Understanding the Effects of Marine Biodiversity on Communities and Ecosystems

John J. Stachowicz,[1] John F. Bruno,[2] and J. Emmett Duffy[3]

[1]Section of Evolution and Ecology, University of California, Davis, California 95616; email: jjstachowicz@ucdavis.edu

[2]Department of Marine Sciences, University of North Carolina, Chapel Hill, North Carolina 27599-3300

[3]Virginia Institute of Marine Sciences, College of William and Mary, Gloucester Point, Virginia 23062

Annu. Rev. Ecol. Evol. Syst. 2007. 38:739–66

First published online as a Review in Advance on August 20, 2007

The *Annual Review of Ecology, Evolution, and Systematics* is online at http://ecolsys.annualreviews.org

This article's doi: 10.1146/annurev.ecolsys.38.091206.095659

1543-592X/07/1201-0739$20.00

Key Words

diversity, ecosystem function, food webs, productivity, stability, trophic cascade, trophic skew

Abstract

There is growing interest in the effects of changing marine biodiversity on a variety of community properties and ecosystem processes such as nutrient use and cycling, productivity, stability, and trophic transfer. We review published marine experiments that manipulated the number of species, genotypes, or functional groups. This research reveals several emerging generalities. In studies of primary producers and sessile animals, diversity often has a weak effect on production or biomass, especially relative to the strong effect exerted by individual species. However, sessile taxon richness did consistently decrease variability in community properties, and increased resistance to, or recovery from disturbance or invasion. Multitrophic-level studies indicate that, relative to depauperate assemblages of prey species, diverse ones (*a*) are more resistant to top-down control, (*b*) use their own resources more completely, and (*c*) increase consumer fitness. In contrast, predator diversity can either increase or decrease the strength of top-down control because of omnivory and because interactions among predators can have positive and negative effects on herbivores. Recognizing that marine and terrestrial approaches to understanding diversity-function relationships are converging, we close with suggestions for future research that apply across habitats.

INTRODUCTION

Diversity: strictly incorporates information about both the number of entities and their relative abundance (evenness); in practice it is used interchangeably with richness

Stability: measure of community variability, sometimes equated to resistance, but more generally measured as the coefficient of variation over time

Richness: number of entities at a particular hierarchical level; often used interchangeably with diversity

Biodiversity: variety of life at any hierarchical level, including genes, species, functional groups, or ecosystems

Ecosystem functioning: aggregate or emergent aspects of ecosystems (e.g., production, nutrient cycling), carrying no inherent judgment of value

Ecosystem services: functions that are judged to have some clear value to humanity, (e.g., water filtration, production of harvestable fish)

Ecologists have long pondered the relationships between species *diversity* (italicized terms are defined in more detail in the **Supplemental Glossary**, follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org/**) or complexity and various measures of the *stability* or performance of an ecosystem. Rapid changes in the biological composition and richness of most of Earth's ecosystems as a result of human activities have breathed new urgency into these questions. Stimulated in part by these transformations, theoretical and empirical research in ecology has turned to the relationship between *biodiversity* and *ecosystem functioning*. Ecosystem functioning, as we consider it, includes aggregate, community or ecosystem-level processes and properties such as production, standing biomass, invasion resistance, food web dynamics, element cycling, resource use, and trophic transfer (Chapin et al. 1998, Loreau et al. 2001, Tilman 1999). An influential series of field experiments, conducted primarily in terrestrial grasslands, has demonstrated that the identity and number of plant species in a system can strongly influence ecosystem functioning (Hooper et al. 2005; Loreau et al. 2001, 2002; Tilman 1999; Tilman et al. 2006). Similarly, experiments in laboratory microcosms show that changing biodiversity in multilevel food webs can also have pervasive ecosystem impacts (Naeem & Li 1997, Naeem et al. 1994, Petchey et al. 2002).

Although early reviews lamented that comparable studies were rare in marine systems (e.g., Emmerson & Huxham 2002), this is no longer the case. Experimental manipulations of biodiversity in marine systems have both provided independent tests of generality of results from terrestrial systems, and exploited advantages of marine systems to develop new frontiers in our understanding of the ecological consequences of biodiversity. For example, the stronger top-down control in the sea relative to terrestrial habitats (Shurin et al. 2002) suggests that traditional measures of ecosystem function such as production or biomass may be influenced more by herbivores or predators than by plant diversity in marine systems (Duffy 2003, Paine 2002). Correspondingly, marine studies have greatly influenced the developing theory and empirical understanding of the role of predator and prey biodiversity in regulating the top-down control of populations and communities. Of course, consumers are also important determinants of plant biomass and species composition in terrestrial habitats (Schmitz et al. 2000), so lessons derived from marine studies of consumer diversity may guide future work in terrestrial systems. The focus on the effects of marine diversity at the consumer level has the potential to more directly address conservation concerns (Srivastava & Vellend 2005) because of the bias in extinctions toward higher trophic levels (Byrnes et al. 2007, Duffy 2003, Lotze et al. 2006). Additionally, in marine communities, the importance of diversity change relative to other stressors may be high because of the widespread harvest of wild plants and animals that still occurs in marine systems. Finally, the long history of detailed observational data collection on multiple trophic levels in oceanography has been exploited to assess the effects of natural diversity gradients at large scales, facilitating a better connection between changes in biodiversity and disruptions of *ecosystem services* than is currently possible in terrestrial systems (e.g., Frank et al. 2006, Worm et al. 2006).

We recognize two principal motivations for understanding the effects of variation in diversity on ecosystem function. One, ultimately motivated by practical and conservation concerns, is understanding and predicting consequences of ongoing diversity loss in nature. We discuss this in more detail below. The second, more basic, rationale involves general understanding of how ecosystems work. For example, biodiversity-function research has spurred experimentalists to compare effects of multiple species together and independently. In the past, such approaches have led to major advances in our understanding of the effects of predators on prey population and community structure (Ives et al. 2005, Sih et al. 1998), and in the maintenance of diversity via intransitive or context-dependent competitive networks (Buss & Jackson 1979). In effect, biodiversity manipulations address the flip side of the coexistence question fundamental to ecology: How do so many species coexist (or not)? Many studies motivated initially by concerns of predicting consequences of declining biodiversity may ultimately prove to have a more enduring value in elucidating the outcome of simultaneous interactions among multiple species and the contingency of the outcome of pairwise interactions on the presence of other species. Additionally, there are well documented natural gradients in marine biodiversity with respect to latitude, longitude, and depth (e.g., Rex et al. 1993, Roberts et al. 2002, Roy et al. 1998, Worm et al. 2003) that are independent of human activity and could affect the stability, consistency, or performance of particular communities. For example, latitudinal gradients in invasion (Sax 2001) or predation pressure and prey defenses (Bertness et al. 1981, Bolser & Hay 1996) that correspond with gradients in diversity are well known, but causal links have rarely been rigorously investigated.

Because the relationship between diversity and ecosystem functioning has been a contentious field, with confusion in terminology often contributing to the contention, we first briefly review key concepts and mechanisms underpinning diversity-function relationships. We then discuss current patterns of biodiversity change in marine systems and how these relate to the types of diversity that have been manipulated in experiments. Next, we review available studies that provide data to assess the effects of marine biodiversity on ecosystem functioning. Finally, we close with a discussion of the generalities that have emerged thus far, and what we perceive to be the most pressing issues for further research.

Richness effect: occurs when diverse communities differ in ecosystem function from the average monoculture. Can be caused by many mechanisms

Identity or composition effects: describe variation among species or particular combinations of species in their influence on an ecosystem function

MECHANISMS AND CONCEPTS

The theoretical basis for a positive relationship between the richness or diversity of plants or sessile invertebrates and production, biomass or resource use is well developed and relatively straightforward (Loreau 2000). Following previous work, we define a *richness effect* as occurring when a mixture (of species, genotypes, functional groups, etc; see definition of biodiversity) performs differently than the average performance of its component species in monoculture (also known as nontransgressive overyielding). Apart from richness, individual species can also differ in their effects on ecosystem processes in different, independent ways; such functional differences among individual species or among combinations of species are often referred to as *identity* or *composition effects*. Richness effects result from two main classes of

Complementarity: greater performance of a species in mixture than expected from its performance in monoculture caused by interactions such as resource partitioning or facilitation

Sampling effect: the greater statistical probability of including a species with a dominant effect in an assemblage as species richness increases

Multivariate complementarity: phenomenon by which a diverse assemblage maximizes multiple ecosystem functions simultaneously, because different species control different functions

Selection effect: a more general version of sampling effect that can be positive or negative

phenomena: (*a*) complementary properties of species including niche partitioning and facilitation (*complementarity*), and (*b*) strong effects of a dominant species on the function of interest (*sampling effect*). These mechanisms are most clearly distinguished in experiments that include diverse mixtures of species as well as each of the component species in monoculture. When the response of the species mixture is greater than the highest performing monoculture (transgressive overyielding), this can be taken as clear evidence that the richness effect is not accounted for purely by the effects of a dominant species, and that some form of complementarity is operating. The sampling effect occurs when the presence of a particular species drives the relationship between richness and ecosystem function, as a result of two conditions: (*a*) a greater statistical probability of including a species with a particular trait (e.g., high productivity) in an assemblage as species richness increases, and (*b*) the species with highest function in monoculture is also the dominant competitor in a mixed species assemblage (Huston 1997, Tilman et al. 1997). When multiple functions are considered, the highest levels of different processes can sometimes be caused by different species. In such cases, when multiple functions are considered simultaneously or combined into a multivariate index of ecosystem functioning, a sort of *multivariate complementarity* results, in which diverse communities simultaneously maximize multiple functions and thus produce an ecosystem state different from any monoculture (e.g., Duffy et al. 2003).

The premise of the sampling effect, that high production in monoculture and competitive dominance are correlated, is not always met, especially given likely trade-offs between growth rate and competitive ability. Thus, the sampling phenomenon has been generalized to *selection effects* (Hector et al. 2002, Loreau & Hector 2001), which can be either positive or negative depending on whether the dominant species in polyculture displays relatively high or low performance, respectively, when grown alone. Importantly, this means that the absence of a significant relationship between species richness and ecosystem function can result from the counteracting mechanisms of positive effects of complementarity driven by resource partitioning and the tendency for productive species to fare poorly in competition in mixed species plots (negative selection; e.g., Bruno et al. 2005, Hector et al. 2002). Additionally, what appears to be a sampling effect in which mixture performance is equivalent to the best performing monoculture may in fact be the result of positive complementarity balanced by negative selection. This can make predicting the consequences of the loss of diversity for function not only complex but dependent on relative extinction risks of different species.

Although these basic mechanisms and experimental approaches originally developed for sessile organisms also apply to mobile consumers, studies of predator richness effects have typically employed one of two distinct experimental design strategies. First, replacement series (or substitutive) designs control the initial abundance or biomass of organisms, but as a result intraspecific density declines with increasing richness. Second, additive designs hold intraspecific density constant with increasing species richness, but as a result total organism density increases with richness. Most within-trophic-level richness experiments begin as replacement designs to avoid explicitly confounding biomass and richness. But the initial design is somewhat irrelevant for these experiments as they often track population-level processes over longer

time frames using organisms with sufficiently rapid generation times that their relative and absolute densities adjust during the experiment owing to birth, death, and recruitment. The choice between additive and replacement designs is more important in experiments of short duration or when density of the manipulated taxon is otherwise prevented from changing over the course of the experiment. A full discussion of the costs and benefits of each design is beyond the scope of our review (see, e.g., Sackville-Hamilton 1994), but we note two cautions. First, additive designs confound total density of organisms with species richness, whereas replacement designs confound intraspecific density with richness, so each is limited in the types of mechanisms and outcomes that it can elucidate. Second, additive designs will become intractable when experiments include a large range of species richness because organism density in polycultures will become unnaturally high and can force interactions that might rarely occur in nature. The optimal design choice may be guided by the particular question of interest or by empirical richness-abundance relationships when known.

Resistance: capacity of a system to resist change in the face of a perturbation

Resilience: capacity of a system to recover from a disturbance or perturbation

In addition to measuring the effects of diversity on processes like production using a single measure approach at the end of an experiment, one can also measure the relationship between richness and variability in these same processes over time (review in Hooper et al. 2005, McCann 2000, Tilman et al. 2006). In general, diversity is predicted to increase the stability (or decrease temporal fluctuations) of aggregate community properties like biomass, while slightly destabilizing population abundance of individual species (Lehman & Tilman 2000, May 1974). This can be the result of several, nonmutually exclusive mechanisms, including statistical averaging (the *portfolio effect*), as well as complementary responses of species to changing environmental conditions (often detected as negative covariances in species abundances in diverse communities), and overyielding, which indicates that species are stably coexisting (Tilman 1999, Tilman et al. 2006). A related idea is that diversity contributes to the *resistance* to, or *resilience* (recovery) from a disturbance (see Pimm 1984 for terminology), which can be caused by the mechanisms above as well as by the inclusion of highly resistant species in diverse assemblages (sampling effect). We group these together because they all involve assessing the effect of richness on variability in ecosystem processes rather than on mean states.

REALISTIC SCENARIOS OF DIVERSITY CHANGE

Even though there have been relatively few documented global-scale extinctions of marine species compared to land, many species are locally extinct and even more have been driven ecologically extinct: Their populations are sufficiently small that they can no longer play a significant ecological role in a particular community (Sala & Knowlton 2006, Steneck et al. 2004). The order in which species go extinct is not likely to be random, and the relative extinction risks of different species can alter the expected correlation between diversity and ecosystem functioning (Solan et al. 2004). For example, the depletion of predators relative to prey by selective harvest and habitat degradation has caused a skewing of trophic structure toward dominance at lower levels and the general alteration of aquatic and terrestrial food webs (Duffy 2003, Jones et al. 2004, Pauly et al. 1998, Petchey et al. 2004).

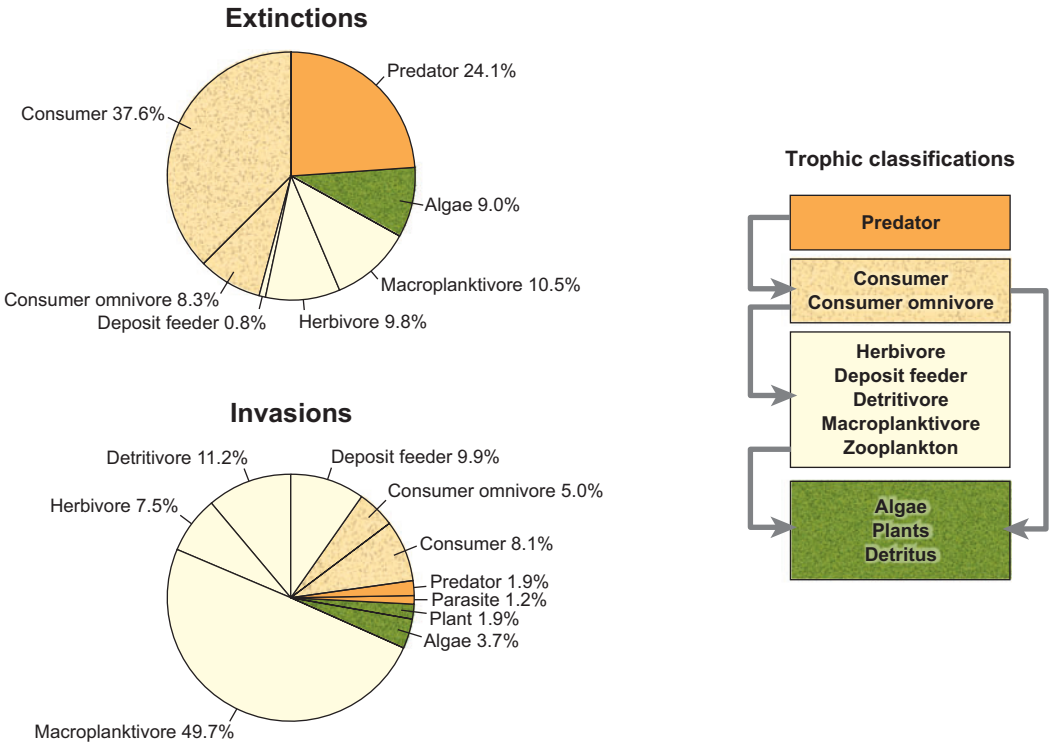

Figure 1

Changing patterns of trophic skew in coastal/estuarine marine ecosystems as the combined result of species introductions and local extinctions. Data replotted from Byrnes et al. (2007). Species loss is biased toward higher trophic levels, whereas species gain is biased toward lower levels (primary consumers). The functional groups most responsible for this skew were top predators (24.1% of extinctions but 6.1% of invasions on average), secondary consumers (37.6% of extinctions but 2.2% of invasions), and suspension feeding macroplanktivores (10.5% of extinctions but 44.6% of invasions). (Percentages may sum to greater than 100% owing to rounding.)

However, at the local to regional scale, diversity gains also occur through species introductions, so the net change in species richness is not always clear cut. Because different processes drive extinctions (e.g., overfishing) and invasion (e.g., ballast water transport), the types of species being gained and lost differ (Lotze et al. 2006). Byrnes et al. (2007) classified all documented marine species extinctions from several regions by trophic level and feeding mode and found that 70% of species lost were high-order consumers (trophic level 3 or 4), whereas 70% of invaders were lower order consumers, particularly suspension feeders or deposit feeders (**Figure 1**). Thus the combined effect of both processes has resulted so far in little net change in richness but an enhancement of *trophic skew* by decreasing predator richness while increasing primary consumers and detritivores. Invasions are most numerous in coastal embayments, so their influence on trophic skew may be reduced in open coast or oceanic

Trophic skew: altered distribution of species richness among trophic levels because of differential effects of invasion and extinction at each level

environments, but the loss of top predators appears to be a global phenomenon. Little is known about how diversity is changing at the local scale at which most experiments are conducted, although local and regional diversity are often strongly correlated.

EMPIRICAL RESEARCH

A summary of results for the most studied ecosystem processes and properties is provided in **Table 1a,b**, and a complete catalog of experimental manipulations is provided in **Supplemental Tables 1–4**. The compilation in **Table 1a,b** includes experimental studies that manipulated the richness of at least three functional groups, species, or genotypes. Though observational studies can be very useful, especially in testing for links between diversity and ecosystem services (see the sidebar, Connecting Diversity to Ecosystem Services), we limit ourselves primarily to experiments in this review. Most experiments manipulate richness in randomly constructed communities, allowing partitioning of effects owing to richness versus identity. We focus on these random assembly experiments, as these more directly address our principal theme of how the number and variety of species per se influence ecosystem properties.

Overall, the majority of experiments and metrics reported in **Table 1a,b** detected a significant effect of richness (85/123). Although publication bias against finding no effect is possible, it is nonetheless clear that richness effects are widespread. Transgressive overyielding, in which the diverse assemblage outperforms the best monoculture was found in far fewer studies (26/105), over half of which were from studies of the effect of animal richness on invasion resistance, resource use, or secondary production.

CONNECTING DIVERSITY TO ECOSYSTEM SERVICES

Worm et al. (2006) analyzed the effects of changes in marine biodiversity on fundamental ecosystem services by combining available data from sources ranging from small scale experiments to global fisheries. At a global scale, they analyzed relationships between species richness and fishery production in 64 large marine ecosystems varying naturally in diversity. Ecosystems with naturally low diversity showed lower fishery productivity, more frequent collapses (strong reductions in fishery yield), and lower resilience than naturally species-rich systems. They suggested that the greater resilience of more diverse ecosystems may result because fishers can switch more readily among target species when there are many species available (high richness), potentially providing overfished taxa with a chance to recover. This mechanism is consistent with theory, small-scale experiments, and with the negative relationship Worm et al. (2006) found between fished taxa richness and variation in catch from year to year. Although the correlative approach employed in their comparison did not allow assignment of causation or mechanisms, it does allow the examination of larger scale processes and the connection between richness and ecosystem services (fish production) with clear value to humans.

Table 1a Summary of experiments manipulating diversity of marine organisms published through early 2007[a]: Within-trophic-level manipulations

Response	Positive	Negative	No effect	Transgressive overyielding
Stability, disturbance, resistance, or resilience[b]	9	1	0	N/A
Plant biomass or production	7	0	6	0/13
Decomposition	0	0	2	0/2
Associated species diversity	0	0	3	0/2
Associated species abundance	2	0	1	0/2
Resource use[b]	6	0	3	4/8[d]
Resource regeneration[c]	4	4	9	1/14
Invader abundance or survival	0	6	1	5/7
Invader settlement	2	0	1	2/3
Secondary production	6	0	1	4/6

[a]Full data for all studies are in **Supplemental Tables 1–4**. Individual studies may be counted multiple times in the table if they either conducted more than one independent experiment or measured more than one potentially independent response variable. Not all studies explicitly tested for transgressive overyielding, and so its existence was inferred in some cases from data available in graphs; in some cases it was impossible to tell because monoculture means were not given, so the total number of possible studies in which trangressive overyielding could be detected is often less than the total number of studies that showed a richness effect (see Supplemental Materials for details).
[b]includes data from plants, sessile and mobile invertebrates.
[c]includes multivariate complementarity.
[d]infauna and epifauna manipulated.

Table 1b Summary of experiments manipulating diversity of marine organisms published through early 2007[a]: Effects of manipulating richness at one level on response by other levels

Taxon manipulated	Response	Positive	Negative	No effect	Transgressive overyielding
Algal prey	Consumer growth	6	0	0	1/6
	Consumer survival	5	0	2	0/7
	Consumer reproduction	5	0	3	1/8
	Integrated production or population growth	6	0	1	5/7
Consumer	Prey biomass	3	8	4	2/15
Predator	Plant biomass (two trophic levels away)	3	2	1	2/5

[a]Full data for all studies are in **Supplemental Tables 1–4**. Individual studies may be counted multiple times in the table if they either conducted more than one independent experiment or measured more than one potentially independent response variable. Not all studies explicitly tested for transgressive overyielding, and so its existence was inferred in some cases from data available in graphs; in some cases it was impossible to tell because monoculture means were not given, so the total number of possible studies in which trangressive overyielding could be detected is often less than the total number of studies that showed a richness effect (see Supplemental Materials for details).

Strikingly, despite a large number of experiments examining plant richness effects on plant community properties or processes, none found evidence of transgressive overyielding (see also Cardinale et al. 2006). The frequency of richness effects also varied among taxa and response metrics, though in most cases the total number of experiments was small. Still, we note that richness effects appear to be less common for within-trophic-level response variables (**Table 1a**, 47/74) than for those that cross trophic levels (**Table 1b**, 38/49), although some experiments were difficult to classify into one of those groups. Nearly all studies (91/99, see data in **Supplemental Tables 1–4**) find significant identity effects, indicating that most experiments find strong effects of particular species, regardless of taxonomic group or metric of response.

Effects of Producer Diversity on Primary Production and Related Processes

The most common ecosystem processes measured in species richness manipulations to date are primary production and biomass accumulation (Hooper et al. 2005). Terrestrial experiments usually measure production as biomass accumulation over a season. Biomass is less reflective of production for algae because the majority of biomass can be removed by a variety of disturbances, transported away from production sites by currents or removed by intense herbivory (Cebrian 1999). For these reasons, experiments examining the effects of marine primary producer (hereafter, plant) diversity on production are often performed in herbivore-free cages or mesocosms that minimize tissue loss due to natural senescence or disturbance. Further, in many marine systems, macrophyte biomass is inversely, or nonlinearly, related to primary productivity due to resource depletion that can limit production when standing stock is high (Carpenter 1986). Production and biomass are thus in some ways separate ecosystem functions in many marine systems, with production measuring energy and material fluxes and biomass measuring habitat characteristics.

Primary production and biomass. A positive relationship between algal richness and biomass was detected in field surveys of highly diverse macroalgal communities in Jamaica (Bruno et al. 2006). This pattern is concordant with the diversity-productivity hypothesis but could clearly be driven by a variety of factors other than algal richness. All the experiments that measured the effects of marine algal or angiosperm richness and identity on primary production detected strong identity effects but only roughly half found evidence for an effect of richness (**Table 1a,b**; **Supplemental Table 1**). In several studies, the relative strength of these was compared, and all found that the magnitude of the identity or composition effects was roughly 10 times stronger than that of richness, which was generally weak and likely ecologically insignificant (e.g., Bruno et al. 2005, 2006). Thus even where richness effects occurred, identity and richness contributed little to primary production. By comparison, a recent meta-analysis across terrestrial and aquatic habitats (Cardinale et al. 2006) detected more consistent richness effects (67/76 studies for biomass) that the researchers argued were largely explained by the strong effects of particular species present in

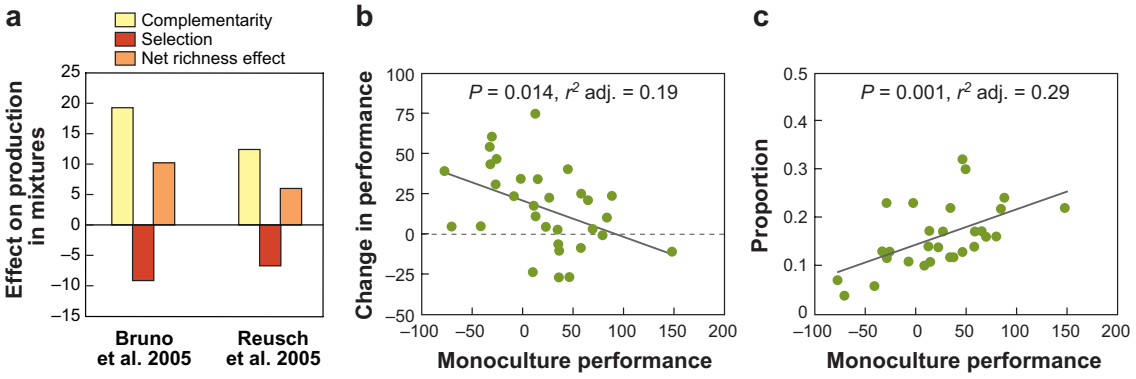

Figure 2

Partitioning of richness effects from two field experiments into complementarity and selection effects. (*a*) Bruno et al. (2005) tested the effects of seaweed richness on production, measured as final wet mass, and Reusch et al. (2005) tested the effects of seagrass genotypic richness on shoot density. Calculations are based on comparing net production in monocultures and mixtures. In both cases the relatively small richness effect is the result of strong positive complementarity offset by negative selection effects. (*b*) Relationship between the performance (% change in wet biomass) of a species in monoculture and its relative performance in polyculture (polyculture% growth-monoculture% growth). (*c*) Relationship between the performance (% change in wet biomass) of a species in monoculture and its proportion of the total final polyculture biomass (that is, dominance). The dashed line in *b* is the 1:1 growth function; points above this line are cases where species grew faster in mixture. (*b* and *c* are redrawn from Bruno et al. 2005.)

polyculture (sampling effects), because species-rich mixtures rarely outperformed the best-performing monoculture.

Simple equations allow the partitioning of diversity effects into components attributable to sampling (or more generally selection) and complementarity (Loreau & Hector 2001). Interestingly, studies that have performed this analysis generally find that complementarity effects are positive and selection effects are negative (**Figure 2**). Positive complementarity occurs when species are more productive on average in mixtures than in monoculture, likely owing to facilitation or resource partitioning (Bruno et al. 2005, Loreau 1998). Negative selection indicates that species that do well in monoculture (e.g., fast growing species) perform relatively poorly when grown with other species. These mechanisms can counteract each other, leading to weak or neutral net richness effects despite strong complementarity among species. This finding contrasts with the sampling effect hypothesis (Huston 1997), which argues that positive effects of richness are driven largely by the random inclusion and ultimate dominance of species with especially high functionality (that is, those with the greatest monoculture performance). In benthic marine communities the most productive genotypes and species often do not dominate polycultures, and species with lower inherent productivity often persist and perform well in diverse communities (**Figure 2**; see also Bracken & Stachowicz 2006, Bruno et al. 2006, Duarte et al. 2000, Hughes

& Stachowicz 2004; Reusch et al. 2005), frequently negating positive effects of biodiversity on algal biomass based on facilitation and complementarity. This could be due in part to trade-offs between fast growth and competitive ability and is not a uniquely marine phenomenon (Hooper & Dukes 2004, Loreau & Hector 2001), although it is not yet known whether positive or negative selection effects are more prevalent in different habitats.

The ability to explicitly partition richness effects between sampling and complementarity is restricted to metrics for which the contribution of each species in polyculture can be unambiguously determined. For some metrics, such as invasion resistance or nutrient uptake or regeneration, partitioning would be impossible because one cannot easily determine the amount of function due to each species in polyculture. However, there are other processes where this partitioning could be profitably applied, including the relative contribution of different predators to prey mortality.

Resistance, resilience, and stability. Virtually all studies that have examined the effects of producer richness on measures of stability have found a positive effect, though the effects on different metrics of stability vary among studies. Allison (2004) manipulated intertidal macroalgal diversity and measured community resistance and resilience in response to thermal stress. Surprisingly, the more diverse plots were less resistant than depauperate ones, losing more biomass to heat stress, but this was largely because they had greater biomass before the stress was imposed. In contrast, there was a positive effect of functional group richness on resilience (recovery), owing to the presence of particularly resilient species and to facilitation promoting recruitment. In contrast, experimentally enhancing eelgrass (*Zostera marina*) genotypic (clonal) richness increased community resistance to grazing by geese (measured as the change in shoot density in response to the disturbances) but had no effect on resilience (rate of recovery) (Hughes & Stachowicz 2004). Two other eelgrass experiments (Reusch et al. 2005, Williams 2001) provide evidence consistent with an effect of intraspecific diversity on processes associated with recovery after disturbance or transplantation.

Kertesz (2006) tested the effects of diversity on stability by crossing macroalgal richness with manipulations of nutrient concentration. The results suggested that richness tended to stabilize biomass production across seasons and in response to variable resource concentrations, as the coefficient of variation in biomass declined with increasing richness. When we compared the results of seven published experiments performed with the same species pool across environmental gradients in time and space (Bruno et al. 2005, 2006), we found that the cross-experiment coefficient of variation in biomass was nearly an order of magnitude higher for algal monocultures, on average, than for the highest-diversity mixtures. Similarly, Worm et al. (2006) reanalyzed the experimental data of Watermann et al. (1999) and found that microalgal biomass accumulation varied less at high than low richness across a factorial combination of three sediment types and three temperatures. Thus, experimental manipulation of marine microalgae, seaweeds, and seagrasses all showed that diversity consistently reduces temporal fluctuations in community biomass (see also Stachowicz et al. 2002) and/or increases stability. This, combined with the relatively weak

contribution of richness to average production, suggests that the effects of richness on marine plant production and biomass may be greatest when considering ecosystem processes that involve variability rather than mean responses (**Table 1a,b**).

Decomposition, nutrient availability, and uptake. Bracken & Stachowicz (2006) directly tested the hypothesis that seaweed species richness is positively related to nutrient depletion by manipulating the richness and composition of macroalgae across a gradient of nutrient concentrations in microcosms. They found that species differed in their use of nitrate and ammonium and that nutrient uptake was 22% greater in polycultures than predicted based on a weighted average of species' uptake rates in monoculture. Complementarity among species in total nitrogen uptake only emerged when the use of multiple forms of nitrogen (ammonium and nitrate) were considered simultaneously (multivariate complementarity); diversity had no effect on uptake of either nitrogen form alone. In a separate study, total soil nitrogen accumulation in a restored salt marsh was positively related to plant species richness (Callaway et al. 2003). Despite this, total soil nitrogen availability was also higher in the most diverse plots, probably reflecting the increased organic matter incorporation into soils as a result of higher total aboveground and litter biomass in the species-rich plots. These diversity effects may have resulted from a mix of sampling and complementarity effects, as one species in monoculture (*Salicornia virginica*) did achieve equal biomass to the mixture, whereas no single species had as great an effect on soil nutrient levels as the mixture. Of two experiments examining the effect of seagrass genotypic diversity on sediment porewater ammonium concentration, one found an inverse relationship suggestive of more complete resource use when diversity is high (Hughes & Stachowicz 2004, but not Reusch et al. 2005).

Facilitation of associated species. Macrophyte diversity could affect the structure of communities of epiphytic algae and animals that inhabit them not only by providing enhanced food through greater primary production, but also via creation of larger and more structurally complex or heterogeneous habitats (Bruno & Bertness 2001, Heck & Orth 1980). Results of experimental studies of this phenomenon are mixed. Two studies found that seagrass genotypic diversity had no effect on the diversity of associated invertebrate species but was positively related to epifaunal abundance (Hughes & Stachowicz 2004, Reusch et al. 2005). Higher shoot density in higher diversity treatments did play some role in this (Reusch et al. 2005), but at least one study found an effect of diversity even when controlling for shoot density (Hughes & Stachowicz 2004). Several studies found little effect of manipulating plant or algal species diversity on the animal community despite strong effects of particular plant or algal species (Moore 2006, Parker et al. 2001). In contrast, intertidal seaweed diversity increased the richness and diversity but not the abundance of associated invertebrates, apparently because each algal species harbored a semiunique invertebrate fauna (J. Stachowicz, M. Bracken and M. Graham, in preparation). The generally weak and inconsistent effects of macrophyte richness on associated species richness could be due to the relative rarity of host specialization in the particular systems studied or the generally low host-specificity of marine consumers compared with

many insects on land (Hay & Steinberg 1992). Interestingly, effects of grassland plant richness on terrestrial insect abundance and diversity are similarly weak and inconsistent (Haddad et al. 2001, Siemann et al. 1998), probably because insect communities consist of multiple trophic levels, which interact among themselves as well as with plant diversity.

Nutrient Regeneration and Bioturbation

A number of experiments in soft-sediment systems have tested the effects of infaunal species richness on fluxes of nutrients out of the sediments (reviewed in Raffaelli et al. 2003, Waldbusser & Marinelli 2006). Broad-scale correlations between infaunal richness and ammonium flux or biomass provide intriguing evidence for a positive diversity-nutrient efflux correlation (Emmerson & Huxham 2002), although whether this relationship is causal or whether both diversity and ammonium flux are controlled by a third variable is unclear. In experiments, richness effects, when they occur, are usually owing to strong effects of a particular species, typically a bioturbator (Emmerson et al. 2001, Ieno et al. 2006). Further investigation in infaunal systems found that functional richness did enhance ammonium flux, but this effect depended on flow (Biles et al. 2003). Similarly, particular species or combinations of epibenthic grazers have stronger effects than grazer richness on sediment organic matter by influencing the quantity and types of algal biomass accumulating in the seagrass canopy and on the sediment surface and its subsequent processing (Canuel et al. 2007). Manipulation of seagrass species richness had no effect on the rate of seagrass detrital decompostion in litterbags (Moore 2006, Moore & Fairweather 2006). Overall, the conclusion from these experiments is that ecosystem processes can often be predicted from species composition, but not from species richness (**Table 1a,b**; **Supplemental Table 2**).

Although experiments with infaunal invertebrates have often found that a single strong interactor dominates ecosystem function, this is not always the case. Several studies have found that interactions among species can result in underyielding or overyielding of nutrient fluxes relative to expectations based on additivity (e.g., Emmerson et al. 2001, Raffaelli et al. 2003). As one example, Waldbusser et al. (2004) manipulated infaunal polychaete richness and measured effects on phosphate and oxygen flux and on sediment profiles of oxygen and pH. They found strong species-specific effects on particular response variables, but different species controlled different processes, leading to multivariate complementarity. Interactions among species also led to underyielding with respect to both oxygen and phosphate flux in the multispecies communities. Waldbusser and colleagues attributed this to the high oxygen permeability of *Clymenella* tubes leading to greater oxygen content in the deeper sediments; oxic porewaters increased the adsorption of phosphate onto particles, decreasing phosphate flux out of the sediments.

Both of the manipulations of infaunal diversity that measure variability in processes found reduced variability in multispecies assemblages relative to monocultures: either reduced spatial variation in fluxes (Waldbusser et al. 2004) or greater proportion of variance explained in regressions (Emmerson et al. 2001). Although the precise

mechanism underlying this effect is unknown, it suggests some sort of complementary effect of species on sediment properties in space (deep versus shallow burrowers) or time, or perhaps owing to context-dependent effects of species (Emmerson et al. 2001).

Resistance to Invasion

Based on the idea that more diverse assemblages more completely use available resources, one might expect diverse communities to be less susceptible than species-poor communities to invasion by new species (Elton 1958). The relationship between species richness and invasibility in terrestrial systems is characterized by apparently contradictory results from experiments, which generally show reduced invasion success with increasing diversity, and observational studies that show the opposite (Fridley et al. 2007). The positive result in surveys is most often explained as a consequence of spatial heterogeneity, which positively affects both native and exotic richness by increasing niche diversity, although alternative explanations exist (Davies et al. 2005; Fridley et al. 2004, 2007).

Marine studies on diversity and invasion do not always follow this pattern, however, and have shed some light on this apparent paradox. Stachowicz et al. (1999, 2002) found that survival and cover of three different sessile invertebrate invaders decreased with increasing resident species richness because resident species were complementary in their temporal patterns of space occupation. Individual species fluctuated in abundance, but these fluctuations were out of phase. Thus, at least one species was always abundant and occupying space in the high-diversity treatments, whereas there were periods of high space availability in the low-diversity treatments. This mechanism appears to operate in the field at larger scales (Stachowicz et al. 2002) driven by complementary temporal niches that arise from seasonal differences in recruitment patterns among species (Stachowicz & Byrnes 2006). Such seasonal or temporal niches may drive diversity effects on invasion resistance in other communities. For example, the biomass of mobile and sessile invertebrate invaders in experimental seagrass mesocosms decreased with increasing species richness of resident mobile invertebrates (France & Duffy 2006a). Grazers in this system do show seasonal abundance patterns (Duffy et al. 2001, Parker et al. 2001), which should produce more complete resource use throughout the season and contribute to this effect.

In contrast to these findings, an experimental study of marine algae found that algal functional group richness did not affect invasion by other native species and that instead functional group identity most strongly affected invasion (Arenas et al. 2006). Although these researchers found that resource availability did control invasion success, algal species identity (and not richness) controlled resource availability. However, in other algal experiments, complementary use of light and space by different functional groups reduced total resource availability and thus invasion success (Britton-Simmons 2006). An overall negative effect of species richness on invader abundance can result even when algal richness enhances initial settlement of invaders through facilitation (White & Shurin 2007). On balance, experimental marine

studies generally support an inhibitory effect of increasing diversity on invasion success, mediated in large part by complementary resource use among taxa (**Table 1a,b**; **Supplemental Table 3**).

Observational studies, while they cannot unambiguously assign causation, can illuminate whether the mechanistic effects of richness identified in experiments are sufficiently strong to generate patterns in the context of natural variation in other important factors. Compared with terrestrial systems, there have been surprisingly few observational studies of resident diversity and invasion in the sea. A survey of sessile marine invertebrates in Tasmania found a positive correlation between the number of native species and the species richness (and to a lesser extent the abundance) of both native and non-native settlers (Dunstan & Johnson 2004). They attributed the positive correlation to a combination of interspecific facilitation and the dominance of low-richness communities by a few large colonies, which were difficult to displace. Likewise, a similar study performed across several spatial scales found that the strength and direction of the relationships between native and exotic plant richness and cover in estuarine shoreline plant communities varied among sites and sampling scale, with negative relationships only occurring at smaller spatial scales (Bruno et al. 2004). Several other small-scale studies have found negative correlations between native richness and invader abundance (White & Shurin 2007) or invader richness (Stachowicz et al. 2002). Thus, the effect of native richness can be strong enough to generate field patterns, whereas in other cases it is overwhelmed by other factors.

Using a multiple regression approach, Stachowicz & Byrnes (2006) examined the context dependency of richness effects on invasion. They found that substrate heterogeneity and the availability of primary space markedly influenced the slope of the relationship. Specifically, the substrate heterogeneity and additional settlement space generated by a structurally complex exotic bryozoan (*Watersipora subtorquata*) caused the native-invader richness relationship to shift from negative to positive (**Figure 3**). A negative relationship was only found when facilitators were rare and space was limiting, suggesting that the conditions under which the effect of species richness on invasion is dominant are restricted. Terrestrial studies often agree, finding that the positive effects of heterogeneity or resource levels on both native and exotic richness drive a positive native-exotic richness correlation, particularly at larger spatial scales, whereas smaller scale negative relationships are often (but certainly not always) found, reflective of the more limited heterogeneity at that scale (e.g., Davies et al. 2005, Fridley et al. 2007, Shea & Chesson 2002).

Within-Trophic-Level Effects of Animal Diversity on Secondary Production and Resource use

Given the generally stronger top-down control in marine than in terrestrial ecosystems (Cyr & Pace 1993, Shurin et al. 2002), a key question regarding marine and other aquatic systems is whether diversity of animal consumers has any consistent effect on resource use and production. Mechanisms that might lead to such an effect are similar to those for sessile species discussed previously (see also Duffy 2002). A growing number of studies have addressed potential effects of consumer species richness on

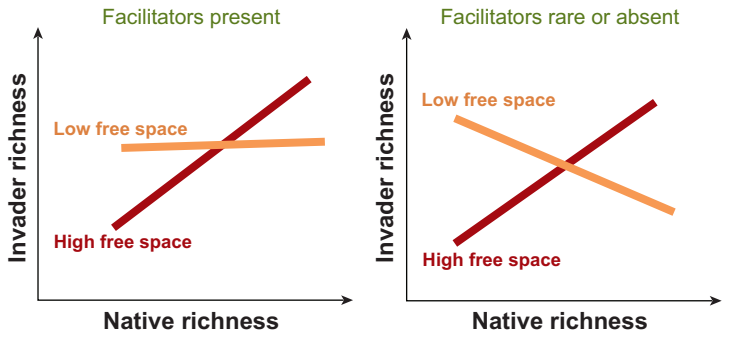

Figure 3

Interactive effects of native richness, resource availability, and facilitation on the richness of exotic species (after Stachowicz & Byrnes 2006). At high levels of open space, there was a strong positive relationship between native and invader richness, likely owing to nonselective disturbance agents that affect native and invader diversity in a similar negative manner, resulting in native and invader richness covarying positively as a reflection of extrinsic factors. At low levels of open space, the slope of the relationship depended on the presence of a foundation species, *Watersipora subtorquata*, which provides secondary space for attachment and thus alleviates space limitation. When *Watersipora* was present there was a consistent positive relationship between native diversity and exotic diversity, regardless of the level of open primary space. When *Watersipora* was absent the native-invader relationship was positive at high levels of open space, but became negative at low levels of open space. One interpretation of these data is that the negative effects of native richness on invasion are only sufficiently strong to be manifest in field patterns when available resources (both primary and secondary space) are in short supply.

ecosystem properties (Duffy et al. 2007), including marine experiments in a variety of estuarine, rocky shore, and subtidal habitats (**Table 1a,b**; **Supplemental Table 4**). One series of experiments manipulated diversity of crustacean herbivores and followed the effects on development of experimental seagrass ecosystems in mesocosms (Duffy et al. 2001, 2003, 2005; France & Duffy 2006a,b). Most of these studies found that, as predicted by theory (e.g., Holt & Loreau 2002), increasing richness of grazer species resulted in greater grazer biomass and lower standing stocks of their algal prey. Because the experimental seagrass ecosystems allowed natural recruitment of algae and sessile invertebrates, they were able to show that grazer richness affected community succession, not only reducing total resource (algal) biomass but also shifting the composition of the assemblage toward unpalatable cyanobacteria and sessile invertebrates and reducing prey diversity (Duffy et al. 2003, France & Duffy 2006a). These experiments also found strong evidence for multivariate complementarity in which particular species influenced individual response variables such as epiphyte or animal biomass, but the most diverse grazer assemblage maximized each of these response variables simultaneously, producing a community state different than that of any single grazer species.

One potentially important pattern emerging from the seagrass grazer studies is that effects of species richness on ecosystem properties were not detectable with three

grazer species (Duffy et al. 2001) but were clear with four (Duffy et al. 2005), six (Duffy et al. 2003), or eight species (France & Duffy 2006b). Results of these experiments suggest that effects of species loss will be less predictable and more idiosyncratic when diversity is initially low, whether naturally or as a result of experimental design (Duffy et al. 2001, O'Connor & Crowe 2005, Schiel 2006).

Within the marine microbial loop, there is also evidence that diversity at a focal trophic level enhances both production and resource use by that level. Increasing richness of herbivorous ciliates strongly decreased total abundance of their algal prey (Gamfeldt et al. 2005), an effect attributable in part to complementarity because the mixture of three ciliate species reduced algal abundance well below the level achieved by any single ciliate species. These researchers also found that total ciliate abundance was strongly enhanced by increasing diversity of either the ciliates themselves or their algal prey. Remarkably, ciliate abundance was more than twice as great than in any other treatment when diversity of both algal prey and herbivorous ciliates was highest.

Diversity in Multitrophic-Level Experiments

Although some of the mechanisms by which diversity acts within trophic levels translate simply to multitrophic-level situations, interactions among mobile heterotrophs can be more varied when considering their effect on adjacent trophic levels (Duffy et al. 2007). A substantial body of experimental work on multiple predator effects (Sih et al. 1998) in a variety of communities including benthic marine systems (e.g., Crowder et al. 1997, Hixon & Carr 1997, Martin et al. 1989) supports many mechanisms by which increasing predator diversity can either decrease (via diet complementarity or predator facilitation) or increase (via intraguild interference or omnivory) herbivory, with correspondingly positive and negative effects on plant biomass. This diversity of potential mechanisms with opposing effects on herbivores can make the prediction of the consequences of changing predator or prey diversity on plant biomass complicated.

Prey diversity and the strength of top-down control. Several hypotheses suggest that prey diversity can affect the strength of top-down control. First, the variance in edibility hypothesis argues that a more diverse prey assemblage is more likely to contain at least one resistant species that can thrive in the presence of consumers (a sampling effect), such that more diverse assemblages will maintain higher biomass under strong consumer pressure (Duffy 2002; Leibold 1989). Thus, in multitrophic systems, the edibility of prey species is expected to be an important mediator of diversity effects because it can foster shifts in species dominance that in turn affect ecosystem functional properties (Thébault & Loreau 2003, 2006). Second, the dilution hypothesis, or its inverse, the resource concentration hypothesis (e.g., Keesing et al. 2006), suggests that a more diverse prey assemblage should reduce the relative and absolute abundances of prey available to specialist consumers, reducing consumer efficiency. When consumers are generalists or have overlapping resource requirements, deletion of a particular species might result in an increase in the abundance of remaining

predator species that can compensate for the loss of top-down control. However, O'Connor & Crowe (2005) found that biomass compensation by remaining grazing limpet species after the removal of a dominant could only maintain grazing pressure in the short term.

Few experiments have explicitly tested effects of prey diversity on consumer control in marine systems. Two experiments come from seagrass beds. First, at the plant level, eelgrass (*Zostera marina*) plots planted with higher genotypic richness lost fewer shoots, on average, than low-richness plots when exposed to grazing by geese (Hughes & Stachowicz 2004). Though the mechanism was unclear it was not driven by the dominance of a resistant genotype in mixed genotype plots. Second, at an intermediate trophic level, increasing richness of an assemblage of crustacean herbivores resulted in higher grazer biomass in the presence of crab predators than did the average herbivore monoculture (Duffy et al. 2005), probably because predator-resistant herbivore species came to dominate the assemblage under intense predation pressure. Both of these studies suggest that diversity at the prey level can dampen ecosystem responses to top-down control, stressing the context-dependence of diversity effects at one trophic level on the activities of other levels. In contrast, manipulation of marine microalgal diversity found that algal diversity did not reduce algal susceptibility to herbivore control (Gamfeldt et al. 2005).

The most comprehensive, albeit indirect, evidence that prey diversity can reduce consumer control of aggregate prey standing stock comes from a meta-analysis of 172 aquatic experiments, which found that herbivore control of algal biomass declined with increasing algal diversity (Hillebrand & Cardinale 2004). The underlying cause of this pattern could not be determined, but more diverse algal communities might be more likely to contain unpalatable algal species, have higher rates of recovery owing to more complete resource use, or have a greater incidence of facilitative interactions. The damping effect of prey diversity on top-down control also appears consistent with the general pattern in terrestrial studies of plant-insect interactions (Andow 1991).

Prey diversity and consumer nutrition and production. Mixed algal diets enhanced herbivore growth, biomass accumulation, and/or reproductive output compared to average algal monocultures in nearly all cases examined for taxa as diverse as protozoa, crustaceans, and sea urchins (see **Table 1a,b**; **Supplemental Table 4**; and Worm et al. 2006 for details). In several cases, grazers fed mixed diets performed no differently than those fed the best single food item, perhaps because grazers selectively consumed only the species that led to highest fitness. However, in many studies monospecific diets that produced highest growth led to low survival and vice-versa. Thus, when considering integrated measures of animal performance (e.g., growth $\times$ survival $\times$ reproductive output) animals fed diverse diets often outperformed even the best single species diet (**Table 1b**). These studies suggest that availability of a diverse prey base may be important to maintaining high production. The mechanisms underlying these effects are unclear, although diverse diets could be better either because of the provision of complementary nutrients, dilution of defensive chemicals, or both (Bernays et al. 1994, DeMott 1998).

Predator diversity and the strength of trophic cascades. Predator diversity could also affect the strength of trophic cascades, either enhancing positive indirect effects on plants where predators have complementary feeding preferences or modes that enhance prey risk, or dampening cascades where predators interfere with or eat one another (Casula et al. 2006, Sih et al. 1998). Only a few experiments have manipulated predator diversity and measured the cascading effects on producers, yet these are clearly critical to understanding the effects of current biodiversity declines on ecosystem functioning (**Figure 1**). These experiments have confirmed that increasing diversity of species that are strict consumers of herbivores (that is, no intraguild predation or omnivory) can indirectly increase plant biomass in salt marsh (Finke & Denno 2005) and subtidal algal ecosystems (Bruno & O'Connor 2005, Byrnes et al. 2006). In most cases, this effect was because predator diversity decreased herbivore activity or per capita feeding rate rather than herbivore density. Positive field correlations between predator diversity and plant biomass (Byrnes et al. 2006) reinforce that these mechanisms likely operate in natural systems.

These manipulations of predator diversity illustrate an important factor influencing the impacts of changing diversity at higher trophic levels that potentially distinguishes them qualitatively from better-studied diversity effects at the plant level, namely the commonness of omnivory and intraguild predation. Experiments in both the subtidal macroalgal system (Bruno & O'Connor 2005) and salt marsh (Finke & Denno 2005) found that when omnivores and intraguild predators were included in the most diverse predator communities, high predator diversity led to lower, not higher, plant biomass. In the algal community this was because some predators also fed on algae, whereas in the salt marsh community predators interfered with or ate other predators, reducing herbivore suppression. Such complex trophic interactions are a hallmark of even very simple natural ecosystems and can, in some cases, reverse expected diversity effects based on niche partitioning and facilitation.

The aspects of food web complexity that lead to predator richness decreasing plant biomass (e.g., omnivory and intraguild predation) and the mechanisms leading to enhanced plant biomass (e.g., complementary prey preferences, predator-predator facilitation), are both predicted to strengthen with increasing species richness. Thus it is perhaps not surprising that a meta-analysis of 114 trophic cascade experiments in a range of systems found no statistical support for an effect of predator diversity on plant biomass (Borer et al. 2005). However, the range of species diversity in the studies analyzed by Borer et al. (2005) was probably insufficient to detect an effect of diversity, even if one existed. Earlier meta-analyses of terrestrial experiments that included a broader range of studies did find greater cascading impacts of predators on plants in systems with low herbivore diversity (e.g., Schmitz et al. 2000). Intriguingly, some oceanographic surveys suggest that at high diversity compensatory population dynamics among predator species contributes to a greater stability of the predator community in the face of intense harvesting, and that this diversity is both a partial cause and a consequence of high primary production and biomass (Frank et al. 2006).

Dispersal and Connectivity

Several recent experiments have explored how connections among habitat patches alter relationships between biodiversity and marine ecosystem properties in metacommunities. In experimental seagrass habitats that were closed to immigration and emigration, more diverse grazer assemblages achieved higher grazer abundance and more effectively cropped algal biomass, compared with less diverse grazer assemblages (France & Duffy 2006a,b), as discussed in detail above. When patches were connected so that grazers could move among them, the dependence of grazer abundance on diversity was erased and patches became more heavily dominated by inedible algae, apparently as grazers were free to move in search of patches with higher quality food (France & Duffy 2006b). Similar results have been found in experiments manipulating grazer diversity and connectivity among habitat patches in Baltic rock pool mesocosms (Matthiessen et al. 2007). Thus, connectivity among habitat patches can strongly modify the biodiversity effects on ecosystem properties found in previous studies of closed systems largely by eliminating differences in realized diversity among patches. Alternatively, variation in connectivity among environments can actually establish local scale variation in diversity, which then affects production and biomass, as shown in a laboratory study of microalgae (Matthiessen & Hillebrand 2006).

SUMMARY POINTS

Recent meta-analyses of biodiversity manipulations [Worm et al. 2006 (see the sidebar, Connecting Diversity to Ecosystem Services), Balvanera et al. 2006, Cardinale et al. 2006], as well as our own compilation (**Table 1a,b**; **Supplemental Tables 1–4**) suggest some generalizations about the effects of marine biodiversity:

1. The richness of species, functional groups, and/or genotypes affects ecosystem functioning in the majority of measurements in the majority of experiments. Diverse assemblages usually perform differently than the average monoculture (85/123 cases, **Table 1a,b**), but are less often better than the best-performing monoculture (26/105 cases). Identity effects were found in nearly all studies (91/99, see **Supplemental Tables 1–4**) and were stronger than richness effects in the few studies for which effect sizes were compared.
2. Positive richness effects in which polycultures outperform the average, but not best, monoculture commonly result from either positive selection (the sampling effect) or a combination of complementarity and negative selection.
3. A significant number of studies provides support for the idea of multivariate complementarity, in which a mixture outperforms all monocultures only when multiple aspects of the total community response are considered simultaneously or integrated into a multivariate index of ecosystem performance. Further research is needed to assess the general frequency and ecological significance of this phenomenon.

4. Although more comparative studies are needed, richness manipulations appear to more strongly and consistently affect metrics related to stability (resistance, resilience, reduced variability) than metrics that reflect mean states.
5. The effect of predator richness on plant biomass is consistently strong, but the direction of the effect is variable (increase versus decrease in plant biomass) and contingent upon the degree of omnivory and intraguild predation.
6. Observational studies suggest that the mechanistic effects of diversity on ecosystem functioning identified in experiments can be strong enough to generate correlations between diversity and function in field surveys. Such studies permit examination of a broader range of richness, larger spatial and temporal scales, more realistic environmental conditions, and provide better potential to test connections with ecosystem services valued by society (see sidebar, Connecting Diversity to Ecosystem Services).

FUTURE ISSUES

Although marine biodiversity-function studies have proliferated in the past 5–10 years and produced some emerging generalizations, these studies also point to gaps in our understanding of biodiversity-ecosystem function relationships in both terrestrial and marine environments. We offer the following suggestions for future work to consider.

1. Incorporate temporal and spatial heterogeneity. Many experiments lack the sort of spatial and temporal heterogeneity within replicates that is often key to coexistence and may enhance the likelihood that complementarity among species will be expressed. Also, experiments over longer timescales will enhance our understanding of whether remaining species can numerically or behaviorally compensate for the loss of superficially similar species, better assessing the degree to which species are redundant.
2. Develop a multitrophic-level perspective. Realistic estimates of diversity change show differential change at different trophic levels at the regional scale. Given that the effect of diversity at a particular trophic level is often contingent on the presence, diversity, and density of organisms at adjacent trophic levels, a better consideration of the food-web context of diversity manipulations is warranted.
3. Assess the relative importance of diversity. Factorial or nested experiments that manipulate richness along with other factors or compare the magnitude of richness and identity effects can help address the importance of diversity relative to other factors. Statistical analysis of survey data using multiple regression, structural equation modeling, data assimilation, or inverse

modeling will also be useful, though care must be taken in inferring causation from correlation.

4. Reconcile reciprocal relationships between diversity and ecosystem processes. Here we reviewed the effect of biodiversity on ecosystem processes, but many of these processes (productivity, stability, nutrient availability, strength of consumer control) are well-known to affect diversity. How these reciprocal relationships are reconciled is an obvious question in need of attention (Worm & Duffy 2003, Hughes et al. 2007).

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors thank Drew Harvell, Matt Bracken, Randall Hughes, and Jarrett Byrnes for constructive criticism on the manuscript. The authors also acknowledge the United States National Science Foundation Biological Oceanography program for funding their work on marine biodiversity ecosystem-function relationships, including this manuscript.

LITERATURE CITED

Allison G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. *Ecol. Monogr.* 74:117–34

Andow DA. 1991. Yield loss to arthropods in vegetationally diverse agroecosystems. *Environ. Entomol.* 20:1228–35

Arenas FI, Sanchez I, Hawkins SJ, Jenkins SR. 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. *Ecology* 87:2851–61

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, et al. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9:1146–56

Bernays EA, Bright KL, Gonzalez N, Angel J. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75:1997–2006

Bertness MD, Garrity SD, Levings SC. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Ecology* 78:1976–89

Biles CL, Solan M, Isaksson I, Paterson DM, Emes C, Raffaelli DG. 2003. Flow modifies the effect of biodiversity on ecosystem functioning: An in situ study of estuarine sediments. *J. Exp. Mar. Biol. Ecol.* 285/286:165–77

Bolser RC, Hay ME. 1996. Are tropical plants better defended? Palatability and defenses of temperate vs tropical seaweeds. *Ecology* 77:2269–86

Borer ET, Seabloom EW, Shurin JB, Anderson KE, Blanchette CA, et al. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528–37
Bracken MES, Stachowicz JJ. 2006. Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium. *Ecology* 87:2397–403
Britton-Simmons KH. 2006. Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. *Oikos* 113:395–401
Bruno JF, Bertness MD. 2001. Habitat modification and facilitation in benthic marine communities. In *Marine Community Ecology*, ed. MD Bertness, SD Gaines, ME Hay, pp. 201–18. Sunderland, MA: Sinauer
Bruno JF, Boyer KE, Duffy JE, Lee SC, Kertesz JS. 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecol. Lett.* 8:1165–74
Bruno JF, Kennedy CW, Rand TA, Grant MB. 2004. Landscape-scale patterns of biological invasions in shoreline plant communities. *Oikos* 107:531–40
Bruno JF, Lee SC, Kertesz JS, Carpenter RC, Long ZT, Duffy JE. 2006. Partitioning effects of algal species identity and richness on benthic marine primary production. *Oikos* 115:170–78
Bruno JF, O'Connor MI. 2005. Cascading effects of predator diversity and omnivory in a marine food web. *Ecol. Lett.* 8:1048–56
Buss LW, Jackson JB. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* 113:223–34
Byrnes JE, Reynolds PL, Stachowicz JJ. 2007. Invasions and extinctions reshape coastal marine food webs. *PloS ONE* 2(3):e295
Byrnes JE, Stachowicz JJ, Hultgren KM, Hughes RA, Olyarnik SV, Thornber CS. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecol. Lett.* 9:61–71
Callaway JC, Sullivan G, Zedler JB. 2003. Species-rich plantings increase biomass and nitrogen accumulation in a wetland restoration experiment. *Ecol. Appl.* 13:1626–39
Canuel EA, Spivak AC, Waterson EJ, Duffy JE. 2007. Biodiversity and food web structure influence short-term accumulation of sediment organic matter in an experimental seagrass system. *Limnol. Oceanogr.* 52:590–602
Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, et al. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–92
Carpenter RC. 1986. Partitioning herbivory and its effects on coral-reef algal communities. *Ecol. Monogr.* 56:345–63
Casula P, Wilby A, Thomas MB. 2006. Understanding biodiversity effects on prey in multi-enemy systems. *Ecol. Lett.* 9:995–1004
Cebrian J. 1999. Patterns in the fate of production in plant communities. *Am. Nat.* 154:449–68
Chapin FS III, Sala OE, Burke IC, Grime JP, Hooper DU, et al. 1998. Ecosystem consequences of changing biodiversity. *BioScience* 48:45–52
Crowder LB, Squires DD, Rice JA. 1997. Nonadditive effects of terrestrial and aquatic predators on juvenile estuarine fish. *Ecology* 78:1796–804

Cyr H, Pace ML. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361:148–50
Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86:1602–10
DeMott WR. 1998. Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology* 79:2463–81
Duarte CM, Terrados J, Agawin NSR, Fortes MD. 2000. An experimental test of the occurence of competitive interactions among SE Asian seagrasses. *Mar. Ecol-Prog. Ser.* 197:23
Duffy JE. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–19
Duffy JE. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* 6:680–87
Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M. 2007. The functional role of biodiversity in ecosystems: Incorporating trophic complexity. *Ecol. Lett.* 10:522–538
Duffy JE, Macdonald KS, Rhode JM, Parker JD. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417–34
Duffy JE, Richardson JP, Canuel EA. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecol. Lett.* 6:637–45
Duffy JE, Richardson JP, France KE. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol. Lett.* 8:301–9
Dunstan PK, Johnson CR. 2004. Invasion rates increase with species richness in a marine epibenthic community by two mechanisms. *Oecologia* 138:285–92
Elton CS. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen. 181 pp.
Emmerson M, Huxham M. 2002. How can marine ecology contribute to the biodiversity-ecosystem functioning debate? See Loreau et al. 2002, pp. 139–46
Emmerson MC, Solan M, Emes C, Paterson DM, Raffaelli D. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* 411:73–77
Finke DL, Denno RF. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol. Lett.* 8:1299–306
France KE, Duffy JE. 2006a. Consumer diversity mediates invasion dynamics at multiple trophic levels. *Oikos* 113:515–29
France KE, Duffy JE. 2006b. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature* 441:1139–43
Frank KT, Petrie B, Shackell NL, Choi JS. 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecol. Lett.* 9:1096–105
Fridley JD, Brown RL, Bruno JF. 2004. Null models of exotic invasions and scale-dependent patterns of native and exotic richness. *Ecology* 85:3215–22
Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom E, et al. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology.* 88:3–17

Gamfeldt L, Hillebrand H, Jonsson PR. 2005. Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol. Lett.* 8:696–703

Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH. 2001. Contrasting effects of plant richness and composition on insect communities: A field experiment. *Am. Nat.* 158:17–35

Hay ME, Steinberg PD. 1992. The chemical ecology of plant-herbivore interactions in marine vs terrestrial communities. In *Herbivores: Their Interaction with Secondary Metabolites*, *Evolutionary and Ecological Processes*, Vol. 2, ed. JA Rosenthal, MR Berenbaum, pp. 371–413. San Diego, CA: Academic

Heck KL Jr, Orth RJ. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In *Estuarine Perspectives*, ed. VS Kennedy, pp. 449–64. New York: Academic

Hector A, Bazeley-White E, Loreau M, Otway S, Schmid B. 2002. Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecol. Lett.* 5:502–11

Hillebrand H, Cardinale BJ. 2004. Consumer effects decline with prey diversity. *Ecol. Lett.* 7:192–201

Hillebrand H, Shurin JB. 2005. Biodiversity and aquatic food webs. In *Aquatic Food Webs: An Ecosystem Approach*, ed. A Belgrano, UM Scharler, J Dunne, RE Ulanowicz, pp. 184–97. New York: Oxford Univ. Press

Hixon MA, Carr MH. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–49

Holt RD, Loreau M. 2002. Biodiversity and ecosystem functioning: the role of trophic interactions and the importance of system openness. In *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*, ed. AP Kinzig, S Pacala, D Tilman, pp. 246–62. Princeton, NJ: Princeton Univ. Press

Hooper DU, Chapin FSI, Ewel JJ, Hector A, Inchausti P, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75:3–35

Hooper DU, Dukes JS. 2004. Overyielding among plant functional groups in a long-term experiment. *Ecol. Lett.* 7:95–105

Hughes AR, Stachowicz JJ. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci. USA* 101:8998–9002

Hughes AR, Byrnes JE, Kimbro DL, Stachowicz JJ. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecol. Lett.* 10:849–64

Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–60

Ieno EN, Solan M, Batty P, Pierce GJ. 2006. How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Mar. Ecol-Prog. Ser.* 311:263–71

Ives AR, Cardinale BJ, Snyder WE. 2005. A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecol. Lett.* 8:102–16

Jones GP, McCormick MI, Srinivasan M, Eagle JV. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA* 101:8251–53
Keesing F, Holt RD, Ostfeld RS. 2006. Effects of species diversity on disease risk. *Ecol. Lett.* 9:485–98
Kertesz JS. 2006. *The role of biodiversity in a fluctuating environment*. MS thesis. San Francisco State Univ. 44 pp.
Lehman CL, Tilman D. 2000. Biodiversity, stability, and productivity in competitive communities. *Am. Nat.* 156:534–52
Leibold MA. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* 134:922–49
Loreau M. 1998. Separating sampling and other effects in biodiversity experiments. *Oikos* 82:600–2
Loreau M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91:3–17
Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76
Loreau M, Naeem S, Inchausti P, eds. 2002. *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives.* New York: Oxford Univ. Press
Loreau M, Naeem S, Inchausti P, eds. 2002. Perspectives and challenges. See Loreau et al. 2002, pp. 237–42
Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–8
Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, et al. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–9
Martin TH, Wright RA, Crowder LB. 1989. Non-additive impact of blue crabs and spot on their prey assemblages. *Ecology* 70:1935–42
Matthiessen B, Gamfeldt L, Jonsson PR, Hillebrand H. 2007. Effects of grazer richness and composition on algal biomass in a closed and open marine system. *Ecology.* 88:178–187
Matthiessen B, Hillebrand H. 2006. Dispersal frequency affects local biomass production by controlling local diversity. *Ecol. Lett.* 9:652–62
May RM. 1974. *Stability and Complexity in Model Systems.* Princeton, NJ: Princeton Univ. Press. 2nd ed.
McCann KS. 2000. The diversity–stability debate. *Nature* 405:228–33
Moore T. 2006. *Seagrass meadows: spatial scaling, biodiversity & ecosystem function*. PhD thesis. Flinders Univ., Adelaide, South Australia. 189 pp.
Moore TN, Fairweather PG. 2006. Decay of multiple species of seagrass detritus is dominated by species identity, with an important influence of mixing litters. *Oikos* 114:329–37
Naeem S, Li S. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507–9
Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–37
O'Connor NE, Crowe TP. 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology* 86:1783–96

Paine RT. 2002. Trophic control of production in a rocky intertidal community. *Science* 296:736–39

Parker JD, Duffy JE, Orth RJ. 2001. Plant species diversity and composition: experimental effects on marine epifaunal assemblages. *Mar. Ecol. Prog. Ser.* 224:55–67

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr. 1998. Fishing down marine food webs. *Science* 279:860–63

Petchey OL, Casey T, Jiang L, McPhearson PT, Price J. 2002. Species richness, environmental fluctuations, and temporal change in total community biomass. *Oikos* 99:231–40

Petchey OL, Downing AL, Mittelbach GG, Persson L, Steiner CF, et al. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* 104:467–78

Pimm SL. 1984. The complexity and stability of ecosystems. *Nature* 307:321–26

Raffaelli D, Emmerson M, Solan M, Biles C, Paterson D. 2003. Biodiversity and ecosystem processes in shallow coastal waters: an experimental approach. *J. Sea Res.* 49:133–41

Reusch TBH, Ehlers A, Haemmerli A, Worm B. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci. USA* 102:2826–31

Rex MA, Stuart CT, Hessler RR, Allen JA, Sanders HL, Wilson GDF. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636–39

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, et al. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295:1280–84

Roy K, Jablonski D, Valentine JW, Rosenberg G. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl. Acad. Sci. USA* 95:3699–3702

Sackville-Hamilton NR. 1994. Replacement and additive designs for plant competition studies. *J. Appl. Ecol.* 31:599–603

Sala E, Knowlton N. 2006. Global marine biodiversity trends. *Annu. Rev. Environ. Resourc.* 31:93–122

Sax D. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *J. Biogeogr.* 28:139–50

Schiel DR. 2006. Rivets or bolts? When single species count in the function of temperate rocky reef communities. *J. Exp. Mar. Biol. Ecol.* 338:233–52

Schmitz OJ, Hamback PA, Beckerman AP. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.* 155:141–53

Shea K, Chesson P. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17:170–76

Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, et al. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* 5:785–91

Siemann E, Tilman D, Haartstad J, Ritchie M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* 152:738–50

Sih A, Englund G, Wooster D. 1998. Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.* 13:350–55

Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS. 2004. Extinction and ecosystem function in the marine benthos. *Science* 306:1177–80

Srivastava DS, Vellend M. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.* 36:267–94

Stachowicz JJ, Byrnes JE. 2006. Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Mar. Ecol. Prog. Ser.* 311:251–62

Stachowicz JJ, Fried H, Whitlatch RB, Osman RW. 2002. Biodiversity, invasion resistance and marine ecosystem function: reconciling pattern and process. *Ecology* 83:2575–90

Stachowicz JJ, Whitlatch RB, Osman RW. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–79

Steneck RS, Vavrinec J, Leland AV. 2004. Accelerating trophic level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems* 7:323–31

Thebault E, Loreau M. 2003. Food-web constraints on biodiversity-ecosystem functioning relationships. *Proc. Natl. Acad. Sci. USA* 100:14949–54

Thebault E, Loreau M. 2006. The relationship between biodiversity and ecosystem functioning in food webs. *Ecol. Res.* 21:17–25

Tilman D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455–74

Tilman D, Lehman C, Thompson K. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. USA* 94:1857–61

Tilman D, Reich PB, Knops JMH. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–32

Waldbusser GG, Marinelli RL. 2006. Macrofaunal modification of porewater advection: Role of species function, species interaction, and kinetics. *Mar. Ecol. Prog. Ser.* 311:217–31

Waldbusser GG, Marinelli RL, Whitlatch RB, Visscher PT. 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnol. Oceanogr.* 49:1482–92

Watermann F, Hillebrand H, Gerdes G, Krumbein WE, Sommer U. 1999. Competition between benthic cyanobacteria and diatoms as influenced by different grain sizes and temperatures. *Mar. Ecol. Prog. Ser.* 187:77–87

White LF, Shurin J. 2007. Diversity effects on invasion vary with life history stage in marine macroalgae. *Oikos.* 116:1193–1203

Williams SL. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecol. Appl.* 11:1472–88

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–90

Worm B, Duffy JE. 2003. Biodiversity, productivity and stability in real food webs. *Trends Ecol. Evol.* 18:628–32

Worm B, Lotze HK, Myers RA. 2003. Predator diversity hotspots in the blue ocean. *Proc. Natl. Acad. Sci. USA* 100:9884–88

Annual Review of Ecology, Evolution, and Systematics

Volume 38, 2007

Contents

Evolution of Animal Photoperiodism
William E. Bradshaw and Christina M. Holzapfel 1

Virus Evolution: Insights from an Experimental Approach
Santiago F. Elena and Rafael Sanjuán 27

The Social Lives of Microbes
Stuart A. West, Stephen P. Diggle, Angus Buckling, Andy Gardner, and Ashleigh S. Griffin 53

Sexual Selection and Speciation
Michael G. Ritchie 79

Kin Selection and the Evolutionary Theory of Aging
Andrew F.G. Bourke 103

Climate Change and Invasibility of the Antarctic Benthos
Richard B. Aronson, Sven Thatje, Andrew Clarke, Lloyd S. Peck, Daniel B. Blake, Cheryl D. Wilga, and Brad A. Seibel 129

Spatiotemporal Dimensions of Visual Signals in Animal Communication
Gil G. Rosenthal 155

Gliding and the Functional Origins of Flight: Biomechanical Novelty or Necessity?
Robert Dudley, Greg Byrnes, Stephen P. Yanoviak, Brendan Borrell, Rafe M. Brown, and Jimmy A. McGuire 179

How Mutational Networks Shape Evolution: Lessons from RNA Models
Matthew C. Cowperthwaite and Lauren Ancel Meyers 203

How Does It Feel to Be Like a Rolling Stone? Ten Questions about Dispersal Evolution
Ophélie Ronce 231

Exploring Cyanobacterial Mutualisms
Kayley M. Usher, Birgitta Bergman, and John A. Raven 255

Human Impacts in Pine Forests: Past, Present, and Future
David M. Richardson, Philip W. Rundel, Stephen T. Jackson, Robert O. Teskey, James Aronson, Andrzej Bytnerowicz, Michael J. Wingfield, and Şerban Procheş 275

Chemical Complexity and the Genetics of Aging
Scott D. Pletcher, Hadise Kabil, and Linda Partridge 299

A Global Review of the Distribution, Taxonomy, and Impacts of Introduced Seaweeds
Susan L. Williams and Jennifer E. Smith 327

The Very Early Stages of Biological Evolution and the Nature of the Last Common Ancestor of the Three Major Cell Domains
Arturo Becerra, Luis Delaye, Sara Islas, and Antonio Lazcano 361

Functional Versus Morphological Diversity in Macroevolution
Peter C. Wainwright 381

Evolutionary Game Theory and Adaptive Dynamics of Continuous Traits
Brian J. McGill and Joel S. Brown 403

The Maintenance of Outcrossing in Predominantly Selfing Species: Ideas and Evidence from Cleistogamous Species
Christopher G. Oakley, Ken S. Moriuchi, and Alice A. Winn 437

Sympatric Speciation: Models and Empirical Evidence
Daniel I. Bolnick and Benjamin M. Fitzpatrick 459

The Evolution of Color Polymorphism: Crypticity, Searching Images, and Apostatic Selection
Alan B. Bond 489

Point, Counterpoint: The Evolution of Pathogenic Viruses and their Human Hosts
Michael Worobey, Adam Bjork, and Joel O. Wertheim 515

The Evolution of Resistance and Tolerance to Herbivores
Juan Núñez-Farfán, Juan Fornoni, and Pedro Luis Valverde 541

Plant-Animal Mutualistic Networks: The Architecture of Biodiversity
Jordi Bascompte and Pedro Jordano 567

Gene Flow and Local Adaptation in Trees
Outi Savolainen, Tanja Pyhäjärvi, and Timo Knürr 595

The Evolution of Multicellularity: A Minor Major Transition?
Richard K. Grosberg and Richard R. Strathmann 621

Developmental Genetics of Adaptation in Fishes: The Case for Novelty
J.T. Streelman, C.L. Peichel, and D.M. Parichy 655

Terrestrial Carbon–Cycle Feedback to Climate Warming
Yiqi Luo 683

Shortcuts for Biodiversity Conservation Planning: The Effectiveness of Surrogates
Ana S.L. Rodrigues and Thomas M. Brooks 713

Understanding the Effects of Marine Biodiversity on Communities and Ecosystems
John J. Stachowicz, John F. Bruno, and J. Emmett Duffy 739

Stochastic Dynamics of Plant-Water Interactions
Gabriel Katul, Amilcare Porporato, and Ram Oren 767

Evolutionary Endocrinology: The Developing Synthesis between Endocrinology and Evolutionary Genetics
Anthony J. Zera, Lawrence G. Harshman, and Tony D. Williams 793

The Role of Behavior in the Evolution of Spiders, Silks, and Webs
Fritz Vollrath and Paul Selden 819

Applications of Flow Cytometry to Evolutionary and Population Biology
Paul Kron, Jan Suda, and Brian C. Husband 847

Indexes

Cumulative Index of Contributing Authors, Volumes 34–38 877

Cumulative Index of Chapter Titles, Volumes 34–38 881

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at http://ecolsys.annualreviews.org/errata.shtml