not affect the recruitment of any species (Table 4, Fig. 5B). Despite differences in the species combinations used in the July and September deployments, results were qualitatively similar. Overall settlement and recruitment was lower for *Botrylloides* and *Ascidella*, and higher for *Diplosoma* in September due to seasonality in the timing of reproduction, yet there was no effect of richness on settlement or recruitment of any

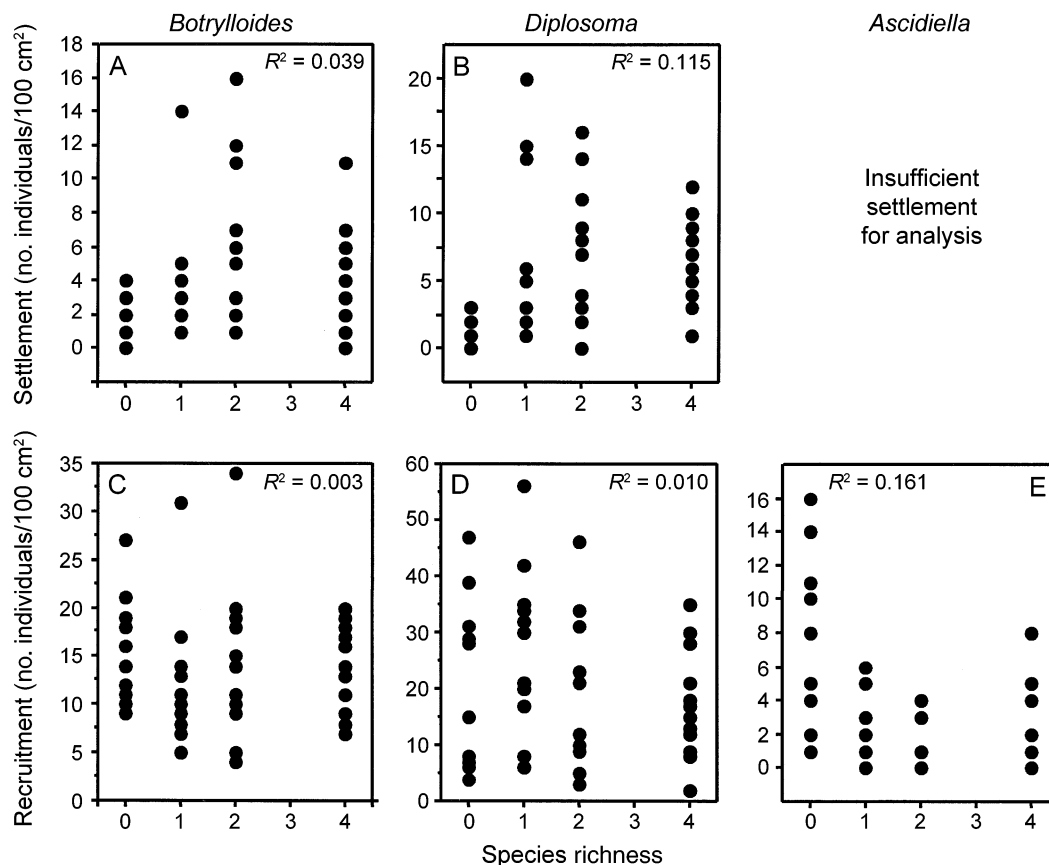


FIG. 5. Effects of native diversity manipulations on (A, B) settlement, and (C–E) recruitment of nonnative species. Analysis was by simple linear regression; partial R^2 for diversity from multiple regression is given in Table 4. Despite weak diversity effects, there were strong effects of individual native species on the settlement and recruitment of native and nonnative species (see Table 4).

of these species ($R^2 < 0.03$, $P > 0.32$; results not depicted).

The abundance of specific native species often strongly influenced settlement and recruitment, although these effects were not always consistent among invaders. *Botrylloides* settlement was enhanced by *Molgula* and *Cryptosula* (Table 4). *Molgula* enhanced both the settlement and recruitment of *Diplosoma* (Table 4), although the strength of the association is much greater for settlement than for recruitment ($R^2 = 0.598$ vs. 0.221). There was a weak negative correlation between *Molgula* abundance and *Ascidiella* recruitment (Table 4), perhaps an indirect consequence of enhanced settlement of *Diplosoma*, which can grow rapidly and smother *Ascidiella* recruits. The total amount of free space differed little among panels, and multiple regression analysis demonstrated that it was never significantly related to the species composition or diversity of that panel ($R^2 \leq 0.08$, $P \geq 0.10$) or the number of recruits ($R^2 \leq 0.05$, $P \geq 0.20$), suggesting that the patterns we have described are the direct result of species-specific interactions, rather than an indirect consequence of differences in space availability.

Although species richness had little direct effect on short-term recruitment and settlement, low diversity communities also experienced periods of relatively high space availability (Fig. 4A and B), which enhanced recruitment. Direct manipulation of space availability independent of diversity strongly influenced settlement and recruitment of both native and introduced species, with decreased space availability resulting in lower settlement and recruitment (Fig. 6A–F). This pattern was especially apparent in species with high recruitment: for example, space availability explains $>80\%$ of the variance in settlement and recruitment of *Diplosoma* (Fig. 6A, B). Settlement of *Botrylloides* and *Ascidiella* after one day was too low to assess the effects of space availability, although recruitment of these species was sufficiently high after one week to discern a negative relationship between native cover and recruitment for both species ($R^2 = 0.18$ for *Ascidiella* and 0.64 for *Botrylloides*; Fig. 6D and E, respectively). A similar pattern emerged for native species settlement and recruitment ($R^2 = 0.76$ and 0.85, respectively; Fig. 6C, F), suggesting that the recruitment–space availability phenomenon is a general prop-

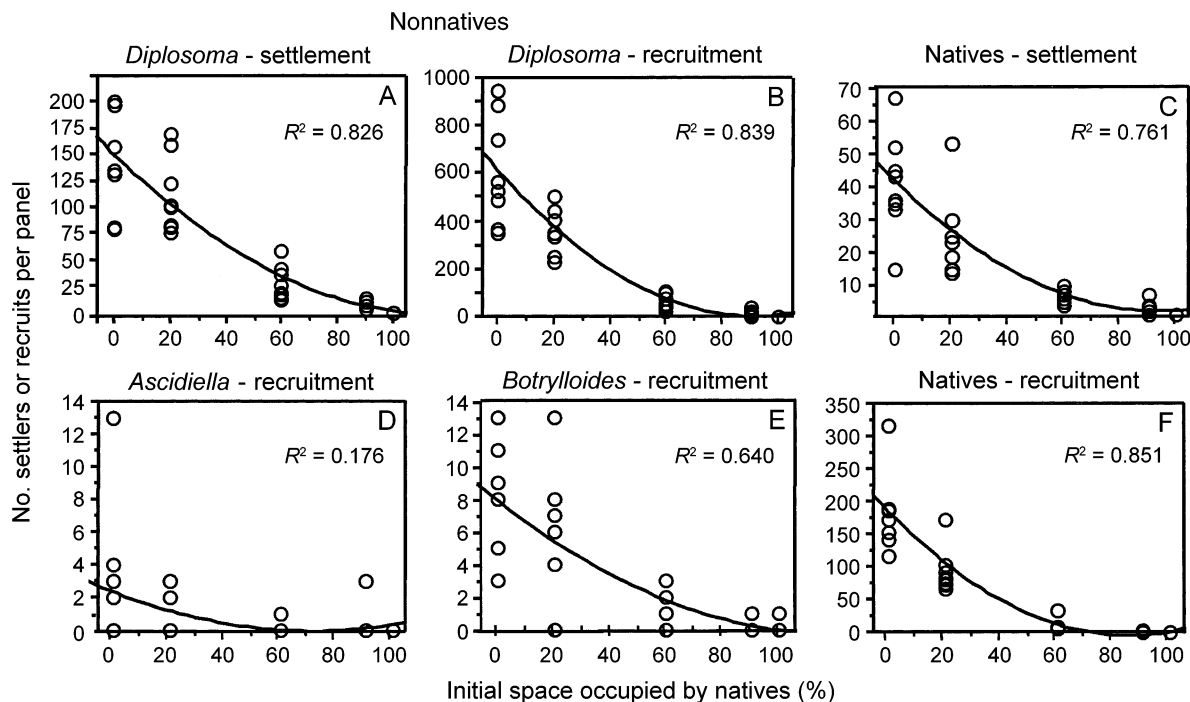


FIG. 6. Effects of the direct manipulation of space on the settlement and recruitment of native and nonnative species. Analysis by quadratic regression demonstrates that space availability reduces the short-term settlement and recruitment of the nonnative species: (A, B) *Diplosoma*, (D) *Ascidella*, and (E) *Botrylloides*, and of (C, F) native species ($R^2 > 0.64$ for all except *Ascidella*, for which recruitment was ≤ 4 individuals/100 cm² for all but one panel).

erty of marine epifaunal communities. However, we did find strong negative species-specific effects of *Ciona* on the recruitment of natives (Table 4), so it is unclear whether this result is attributable to declining space availability or increasing *Ciona* abundance. For nonnative species, there were only weak negative effects of *Ciona* abundance ($R^2 = 0.071$ for *Ascidella* recruitment; Table 4), so the strong patterns observed are likely a consequence of space availability rather than *Ciona* abundance, per se.

After two months, there was a strong negative relationship between initial native cover and percent cover of invaders. Native cover explained 61%, 46%, and 80% of the variation in the final percent cover of *Botrylloides*, *Ascidella*, and *Diplosoma*, respectively (Fig. 7A–C, respectively; $P < 0.001$ in all cases). Quadratic functions fit the data significantly better than linear models. Despite initial differences, no space was available in any of the communities within three to four weeks (Fig. 7D), due to lateral expansion of *Ciona* and recruitment of both native and nonnative species. Initial differences in cover were similar in duration and magnitude to the peaks in the availability of space in our experimental communities (compare Fig. 4A, B with Fig. 7D). The negative effect of space availability on recruitment (Fig. 6B, D–F) probably contributed to these final differences in invader cover, although post-settlement effects were likely important as well (see Discussion).

DISCUSSION

This study demonstrates that diversity reduces the survival and percent cover of invaders (Fig. 3) and may decrease their settlement and recruitment indirectly (Figs. 6 and 7). Underlying both of these patterns is the fact that the availability of open space is lower, and more consistent over time, in communities with more species. Available space is often the limiting resource in subtidal epifaunal communities like the one studied here (e.g., Dayton 1971, Osman 1977, Sutherland and Karlson 1977, Buss and Jackson 1979). Although the means by which diversity decreases invasion success appear to operate at fairly small spatial scales (possibly even $<10 \times 10$ cm), the concurrence of experimental data with field surveys at multiple spatial scales suggests that diversity is important in determining larger scale patterns of invader distribution in this community.

Few studies have experimentally attempted to decouple the effects of diversity, per se, from environmental variables correlated with diversity to determine the relative importance of each. In one California riparian plant community, diversity did reduce invasion success in randomly assembled plant communities that were seeded with an equal number of seeds of an invader (Levine 2000). However, in natural communities the effect of native diversity on invasibility was weak relative to propagule supply, which was the primary

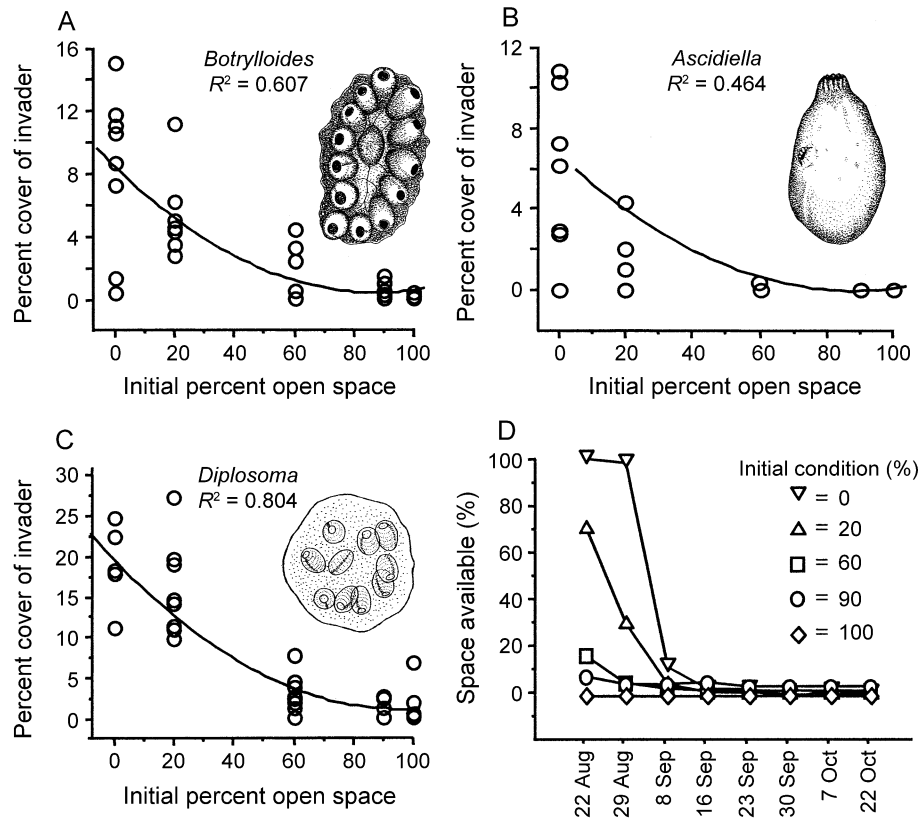


FIG. 7. Effects of the direct manipulation of space on space occupation by nonnative species. Percent cover of (A) *Botrylloides*, (B) *Ascidiella*, and (C) *Diplosoma* all decreased with decreasing space availability after two months ($R^2 = 0.46$ – 0.80). This occurred despite the fact that a plot of (D) open space availability over time showed that initial differences in space availability among treatments persisted for only a few weeks at most.

determinant of field patterns of both native and introduced species richness. This, combined with previous experimental results (McGrady-Steed et al. 1997, Stachowicz et al. 1999, Naeem et al. 2000), suggests that negative effects of diversity on invasion success may be common and translate across systems, but that the relative importance of diversity vs. other factors in determining overall invasion success may vary. The positive correlation between native richness and invader frequency in many terrestrial plant communities (Plant-Tabacchi et al. 1996, Rejmanek 1996, Lonsdale 1999, Stohlgren et al. 1999; review in Levine and D'Antonio [1999]) suggests that the effect of diversity on invasion in these systems may be relatively unimportant. Diversity per se may still reduce invasion of these communities, but its effect at large spatial scales is obscured by other processes that facilitate invasions but are positively correlated with diversity at this scale (e.g., Levine 2000).

In our experiments, the number of native species explained the majority of the variation in invader survival (79% for *Botrylloides*; 63% for *Ascidiella*), whereas the abundance of individual species was a poor predictor of invader survival (Table 2). Species that were best at resisting invasion in monospecific com-

munities were not necessarily members of the most resistant multispecies communities, and species that were highly susceptible to being invaded in monoculture were often members of highly resistant multispecies communities. Furthermore, diverse communities (four species) were almost always more resistant to invasion than the most resistant monoculture (Fig. 3F). This suggests that the effects of diversity we observed here are not the result of more diverse communities being more likely to contain highly resistant species (the sampling effect; see, e.g., Huston 1997, Tilman et al. 1997). Rather, we suggest that invasion resistance arises in diverse communities because individual species are complementary in their temporal patterns of space occupation. All native species fluctuated in abundance over the course of the experiments (Fig. 4D), so all one-species communities experienced periods of high space availability (Fig. 4A, B). Because each species differs in growth rate, timing, duration, and magnitude of reproductive output, the degree to which they are capable of local replacement, and in their response to biotic and physical stresses, the seasonal fluctuations in abundance of each species tend to be out of phase with each other (Fig. 4C, D). Thus, diverse communities exhibit changes in the relative abundance of spe-

cies over time, but maintain high cover of space relative to communities with fewer species.

Space occupation itself can be considered an important measure of ecosystem function. That more diverse communities are less variable in their coverage of space over time suggests that they may be more stable over longer temporal and spatial scales. Although our high-diversity communities are by no means stable with respect to species composition, they likely are more temporally stable with respect to biomass and productivity because of their more consistent coverage of space. This suggests that there may be additional enhancement of ecosystem function by diversity in this system, beyond just invasion resistance.

Although our experiments took place on 10×10 cm substrates and ran for only two to three months, that native and invasive species richness were negatively correlated in the field suggests that the processes and mechanisms operating in our experiments also operate over larger spatial and temporal scales. This is supported by the observation that natural communities at these sites undergo similar fluctuations in community composition as a result of inter and intra-annual variability in growth and recruitment (Osman 1977, 1978; J. Stachowicz, H. Fried, R. Osman, and R. Whitlatch, *unpublished data*). Also, multiyear studies show a negative correlation between species diversity and the availability of free space (Osman 1977; R. Osman, *unpublished data*). This appears to be not because species differ in resource utilization or that classical niche partitioning is occurring (e.g., Tilman et al. 1997), but rather because species have more or less distinct temporal niches defined by seasonal patterns in reproduction and recruitment (J. Stachowicz, H. Fried, R. Osman, and R. Whitlatch, *unpublished data*). The extent to which temporal patterns of recruitment translate into temporal variation in adult densities will depend on a variety of factors, but our personal observations suggest that seasonal patterns of adult abundance roughly lag behind those of recruitment by a few weeks to a month. Regardless, high recruitment of individual species is probably capable of depressing space availability to low levels for a short period of time. However, a collection of species with different temporal patterns of abundance will keep space consistently occupied (Fig. 4C), and over larger spatial and temporal scales increase the likelihood that what space becomes available will be colonized by a native species.

Despite the lack of a direct effect of diversity on the recruitment of any invader (Table 4), the consistently high cover in more species-rich communities probably decreases recruitment of new invaders into these communities (Figs. 6 and 7). Although our space manipulation experiments did not allow us to distinguish the relative importance of the effects of space on recruitment vs. survival of invaders, the data do strongly suggest that the consistent occupation of primary space is the key to enhancing invasion resistance. A high degree

of space occupation can reduce colonization in a wide array of other marine invertebrate communities (e.g., Jackson 1977, Sutherland 1978, Osman and Whitlatch 1995a, b), so this means of increasing invasion resistance may be widespread if diversity commonly increases the temporal occupancy of space. Space influences invasion success in other communities (e.g., Burke and Grime 1996), but the degree to which diversity affects space availability in these systems is less well understood.

Other factors such as predation and disturbance can affect the availability of space (see review in Sousa [2001]), and potentially the success of invaders. The intensity of both these forces in protected harbors and estuaries like the one where this study was conducted is typically low (Osman and Whitlatch 1996; R. Osman and R. Whitlatch, *unpublished manuscript*). Natural disturbance and predation are more intense at subtidal locations along the open coast (Osman et al. 1992, Osman and Whitlatch 1995c), with disturbance more important in shallower areas and predation in deeper areas (Witman and Dayton 2001). This could create a gradient in the relative importance of different factors determining invasion success, both within and among sites, although this remains to be tested. Clearly, though, the importance of diversity in determining invasion success is likely to depend on environmental context.

In theory, a single, competitively dominant species that could monopolize space for a long period of time would resist invasion at least as well as a multispecies assemblage (e.g., Paine 1966). However, the existence of such species in shallow-water epifaunal communities such as these appears unlikely, due to the short life span of most individuals, the importance of “priority” effects, and intransitive competitive relationships (Osman 1977, Sutherland and Karlson 1977, Sutherland 1978, Buss and Jackson 1979, Russ 1982). Although monospecific stands can be generated when disturbance is eliminated, that this situation is unlikely to occur in nature is supported by the fact that most natural subtidal substrates do not support monocultures (Jackson 1977, Osman 1977). In fact, we observed no strong effects of individual species (positive or negative) on the survival of planted invaders, suggesting the absence of a competitively superior species in this particular system. Many communities do lack strong competitive dominants (e.g., Sale 1977, Connell 1978, Peterson 1979), although many others do not (Connell 1972, Whittaker 1975, Sebens 1986). Yet the deletion of even rare species from systems with strong dominants can significantly enhance invasion success (Lyons and Schwartz 2001). This may occur because “rare” and “common” species frequently change roles (Schwartz et al. 2000), or because rare species occupy a similar niche to invaders (e.g., Theodose et al. 1996). Our manipulations began with an even distribution of species and allowed species’ abundances to change over time, which was

the key to understanding the effects of diversity on invasion in this system. Manipulations that force an even distribution of species in systems that normally have strong competitive dominants may reach erroneous conclusions (Schwartz et al. 2000).

We did find strong effects of individual resident species on settlement of propagules, suggesting that particular species could play a disproportionate role in determining invasion success. Most of the negative effects of adults on settlement of larvae in these communities are likely due to preemption of space or overgrowth, rather than direct consumption (Osman and Whitlatch 1995a, b). Although many of the effects of individual species were idiosyncratic, and their underlying mechanisms unclear, *Molgula manhattensis* consistently facilitated colonial invaders. This effect is much stronger for settlement than recruitment, suggesting that *Molgula* facilitates *Diplosoma* larval settlement rather than postsettlement survival. A possible mechanism for this facilitation is that tunic of *Molgula* is covered with papillae (tiny, hair-like projections) that trap sediment and detritus (Van Name 1945), and may trap con- and heterospecific larvae (J. Stachowicz, *personal observations*). The decrease in the strength of association between *Molgula* and settlement vs. recruitment may be due to the overgrowth of new settlers by resident adults (e.g., Grosberg 1981, Osman and Whitlatch 1995b).

Many previous studies of the importance of diversity on invasion success used native species as model invaders (Robinson et al. 1995, McGrady-Steed et al. 1997, Knops et al. 1999, Lavorel et al. 1999, Symstad 2000), operating under the assumption that natives and invaders differ little in terms of the processes that govern their success. Our results suggest natives and new invaders are similar in that resident species richness decreases their survival and does not affect their recruitment (Tables 2 and 4), although diversity effects on survival were weaker for native than nonnative species. The correlations between individual species abundances and recruitment that we observed for nonnative species often held true for natives as well (e.g., *Mytilus* inhibited recruitment of both *Asciidiella* and *Botrylloides*; Table 4). However, individual native species had stronger negative effects on native than on nonnative invaders, explaining 73% vs. 28–38% of the variance in recruitment and 38% vs. 0–5% of the variance in of native and nonnative “invaders,” respectively (summed R^2 from individual species effects in Table 4). This suggests that nonindigenous invaders may be less susceptible to negative interactions with resident adults. Similarly, some terrestrial plants appear more susceptible to competitive effects from species in their native range than in areas to which they are introduced (Callaway and Aschehoug 2000). These results urge caution in the interpretation of results from studies using resident species as model invaders.

CONCLUSIONS

It is increasingly apparent that experimental manipulations support the idea that diversity directly increases the resistance of communities to invasions (McGrady-Steed et al. 1997, Knops et al. 1999, Stachowicz et al. 1999, Levine 2000, Naeem et al. 2000, Lyons and Schwartz 2001). Our results demonstrate that this can occur because species differ in their temporal patterns of space occupation and the inclusion of more species provides more consistent utilization of space, which is the limiting resource in this system. In addition to conferring enhanced invasion resistance, the increased temporal stability characteristic of more diverse communities may enhance other ecosystem functions, such as productivity. Field observations at small (quadrat) and larger (individual site) spatial scales are consistent with the results of our manipulations of diversity and suggest that resident community diversity can play a large role in determining patterns of invader distribution in the field. The question now is not whether diversity is important, but how important is it relative to predation, disturbance, productivity, propagule supply, and other factors known to affect invasion success? Unfortunately, this question is difficult to address at present, as few other studies provide experimental evidence for the process(es) underlying the diversity–invasibility relationship. By focusing on a more mechanistic level, we can predict that the dominant factor controlling the availability of space (e.g., diversity, predation, disturbance) should control invasion success in this community. This approach should be applicable to many systems. Where possible, experimental approaches to the study of community susceptibility to invasion should be encouraged as a complement to larger scale observational studies, as this synthesis will allow a broader, more predictive approach to the study of invasion biology. Indeed, conflicts between experimental and observational studies are not unique to the diversity ecosystem function debate; studies that apply both approaches could result in progress in other areas of controversy in ecology.

ACKNOWLEDGMENTS

This research was funded by grants from the National Sea Grant program (to J. J. Stachowicz, R. W. Osman, and R. B. Whitlatch) and the National Science Foundation Biological Oceanography program (separate grants to J. J. Stachowicz and to R. B. Whitlatch and R. W. Osman). We thank Stephan Bullard, Kari Heinonen, Sarah Johnson, Chunpei Wang, and William Lei for help in the field and in the lab. Discussions with, and comments from, Rick Grosberg, Peter Chesson, Andy Suarez, Melissa Frey, Kelly Lyons, Elizabeth Brusati, Emmett Duffy, and two anonymous reviewers improved the manuscript. Jun Bando drew the pictures of our study organisms.

LITERATURE CITED

- Berman, J., L. Harris, W. Lambert, M. Buttrick, and M. Dufresne. 1992. Recent invasions of the Gulf of Maine: three contrasting ecological histories. *Conservation Biology* 6: 435–441.

- Binney, W. G. 1870. Mollusca. Figures 350–755 and Plates 14–27 in A. A. Gould Report on the Invertebrata of Massachusetts. Second edition. Boston, Massachusetts, USA.
- Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**:776–790.
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist* **113**:223–234.
- Byers, J. E. 2000. Competition between two estuarine snails: implications for invasions of exotic species. *Ecology* **81**:1225–1239.
- Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* **290**:521–523.
- Carlton, J. T. 1979. Introduced invertebrates of San Francisco Bay. Pages 427–444 in T. J. Conomos, editor. San Francisco Bay: the urbanized estuary. California Academy of Sciences, San Francisco, California, USA.
- Carlton, J. T. 1996. Pattern, process, and prediction in marine invasion ecology. *Biological Conservation* **78**:97–106.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competitive systems. *Proceedings of the National Academy of Sciences* **87**:9610–9614.
- Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biological Conservation* **78**:69–96.
- Case, T. J., and D. T. Bolger. 1991. The role of introduced species in shaping the distribution and abundance of island reptiles. *Evolutionary Ecology* **5**:272–290.
- Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* **279**:555–558.
- Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* **3**:169–192.
- Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science* **199**:1302–1310.
- Couthouy, J. T. 1838. Descriptions of new species of Mollusca and shells. *Boston Journal of Natural History* **2**:53–111.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass–fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63–87.
- Dayton, P. K. 1971. Competition, disturbance and community organization: the provision of and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351–389.
- DeKay, J. E. 1843. *Zoology of New York, or the New York fauna. Part 5. Mollusca*. Albany, New York, USA.
- Drake, J. A. 1990. The mechanics of community assembly and succession. *Journal of Theoretical Biology* **147**:213–233.
- Duffy, J. E., K. S. Macdonald, J. M. Rhode, and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* **82**:2417–2434.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Emmerson, M. C., M. Solan, C. Emes, D. M. Patterson, and D. G. Raffaelli. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* **411**:73–77.
- Grosberg, R. K. 1981. Competitive ability influences habitat choice in marine invertebrates. *Nature* **290**:700–702.
- Grosberg, R. K. 1988. Life-history variation within a population of the colonial ascidian *Botryllus schlosseri*. I. The genetic and environmental control of seasonal variation. *Evolution* **42**:900–920.
- Grosholz, E. D., G. M. Ruiz, C. A. Dean, K. A. Shirley, J. L. Maron, and P. G. Connors. 2000. The impacts of a non-indigenous marine predator in a California bay. *Ecology* **81**:1206–1224.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449–460.
- Jackson, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *American Naturalist* **111**:743–767.
- Kareiva, P. 1996. Developing a predictive ecology for non-indigenous species and ecological invasions. *Ecology* **77**:1651–1652.
- Knops, J. M. H., J. R. Griffin, and A. C. Royalty. 1995. Introduced and native plants of the Hastings reservation, central coastal California, a comparison. *Biological Conservation* **71**:115–123.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**:286–293.
- Lavorel, S., A.-H. Prieur-Richard, and K. Grigulis. 1999. Invasibility and diversity of plant communities: from patterns to processes. *Diversity and Distributions* **5**:41–49.
- Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* **77**:762–775.
- Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* **288**:852–854.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**:15–26.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522–1536.
- Loreau, M. 1998. Separating sampling effects and other effects in biodiversity experiments. *Oikos* **82**:600–602.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**:3–17.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function—involution resistance. *Ecology Letters* **4**:358–365.
- McGrady-Steed, J., P. M. Haris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* **390**:162–165.
- Morgan, J. W. 1998. Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. *Journal of Vegetation Science* **9**:181–190.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**:97–108.
- Nichols, F. H., and M. M. Pamatmat. 1988. The ecology of the soft-bottom benthos of San Francisco Bay: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.19).
- Nichols, F. H., J. K. Thompson, and L. E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. *Marine Ecology Progress Series* **66**:95–101.
- Niermann-Kerkenberg, E., and D. K. Hofmann. 1989. Fertilization and normal development in *Ascidella aspersa*

- (Tunicata) studied with Nomarski-optics. *Helgolander Meeresuntersuchungen* **43**:245–258.
- Office of Technology Assessment (OTA). 1993. Harmful non-indigenous species in the United States. OTA, United States Congress, Washington, D.C., USA.
- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* **47**: 37–63.
- Osman, R. W. 1978. The influence of seasonality and stability on the species equilibrium. *Ecology* **59**:383–399.
- Osman, R. W., and R. B. Whitlatch. 1995a. The influence of resident adults on settlement: experiments with four species of ascidians. *Journal of Experimental Marine Biology and Ecology* **190**:199–220.
- Osman, R. W., and R. B. Whitlatch. 1995b. The influence of resident adults on recruitment: a comparison to settlement. *Journal of Experimental Marine Biology and Ecology* **190**: 169–198.
- Osman, R. W., and R. B. Whitlatch. 1995c. Predation on early ontogenetic life-stages and its effect on recruitment into a marine community. *Marine Ecology Progress Series* **117**: 111–126.
- Osman, R. W., and R. B. Whitlatch. 1996. Processes affecting newly-settled juveniles and the consequences to subsequent community development. *Invertebrate Reproduction and Development* **30**:217–225.
- Osman, R. W., R. B. Whitlatch, and R. J. Malatesta. 1992. Potential role of micropredators in determining recruitment into a marine community. *Marine Ecology Progress Series* **83**:35–43.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. Pages 233–264 in R. J. Livingston, editor. *Ecological processes in coastal and marine systems*. Plenum, New York, New York, USA.
- Planty-Tabacchi, A.-M., E. Tabacchi, R. J. Naiman, C. De-ferrari, and H. Decamps. 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* **10**: 598–607.
- Post, W. M., and S. L. Pimm. 1983. Community assembly and food web stability. *Mathematical Biosciences* **64**:169–192.
- Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* **11**:193–203.
- Rejmanek, M. 1996. Species richness and resistance to invasions. Pages 153–172 in G. H. Orians, R. Dirzo, and J. H. Cushman, editors. *Biodiversity and ecosystem processes in tropical forests*. Springer-Verlag, Berlin, Germany.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive. *Ecology* **77**:1655–1661.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* **76**:786–794.
- Robinson, J. V., and W. D. Valentine. 1979. The concepts of elasticity, invulnerability, and invadability. *Journal of Theoretical Biology* **81**:91–104.
- Russ, G. R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia* **53**:12–19.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111**:337–359.
- Schlapfer, F., and B. Schmid. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecological Applications* **9**:893–912.
- Schwartz, M. W., C. A. Bringham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**:297–305.
- Sebens, K. P. 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs* **56**:73–96.
- Sousa, W. P. 2001. Natural disturbance and the dynamics of marine benthic communities. Pages 85–130 in M. D. Bertness, M. E. Hay, and S. D. Gaines, editors. *Marine community ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* **286**:1577–1579.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schnell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25–46.
- Sutherland, J. P. 1978. Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, North Carolina. *Ecology* **59**:257–264.
- Sutherland, J. P., and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, N.C. *Ecological Monographs* **47**:425–446.
- Symstad, A. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* **81**:99–109.
- Theodose, T. A., C. H. Jaeger III, W. D. Bowman, and J. C. Schardt. 1996. Uptake and allocation of ^{15}N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. *Oikos* **75**:59–66.
- Tilman, D., C. Lehman, and K. Thompson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences USA* **94**:1857–1861.
- Travis, J. 1993. Invader threatens Black, Azov Seas. *Science* **262**:1366–1367.
- Usher, M. B. 1988. Biological invasions of nature reserves: a search for generalizations. *Biological Conservation* **44**: 119–135.
- Van Name, W. G. 1945. The north and south American ascidians. *Bulletin of the American Museum of Natural History* **84**:1–475.
- Vermeij, G. J. 1991. When biotas meet: understanding biotic interchange. *Science* **253**:1099–1104.
- Whitlatch, R., R. Osman, A. Frese, R. Malatesta, P. Mitchell, and L. Sedgewick. 1995. The ecology of two introduced marine ascidians and their effects on epifaunal organisms in Long Island Sound. Pages 29–48 in *Proceedings of the Northeast Conference on Non-Indigenous Aquatic Nuisance Species*. Connecticut Sea Grant Publication Number CT-SG-95-04.
- Whittaker, R. H. 1975. *Communities and ecosystems*. Second edition. MacMillan, New York, New York, USA.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* **48**:607–615.
- Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* **79**:2071–2081.
- Witman, J. D., and P. K. Dayton. 2001. Rocky subtidal communities. Pages 339–366 in M. D. Bertness, M. E. Hay, and S. D. Gaines, editors. *Marine community ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Woods, K. D. 1993. Effects on invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist* **130**:62–74.
- Worcester, S. E. 1994. Adult rafting versus larval swimming: dispersal and recruitment of a botryllid ascidian on eelgrass. *Marine Biology* **121**:309–317.