Moving species redundancy toward a more predictive framework

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Abstract

Human activities are driving rapid changes in species diversity in a wide range of habitats globally. These changes in species diversity raise questions about the ability of altered systems to continue to offer valuable ecosystem services. Maintenance of ecosystem services under changing biodiversity depends largely on the ability of persisting species to fill the functional gaps left by species in decline, and thus on the ecological or functional redundancy of species. Previous work suggests that the concept of species redundancy holds little applied value because, among other reasons, this concept is highly context dependent. Our goal in this chapter is to demonstrate a conceptual framework in which the prevalence and importance of redundancy is examined across example environmental and biological gradients to determine conditions or situations in which redundancy should play a significant role. By exploring general conditions that should elevate the importance or prevalence of redundancy, we hope to demonstrate that this concept can be used predictively, despite its context-dependent nature.

The needs of a growing human population are having strong impacts on ecosystems worldwide. The biological endpoints of many of these impacts are either a local increase in species richness through species invasion, or a local (as well as global) decrease in species richness through population extinction. Both invasion and extinction therefore represent changes in local levels of biodiversity. Changes in species abundance and/or composition raise questions about the importance of biodiversity, both for the ability of natural systems to persist and their ability to provide important ecosystem services that directly or indirectly benefit humans through provisioning services (e.g., hydrologic cycles, atmos-

pheric composition, soil genesis), regulating services (e.g., climate regulation, water and air purification), supporting services (e.g., pollination, storing and cycling of nutrients), and cultural services (e.g., ecotourism, aesthetics) (Millennium Ecosystem Assessment 2003; Hooper et al. 2005).

The consequences of changing biodiversity have received considerable and increasing attention over the past couple of decades. Much of this work has alluded to, or acknowledged, that multiple species can perform similar functions in natural systems (Walker 1992). Species that perform similar functions are ecologically redundant. By definition then, redundant species are similar in function so that if one species is removed and replaced by another, no loss of ecosystem function would be observed (Lawton and Brown 1993). This is equivalent to "functional degeneracy" as recently described by Gonzalez and Loreau (2009). This situation does not imply that each redundant species has redundant impacts. For example, four individuals of species B may be required to replace the function of a single individual of species A. Thus, the provision of ecosystem services must be considered within the context of both population dynamics and community interactions (Kre-

men and Ostfeld 2005; Griffen and Byers 2006). The level of redundancy in ecological communities therefore determines whether, for example, the loss of species alters ecosystem function (Larsen et al. 2005), and whether there is little or no change to ecosystem function (e.g., Schindler 1990).

As reviewed by Gitay et al. (1996), the concept of species redundancy grows from three main concepts. First, that species with similar functions can be classified into functional guilds that may be followed as single units without regard to individual species within the guild. This approach has commonly been employed (e.g., aquatic invertebrates: Cummins 1973; amphibians and reptiles: Inger and Colwell 1977; stream fish: Winemiller and Pianka 1990; marine fish: Greenstreet 1996). Second, species with similar competitive abilities can be considered ecologically equivalent (Goldberg and Werner 1983). And third, species that share a common niche may also be considered ecologically equivalent (Alley 1982). The confluence of these three related concepts, together with the search for simplifying principles in theoretical attempts to simulate ecosystem processes (for example, using programs such as Ecopath), gave rise to the idea of species redundancy.

Originally, redundancy was a conceptual idea used to simplify effort needed to track complex ecosystems. However, more recently, species redundancy has been applied to conservation. From a conservation perspective, species redundancy is a desirable property, diversifying ecological risk (Hummel et al. 2009) and providing insurance against the loss of ecosystem function with the loss of a species (i.e., the insurance hypothesis, Yachi and Loreau 1999). However, the notion that some species are redundant is a two-edged sword (Rosenfeld 2002)—although it does provide some level of insurance against loss of ecosystem function, it also suggests that not all species are necessary, and that systems may function equally well with fewer species (Chapin et al. 1992; West 1993; Bowman 1994; Cowling et al. 1994; Kennedy and Smith 1995), reducing the need for species conservation. In addition, implementing the concept of species redundancy for conservation is not without problems. Gitay et al. (1996) suggested that this concept is of limited use to applied science for three reasons. First, all of the available measures of redundancy are too difficult to implement. Second, the term is misunderstood by policymakers to mean that there are some species we don't need. Third, species redundancy is highly context dependent and it is therefore hopeless to try to be predictive about when species will be redundant. Although species redundancy has been and will undoubtedly remain a useful intellectual concept within ecology, its utility for conservation therefore remains uncertain.

We agree with Gitay et al. (1996) that these problems could limit the utility of species redundancy in applied circumstances. However, we also posit that these problems are not insurmountable. In fact, considerable progress has recently been made toward solving the first problem. Petchey and Gaston (2006) provide a summary of recent efforts to develop quantitative methods for assessing functional redundancy/diversity and highlight several areas where progress may be facilitated by future research efforts. Additional suggestions are provided by Kremen and Ostfeld (2005). There is still a very long way to go, but we are confident that measures of redundancy will be developed that may be practically implemented on reasonable and useful temporal and spatial scales.

The second concern raised by Gitay et al. (1996) is potentially much more serious, and the responsibility for addressing this concern rests on the collective shoulders of ecologists. As experts in the field, it is our responsibility to clarify misunderstandings about the importance of biodiversity and the value of redundancy. An important distinction in any discussion of redundancy is that redundancy in species function does not necessarily equate with redundancy in environmental tolerance. Therefore, although species may be functionally redundant under a limited set of conditions, they may exhibit complementarity/diversity under different conditions (Rosenfeld 2002). Thus, redundancy not only provides insurance against the loss of ecosystem function with the loss of species richness, it also provides insurance against the loss of ecosystem function under changing environmental conditions, independent of changes in species richness.

Our purpose is not to directly address either of these first two concerns raised by Gitay et al. (1996). Rather, our goal is to address their third concern—that the context dependency of redundancy prohibits a predictive approach. We agree that redundancy is likely highly context dependent. However, we suggest that conditions can be identified for which redundancy is more or less likely and in which it may be more or less important for preserving ecosystem function. Identifying these conditions may therefore increase the predictability of this concept.

Previous work has also attempted to place redundancy in a predictive context (Petchey and Gaston 2006). For example, Fonseca and Ganade (2001) predicted the probability of losing entire functional groups when species randomly go extinct. They predicted that as many as 75% of species could be lost from a particular study system (they used a South American plant community as an example) before the disappearance of the first functional group, speaking to the importance of redundancy. While their quantitative, predictive approach should be lauded, the applicability of their random-extinction approach to natural systems with multiple trophic levels is questionable, given that species extinction is a decidedly non-random process (Purvis et al. 2000). Given the increasing threat of species loss, studies are needed that identify organisms and/or systems in which redundancy may be more prevalent and where it may be more crucial to the maintenance of ecosystem function.

This chapter will proceed as follows. Ecological systems can conveniently be characterized by several environmental and/or organismal characteristics or variables that describe

ecological gradients. We identified two environmental and two biological gradients within aquatic systems that may influence the importance of redundancy (environmental: material transport and disturbance; biological: life history and evolution). Our task is to examine the likely importance of redundancy at different ends of these gradients. This is an attempt to move redundancy from a system-specific science to a more predictive science. In Part One of this chapter, we therefore examine each of these four gradients and make predictions about where redundancy may be most prevalent or influential along each gradient. The choice of these four gradients is not meant to be exhaustive, but provides examples of a technique that may usefully be applied to other environmental or biological gradients as well. In Part Two of this chapter, we then demonstrate how these predictions may be applied. We do this in two ways. First, we explore the ability of these predictions to explain redundancy within microbial communities. Second, we demonstrate how these predictions can be further extended to make predictions related to applied ecological problems. Specifically, we extend our predictions to address the likely importance of redundancy in determining the susceptibility of an ecosystem to species invasion.

PART ONE: Predictions

Material transport in ecosystems—Like all living organisms, ecosystems receive, recycle, and release materials (energy and nutrients) with respect to their surrounding environment. Yet, despite this broad generality, the underpinnings of how ecosystems function often depend on their unique characteristics, which internally regulate the abundance, transport, and retention of materials. These also govern community composition by selecting species from regional pools that: (1) are well adapted to local conditions; and (2) vary in the degree for which their traits overlap (assumed functional redundancy). Although the roles of species within ecosystems span a variety of functions, which include providing physical structure, habitat modification, community regulation, and population control among many others, often the most salient contribution is the cycling and storage of energy and materials (Cebrian 2004). The significance of organisms as nutrient and carbon capacitors may be especially prevalent in ecosystems that are susceptible to disturbance and lack physical mechanisms to retain materials. As such, we would expect the importance of biological redundancy to differ among ecosystems with variable material inputs and physical characteristics (Poff et al. 2003). Here we provide a conceptual framework for identifying ecosystems in which functional redundancy in material cycling should be important (Fig. 1).

Magnitude of incoming resources: Establishing a mechanistic understanding of the relationship between biological diversity and ecosystem function has been a longstanding theme in ecology (Tilman 1986; Naeem 2003). Up to now, our discussion has focused on ecological similarity among species in the context of redundancy in the ecological services they confer
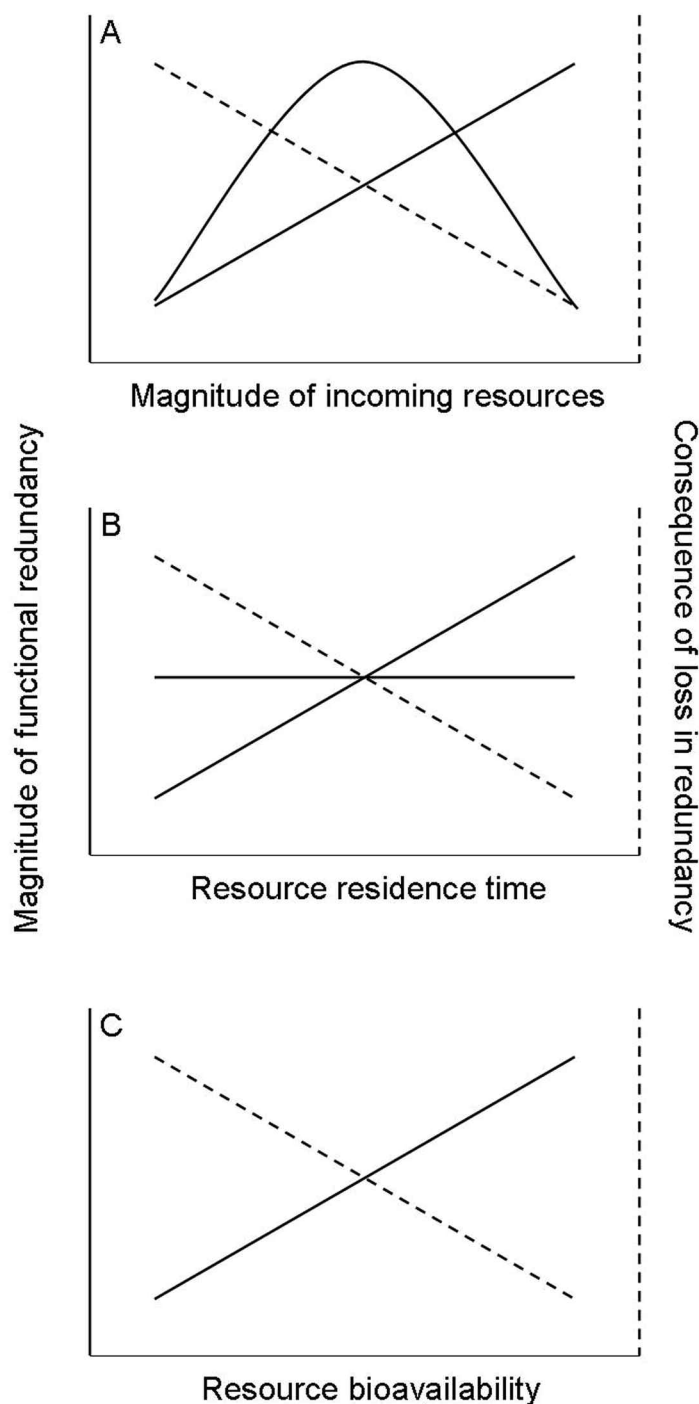

Fig. 1. Hypothetical relationships between magnitude of functional redundancy (left y-axis solid line), ecological consequences of loss in redundancy (right y-axis dashed line) and three ecosystem characteristics: (A) magnitude of incoming resources, (B) residence time, and (C) resource bioavailability.

to ecosystems. This is somewhat of a circular argument, however, as productivity regimes within ecosystems can also set the stage for species coexistence and community composition (Schmidt 1996). The coevolutionary trajectory of species is

intimately linked to the degree of resource availability such that ecosystems with a larger resource base, and thus greater carrying capacity, can support more trophic levels with greater numbers of species (Brown et al. 2001; Loreau 2004). For example both ecosystem size and magnitude of productivity are positively related to the number of species and trophic levels within lakes (Dodson et al. 2000; Post et al. 2000). Often, however, these relationships become unimodal due to more complex species interactions (predation and competition) at higher levels of productivity (Fig. 1A). Nonetheless, we predict that ecosystems that receive greater external resources, either as nutrients or light availability, should have a greater resource base to support more species. Consequently, these systems should also have a higher magnitude of redundancy and a greater buffering capacity against species loss (Fig. 1A). Although the magnitude of redundancy may be greater in highly productive ecosystems, as ecosystems become perturbed, the consequence of a lack of redundancy may be greater in less productive ecosystems (Fig. 1A).

Residence time within ecosystems: While all ecosystems are theoretically open, some retain materials better than others. This is largely a function of a series of transport processes (local disturbance and climate regimes) that physically influence the residence time of materials as they pass through an ecosystem (Padisak 1993). Ultimately, these processes determine the encounter rate, duration, and availability of materials for biological processing. For example, ecosystems with short residence times either undergo net losses, or fail to retain nutrients and energy that move through the ecosystem. These "leaky systems" are typically characterized by high transport agents including wind or water that keep materials moving in suspension. Consequently, these agents can also dictate the variety of foraging modes used by resident species to obtain resources. For example, streams, rivers, and estuaries have relatively low residence times due to high flow and turnover rates compared to slow-moving open oceans, lakes, and ponds (Allan 1995). Some species that reside within these systems depend on the delivery of materials and therefore use sit-and-wait or filter-feeding strategies to capture food items. Consequently, these organisms facilitate the cycling or retention of materials that may otherwise be lost to adjacent ecosystems by other organisms that are more mobile and therefore transport nutrient (e.g., fish, crabs, birds). Conversely, ecosystems with longer residence times are better suited to retain materials because (1) they are either very large (pelagic oceans) or are terminal recipient ecosystems (kettle lakes), (2) they have low turnover rates (ponds and wetlands), or (3) they receive large refractory materials that are not easily transported (wetlands). Unlike leaky ecosystems, ecosystems with longer residence times (storage ecosystems) allow for greater encounter rates for material processing by their inhabitants, resulting in net storage of materials.

Overall, we would expect functional redundancy to be greater in ecosystems with high residence times due to

increased consumer-resources interaction associated with resource availability (Fig. 1B). However, this relationship may be complicated by the fact that species inhabiting these contrasting environments are likely to be highly specialized and reflect completely different species pools, which may negate any observable trend (Fig. 1B). Although the degree of redundancy across the gradient of resource residence times may not be predictable, the ecological consequences associated with reduced redundancy should be. The loss of redundant species may have profound impacts on many aspects of the functioning of ecosystems, yet from the perspective of our target function "material cycling and retention," we argue that there is less concern with species loss in high–residence time "storage" ecosystems because there is a lower probability that the materials will be physically transported from the ecosystem (Fig. 1B).

Bioavailability of incoming materials: Materials entering ecosystems are generally lumped into two distinct categories, those that are labile and readily assimilated into new biomass by producers and consumers and those that are refractory and require further processing before consumption and assimilation can occur (Lennon and Pfaff 2005). Although materials in both categories move through ecosystems via a variety of pathways, the extent of their bioavailability often reflects the source from which they originated. Many aquatic ecosystems are nested within terrestrial biomes (headwater streams, lakes, ponds, and bogs) and are therefore highly influenced by the landscape from which they drain. For example, wooded and wetland-dominated lakes and streams receive a substantial amount of their carbon from detrital particulate organic material that is often unpalatable due to high lignin content and other structural components (Cross 2003; Crump et al. 2003). Conversely, watersheds that drain agricultural landscapes transport more nutrients and more simply structured, bioavailable organic matter (Rier and Stevenson 2002). These differences in character and bioavailability can influence microbial and primary-producer community composition, which in turn can have cascading effects on material cycling at higher trophic levels within ecosystems (Legendre and Rivkin 2002; Wilson and Xenopoulos 2009).

The recurring theme of species traits and foraging modes is central to understanding how resource bioavailability relates to the concept of functional redundancy. We predict that, like our expected relationship with the magnitude of incoming resources, ecosystems with readily available resources would support more redundant species compared to those with less palatable resources (Fig. 1C). For example, ecosystems with resources that are less bioavailable often contain species with specific traits that are uniquely adapted to consuming less palatable materials (Covich et al. 1999). These species contribute to at least three important ecological functions: (1) acquiring, assimilating, and retaining materials that otherwise may be lost to adjacent ecosystems; (2) subsidizing co-occurring species by modifying materials and making them biologically available; and (3) remineralizing nutrients and stimulat-

ing primary production. Although there is ample evidence suggesting that ecosystems with labile resources support many species with similar foraging strategies, we predict that ecosystems containing refractory resources have fewer redundant species and thus have a reduced ability to buffer against species declines (Fig. 1C).

While each of the above characteristics influences the retention of materials within ecosystems, considering all three in concert may provide particular insight into which ecosystems are susceptible to disturbance and warrant concern for loss of functional redundancy. For example ecosystems with high residence times that receive a large amount of labile resources should be significantly less threatened than those receiving refractory materials that are quickly transported away (Fig. 2). This conceptualization, while helpful, is further complicated by the fact that ecosystems are undergoing changes that influence where they fall out along our hypothesized gradients. For example, cultural eutrophication threatens to increase both the magnitude and bioavailability of resources in historically oligotrophic systems. In addition, impoundments and the increase of impervious substrates associated with urbanization are changing the extent to which resources are delivered among ecosystems.

Disturbance and environmental variability—Changes in local or regional climate, habitat structure, and the frequency and extent of disturbances may alter the composition of plant and animal communities, because organisms are sensitive to environmental conditions (e.g., temperature, irradiance, precipita-

tion, salinity, etc; Gonzalez and Loreau 2009). For example, systems that experience frequent and severe disturbances may be dominated by fast-growing, early successional species, whereas systems with a low-disturbance regime may be comprised of slower-growing, longer-lived species. However, systems with moderate rates of disturbance may be the most diverse, being populated by both fast- and slow-growing species; this is in accordance with the intermediate disturbance hypothesis (Pianka 1966; Connell 1978; Huston 1979; Fig. 3). We predict that, like diversity, functional redundancy will be maximized at intermediate rates of disturbance (but see Loreau 2004; Hughes et al. 2007). It is likely that frequent or severe disturbances will reduce redundancy by having a negative impact on species survivorship. Similarly, in a low-disturbance environment, competitive interactions may reduce species abundance and richness (Connell 1978). Because niches of functionally redundant species may not overlap exactly, it is possible that redundant species may be competitively excluded from the habitat (Cole et al. 2006). Thus, conditions that maximize diversity may also enhance functional redundancy and, as a result, system stability (e.g., Ives and Hughes 2002). Although it is convenient to envision measures of redundancy and ecosystem stability over a gradient of disturbance, it is more likely that a variety of factors, including species composition and disturbance identity, duration, and severity, will moderate the coexistence and success of redundant species.

Overlap in species functional roles may confer stability to ecosystem processes by buffering those processes against dis-
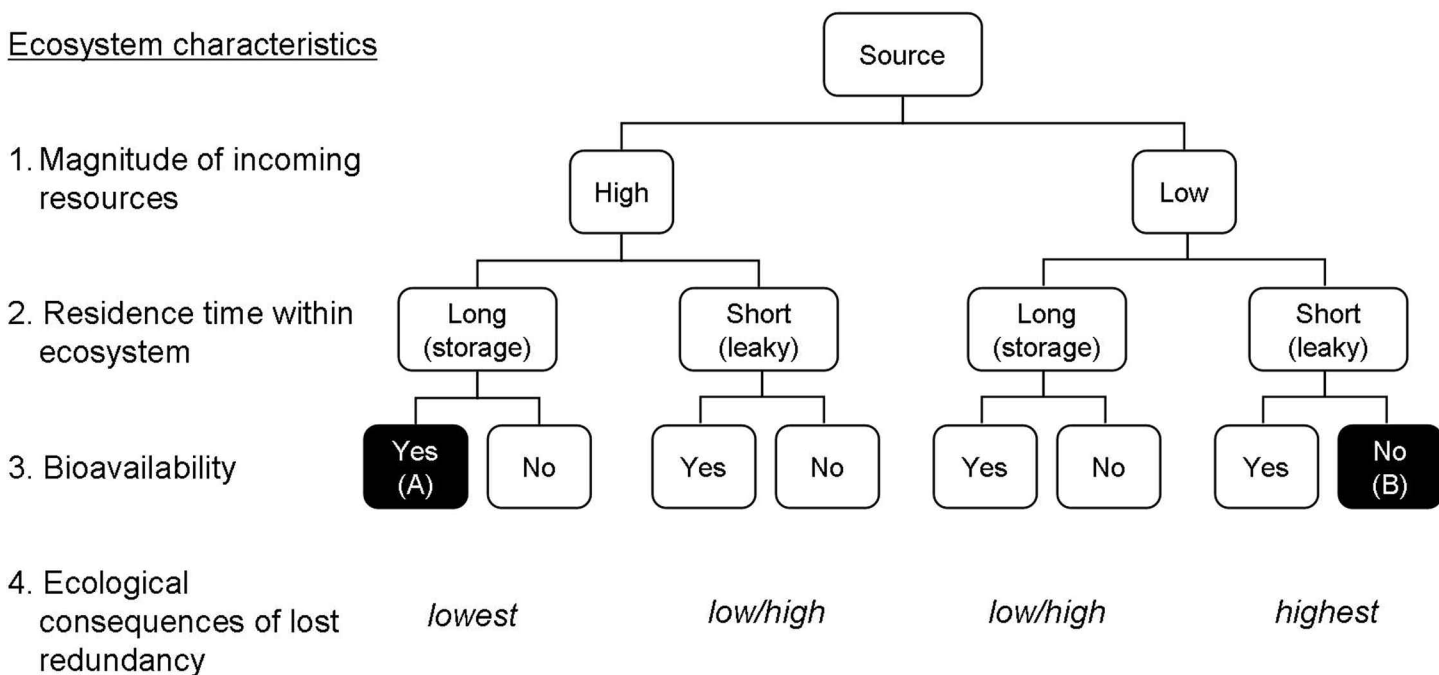

Fig. 2. Conceptual flow diagram illustrating the relative importance of ecosystem level characteristics on ecological redundancy. We predict that ecosystems with long residence times that receive lots of labile resources (A) will be relatively less susceptible to disturbance compared to those that are leaky and receive low amounts of refractory materials (B).
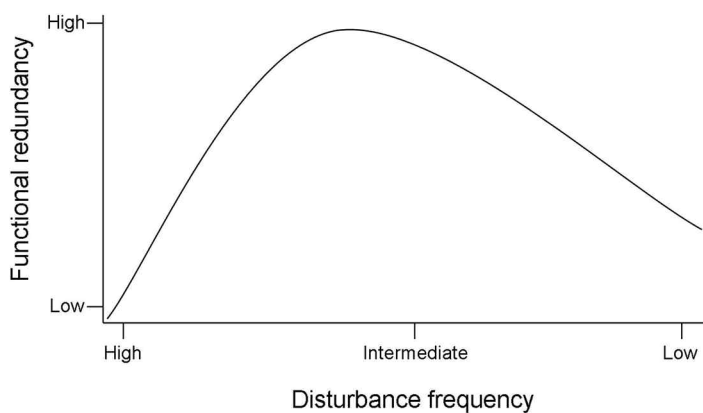
Fig. 3. Proposed relationship between the occurrence of functionally redundant species and disturbance frequency. Based on Connell (1978).

turbances and reducing the time required for a process to return to a predisturbance level (Walker et al. 1999; Fonseca and Ganade 2001, Palumbi et al. 2008; Winfree and Kremen 2009). In part, this depends upon functionally redundant species differing in their susceptibility to ecosystem disturbances and to temporal asynchronies (e.g., seasonality) in abundance (Ives et al. 2000; Loreau 2000; Palumbi et al. 2008). Following a disturbance that severely reduces the abundance of a numerically dominant species, compensatory population growth of other species may occur and, as a result, ecosystem processes may be maintained in the long term (Naeem 1998; Walker et al. 1999; Hooper et al. 2005, Gonzalez and Loreau 2009). However, ecosystem functioning will likely decline after a severe disturbance because other species may not be able to immediately fill the process of the reduced or extinct species. The time required for an ecosystem process to return to a predisturbance state may depend on the growth and reproductive patterns of less abundant or donor species. In addition, competitive interactions between the less abundant but functionally redundant species may affect the rate of recovery because the species may exist in different proportions before and after a perturbation (Allison 2004; Hughes et al. 2007). Consequently, functional redundancy may operate as a stability mechanism over long time periods.

The notion that functionally redundant species buffer ecosystem processes against disturbances is in accordance with the insurance hypothesis (Yachi and Loreau 1999; Borrvall et al. 2000; Ives et al. 2000; Wohl et al. 2004; Hooper et al. 2005; Winfree and Kremen 2009). In part, the "insurance" in more diverse systems is due to a greater likelihood that there will be some functional overlap between species that survive a disturbance (Walker et al. 1999; Borrvall et al. 2000; Ives et al. 2000). Consequently ecosystem functions may be more constant in systems with diverse species assemblages as opposed to more depauperate communities (Duarte 2000). However there is experimental evidence that functional (versus ecological) diversity and composition strongly influences ecosystem processes (Tilman et al. 1997; Petchey and Gaston 2002). This suggests that a better predictor of ecosystem response to disturbance may be functional diversity or functional redundancy rather than biodiversity (ecological redundancy), per se.

The usefulness of functional redundancy as a stability mechanism may depend on the frequency and extent of disturbance as well as community composition (Diaz et al. 1999). For example, particularly strong disturbances (e.g., hurricanes, bulldozers, etc) may eliminate the buffering capacity of functionally redundant species. In addition, disturbances that occur over longer timeframes may alter ecosystem processes by changing community composition or interactions between species (e.g., Slik 2004). For instance, constant and high fishing pressure may remove entire functional groups (i.e., top predators) from coastal and oceanic systems (Micheli and Halpern 2005; Scheffer et al. 2005; Worm et al. 2006). Predator removal may lead to higher herbivore biomass and consumption of primary producers, in simple three-level food chains. However, simple trophic food-web theory is complicated by interactions between species both within and across trophic levels (Bascompte et al. 2005; Duffy et al. 2007; Stachowicz et al. 2007; Otto et al. 2008). The effects of single disturbances, such as predator removal, may be diminished or exaggerated by changes in environmental conditions. For example, rising temperatures may increase metabolic rates, resulting in stronger interactions between herbivores and primary producers (O'Connor 2009). By extension, we may hypothesize that plant and algal biomass may be more strongly reduced in systems experiencing both predator removal and warming than in systems with either single disturbance. Thus, the identity, severity, and duration of disturbances may affect community composition and, in turn, interactions between species. Functionally redundant species may stabilize ecosystem processes after a disturbance; however, the ability of a species to become established, build biomass, and substitute for an extinct species may depend on community interactions and food-web stability. Shifts in community composition and species interactions may also affect the success of a species to reestablish following a disturbance. Consequently, the presence of functionally redundant species does not necessarily ensure that ecosystem functioning will be maintained after one or multiple disturbances.

The ability to predict how disturbances may affect the degree of functional redundancy within an ecosystem may be aided by studies on community composition in pre- and post-disturbance habitats. For example, experiments that simultaneously alter the degree of redundancy and the severity of the disturbance (e.g., drought versus wet conditions, warm versus cold, etc.) may be useful in predicting the survivorship and buffering capacity of redundant species (see Bestelmeyer and Wiens 1996; Kreyling et al. 2008). Such studies may be best served by employing designs using realistic combinations of species instead of random community assemblages (Loreau et al. 2001; Gross and Cardinale 2005; Larsen et al. 2005;

Ellingsen et al. 2007). In addition, comparative studies on community composition in extreme and moderate environments may be fruitful. Since the frequency and severity of extreme weather events are predicted to increase, comparing the occurrence of redundant species in moderate and extreme (i.e., end-point) environments may provide insight to environmental change. Combined, experimental and comparative studies may increase our understanding of the disturbance effects on functionally redundant species and ecosystem functioning.

Evolutionary relatedness—As the source of species traits and an influence on many of the interactions structuring communities, evolution plays an important role in ecosystem function and seems likely to be equally important in determining the degree of functional redundancy present. Across communities and ecosystems we observe similar functional roles being filled both by close relatives and very diverse species, which suggests that any relationship between evolutionary relatedness and redundancy is likely complex. At the same time, establishing a predictable relationship between evolutionary history and redundancy within a community or functional group would be particularly valuable because, in many cases, constructing phylogenies and estimating relatedness of the species may be easier than assessing functional rates and interaction strengths among all the species. Here we consider whether information about evolutionary history and relatedness can suggest whether species in a community are more or less likely to be redundant.

Close relatives are often expected to be ecologically similar (Webb 2000; Ackerly et al. 2006) due to conservatism in species traits (Webb 2000), but phylogenetic overdispersion, in which close relatives are less similar than more distant relatives, has also been observed (Cavender-Bares et al. 2004). The fundamental nature of the traits involved in several commonly measured ecosystem functions, e.g., primary productivity, nutrient cycling, and trophic level, may make these traits more likely to be conserved. This suggests that closely related species are likely to possess the functional traits enabling them to be redundant. However, redundant species must be capable of reacting to species loss by increasing their own rate of influence on ecosystem function, and thus must also be similar in the suite of traits affecting spatial and environmental niches and interspecific interactions. Predictions for whether closely related species will coexist in a community depend on how the community is assembled and whether traits are conserved or convergent (Cavender-Bares et al. 2004; Kraft et al. 2007). When traits are conserved, communities in which environmental filtering is most important, such as extreme environments, will tend to have species more closely related than by chance, whereas communities in which competitive exclusion limits ecological similarity will have more distantly related species (Webb et al. 2002; Kraft et al. 2007). When traits are convergent among clades the expectation is reversed, leading to phylogenetic overdispersion (Cavender-Bares et al. 2004). Alternatively, neutral models of assembly (Hubbell 2001)

should result in a random relationship between phylogenetic distance and the species in a community.

This context dependence is supported by empirical evidence for contrasting relationships between ecological similarity and evolutionary relatedness across communities (reviewed in Webb et al. 2002) and in different habitats within a rainforest (Kembel and Hubble 2006). The theory and data do support niche differentiation in adaptive radiation (Schluter 2000; Ackerly et al. 2006), which should lead to reduced redundancy among the radiating species due to niche specialization. So although the species may be complementary and all contributing to the same ecosystem service, the other species in the community are unlikely to be able to compensate for a loss or reduction of a given species. However, on evolutionary time scales, a new related species is likely to reclaim the niche. The dependency of predictions on specifics of individual communities and traits implies that simply estimating evolutionary relatedness alone may not facilitate prediction of the functional redundancy across communities or functional groups, but it may improve predictions when other information is also available. As more data on functional redundancy is collected, it will be useful to look at the correlation with phylogenetic relatedness across communities and functional groups.

Life History—Redundancy in ecosystem function following a perturbation, such as species loss, requires the remaining organisms to replace the lost function (Gitay et al. 1996). Assuming the existence of species physiologically capable of performing the function, this replacement of lost function can happen through some combination of three processes: increased rates by individuals already performing the function, increased abundance of individuals performing the function, performance of the function by previously uninvolved individuals or species. Which of these processes can occur and the likelihood that they will compensate for the lost species depends on the life history traits of the potentially redundant organisms.

Phenotypic plasticity is one way in which individuals can increase a functional rate or perform a "new" function. The existence of phenotypic plasticity in a functional group is most likely to allow for uninterrupted ecosystem functioning, because compensation can be immediate. An example is a plant species that is able to alter its foliar characteristics in response to the characteristics of co-occurring plants (Herault et al. 2008). A corollary of this idea is that generalists are more likely to be redundant because they can adjust their resource use in response to changes in community structure. The propensity of generalists to be redundant has led to conflicting predictions, with Johnson (2000) hypothesizing that the lower amount of energy available to higher trophic levels results in more generalists and higher redundancy. Conversely, Hooper et al. (2005) hypothesize that higher trophic levels will be less redundant simply because species richness is lower. Commonly cited examples of redundancy tend to occur in more species with rich functional groups of producers (e.g., rainforest trees, grasses), but these also seem to represent generalists, suggesting

that the link between generalism and redundancy at higher trophic levels needs to be assessed empirically.

While plasticity allows a specific function to be retained with potentially very little disruption, it should often result in a change away from another function for the individuals making the shift. Maintaining ecosystem function across the whole functional group depends on additional characteristics. If individuals can respond to disruption of community structure by increasing their average body size there is the potential for increased contribution to ecosystem function without an increase in population size. In this case redundant organisms with rapid somatic growth can maintain ecosystem function over short time periods, while slower-growing species will take longer to compensate for the lost function. If growth is limited by a factor other than the resources made available by the perturbation, redundancy is likely to be limited or extremely slow. For example, individuals may not be able to respond to increased nitrogen availability if light is a limiting factor, or to an increased food resource if predation limits body size.

Reproductive rates are likely to be a primary determinant of redundancy on time scales relevant to human activities and management. A potentially redundant species with a high population growth rate will be more likely to replace the functional role of the lost species in a short time period. Functional groups in which all members have low reproductive rates are likely to experience extended loss of ecosystem function, even if they possess phenotypic plasticity and high somatic growth rates, if the species lost from the system had a large biomass. It is likely that asexual species will be more redundant due to reproductive advantage of single-sex reproduction (Smith 1978) and because clones best suited to the environment are likely to be present already (e.g., Parejko and Dodson 1991). Over short time scales, population growth rate of sexual species at low density may be limited by an Allee effect due to male-female encounter rates (Courchamp et al. 2008). In plant communities the distinction between r- and K- selected species depends partly on reproductive rate (MacArthur and Wilson 1967), suggesting that K-selected species may be less redundant over relevant time scales unless individuals are already present and can grow quickly in response to an open niche.

Dispersal is also likely to be an important determinant of potential redundancy. High dispersal rates will allow redundant species to occupy open spatial niches or to enter the system from nearby communities. Species with low dispersal will take longer to arrive or spread from their current location. In cases in which the potentially redundant species has been excluded by a superior competitor, or in which species loss has resulted from environmental change, sufficiently high dispersal is necessary for redundant species to arrive from nearby habitats. While functional groups with high dispersal are likely to reach suitable habitats, which allows them to replace lost function, in some cases high dispersal may oppose the presence of functionally redundant species. For example, Hubbell's (2001) neutral theory relies on dispersal and recruit-ment limitation for ecologically equivalent species to coexist. If species have high dispersal and high reproductive rates a superior competitor is likely to exclude other species, reducing the potential pool of redundant species if that dominant species is perturbed.

The importance of growth, reproduction, and dispersal has been considered in the context of a specific aspect of redundancy: density compensation. Density compensation occurs when the total density or biomass of a community attains a level equal to that of the community prior to a loss of species (Gonzalez and Loreau 2009). In the case in which biomass is the ecosystem function of interest, density compensation means the extant species pool is functionally redundant, and in all cases the ability to reach original density or biomass is likely to be correlated with redundancy of most ecosystem functions.

PART TWO: Applications

Microbial functional redundancy in aquatic ecosystems—In previous sections, we discussed four axes or gradients along which we might predict variations in the degree of functional redundancy. If such a framework is useful, its predictive power would be particularly important for organisms whose individual functional roles in ecosystems are often difficult to determine. One such example is microbes, whose functional traits cannot be determined solely on the basis of morphology or phylogeny, and yet, microbes are often lumped into functional groups (e.g., denitrifiers, anaerobic, etc.). Allison and Martiny (2008) recently reviewed our current understanding of resistance, resilience, and redundancy in microbial communities. Only 9 of 79 studies considered in their quantitative review involved aquatic microbes, broadly defined to include river, lake, marine, benthic, and pelagic environments. This relative paucity of experimental data suggests there are fundamental obstacles to measuring redundancy in aquatic microbes. In this section, we apply the predictive framework outlined above to compare microbial communities between ecosystems and ask both whether a given functional group (i.e., denitrifiers) is more redundant in some environments than others as well as if some environments contain more functional redundancy than others.

Material transport: The microbial literature offers support to the hypothesis presented above that functional redundancy will be greatest at intermediate levels of incoming resources. Hewson and Fuhrman (2004) found in a study along an estuarine gradient that planktonic bacterial diversity followed a bell-shaped curve, with the greatest diversity at intermediate productivity. Some groups of freshwater bacteria (such as the Cytophaga-Flavobacteria) also appear to follow a similar bell-shaped curve, while others (such as the β-Proteobacteria) display no relationship with productivity (Horner-Devine et al. 2003). With respect to residence time, this important physical parameter is only rarely taken into consideration in aquatic microbial diversity studies. One exception is a study in the Plum Island Sound estuary (Crump et al. 2003) where a micro-

bial community unique to the estuary, distinct from the adjoining river and ocean communities, developed only when the residence time was greater than the bacterial doubling time. The links between these patterns in community structure and functional redundancy, however, remain unexplored.

Environmental variability: Our second predictor of redundancy is environmental variability, with the prediction that systems that experience an intermediate degree of environmental variability are more likely to have functionally redundant communities. To the extent that overall species richness is an indicator of functional redundancy, this prediction may hold true for aquatic microbes. To take the example of estuarine systems, the middle of the estuary experiences variations in salinity and temperature, while the river and ocean end-members are comparatively more stable. Studies of bacterioplankton richness in general (Crump et al. 1999) and functional groups such as denitrifiers (Santoro et al. 2006) have shown greater species richness at zones of mixing between fresh and salt water. However, the link between total species richness and functional richness is almost completely untested for microbial communities.

Acid mine drainage (AMD) biofilms are particularly well-studied systems that demonstrate that a low degree of environmental variability can lead to low functional redundancy in microbial communities. AMD biofilms have become a model system for developing methods in environmental genomics because their low complexity means that the genomes of every member of the community can be reconstructed (Tyson et al. 2004), unlike complex marine communities, which recover only a small fraction of the total community (Venter et al. 2004). Tyson et al. (2004) showed at the Richmond mine site in California, that the AMD community consists primarily (<95%) of two types of *Leptospirillum* and one Archaea. These investigators discovered that a key function of the community—nitrogen fixation—was carried out by only one of the members. In an essentially inorganic nitrogen-free environment such as the AMD system, one might have predicted that multiple community members would carry out this important function. This system appears to provide evidence that contradicts the prediction of Fonseca et al. (2001), who suggested that communities with fewer functional groups have more functional redundancy. In the model AMD community, it instead appears that in simple microbial communities with fewer functional groups, each member may carry out just one key function.

Despite the preceding examples that support a link between environmental variability and functional redundancy, aquatic environments that are seemingly stable over timescales of hundreds of years, such as the deep sea, harbor tremendous diversity (Sogin et al. 2006), thus the predictive power of environmental variability to predict redundancy between biomes may not apply to all system.

Evolutionary descent: We predicted that under phylogenetic overdispersion, ecosystems containing many closely related species may be less functionally redundant as niche specialization occurs. This is a prediction that is difficult to test with microbes. Genetic similarity in macroorganisms is much greater than in microorganisms; the chimp and human genomes share 95% identity (Britten 2002), while different *Escherichia coli* strains may share less than 40% protein identity (Welch et al. 2002) due to a high degree of lateral gene transfer among strains. As we gain a better understanding of how to separate out microbial species based on niches or ecotypes (Hunt et al. 2008), the relevancy of this prediction to microbial systems can be better assessed. Evolutionary history, to the extent that it is reflected in the phylogenetic tree of life, likely still offers predictive information on microbial functional redundancy. Functions that are distributed among broad taxonomic groups, such as heterotrophic carbon acquisition, are probably more functionally redundant (Bell et al. 2005) than those that are phylogenetically constrained, such as nitrogen metabolism (Balser and Firestone 2005).

Life history: We predicted that within ecosystems, organisms with high intrinsic growth rates and high dispersal rates have a high potential to be functionally redundant. When microorganisms are compared to macroorganisms in the same environment, they clearly have higher growth rates, which would lead to the prediction that microbial communities should be more functionally redundant than macroorganisms. However, if one wants to compare microbial communities from different environments, or compare different microbial functional groups in the same environment, the question is much more challenging due to the difficulty of determining in situ growth rates for specific organisms. If we rely solely on the cultured representatives of different functional groups, there is some evidence that functional groups with relatively rapid growth rates are more redundant. Looking specifically at the marine water column environment, relatively fast-growing phytoplankton serving the function of carbon fixation are much more redundant in terms of both species richness and total biomass than a slow-growing carbon-fixing group such as nitrifying bacteria, which may comprise as little as 0.1% of the bacterioplankton (Ward 2002).

Improving our understanding of functional redundancy in aquatic microbial communities: Microbial ecology has a long way to go before our understanding of functional redundancy in microbial communities approaches that of macroorganisms. Although the struggle to understand all the functions of microbial communities is worthwhile, it may be possible to move forward without understanding every functional group by defining functional groups very broadly. To do this, a consensus about what constitutes a functional group of microbes needs to be developed. For example, are all heterotrophic microorganisms equivalent, or should the oxidation of individual carbon compounds be considered a different function? Should we consider "nitrogen removal" a functional trait, or is process actually attributable to multiple functional traits of denitrification and anammox? Ducklow (2008) provides an

interesting start to this task by adapting the ecosystem service approach to microbial communities.

Increasing the use of functional genes to survey microbial communities instead of community fingerprinting approaches is essential to advancing our understanding of functional redundancy. It is unlikely that a macro ecologist would consider "trees" or "mammals" a functional group, yet the resolution of the community fingerprinting techniques used in many designs for experiments for testing microbial community composition probably makes an equivalent generalization. Investigation of functional genes targeting enzymes involved in key ecological functions such as dissimilatory sulfate reductase (*dsr*) or nitrite reductase (*nir*) are much more useful in understanding both functional richness and redundancy, as well as providing important tools with which to interpret the growing number of environmental genomic sequences.

Finally, although in microbial aquatic systems there may be more hurdles to conducting meaningful ecological experiments than in terrestrial systems, the reality is the experiments have simply not been done. Karl (2007) noted that the experimental phase of microbial oceanography has lagged behind other fields. Often, in the cases in which manipulative experiments have been conducted, their value for advancing our theoretical knowledge of concepts such as functional redundancy is lost because of differences in terminology between the applied and ecological research communities (Prosser and Head. 2007). Continued interaction among aquatic microbial ecologists and ecologists from other fields will help minimize these differences.

Redundancy and biological resistance to species invasion—Biological invasions are one of the greatest threats to global biodiversity (Wilcove et al. 1998). While their effects vary, invasive species have the potential to negatively affect populations, communities, and ecosystems of native species in aquatic environments (Parker et al. 1999; Grosholz 2002; Reise et al. 2006). Maintaining ecosystem functioning is vital to the effective management of aquatic ecosystems, yet accurate predictions of future invasions remain elusive. In this section, we examine how redundancy may influence the ability of aquatic communities to resist biological invasions (redundancy-invasion relationship), and then explore how three concepts discussed in Part One, which directly affect the success of species invasions, influence this relationship: material transport, disturbance and environmental variation, and biological interactions and niche specialization.

A long-standing idea in ecology is that species-rich communities are less susceptible to invasion than species-poor ones (Elton 1958). This "biotic resistance" hypothesis predicts that highly diverse communities will decrease the probability of success of new invaders due to a more complete use of resources, and have a greater likelihood of containing competitors or predators that can exclude potential invaders (Case 1990; Naeem et al. 2000; Shea and Chesson 2002; Stachowicz et al. 2002). Experimental and observational evidence for sup-

port of this theory has remained equivocal, despite a large amount of recent attention (reviewed in Levine and D'Antonio 1999; Herben et al. 2004; Fridley et al. 2007). Emerging from this debate is increasing interest in the functional roles that species or groups of species play in communities (e.g., Arenas et al. 2006; Britton-Simmons 2006). Because resource use is central to the "biotic resistance" hypothesis, the number and identity of functional groups within a community may dictate the level of resistance to invasion.

Using principles of niche theory, Shea and Chesson (2002) corroborated the link between high species diversity and biotic resistance to invasion, such that communities with high species richness reduce the number of resource or niche opportunities available, thus preventing invaders from becoming established or increasing in abundance. Consequently, increasing functional redundancy within communities would not only provide insurance against the loss of ecosystem function with the loss of species, but would also ensure that few niche opportunities or resources become available after disturbance or species loss, preventing new colonizers from becoming established (Elton 1958). Resource limitation has been found to limit the success of species invasions in aquatic environments, via direct reductions in resources, or through increases in native species diversity (and presumably redundancy) within a community, which alters the partitioning and consumption of available resources over time (Stachowicz et al. 1999, 2002; Clark and Johnston 2005; Romanuk and Kolasa 2005; Arenas et al. 2006; Stachowicz and Byrnes 2006). Thus, a better predictor of community resistance to invasion may not be solely the number of species in a community but may also involve the functional diversity and degree of functional redundancy among species.

The relationship between species functional redundancy and community resistance to invasion (the redundancy-invasion relationship) depends on the extent of ecologically similar species fulfilling the same functional role (ecological redundancy) and occupying the same spatial niches (functional redundancy) versus the level of complementarity (e.g., species each possessing a unique ecological function and occupying nonoverlapping spatial niches) among species at a given level of diversity. At one extreme, high complementarity but no ecological similarity among species (e.g., redundancy is zero) results in communities with low resistance to invasion (Fig. 4A). At the other extreme, high ecological similarity among species and no complementarity (e.g., functional redundancy is maximized) leads to communities with a very high resistance to invasion (Fig. 4B). Overall, this relationship predicts that loss of species or functional groups at lower levels of redundancy would have a greater impact on invasion resistance than an equivalent loss at higher levels of redundancy (Fig. 4). The nonlinear transition between the two endpoints of the redundancy-invasion relationship implies the existence of a critical minimum threshold in functional redundancy necessary to protect against species invasions. Identification of such
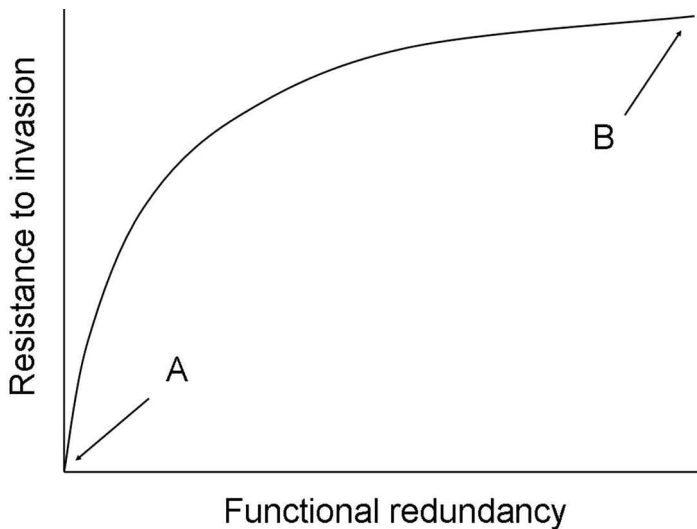
Fig. 4. Theoretical relationship between community resistance to invasion and functional redundancy, illustrating two endpoints of community functional organization: (A) high complementarity and no ecological similarity among species and (B) high ecological similarity and no complementarity among species.

a threshold would be context dependent, but could become a valuable tool for managers seeking to prevent invasions in aquatic ecosystems. For example, in nature most communities are likely never completely saturated with species (Lodge 1993; Gido and Brown 1999), never monopolizing all available resources or filling all available niches, and the loss of even a few species or an entire functional group would result in a rapid decline in community resistance to invasion. However, resistance to invasion may always be low, regardless of the level of functional redundancy, if many vacant niches are present within an ecosystem, which not only increases the probability of establishment of an invader, but also the opportunity to introduce a new functional role into the ecosystem.

Material transport: Any resource not used by a resident species provides an opportunity for a potential invader (Shea and Chesson 2002). As the degree of species redundancy within communities shifts along a gradient of resource abundance and availability, which would alter the fraction of resources and open niches within an ecosystem, biotic resistance to invasion would be expected to change correspondingly. The risk of species invasion would be greatest where the ecological consequences (to ecosystem functioning) of lost redundancy are highest (e.g., leaky ecosystems that receive low amounts of refractory materials; Fig. 2). In contrast, ecosystems with high residence times that receive a large amount of labile resources are more likely to harbor a diverse assemblage of redundant species. These ecosystems should be more resistant to species invasions because differences among functionally redundant species in their temporal pattern of resource use would result in a more consistent use of resources and limit available niches over time (Stachowicz et al. 2002; Romanuk

and Kolasa 2005; Stachowicz and Byrnes 2006). Given that resource use relates to many other ecosystem functions, promoting functional redundancy among species within a community would have important consequences not only for the control of invasive species, but also has the potential to enhance ecosystem productivity and community stability.

Disturbance and environmental variability: Disturbance is an important mechanism promoting the coexistence of particular species and maintaining species diversity within a community over time (the intermediate disturbance hypothesis: Connell 1978). However, disturbance can also facilitate species invasions through the release of resources (e.g., nutrients, light, space, etc), mediate interactions between native and invasive species, and/or alter the environment in ways that favor invaders (Elton 1958; Clark and Johnston 2005; Bando 2006). Ecosystems that experience either low or high levels of disturbance and environmental variability are characterized by low species diversity and redundancy (Fig. 3), resulting in the release of multiple resources and opened spatial niches following a disturbance event, facilitating the colonization and establishment of inferior competitors. In contrast, species that are functionally redundant may differ in their response to environmental variation, (the "insurance hypothesis"; see Disturbance and environmental variability section above), suggesting that high species redundancy within a community would ensure that at least one species could maintain its functioning and access to resources following a disturbance, maintaining some level of community resistance to invasion. Thus, we theorize that the greatest biotic resistance to invasion occurs at intermediate levels of disturbance, which promotes the highest species diversity and functional redundancy within a community (Fig. 3). Given these predictions, we suggest that the role of species redundancy should be considered carefully in the future management and conservation of aquatic communities to control the future spread of invasive species in systems that experience high rates of natural and anthropogenic change.

Biological interactions and niche specialization: The degree of redundancy in niche specialization within the native community is influential in determining the outcome of biological interactions and thus biotic resistance to invasion. The outcomes of biological interactions promoting biotic resistance to invasion would occur anytime a native species inhibited a potential invader's survival or growth rates, or under any combination of species in the native community that can keep resource and niche opportunities low (Shea and Chesson 2002). For example, the presence of strong predators (or grazers) that could directly attack or consume potential invaders would directly affect an invader's abundance, biomass, or mortality rate, while native species that are strong competitors could directly or indirectly decrease invader growth rates through competition for resources (Drake 1990; Baltz and Moyle 1993; Shurin 2000; Byers and Noonburg 2003; Bando 2006). Multiple specialists may be

more effective in controlling a specific resource than one generalist, but generalists may have broader niches, making them more readily able to alter their resource use, and more likely to be in a position to consume a potential invader once it is introduced (Shea and Chesson 2002; see also Evolution relatedness and Life history sections above). Functional redundancy within the native community would be expected to increase the strength of competition between functionally similar native and potential invaders (Bando 2006), which could inhibit invasion even for a superior competitor (Case 1990, 1991). In addition, given that species within a community vary in their competitive abilities and resource use, functional redundancy within the native community would also increase the probability that a potential invader would encounter a native competitor or predator once introduced, resulting in a higher resistance to invasion.

Based on these predictions, the ecosystems that should be most resistant to species invasions are expected to experience intermediate levels of disturbance, contain a small fraction of available resources or niche opportunities, and have few specialists and many generalists, as well as a high degree of functional redundancy within the native community. It is presently difficult to find examples of such ecosystems in the literature, given the paucity of current studies that have considered the role of functional redundancy in resisting species invasions, as well as the fact that failed invasions are rarely reported, potentially obscuring evidence of communities that have resisted invasion (Ricciardi 2001). In lieu of such evidence, we reexamined eight studies that explicitly tested the effects of species richness or functional diversity on biotic resistance to invasion in aquatic environments (marine: Stachowicz et al. 1999, 2002; Dunstan and Johnson 2004; Arenas et al. 2006; Britton-Simmons 2006; freshwater: Shurin 2000; Baltz and Moyle 1993; Romanuk and Kolasa 2005). By regrouping their measures of species richness or diversity into a measure of redundancy (approximated as the number of species per functional group; e.g., filter feeders versus grazers, canopy versus turf species, etc), we examined whether redundancy may be a better predictor of resistance to invasion. Although this reexamination is rather coarse and includes only a small number of available studies, the general trend that emerges demonstrates that systems that were successful in preventing species invasions exhibited higher redundancy (Fig. 5). Formal testing of the redundancy-invasion hypothesis may prove fruitful for the future control and management of invasive species and conservation of aquatic ecosystems.

Summary

In conclusion, contrary to the assertion by Gitay et al. (1996), it may be possible and quite feasible to conceptually apply the concept of redundancy in a predictive way. By reasoning how redundancy should change across environmental and biological gradients, we have posited predictions about
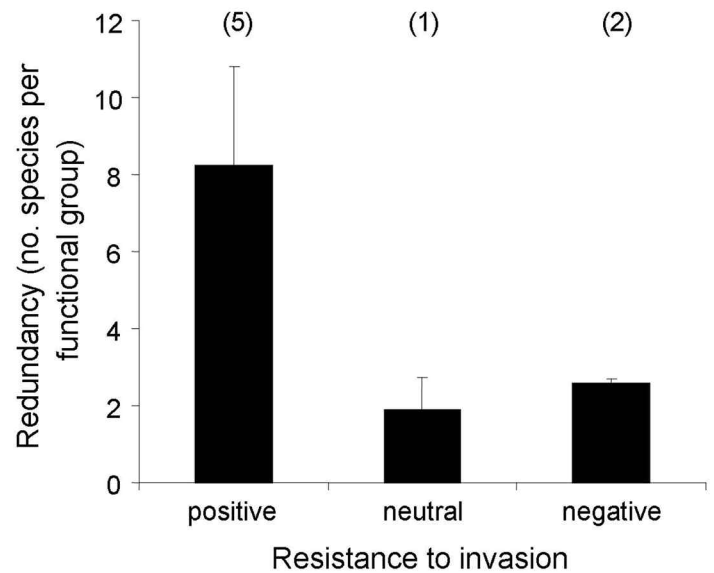

Fig. 5. Mean redundancy (number of species per functional group) (±SD) in experimental treatments in studies conducted in aquatic environments reporting a positive, neutral, or negative effect on resisting species invasions. Numbers above bars indicate the number of studies reporting that effect on invasion.

the importance of redundancy across broad-based ecological conditions. We emphasize that the gradients chosen for use here (environmental: material transport and disturbance; biological: life history and evolution) were chosen for illustrative purposes only, and other gradients may prove equally useful. Thus, our approach not only provides specific predictions about the importance of redundancy along these gradients, but provides an example of how this approach may be applied to other environmental or biological gradients. This approach appears promising, because our predictions were largely upheld when applied to microbial communities. Further tests of these hypotheses in other systems may also prove fruitful. In addition, we illustrated how these predictions can be extended to inform specific applied problems by extending them to predict the importance of species redundancy in prohibiting the establishment of invasive species. While these extended predictions appear to be supported based on the rough analysis given with the limited data available on species invasion and species redundancy (Fig. 5), much more data are needed to determine the role of redundancy in species invasion, as well as in other applied problems addressed by ecologists. In sum, species redundancy is a well-established and broadly relevant ecological concept. Elevating this concept to a predictive level could play an important role in tying conservation practices to ecological concepts more firmly.

References

Ackerly, D. D., D. W. Schwilk, and C. O. Webb. 2006. Niche evolution and adaptive radiation: testing the order of trait

divergence. Ecology 87:S50-S61 [doi:10.1890/0012-9658 (2006)87[50:NEAART]2.0.CO;2].

Allan, J. D. 1995. Stream ecology. Structure and function of running waters. Chapman and Hall.

Alley, T. R. 1982. Competition theory, evolution, and the concept of an ecological niche. Acta Biotheor. 31:165-179 [doi:10.1007/BF01857239].

Allison, S. D., and J. B. H. Martiny. 2008. Resistance, resilience, and redundancy in microbial communities. Proc. Natl. Acad. Sci. U.S.A. 105:11512-11519 [doi:10.1073/pnas.0801 925105].

Allison, G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. Ecol. Monogr. 74:117-134 [doi:10.1890/02-0681].

Arenas, F., I. Sanchez, S. J. Hawkins, and S. R. Jenkins. 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. Ecology 87:2851-2861 [doi:10.1890/0012-9658(2006)87[2851:TIOMAA]2.0.CO;2].

Balser, T.C., and M. K. Firestone. 2005. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. Biogeochemistry. 73:395-415 [doi:10.1007/s10533-004-0372-y].

Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecol. Appl. 3:246-255 [doi:10.2307/1941827].

Bando, K. J. 2006. The roles of competition and disturbance in a marine invasion. Biol. Invasions 8:755-763 [doi:10.1007/s10530-005-3543-4].

Bascompte, J., C. J. Melian, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. Proc. Natl. Acad. Sci. U.S.A. 102:5443-5447 [doi:10.1073/pnas.0501562102].

Bell, T., J. A. Newman, B. W. Silverman, S. L. Turner, and A. K. Lilley. 2005. The contribution of species richness and composition to bacterial services. Nature 436:1157-1160 [doi:10.1038/nature03891].

Bestelmeyer, B. T., and J. A. Wiens. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. Ecol. Appl. 6:1225-1240 [doi:10.2307/2269603].

Borrvall, C., B. Ebenman, and T. Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. Ecol. Lett. 3:131-136 [doi:10.1046/j.1461-0248.2000. 00130.x].

Bowman, D. 1994. Cry shame on all humanity. New Sci. 144:59-59.

Britten, R. J. 2002. Divergence between samples of chimpanzee and human DNA sequences is 5%, counting indels. Proc. Natl. Acad. Sci. U.S.A. 99:13633-13635 [doi:10.1073/pnas.172510699].

Britton-Simmons, K. H. 2006. Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. Oikos 113:395-401 [doi:10.1111/j.2006.0030-1299.14203.x].

Brown, J. H., S. K. M. Ernest, J. M. Parody, and J. P. Haskell. 2001. Regulation of species diversity: Maintenance of species richness in changing environments. Oecologia 126:321-332 [doi:10.1007/s004420000536].

Byers, J. E., E. G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasion. Ecology 84:1428-1433 [doi:10.1890/02-3131].

Case, T. J. 1991. Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. Biol. J. Linn. Soc. 42:239-266 [doi:10.1111/j.1095-8312.1991.tb00562.x].

———. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proc. Natl. Acad. Sci. U.S.A. 87:9610-9614 [doi:10.1073/pnas.87.24.9610].

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. Am. Nat. 163:823-843 [doi:10.1086/386375].

Cebrian, J. 2004. Role of first-order consumers in ecosystem carbon flow. Ecol. Lett. 7:232-240 [doi:10.1111/j.1461-0248.2004.00574.x].

Chapin, F. S., E. D. Schulze, and H. A. Mooney. 1992. Biodiversity and ecosystem processes. Trends Ecol. Evol. 7:107-108 [doi:10.1016/0169-5347(92)90141-W].

Clarke, K. R., and R. M. Warwick. 1998. Quantifying structural redundancy in ecological communities. Oecologia 113:278-289 [doi:10.1007/s004420050379].

Cole, L., M. A. Bradford, P. J. A. Shaw, and R. D. Bardgett. 2006. The abundance, richness and functional role of soil meso- and macrofauna in temperate grassland - a case study. Appl. Soil Ecol. 33:186-198 [doi:10.1016/j.apsoil.2005.11.003].

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310 [doi:10.1126/science.199. 4335.1302].

Courchamp, F., L. Berec, and J. C. Gascoigne. 2008. Allee effects in ecology and conservation. Oxford Univ. Press [doi:10.1093/acprof:oso/9780198570301.001.0001].

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems. BioScience 49:119-127 [doi:10.2307/1313537].

Cowling, R. M., P. J. Mustart, H. Laurie, and M. B. Richards. 1994. Species-diversity—functional diversity and functional redundancy in fynbos communities. S. Af. J. Sci. 90:333-337.

Cross, W.F., J.P. Benstead, A.D. Rosemond, and J.B. Wallace. 2003. Consumer-resource stoichiometry in detritus-based streams. Ecol. Let. 6:721-732 [doi:10.1046/j.1461-0248.2003.00481.x].

Crump, B. C., G. W. Kling, M. Bahr, and J. E. Hobbie. 2003. Bacterioplankton community shifts in an Arctic lake correlate with seasonal changes in organic matter source. Appl. Environ. Microbiol. 69:2253-2268 [doi:10.1128/AEM.69.4. 2253-2268.2003].

———, E. V. Armbrust, and J. A. Baross. 1999. Phylogenetic analysis of particle-attached and free-living bacterial com-

munities in the Columbia river, its estuary, and the adjacent coastal ocean. Appl. Environ. Microbiol. 65:3192-3204.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Ann. Rev. Ent. 18:183-206 [doi:10.1146/annurev.en.18.010173.001151].

Díaz, S., C. Marcelo, Z. Marcelo, M. C. Eduardo, and A. Julieta. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. J. Veg. Sci. 10:651-660.

Dodson, S. I., S. E. Arnott, and K. L. Cottingham. 2000. The relationship in lake communities between primary productivity and species richness. Ecology 81:2662-2679 [doi:10.1890/0012-9658(2000)081[2662:TRILCB]2.0.CO;2].

Drake, J. A. 1990. The mechanics of community assembly and succession. J. Theor. Biol. 147:213-233 [doi:10.1016/S0022-5193(05)80053-0].

Duarte, C. M. 2000. Marine biodiversity and ecosystem services: an elusive link. J. Exp. Mar. Biol. Ecol. 250:117-131 [doi:10.1016/S0022-0981(00)00194-5].

Ducklow, H. 2008. Microbial services: challenges for microbial ecologists in a changing world. Aquat. Microb. Ecol. 53:13-19 [doi:10.3354/ame01220].

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thebault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecol. Lett. 10:522-538 [doi:10.1111/j.1461-0248.2007.01037.x].

Dunstan, P. K., and C. R. Johnson. 2004. Invasion rates increase with species richness in a marine epibenthic community by two mechanisms Oecologia 138:285-292 [doi:10.1007/s00442-003-1400-7].

Ellingsen, K. E., J. E.Hewitt, and S. F. Thrush. 2007. Rare species, habitat diversity and functional redundancy in marine benthos. J. Sea Res. 58:291-301 [doi:10.1016/j.seares.2007.10.001].

Elton C. S. 1958. The ecology of invasions by plants and animals. Chapman Hall.

Fonseca, C. R., and G. Ganade. 2001. Species functional redundancy, random extinctions and the stability of ecosystems. J. Ecol. 89:118-125 [doi:10.1046/j.1365-2745.2001.00528.x].

Fridley, J. D., and others. 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3-17 [doi:10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2].

Gido, K. B., and J. H. Brown. 1999. Invasion of North American drainages by alien fish species. Freshw. Biol. 42:387-399 [doi:10.1046/j.1365-2427.1999.444490.x].

Gitay, H., J. B. Wilson, and W. G. Lee. 1996. Species redundancy: A redundant concept? J. Ecol. 84:121-124 [doi:10.2307/2261706].

Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant-communities—a null hypothesis and a field experimental approach. Am. J. Bot. 70:1098-1104 [doi:10.2307/2442821].

Gonzalez, A., and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. Ann. Rev. Ecol. Evol. Syst. 40:393-414 [doi:10.1146/annurev.ecolsys.39.110707.173349].

Greenstreet, S. P. R. 1996. Estimation of the daily consumption of food by fish in the North Sea in each quarter of the year. Scott. Fish. Res. Rep. 55:16.

Griffen, B. D., and J. E. Byers. 2006. Intraguild predation reduces redundancy of predator species in multiple predator assemblage. J. Anim. Ecol. 75:959-966 [doi:10.1111/j.1365-2656.2006.01115.x].

Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. Trends Ecol. Evol. 17:22-27 [doi:10.1016/S0169-5347(01)02358-8].

Gross, K., and B. J. Cardinale. 2005. The functional consequences of random vs. ordered species extinctions. Ecol. Lett. 8:409-418 [doi:10.1111/j.1461-0248.2005.00733.x].

Herault, B., A. Bornet, and M. Tremolieres. 2008. Redundancy and niche differentiation among the European invasive Elodea species. Biol. Invasions 10:1099-1107 [doi:10.1007/s10530-007-9187-9].

Herben, T. S., B. Mandak, K. Bimova, and Z. Munzbergova. 2004. Invasibility and species richness of a community: a neutral model and a survey of published data. Ecology 85:3223-3233 [doi:10.1890/03-0648].

Hewson, I., and J. A. Fuhrman. 2004. Richness and diversity of bacterioplankton species along an estuarine gradient in Moreton Bay, Australia. Appl. Environ. Microbiol. 70:3425-433 [doi:10.1128/AEM.70.6.3425-3433.2004].

Hooper, D. U, and others. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. 75:3-35 [doi:10.1890/04-0922].

Horner-Devine, M. C., M. A. Leibold, V. H. Smith, and B. J. M. Bohannan. 2003. Bacterial diversity patterns along a gradient of primary productivity. Ecol. Lett. 6:613-622 [doi:10.1046/j.1461-0248.2003.00472.x].

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton Univ. Press.

Hughes, R. A., J. E. Byrnes, D. L. Kimbro, and J. J. Stachowicz. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecol. Lett. 10:849-864 [doi:10.1111/j.1461-0248.2007.01075.x].

Hummel, S., G. H. Donovan, T. A. Spies, and M. A. Hemstrom. 2009. Conserving biodiversity using risk management: hoax or hope? Front. Ecol. Environ. 7:103-109 [doi:10.1890/070111].

Hunt, D. E., L. A. David, D. Gevers, S. P. Preheim, E. J. Alm, and M. F. Polz. 2008. Resource partitioning and sympatric differentiation among closely related bacterioplankton. Science 320:1081-1085 [doi:10.1126/science.1157890].

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113:81-101 [doi:10.1086/283366].

Inger, R. F., and R. K. Colwell. 1977. Organization of contigu-

ous communities of amphibians and reptiles in Thailand. Ecol. Monogr. 47:229-253 [doi:10.2307/1942516].

Ives, A. R., and J. B. Hughes. 2002. General relationships between species diversity and stability in competitive systems. Am. Nat. 159:388-395 [doi:10.1086/338994].

———, J. L. Klug, and K. Gross. 2000. Stability and species richness in complex communities. Ecol. Lett. 3:399-411 [doi:10.1046/j.1461-0248.2000.00144.x].

Johnson K. H. 2000. Trophic-dynamic considerations in relating species diversity to ecosystem resilience. Biol. Rev. 75:347-376 [doi:10.1017/S0006323100005508].

Karl, D. M. 2007. Microbial oceanography: paradigms, processes and promise. Nat. Rev. Microbiol. 5:759-769 [doi:10.1038/nrmicro1749].

Kembel, S. W., and S. P. Hubbell. 2006. The phylogenetic structure of a neotropical forest tree community. Ecology 87:S86-S99 [doi:10.1890/0012-9658(2006)87[86:TPSOAN]2.0.CO;2].

Kennedy, A. C., and K. L. Smith. 1995. Soil microbial diversity and the sustainability of agricultural soils. Plant Soil 170:75-86 [doi:10.1007/BF02183056].

Kraft, N. J. B., W. K. Cornwall, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. Am. Nat. 170:271-283 [doi:10.1086/519400].

Kremen, C., and R. S. Ostfeld. 2005. A call to ecologists: measuring, analyzing, and managing ecosystem services. Front. Ecol. Environ. 3:540-548 [doi:10.1890/1540-9295(2005)003[0540:ACTEMA]2.0.CO;2].

Kreyling, J., M. Wenigmann, C. Beierkuhnlein, and A. Jentsch. 2008. Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. Ecosystems 11:752-763 [doi:10.1007/s10021-008-9157-9].

Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol. Lett. 8:538-547 [doi:10.1111/j.1461-0248.2005.00749.x].

Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems, p. 255-270. In E. D. Schulze and H. A. Mooney, [eds]. Biodiversity and ecosystem function. Springer.

Legendre, L., and R. B. Rivkin. 2002. Pelagic food webs: Responses to environmental processes and effects on the environment. Ecol. Res. 17:143-149 [doi:10.1046/j.1440-1703.2002.00474.x].

Lennon, J. T., and L. E. Pfaff. 2005. Source and supply of terrestrial organic matter affects aquatic microbial metabolism. Aquat. Microb. Ecol. 39:107-119 [doi:10.3354/ame039107].

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15-26 [doi:10.2307/3546992].

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends Ecol. Evol. 8:133-137 [doi:10.1016/0169-5347(93) 90025-K].

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3-17 [doi:10.1034/j.1600-0706.2000.910101.x].

———. 2004. Does functional redundancy exist? Oikos 104:606-611 [doi:10.1111/j.0030-1299.2004.12685.x].

———, and others. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804-808 [doi:10.1126/science.1064088].

Macarthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press.

Micheli, F., and B. S. Halpern. 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8:391-400 [doi:10.1111/j.1461-0248.2005.00731.x].

Millennium. Ecosystem Assessment. 2003. Ecosystems and human well-being: a framework for assessment. Island Press.

Naeem, S., and J.P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecol. Let. 6:567-579 [doi:10.1046/j.1461-0248.2003.00471.x].

———, J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97-108 [doi:10.1034/j.1600-0706.2000.910108.x].

O'Connor, M. I. 2009. Warming strengthens an herbivore-plant interaction. Ecology 90:388-398 [doi:10.1890/08-0034.1].

Otto, S. B., E. L. Berlow, N. E. Rank, J. Smiley, and U. Brose. 2008. Predator diversity and identity drive interaction strength and trophic cascades in a food web. Ecology 89:134-144 [doi:10.1890/07-0066.1].

Padisak, J. 1993. The influence of different disturbance frequencies on the species richness, diversity and equitability of phytoplankton in shallow lakes. Hydrobiologia 249:135-156 [doi:10.1007/BF00008850].

Palumbi, S. R., K. L. McLeod, and D. Grunbaum. 2008. Ecosystems in action: Lessons from marine ecology about recovery, resistance, and reversibility. Bioscience 58:33-42 [doi:10.1641/B580108].

Parejko, K., and S. I. Dodson. 1991. The evolutionary ecology of an antipredator reaction norm: *Daphnia pulex* and *Chaoborus americanus*. Evolution 45:1665-1674 [doi:10.2307/2409787].

Parker, I. M., and others. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biol. Invasions 1:3-19 [doi:10.1023/A:1010034312781].

Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5:402-411 [doi:10.1046/j.1461-0248.2002.00339.x].

——— and ———. 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9:741-758 [doi:10.1111/j.1461-0248.2006.00924.x].

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a

review of concepts. Am. Nat. 100:33-46 [doi:10.1086/282398].

Poff, N. L., T. Wellnitz, and J. B. Monroe. 2003. Redundancy among three herbivorous insects across an experimental current velocity gradient. Oecologia 134:262-269.

Post, D. M., M. L. Pace, and N. G. Hairston. 2000. Ecosystem size determines food-chain length in lakes. Nature 405:1047-1049 [doi:10.1038/35016565].

Prosser, J. I., and I. M. Head. 2007. Microorganisms, macroorganisms and ecology. Fems Microbiol. Ecol. 62:133-134 [doi:10.1111/j.1574-6941.2007.00395.x].

Purvis, A., P. M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. Science 288:328-330 [doi:10.1126/science.288.5464.328].

Reise, K., S. Olenin, and D. W. Thieltges. 2006. Are aliens threatening European aquatic coastal ecosystems? Helg. Mar. Res. 60:77-83 [doi:10.1007/s10152-006-0024-9].

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Can. J. Fish. Aquat. Sci. 58:2513-2525 [doi:10.1139/cjfas-58-12-2513].

Rier, S. T., and R. J. Stevenson. 2002. Effects of light, dissolved organic carbon, and inorganic nutrients on the relationship between algae and heterotrophic bacteria in stream periphyton. Hydrobiologia 489:179-184 [doi:10.1023/A:1023284821485].

Romanuk, T. N., and J. Kolasa. 2005. Resource limitation, biodiversity, and competitive effects interact to determine the invasibility of rock pool microcosms. Biol. Invasions 7:711-722 [doi:10.1007/s10530-004-0997-8].

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. Oikos 98:156-162 [doi:10.1034/j.1600-0706.2002.980116.x].

Santoro, A. E., A. B. Boehm, and C. A. Francis. 2006. Denitrifier community composition along a nitrate and salinity gradient in a coastal aquifer. Appl. Environ. Microbiol. 72:2102-2109 [doi:10.1128/AEM.72.3.2102-2109.2006].

Scheffer, M., S. Carpenter, and B. D. Young. 2005. Cascading effects of overfishing marine systems. Trends Ecol. Evol. 20:579-581 [doi:10.1016/j.tree.2005.08.018].

Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. Oikos 57:25-41 [doi:10.2307/3565733].

Schluter, D. 2000. Ecological character displacement in adaptive radiation. Am. Nat. 156:S4-S16 [doi:10.1086/303412].

Schmid, B., and A.B. Pfisterer. 2003. Species vs. community perspectives in biodiversity experiments. Oikos. 100:620-621 [doi:10.1034/j.1600-0706.2003.12284.x].

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends Ecol. Evol. 17:170-176 [doi:10.1016/S0169-5347(02)02495-3].

Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecol-

ogy 81:3074-3086 [doi:10.1890/0012-9658(2000)081[3074:DLIRAT]2.0.CO;2].

Slik, J. W. F. 2004. El Nino droughts and their effects on tree species composition and diversity in tropical rain forests. Oecologia 141:114-120 [doi:10.1007/s00442-004-1635-y].

Smith, J.M. 1978. The evolution of sex. Cambridge Univ. Press.

Sogin, M.L., and others. 2006. Microbial diversity in the deep sea and the underexplored "rare biosphere". Proc. Nat. Acad. Sci. U.S.A. 103:12115-12120 [doi:10.1073/pnas.0605127103].

Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286:1577-1579 [doi:10.1126/science.286.5444.1577].

———, H. Fried, R. W. Osman, and R. B. Whitlatch. 2002. Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83:2575-2590 [doi:10.1890/0012-9658(2002)083[2575:BIRAME]2.0.CO;2].

———, J. F. Bruno, and J. E. Duffy. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Ann. Rev. Ecol. Evol. Syst. 38:739-766 [doi:10.1146/annurev.ecolsys.38.091206.095659].

———, and J. E. Byrnes. 2006. Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. Mar. Ecol. Prog. Ser. 311:251-262 [doi:10.3354/meps311251].

Tilman, D., 1986. A consumer-resource approach to community structure. Am. Zool. 26:5-22.

———, J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277:1300-1302 [doi:10.1126/science.277.5330.1300].

Tobor-Kaplon, M. A., J. Bloem, P. Romkens, and P. C. de Ruiter. 2005. Functional stability of microbial communities in contaminated soils. Oikos 111:119-129 [doi:10.1111/j.0030-1299.2005.13512.x].

Tyson, G. W., and others. 2004. Community structure and metabolism through reconstruction of microbial genomes from the environment. Nature 428:37-43 [doi:10.1038/nature02340].

Venter, J. C., and others. 2004. Environmental genome shotgun sequencing of the Sargasso Sea. Science 304:66-74 [doi:10.1126/science.1093857].

Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2:95-113 [doi:10.1007/s100219900062].

Walker, B. H. 1992. Biodiversity and ecological redundancy. Cons. Biol. 6:18-23 [doi:10.1046/j.1523-1739.1992.610018.x].

Ward, B.B. 2002. Nitrification in aquatic environments, p. 2144-2167. *In*: D.G. Capone [ed.], Encyclopedia of Envi-

ronmental Microbiology. Wiley and Sons.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. Am. Nat. 156:145-155 [doi:10.1086/303378].

———, D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Ann. Rev. Ecol. Syst. 33:475-505 [doi:10.1146/annurev.ecolsys.33.010802. 150448].

Welch, R. A., and others. 2002. Extensive mosaic structure revealed by the complete genome sequence of uropathogenic *Escherichia coli*. Proc. Natl. Acad. Sci. U.S.A. 99:17020-17024 [doi:10.1073/pnas.252529799].

West, N. E. 1993. Biodiversity of rangelands. J. Range Manag. 46:2-13 [doi:10.2307/4002440].

Wilcove D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience. 48:607-615 [doi:10.2307/131 3420].

Wilson, H. F., and M. A. Xenopoulos. 2009. Effects of agricultural land use on the composition of fluvial dissolved organic matter. Nat. Geosci. 2:37-41 [doi:10.1038/ngeo391].

Winemiller, K. O., and E. R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecol. Monogr. 60:27-55 [doi:10.2307/1943025].

Winfree, R., and C. Kremen. 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. Proc. R. Soc. B 276:229-237 [doi:10.1098/rspb. 2008.0709].

Wohl, D. L., S. Arora, and J. R. Gladstone. 2004. Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. Ecology 85:1534-1540 [doi:10.1890/03-3050].

Worm, B., and others. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787-790 [doi:10.1126/science.1132294].

Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc. Natl. Acad. Sci. U.S.A. 96:1463-1468 [doi:10.1073/pnas.96.4.1463].