Ecosystem Responses to Community Disassembly

Erika Zavaleta,[a] Jae Pasari,[a] Jonathan Moore,[b] Daniel Hernández,[a] K. Blake Suttle,[a] and Christopher C. Wilmers[a]

[a]*Environmental Studies Department, University of California, Santa Cruz, California, USA*

[b]*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California, USA*

Ecosystems around the world are experiencing unprecedented rates of extinction and species decline. The question of how community disassembly—the ongoing process of nonrandom species losses and declines—affects ecosystem functions, including those that influence persistence of other species, is addressed. The order in which species disappear from a community depends on their vulnerability to specific stressors and on traits associated with inherent susceptibility to decline. Information on species characteristics associated with vulnerability (response traits) is synthesized, and it is asked whether they are associated with characteristics that underpin significant contributions to ecosystem functioning (effect traits). Direct evidence that community disassembly affects ecosystem functioning comes from a variety of sources, ranging from documentation of long-term changes following the loss of an initial species or fragmentation of a landscape, to modeling and manipulative experiments that simulate species losses and observe their consequences. The usefulness to conservation and restoration practice of community disassembly as a concept is evaluated, and it is asked whether and how community disassembly can provide guidance about species loss order, its consequences, what each of these depends on, and whether a positive link exists between vulnerability and contribution to function—a link that would exacerbate the consequences of the ongoing extinction crisis.

***Key words*: community disassembly; extinction risk; vulnerability; species loss; biodiversity; ecosystem functioning; trophic cascades; functional traits**

Ecology has long recognized that the loss of biological diversity can compromise ecosystem functioning. Half a century ago, Charles Elton (1958) asserted, "The balance of relatively simple communities of plants and animals is more easily upset than that of richer ones" (p. 145), and nearly a century before him Darwin (1859) recognized more biodiverse grasslands as more productive than others. In more recent years, as species declines and losses accelerate worldwide, large literatures have emerged on the question of whether species losses are nonrandom with respect to traits or taxonomy, and the effects of diversity losses on ecosystem functioning (Loreau *et al.* 2002; Balvanera *et al.* 2006). However, ecologists have only begun to link these areas of inquiry (Schwartz *et al.* 2000; Hector *et al.* 2001; Lawler *et al.* 2001, Raffaelli 2004, Srivastava and Vellend 2005). A more comprehensive bridge between work on biodiversity–ecosystem functioning relationships and our understanding of ongoing and potential species losses could advance conservation science and practice by enhancing (1) understanding of how ongoing and future species losses affect ecosystem processes, including those linked to the persistence of other species, (2) ability to consider both species

---

Address for correspondence: Erika Zavaleta, Environmental Studies Department, University of California, 1156 High St., Santa Cruz, CA 95064. zavaleta@ucsc.edu

The Year in Ecology and Conservation Biology, 2009: Ann. N.Y. Acad. Sci. 1162: 311–333 (2009).
doi: 10.1111/j.1749-6632.2009.04448.x

vulnerability and species contributions to ecosystem processes as criteria for restoration and conservation priority setting, and (3) insight into whether and how species vulnerability and contributions to ecological processes are linked.

Not all species are equally likely to experience decline or extinction. Rapid biodiversity losses at both local and global scales disproportionately involve species with particular values of traits such as size, trophic position, rarity, distribution, and degree of specialization (Fox 1987; McDonald and Brown 1992; Belyea and Lancaster 1999; Lawler *et al.* 2001; Henle *et al.* 2004). The order of species declines and losses also depends on what specific drivers of biodiversity loss affect an assemblage, such as habitat destruction, eutrophication/nitrogen deposition, invasive species, climate change, and overharvesting (Chapin *et al.* 1997; Vitousek *et al.* 1997). This interaction of traits and drivers produces nonrandom species declines and losses, a phenomenon often referred to as community disassembly. Similarly, not all species are equally likely to contribute to ecosystem functioning or to affect it when they decline or disappear. *Ecosystem functioning* refers broadly to ecological processes, including levels and stability of productivity, nutrient cycling, invasion resistance, support for higher trophic levels, and so on, that depend on the contributions, abundances, and identities of species in an ecosystem (Chapin *et al.* 2000). From a conservation perspective, characteristic ecosystem functioning itself can be a target to restore or sustain or can serve as an integrative indicator of ecological condition. Alternatively, ecosystem functioning can enter conservation to the extent that it enhances the persistence or restoration of native biodiversity or particular species of concern. Many ecosystem functions are linked to, but not synonymous with, ecosystem services to society that are also increasingly the targets of conservation and restoration action (Chan *et al.* 2006). These ecosystem services range from food production and clean-water provision to climate regulation and soil stabilization (Hassan *et al.* 2005).

In this chapter, we address the question of how ongoing, non-random species losses and declines—community disassembly—affect and are likely to affect ecosystem functioning. We tackle this question in three parts: first, we ask how predictable disassembly is by synthesizing information on species characteristics associated with vulnerability to population decline or extirpation. Second, we review literature on species characteristics associated with significant contributions to ecosystem functioning. Finally, we review direct evidence that actual or simulated community disassembly affects ecosystem functioning. We evaluate the usefulness to conservation and restoration practice of community disassembly as a concept, like other concepts such as ecosystem, community, and habitat. We ask whether and how community disassembly can provide guidance or rules of thumb about the order of species loss, what are its consequences, what each of these depends on (such as taxonomic group, stressor, or ecosystem type), and whether a positive link exists between vulnerability and contribution to function, exacerbating the consequences of the ongoing extinction crisis.

What is Community Disassembly?

While the term *community disassembly* has been used to describe processes ranging from emigration (Buzas and Culver 1998) to local extinctions, ecologists have begun to focus the term on the process and consequences of species declines in native communities. For example, Mikkelson (1993) and Ostfield and LoGiudice (2003) use the phrase to refer to progressive species loss during habitat destruction/fragmentation. Others highlight the attrition of species interactions (Belyea and Lancaster 1999) and the associated loss of community structure as critical elements of disassembly (Sanders *et al.* 2003). Because declines in species abundance, richness, and interactions often depend critically on both species traits and environmental and anthropogenic stressors, many ecologists stress that community disassembly is a nonrandom process and that patterns or rules in the disassembly process may be discoverable (Belyea and Lancaster 1999; Lomolino and Perault 2000; Duffy 2002; Ostfeld and LoGiudice 2003).

Because the term *community disassembly* has been used in several ways, we propose the following working definition: Community disassembly is the nonrandom process of progressive species declines and losses. We emphasize that disassembly is a process of successive species losses, not a single event; and that these successive losses can reflect progressive habitat degradation or direct cascading responses to previous species losses. While previous disassembly studies have focused mainly on local species extinctions, we suggest that the disassembly process also includes species abundance declines and range contractions. Community disassembly drives a reshuffling of interaction webs (following Belyea and Lancaster 1999; Sanders *et al.* 2003); however, for clarity we treat these altered interaction webs as first-order consequences of disassembly, rather than as the process itself.

Disassembly can be applied to and observed at many scales, from an ecological "neighborhood" such as a single forest patch to an entire region, such as the Arctic or the northern Atlantic. However, it makes sense only as applied to systems that contain interactions (weak or strong) among the species that make up an assemblage—a "community," rather than, for instance, the global amphibian fauna. While we do not restrict its definition to losses driven by human activity, the disassembly concept is most relevant to conservation when used to understand the consequences of anthropogenic drivers. These include, most notably, direct harvest, habitat destruction, biological invasion, and climate and atmospheric changes, acting alone or in concert with other forces such as variable weather and extreme events. Just as disassembling a stereo will reduce its function as a music-producing entity, disassembling a community will likely produce progressive and nonlinear changes in ecosystem functioning (Gonzalez and Chaneton 2002; Solan *et al.* 2004; McIntyre *et al.* 2007).

Disassembly Rules

The literature on community disassembly asserts that it is not a random process, but rather follows "disassembly rules"—principles that govern the order of species loss (Belyea and Lancaster 1999; Duffy 2002; Ostfeld and LoGiudice 2003). Specifically, the sensitivity of a species to particular drivers or stresses is expected to be linked to characteristics (i.e., life-history traits) of that species, termed "response traits" (Hooper *et al.* 2005). For example, in fishes large body size is correlated to population decreases and extinction risk under pressure from harvest (Jennings *et al.* 1999a; Dulvey and Reynolds 2002; Reynolds *et al.* 2005a; Olden *et al.* 2007). These response traits may also be—or be associated with—"effect traits" (Hooper *et al.* 2005) that govern species effects on ecosystem structure and processes (e.g., Duffy 2003; Solan *et al.* 2004; Dobson *et al.* 2006; McIntyre *et al.* 2007), creating a relationship between disassembly and changes in ecosystem functioning.

To the degree that assembly and disassembly pathways are mirrors, the concept of disassembly can borrow from the well-developed community assembly literature (Fox 1987; Mikkelson 1993; Belyea and Lancaster 1999). However, communities are most likely not disassembled by retracing the pathway by which they were assembled (Saavedra *et al.* 2008), not least because disassembly is most often governed by anthropogenic drivers not in force at the time of assembly. Similarly, species susceptibilities to loss are likely different from their original probabilities of colonization during community assembly. We caution against using community assembly "rules" to extrapolate to probable species loss orders, especially when identifiable drivers of loss are involved.

Community disassembly is likely influenced by many factors. First, initial species loss may change the trajectory of disassembly, and small changes in the order of species loss may have large consequences for disassembly trajectories (Samuels and Drake 1997; Chase 2003). Loss of a keystone species can cause cascading extinction (e.g., Paine 1966; Thébault *et al.* 2007; Petchey *et al.* 2008), loss of a dominant ecosystem engineer can change biogenic habitat (Hastings *et al.* 2007), and loss of a strong competitor can allow for compensatory dynamics by opening up resources (e.g., Tilman 1996). Second, patterns of community disassembly likely depend on the driver or combination of drivers involved. Different drivers determine which species traits influence susceptibility (Olden *et al.* 2007), which would in turn control the order of species loss. Third, the rate of disassembly will likely be a key factor in influencing dynamics. Rapid disassembly may not allow time for compensatory dynamics to be important. Slow disassembly may allow for more evolutionary dynamics to influence outcomes (Fox 1987). Fourth, environmental conditions will provide the abiotic context for disassembly. Finally, contingency likely plays a strong role in trajectories of community disassembly. Chance events, especially for small population sizes, can determine whether species go extinct or not.

Thus, the concept of disassembly "rules" suggests that the order of species loss is predictable, but in practice it will vary as a function of ecosystem type, taxonomic group, driver, and environmental and geographic context. The question, then, is whether disassembly rules are useful for conservation—useful for guiding prioritization of species or sites to protect, stresses and drivers to alleviate, and ecosystem functions and services to actively restore or replace.

What Makes Species Vulnerable?

Certain types of species seem to disappear early in the face of human impacts. For example, large, mobile top predators, such as grizzly bears in the continental United States and tigers in Asia, are often early victims of human settlement, hunting, and land use. How consistent are these patterns of disassembly, what do they depend on, and how do they extend to other types of species in other taxonomic groups and ecosystem types? Mountain lions, also large, mobile top predators, are thriving in many areas that lost bears and wolves long ago. Another widely recognized "rule" is that rare and restricted species (which also make up most of the biotic diversity in most ecosystems) are more vulnerable than common dominants (Smith and Knapp 2003). Many examples support this pattern, yet superabundant, widespread, relatively generalist species such as the passenger pigeon (*Ectopistes migratorius*) and American bison (*Bison bison*) have also gone rapidly extinct or nearly so when faced with particular drivers. Differences in behavior or life history traits could explain these disparities. Alternatively, they could be products of chance or historical events that would not be predicted based on ecological principles.

A sizable literature explores the relationship between species vulnerability and biological factors (O'Grady *et al.* 2004) (Table 1). At a minimum, to identify consistent patterns in species vulnerability usually requires information about both intrinsic (species or population trait) and extrinsic (threat-linked) factors (Tracy and George 1992; Beissinger 2000; Blackburn and Gaston 2002; Owens ad Bennett 2000; Gage *et al.* 2004; Purvis *et al.* 2005; Feeley *et al.* 2007; Freville *et al.* 2007). Andrew Purvis and colleagues (2005) conceptualize extinction risk as a function of intrinsic species susceptibility, extrinsic threat, and the interaction between these two:

$$\begin{aligned}\text{Risk} = {} & \text{Susceptibility} + \text{Threat}\\ & + (\text{Susceptibility} \times \text{Threat}).\end{aligned}$$

They point out that the interaction term is likely to be much larger than intrinsic susceptibility in the absence of threat (since background extinction rates are quite low). However, we argue that susceptibility is best viewed as general susceptibility—not in the absence of threat, but to any type of threat. From this perspective, a species can be vulnerable from a trait-based perspective in at least three ways, which correspond in order to the three terms in the equation of Purvis and colleagues:

1. General or inherent susceptibility, such as life-history traits that make population recovery slow or a small distribution that is inherently vulnerable to chance events that would cause extinction.
2. Association with habitat or areas that are sensitive to or targeted by a particular threat. For instance, regardless of life-history traits, species endemic to a river experiencing heavy pollution or a forest region experiencing widespread clearing are generally at greater risk than others.
3. Traits that increase vulnerability to specific drivers, such as possession of valued fur or meat stores by bison or bears. These traits do not in and of themselves increase extinction risk, but when paired with a specific driver they do.

A species can experience more than one of these types of vulnerability at once, as do sperm whales with both inherent susceptibility (slow reproductive rates) and fat and meat stores that make them the targets of direct exploitation. For species with high inherent susceptibility, information about threats might not be necessary to conclude that they are vulnerable in general.

Some factors emerge consistently as correlates of greater species vulnerability to local, regional, or global extinction or decline (Table 1). Most notably, large body size is associated with increased vulnerability in at least one study each of reptiles, amphibians, birds, mammals, and freshwater and marine fishes. Small geographic range size, including narrow elevational range, latitudinal range, or habitat specificity, is associated with higher vulnerability in at least some assemblages of amphibians, reptiles, birds, mammals, marine fishes, plants, and prehistoric invertebrates. Not surprisingly, distributional overlap with specific threats has also been linked to increased vulnerability in frogs, reptiles, birds, mollusks, and plants—and with analysis, would probably emerge as a factor for other taxa. Low population abundance or density increases the vulnerability of at least reptiles, birds, plants, and larger (>3 kg) mammals. A suite of demographic traits related to slow population-growth rates, including slow reproductive rates, is also linked to greater vulnerability among at least amphibians, plants, marine fishes, and mammals >3 kg.

The roles of certain factors in influencing vulnerability appear to depend on taxon or context. Although large body size predisposes many taxonomic groups to extinction risk, plants are a notable exception—and are more vulnerable when smaller in size (Leach and Givnish 1996; Turner *et al.* 1996; Duncan and Young 2000). The effect of body size can be threat dependent: small size makes marine and freshwater fishes more vulnerable to habitat loss or degradation, but less vulnerable to the effects of direct harvest (Olden *et al.* 2007). At very low population sizes (<7–10 breeding pairs), there is some evidence that large body size confers increased individual resilience and reduces vulnerability in birds (Pimm *et al.* 1988; Owens and Bennett 2000). Long life span also has taxon-dependent effects, increasing vulnerability of marine fishes to direct harvest, but reducing vulnerability of mammals, plants, and perhaps invertebrates (Pimm *et al.* 1988; Turner *et al.* 1996; Dulvy *et al.* 2003; Reynolds *et al.* 2005a; Bossuyt and Honnay 2006; Morris *et al.* 2008). And while plants in species-rich lineages appear more vulnerable, birds in species-poor lineages are at greater risk, possibly because of correlation with smaller range size in the latter case (Bennett and Owens 1997; Russell *et al.* 1998; Schwartz and Simberloff 2001). Results of different studies directly conflict in just one case we could find: both monoecious and dioecious reproduction have been linked to greater vulnerability in plants by different studies based in different regions (Sakai

TABLE 1. Factors Associated with Species Vulnerability[a]

Category	Factor	Type	Taxon	Sources	Notes
Distribution	Small geographic range size	S	Frogs	Cooper *et al.* 2008	But Feeley *et al.* 2007 also found positive relationship with large range size in some cases.
			Birds	Diamond 1984; Blackburn and Gaston 2002; Keane *et al.* 2005; Feeley *et al.* 2007; Jetz *et al.* 2007	Prehistoric (Jurassic, Triassic); selectivity diminished during Triassic mass extinction
			Invertebrates	Kiessling and Aberhan 2007	Both endemism to Hawaii, habitat size
			Mammals > 3 kg	Cardillo *et al.* 2005	
			Plants	Sakai *et al.* 2002	
	Narrow latitudinal range	S	Marine fishes	Reynolds *et al.* 2005	But see Dulvy and Reynolds 2002: skates do not fit this pattern.
	Small elevational range	S	Amphibians	Lips *et al.* 2003	
	High habitat specificity	S	Reptiles	Foufopoulos and Ives 1999	
			Birds	Owens and Bennett 2000; Feeley *et al.* 2007; Jiguet *et al.* 2007	
	Distribution overlap with specific threats	T	Frogs	Murray and Hose 2005	Vulnerable to projected land-use change
			Elapid snakes	Reed and Shine 2002	New Zealand
			Tropical endemic birds	Jetz *et al.* 2007	Australian grassland
			Gastropod mollusks	Carlton 1993	
			Plants	Duncan and Young 2000 Williams *et al.* 2005	
	Island-breeding, burrow-nesting	S × T	Seabirds	Jones *et al.* 2008	Vulnerable to exotic predators

Continued

TABLE 1. *Continued*

Category	Factor	Type	Taxon	Sources	Notes
Demographic	Low population abundance	S	Reptiles	Foufopoulos and Ives 1993	Correlated with large size
			Plants	Duncan and Young 2000	Low abundance and small distribution not distinguished.
				Williams *et al.* 2005	Measured as percent of sample plots containing sp.
	Low population density	S	Birds	Diamond 1984; Pimm *et al.* 1988; Bolger *et al.* 1991; Tracy and George 1992; Feeley *et al.* 2007	Vulnerable to demographic, environmental stochasticity
			Mammals > 3 kg	Cardillo *et al.* 2005	
	Variable population density	S	Birds	Pimm *et al.* 1988	But see Tracy and George 1992
	Small clutch size	S	Amphibians	Hero *et al.* 2005	Through correlation with small range
			Frogs	Cooper *et al.* 2008	Not significant in one study of Australian endemic frogs (Murray and Hose 2005)
	Short life span	S × T, S	Mammals	Pimm *et al.* 1988	
			Plants	Turner *et al.* 1996; Bossuyt and Honnay 2006	Based on models estimating time to extinction. Sampling bias may play a role
			Insects, plants	Morris *et al.* 2008	Increases vital rate variability; vulnerable to climate variability; qualitative.
	Long life span	S	Marine fishes	Reynolds *et al.* 2005a; Dulvy *et al.* 2003	Focused on vulnerability to fishing
	Late maturation	S	Marine fishes	Jennings *et al.* 1998; Reynolds *et al.* 2005a	Focused on vulnerability to fishing
	Late weaning age	S	Mammals > 3 kg	Cardillo *et al.* 2005	
	Long gestation	S	Mammals > 3 kg	Cardillo *et al.* 2005	
	Slow reproductive rate	S	Mammals	Johnson 2002	Pleistocene
	Low population growth rate	S	Marine fishes	Jennings *et al.* 1998	Focused on vulnerability to fishing
			Plants	Bossuyt and Honnay 2006	European coastal dunes
	Low r (instrinsic rate of increase)	S	Mammals	Pimm *et al.* 1988	Based on models estimating time to extinction

Continued

TABLE 1. *Continued*

Category	Factor	Type	Taxon	Sources	Notes
Phenotype	Large body size	S, S × T	Frogs	Cooper *et al.* 2008	Through correlation with small range
			Amphibians	Lips *et al.* 2003	Through correlation with low abundance
			Reptiles	Foufopoulos and Ives 1993	Through higher risk of human predation
			Elapid snakes	Reed and Shine 2002	When population is >7–10 pairs.. Often correlated with low fecundity, long generation time.
			Birds	Pimm *et al.* 1988; Bennett and Owens 1997; Owens and Bennett 2000; Duncan *et al.* 2002; Keane *et al.* 2005; Feeley *et al.* 2007.	Increases vulnerability to predation, direct exploitation. But see Tracy & George 1992; Cook and Hanski 1995.
			Marine fishes	Jennings *et al.* 1998, 1999b; Reynolds *et al.* 2005a; Dulvy and Reynolds 2002	Increases vulnerability to harvest, pollution. In skates, correlates with late maturation
			Freshwater fishes	Olden *et al.* 2007	Increases vulnerability to harvest
			Mammals	Cardillo and Bronham 2001	Pleistocene; but see Johnson 2002: no effect
	Small body size	S × T	Birds	Pimm *et al.* 1988; Owens and Bennett 2000.	When population is <7–10 pairs,. but see Tracy and George 1992.
			Freshwater fishes	Olden *et al.* 2007	Increases vulnerability to habitat loss/change, invasive species, pollution
			Marine fishes	Olden *et al.* 2007	Increases vulnerability to habitat loss/change
			Plants	Duncan and Young 2000; Leach and Givnish 1996	Short vs. tall species at greater risk
				Turner *et al.* 1996	Shrubs, climbers at greater risk than trees
	Small seed size	S	Plants	Leach and Givnish 1996	Wisconsin prairie
				Williams *et al.* 2005	Australian grassland
	Attractiveness to hunters	S × T	Birds	Duncan *et al.* 2002; Keane *et al.* 2005	Independent of habitat use, body mass, taxa; especially in prehistoric times
	Low individual growth rate	S	Plants	Bossuyt and Honnay 2006	Coastal dunes
	Low thermal maxima	S ×T	Birds	Jiguet *et al.* 2007	Vulnerable to climate change
	Large testes size	S	Birds	Morrow and Pitcher 2003	Higher postmating sperm competition

Continued

TABLE 1. *Continued*

Category	Factor	Type	Taxon	Sources	Notes
Life history	Wet/aquatic habitat	S × T	Frogs	Hero *et al.* 2005	E. Australia; development in aquatic vs. terrestrial habitats, especially in ephemeral pools/ponds
			Plants	Lips *et al.* 2003	Lifetime aquatic index; driver-specific
				Walker and Preston 2006; Sakai *et al.* 2002	England Hawaii
	Reliance on stress-tolerant host plant vs. ruderal or competitive host plant	S	Butterflies	Dennis *et al.* 2004	Stress-tolerant host-plant dependence linked to (and inferred as cause of) long development time, fewer broods, lower mobility, monophagy, small geographical range, low population density
	Sensitivity to specific threats	T	Herps	Lehtinen *et al.* 2003	Edges
	Habitat overlap with specific threats	T, S × T	Beetles	Driscoll and Weir 2005	Flightless and subterranean beetles more susceptible to agricultural conversion
	Feeding strategy	S	Elapid snakes	Reed and Shine 2002	Strategy associated with cluster of life-history traits limiting population resilience
	Diurnal	S × T	Mammals	Johnson 2002	Pleistocene
	Nonarboreal	S × T	Mammals	Johnson 2002	Pleistocene
	Low natal dispersal distance	S × T	Birds	Jiguet *et al.* 2007	Vulnerable to climate change
					No effect in plants (Walker and Preston 2006)
	Migratory	S	Birds	Pimm *et al.* 1988	May be associated with higher population variability, but see Tracy and George 1992
	Specialist diet	S × T	Pollinating insects	Memmott *et al.* 2007	Predicted to be more vulnerable to climate change

Continued

TABLE 1. *Continued*

Category	Factor	Type	Taxon	Sources	Notes
	Sexual reproduction	S	Plants	Williams *et al.* 2005	Australian grassland
	Dioecious with showy flowers	S	Plants	Vamosi and Otto 2002	But see Walker and Preston 2006 no effect in English flora
	Monoecious	S	Plants	Sodhi *et al.* 2008 Sakai *et al.* 2002	Tropical angiosperms Hawaii only
	Epiphytic	S, ?S × T	Plants	Sodhi *et al.* 2008 Turner *et al.* 1996	Tropical angiosperms
	Mammal-pollinated	S	Plants	Sodhi *et al.* 2008	Tropical angiosperms
	Shade tolerance (shrubs, rattans)	S, ?S × T	Plants	Turner *et al.* 1996	Tropics
	Nitrogen-fixing	S	Plants	Leach and Givnish 1996	Prairie
Taxonomic	In a species-poor genus/lineage	S	Birds	Bennett and Owens 1997; Russell *et al.* 1998	Often correlated with small range size
	In a species-rich lineage	S	Vascular plants	Schwartz and Simberloff 2001	But see Sakai *et al.* 2002 no such relationship for Hawaiian plants
	Clustered taxonomically	S, S × T	Amphibians	Bielby *et al.* 2006; Hero *et al.* 2005	
	Dicots vs. monocots	S	Plants	Duncan and Young 2000	New Zealand
Evolutionary history	No evolutionary experience with stressor	S × T, T	Birds, others	Balmford 1996	

[a] Grouped into those categories associated with species distribution, demography, phenotype (individual physical characteristics), life history, taxonomic features, and evolutionary history. Factor types S = inherent susceptibility; T = threat-associated, extrinsic vulnerability; S × T = vulnerability arising from interactions between extrinsic threats and species susceptibility. See text for details.

et al. 2002; Vamosi and Otto 2002; Sodhi *et al.* 2008).

In addition to the direct evidence of worldwide species decline and loss patterns, dozens of nested subset analyses have investigated the degree to which patterns of species losses are ordered. A group of species assemblages or communities is nested to the degree that less species-rich assemblages are composed only of subsets of more species-rich assemblages (Wright *et al.* 1998). For example, a series of mountaintop islands of varying size in the Great Basin contain a strongly nested set of small mammal assemblages, with species disappearing largely in a particular order from the largest to the smallest islands (Patterson and Atmar 1986). A review of 279 species presence/absence data sets across taxa concluded that nestedness was common. Moreover, it appeared to be generated most often by patterns of species losses following fragmentation, such as through isolation of land-bridge islands from a mainland, and least often by assembly processes such as immigration (Wright *et al.* 1998). This suggests that not only are nested patterns common in nature, but also that they are a product of a disassembly process.

Nested subset patterns are seldom perfect and reflect only presence and absence rather than relative abundances. The declines or losses of some species that occur in response to fragmentation, for example, can be accompanied by increases in the abundance of other, ruderal or stress-tolerant species (e.g., Lomolino and Perault 2000). Thus, the ecosystem consequences of community disassembly can reflect both losses of vulnerable species' functional roles and associated increases in the functional roles of tolerant species.

What Makes Species Functionally Important?

Species losses can have widely varying effects on ecosystem functioning. Individual species make a range of magnitudes and types of contributions to diverse functions. Some species appear to have little effect on ecosystem processes, while others have wide-ranging roles in regulating and maintaining the character of an ecosystem (Estes and Duggins 1995; Terborgh *et al.* 2001; Simberloff 2003; Hooper *et al.* 2005). Losses of the latter species can change biotic and abiotic conditions such as trophic patterns and dynamics, disturbance regimes, and rates of nutrient cycling in ways that affect many or all other species in the community (Chapin *et al.* 1997).

The large influence on ecosystem functioning of certain types of species, such as dominants and keystones, has been well documented. These species are often the focus of management efforts emphasizing the restoration or maintenance of ecosystem functioning or character. However, comprehensively identifying functionally important species in a community can be difficult. Sometimes the functional role of a species varies widely in different times and places, or the species may periodically provide critical redundancy when another species dips in abundance (Walker *et al.* 1999; Gunderson and Holling 2002; Luck *et al.* 2003). Sometimes the fundamental role of a species is not apparent until the species is removed (Zavaleta *et al.* 2001). Attributes such as functional uniqueness, the ability to alter abiotic conditions, and strong interactions with dominants can also confer functional importance and may be overlooked in conservation efforts. Finally, functional importance can depend on how many and what functions one defines as important. While evidence of a strong role in maintaining ecosystem processes or character can identify a species as functionally important, the absence of such evidence does not necessarily confirm a species as functionally unimportant.

Certain kinds of species play a consistent strong role in ecosystem functioning. Dominant or foundation species (Dayton 1975), through sheer numbers or biomass, generally play a central role in the regulation of ecosystem dynamics (Paine and Suchanek 1983; Wardle *et al.*

1997; Smith and Knapp 2003; Ellison *et al.* 2005). Dominant species are not commonly lost from communities, but they can decline in extent or disappear, as did the American chestnut from eastern deciduous forests when an exotic blight reached the United States (Paillet 2002). While it may seem intuitive that the loss of dominant and extremely abundant species such as the American chestnut and the passenger pigeon would have strong effects on ecosystem function, the empirical evidence for this is usually anecdotal and unclear (Simberloff 2003). It is also possible for one species loss to trigger a decline in another, dominant species: the loss of giant tortoises from the Mascarene Islands led to declines of a tortoise-dependent tree, the Ile aux Aigrettes ebony (*Diospyros egrettarum*) (Zavaleta *et al.* 2001). In this sense, species that interact strongly with dominants also play important roles in ecosystem functioning. Clark's nutcracker, (*Nucifraga columbiana*) maintains whitebark pine (*Pinus albicaulis*) regeneration in high-elevation western U.S. forests, which in turn support populations of grizzly bears (*Ursus arctos horribilis)* (Hutchins and Lanner 1982). In tallgrass prairie communities, mycorrhizal fungi facilitate the dominance of certain grasses over other species (Hartnett and Wilson 1999).

Dominants commonly affect ecosystem functioning by shaping and altering the abiotic environment (Stachowicz 2001). Minor species with strong effects on the abiotic environment are also often functionally important. These can include species that alter resource availability, such as nitrogen-fixing plants (Chapin *et al.* 1997); species that alter disturbance regimes, such as highly flammable species (Bond and Keeley 2005); and ecosystem engineers that shape the physical environment, such as gophers in California grasslands (Hobbs and Mooney 1995). The functional effects of these types of species are context dependent—nitrogen fixers might play pivotal roles in low-nutrient ecosystems without other nitrogen-fixing species, but might otherwise play less key functional roles.

Keystone species by definition have disproportionately large effects on ecosystem functioning given relatively low abundances (Mills *et al.* 1993; Power *et al.* 1996) and may be more vulnerable to extirpation than dominants (Miller *et al.* 1994; Ripple and Beschta 2003). Keystones generally play unique ecological functions, such as unique trophic roles (e.g., sea otters, Estes *et al.* 1998) or roles in structuring the physical environment (e.g., beavers, Bridgham *et al* 1995). Loss of a keystone can be expected to have far-reaching functional effects. More generally, losses in general of functionally unique species are likely to affect ecosystem processes due to the absence of other species that can fill their roles (Walker 1995; Tilman *et al.* 1997). Moreover, certain kinds of functional specialists are often particularly sensitive to environmental perturbations, such as specialist pollinators dependent on consistent availability of a host plant species (Thompson 1998; Memmott *et al.* 2007).

Are Vulnerability and Functioning Associated?

The extent to which community disassembly affects ecosystem processes depends on the correlation between species' vulnerability (response traits) and importance to ecosystem functioning (effect traits). This relationship has not been directly studied to much extent. Models of the link between response and effect traits in the marine benthos suggest, unsurprisingly, that function will decline precipitously when important species are highly vulnerable (in this case, due to body size), but will decline much more slowly when the traits of important species make them more tolerant of stresses (Solan *et al.* 2004). Furthermore, community compensation for the lost functions of important species can only occur if the remaining species have the capacity to increase their functionality and the tolerance to avoid stress (Solan *et al.* 2004). Limited, direct empirical evidence also suggests that large body size is correlated with both function and vulnerability. For example, the large size of *Dialium guianense*, a tropical Mexican tree responsible for the majority of carbon storage in some forests, makes it more vulnerable to extraction through ongoing forestry intensification (Balvanera *et al.* 2005). Likewise, body size appears to be linked to both function and vulnerability to land-use change among bee and dung beetle populations (Larsen *et al.* 2005).

This direct evidence is bolstered by the evidence that large body size corresponds to increased extinction risk in a range of taxa and that large size is often associated with unique functional roles, from trophic position to effects on nutrient cycling (Taylor *et al.* 2006). Other traits that emerge as potentially linked to both vulnerability and ecosystem functioning include nitrogen fixation in plants and host specialization in insects (Table 1). Emerging evidence thus indicates that vulnerability and contribution to functioning can be correlated. More detailed studies of the relationship between response and effect traits within particular assemblages could test the extent of positive correlation between vulnerability and importance to functioning.

Ecosystem Effects of Community Disassembly

Although the evolutionary consequences of nonrandom biodiversity loss have been explored recently (Purvis *et al.* 2000), our understanding of the functional consequences of nonrandom biodiversity loss is largely limited to studies of declines in individual species (Blockstein 1998; Estes *et al.* 1998). These studies focus mainly on keystone species or on species that were once widespread and abundant (Simberloff 2003). However, most species in ecosystems—and most at-risk species—are relatively uncommon and exert what influence they have on ecosystem functioning in relatively small numbers (Magurran 1988). Experimental studies have begun to address the latter category of species losses and declines, complementing observational studies.

Many of the ecosystems that twenty-first century ecologists observe have already been partly disassembled. In many documented cases, the species that have noticeably declined or disappeared are top predators and/or large-bodied animals. The functional consequences of these losses vary widely from top-down trophic cascades to altered ecosystem biogeochemistry, involve many taxa, and affect both marine and terrestrial ecosystems (Box 1). In the aggregate, these examples show that documented losses of top predators and large-bodied animals generally produce significant ecosystem consequences. Of course, losses of other species might go unnoticed, either because they do not produce noticeable consequences or because the species themselves are less visible than large predators. It is therefore difficult to draw on these studies to test whether disassembly has greater ecosystem consequences than random species losses, and whether species losses in general should be expected to produce ecosystem consequences.

Box 1. Observed Examples of Community Disassembly and Its Consequences

While other examples of community disassembly and its consequences have been described, we focus here on three unusually well documented and illustrative cases. Few examples of the functional effects of community disassembly are as dramatic as the decline of the great whales through overharvesting. By the mid-1970s all species of North Pacific great whales had declined to ~14% of preexploitation levels. Ensuing declines in harbor seals, fur seals, sea lions, and finally sea otters were originally attributed to nutritional limitation (Anonymous 1993), but this hypothesis was unsupported by behavioral and physiological information (Council 2003). New evidence indicates that that the reduction in great whales forced killer whales to switch to other prey. Killer whales fed on progressively smaller species as each prey population declined, down to sea otters (Springer *et al.* 2003). Declines in sea otters have in turn released sea-urchin populations, which graze kelp holdfasts and have since transformed underwater kelp forests replete with fish biodiversity to urchin barrens devoid of marine life (Estes *et al.* 1998).

Large marine predator declines have also disassembled tropical coral-reef ecosystems. Comparisons of South Pacific islands with and without heavy depletion of sharks by fishing have revealed extensive compositional and functional differences between them. Islands with sharks had few small fish and abundant corals because sharks consume the majority of fish biomass (Sandin *et al.* 2008). Islands with few sharks had many small, colorful reef fishes, fewer corals, more coral disease, and increased algal cover. This finding suggests that much of the work to date on reefs with abundant, colorful, small fishes could be characterizing already disassembled ecosystems. This study also highlights processes by which declines of some species (in this case, sharks and corals) can drive or be accompanied by gains in others (in this case, small reef-fishes and algae).

Research in Yellowstone National Park on the ecosystem impacts of reintroduced gray wolves and recolonizing mountain lions has illustrated community disassembly dynamics in a terrestrial system. Extirpation of wolves and mountain lions in the early twentieth century along with reduced human hunting pressure led to numerical increases and behavioral changes in elk. Elk became less vigilant (Laundre *et al.* 2001) and heavily browsed willow along stream courses (Beyer *et al.* 2007). This in turn is thought to have competitively excluded beaver, causing hydrological changes in streams from the absence of beaver dams (Wolf *et al.* 2007). Streams became more channelized, reducing alluvial sediment availability for willow establishment. The further decline in willows in turn led to declines in nesting song birds (Berger *et al.* 2001) and to increased water temperatures and bank erosion, with possible implications for trout species that require cool temperatures.

Life-size "experiments" involving species losses brought about by anthropogenic fragmentation have occasionally provided special insight into both community disassembly orders and their functional consequences. Studies of both temperate and Amazonian rain forest reveal that the effects of forest fragmentation on species composition and diversity are immediate, persistent, and exacerbated by landscape-scale influences such as fire, drought, and human activity (Lomolino and Perault 2000; Laurance *et al.* 2002). Predators that are also large-bodied with large individual ranges are often the first species to disappear from fragmented habitats. For example, a series of land-bridge islands were created suddenly in Lago Guri, Venezuela, by a hydroelectric impoundment. Terborgh and colleagues (2001) reported a "meltdown" of island ecosystems following the disappearance of top predators from these small islands. Loss of predators of vertebrates led to increases in densities of rodents, iguanas, and leaf-cutter ants on the order of 10 to 100 times ambient levels on the nearby mainland. Seedlings and saplings of canopy trees continue to decline steeply, presumably due to the tremendous increase in leaf-cutter ant densities (Terborgh *et al*. 2006). Terborgh and colleagues (2001) suggest that the increase in herbivores will lead to an overall reduction in plant species adapted to a low-herbivory environment through relatively low investments in chemical and mechanical defenses. Subsequently, plants that are prickly or poisonous will increase in density, ultimately reducing herbivore populations through bottom-up limitation. Increases in howler monkey density have already coincided with increases in the relative abundance of several nonpreferred tree species (Feeley and Terborgh 2005) and in the overall richness of bird species (Feeley and Terborgh 2006) compared to the adjacent mainland. Other researchers on these islands report changes in dung burial rates following nonrandom losses among dung beetles of larger-bodied species (Larsen *et al.* 2005). In the case of the beetles, large-bodied species proved both more extinction-prone and more functionally significant than small-bodied species. This has meant disproportionate functional loss relative to random extinction scenarios.

In addition to research on the consequences of past disassembly, experimental work forcing one or more species losses has also informed our understanding of disassembly and its consequences. For example, healthy populations of nursery-web spiders in northeastern North American old field force the red-legged grasshopper (*Melanoplus femurrubrum*) to pursue a vigilance-maximizing diet, in which it feeds mainly on the competitively dominant forb, goldenrod (*Solidago rugosa*) (Beckerman *et al.* 1997; Schmitz 2008). When nursery-web spiders were experimentally removed, the grasshopper switched to an energy-maximizing diet of preferred host grasses and forbs (Schmitz *et al.* 1997). This released goldenrod from herbivory and ultimately allowed it to eliminate competitively inferior grasses and forbs. This in turn led to a loss of plant diversity, increased net primary productivity (NPP), and increased nitrogen mineralization rates (Schmitz 2008). Similar cascading effects have been documented in coastal rivers in northern California, from which fish removals trigger cascading community changes that dramatically increase ecosystem NPP (Power 1990; 1992).

Further experimental insight into the effects of community disassembly is provided by experiments that create multiple assemblage of progressively lower species diversity and observe ecosystem responses. With few exceptions (Lyons and Schwartz 2001; Solan *et al.* 2004; Zavaleta and Hulvey 2004; Bunker *et al.* 2005; Schlapfer *et al.* 2005) biodiversity–ecosystem functioning experiments have not explored realistic biodiversity-loss orders. However, existing studies in this area make clear that the order of species losses can critically influence their functional consequences, because the effects of species richness decline depend on the identity and functional traits of species that remain.

In a tallgrass prairie study, NPP was unaffected by losses of rare and uncommon species (Smith and Knapp 2003) because abundant grasses replaced their contributions to productivity. When abundances of dominant plants were reduced, there was no such compensatory response from rare species, reducing NPP. In an exotic-dominated California grassland, Zavaleta and Hulvey (2007) simulated disassembly by removing species in a nested order observed in the field. Because whole functional groups disappeared quickly in this loss scenario, primary production and invasion resistance declined faster than expected from randomly ordered species removals. In a semiarid grassland, production was calculated to decline more steeply when species were lost randomly than it did following ordered removals based on risk criteria (Schlapfer *et al.* 2005). In California coast tide pools, nitrogen uptake rates differed between random and realistic patterns of richness change. Random reductions in seaweed diversity had no effect on nitrogen use, while declines that mirrored natural diversity gradients resulted in reduced nitrogen uptake rates (Bracken *et al.* 2008).

Models based on field data also provide insight into the effects of ordered disassembly versus random removals of species. In a study based on empirically derived models of tropical forest change, the effect of extinctions on forest carbon storage depended on whether species were lost randomly: according to population traits such as growth rate, density, and endemism; according to appeal to humans; or according to vulnerability to environmental change (Bunker *et al.* 2005). Disassembly order could thus be an important determinant of carbon sequestration or release in tropical forests. Models derived from marine invertebrate communities likewise suggest that specific extinction scenarios matter to ecosystem function. Researchers examined benthic sediment bioturbation under various random and realistic scenarios of species loss. Bioturbation influences sediment oxygen content, an important determinant of primary and secondary production, decomposition, and nutrient cycling in these systems. Bioturbation declined under all scenarios of species diversity loss, but the extent of reduction in this function varied based on whether disassembly occurred according to stress sensitivity, body size, rarity, or random processes (Solan *et al.* 2004). Finally, Ostfeld and LoGiudice (2003) used an empirically based disease model to show that species loss order in vertebrate communities influenced the proportion of ticks carrying Lyme disease bacteria. Vertebrate disassembly patterns thus governed human exposure to the disease. Random scenarios of disassembly reduced human disease risk as vertebrate diversity declined, but more realistic scenarios increased in human exposure. Disassembly order can therefore be critically important when effects cascade across trophic levels or through interaction webs to impact function.

Conclusions

The body of evidence synthesized in this chapter points to several important conclusions. First, the consequences of community disassembly—a nonrandom process—can differ markedly from the consequences of random biodiversity declines. Most often, the consequences of ordered disassembly are greater than those of random species removals, providing direct evidence to support correlations between species vulnerability (response traits) and contribution to ecosystem functioning (effect traits). To the extent that these two characteristics of species are correlated, ongoing species losses will have greater effects on ecosystem functioning than what might be expected based on chance losses. A second key conclusion is that disassembly can be a self-perpetuating process, one in which progressive species losses result not only from worsening stressors, but also from the ripple effects of previous species losses. Previously articulated concepts, including trophic cascades (Estes *et al.* 1998) and invasional meltdown (Simberloff and van Holle 1999), describe particular ways in which an initial change in species richness or abundance can initiate such a self-perpetuating chain of ecological impact. These dynamics provide one paradigm for understanding why disassembly and ecosystem change may or may not be stemmed simply by mitigating stresses on an altered ecosystem.

What, If Any, Are the Rules of Disassembly?

Most species characteristics that affect vulnerability depend at least somewhat on what the driver of decline is. However, certain characteristics emerge consistently across drivers and for multiple taxa, including large body size, small range size, low population abundance or density, and other population or life-history characteristics that limit population growth and recovery rates. Empirical examples often focus on losses of large-bodied and/or predator species, largely because these are commonly the first species to decline or disappear in response to environmental degradation. These same examples often highlight far-reaching, sometimes cascading effects of these species losses, underscoring that this particular group of species is both vulnerable and functionally important. The cascading changes that can occur involve both classic top-down trophic cascades and more idiosyncratic changes in species interactions, biogeochemistry, and ecosystem structure that depend on the particular ecosystem and its web of interactions.

In the cases reviewed here, initial species losses trigger a variety of community and ecosystem changes that can include both increases in former prey and competitor species and declines in species that benefited from positive interactions or conditions fostered by the lost species. Disassembly can thus both increase and reduce the likelihood of declines in other species, depending on their identities and on interaction webs. Regardless, what does occur consistently after species loss is further change—from small to large in magnitude, and with varying extent of cascading effects. The literature contains few examples of species losses that had no follow-on effects. We assert that it is prudent to assume any species extirpation or loss will have measurable ecological effects.

Priority Research Needs in This Area

Relatively few studies have taken advantage of ongoing habitat fragmentation or decline to capture information about how successive or multiple species losses occur and are linked, to each other and to other changes in ecosystem functioning. Likewise, no study has yet looked across case studies systematically to ask whether the rate of extinctions, all else being equal, accelerates with each new species loss. Such a pattern would be a robust indication that in general, extinctions fuel further extinctions.

There have also been only a handful of field-scale (vs. plot-scale) manipulations of community composition that provide insight into the cascading effects that can follow one or more species losses. Finally, manipulative experiments of successive, realistic species losses at any scale have involved almost entirely herbaceous plants and deserve to be augmented by studies of other taxa. In all of these studies, long-term data collection and monitoring are key to understanding effects beyond the short-term and transient responses detectable in a one- to three-year study. Attention to both the characteristics correlated with risk of decline and the characteristics associated with effects on ecosystem processes will refine understanding of how vulnerability and contribution to functioning are related in different taxa. In particular, more studies within particular assemblages of the relationship between response and effect traits—particularly where response traits are measured at conservation-relevant spatial and temporal scales—would help to clarify the correlation between vulnerability and functional contribution.

Disassembly, Conservation, and Restoration

Ultimately, an understanding of ecological disassembly helps conservation and restoration to consider both vulnerability and functional importance alongside taxonomic uniqueness in setting priorities for action. Conservation planning tools are already under development to guide geographic priority setting based on both biodiversity and delivery of ecosystem services (Chan *et al.* 2006). Species-based conservation prioritization tools, such as the International Union for Conservation of Nature and Natural Resources (IUCN) classification scheme, do not yet explicitly consider the potential for a species' decline or loss to trigger further disassembly or altered ecosystem functioning. Species conservation and restoration priorities can be set with respect to either or both of vulnerability and functional importance, depending on goals (Fig. 1). Rough characterization of the functional role or importance of a species could be based on existing literature, a conceptual summary of its place in existing interaction webs, and/or rapid assessment.

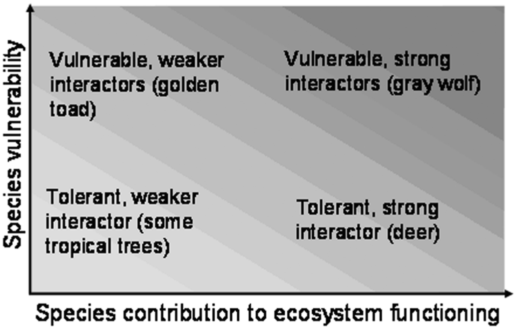

Figure 1. Species classes defined in relation to axes of vulnerability and contribution to ecosystem functioning. Species conservation and restoration priorities can be set with respect to either or both axes. *Shading* indicates conservation importance if both axes are considered. Vulnerability can be assessed in general or with respect to a particular threat, depending on goals. Similarly, species contribution to ecosystem functioning can be assessed per capita or in the aggregate.

Because conservation often relies on geographic priority setting, another key question—which we have not addressed in this review—is whether certain ecosystem types are more vulnerable than others to the effects of disassembly. For example, a species loss in an island assemblage of relatively few, functionally broad species could have more severe follow-on effects than the same species loss in a more speciose continental setting. Inherently low-diversity systems, islands, systems experiencing multiple stresses, and previously "unfiltered" or ecologically naïve systems with respect to human stressors (such as grasslands with no history of large grazing mammals), could be more likely to experience both species declines or losses and cascading effects when such losses occur.

A focus on species' functional roles can also guide restoration priorities by informing when and where restoration of one, well-selected species can lead to extensive restoration of other ecosystem characteristics and processes. Restoration practice focuses increasingly on restoring processes as well as lists of species, and in this vein taxon substitution has even entered into some restoration projects as a way to restore functions of extinct species (Zavaleta *et al.* 2001). Conversely, when species declines are linked by disassembly processes, it may be impossible to restore one without restoring another whose decline preceded it. For example, when declines of certain plant species are linked to losses of top predators that formerly limited herbivore populations (Terborgh *et al.* 2001), plant restoration might be impossible or difficult without concurrent predator restoration or other steps to restore smaller herbivore populations.

Most systems are already partly disassembled; restoration efforts might benefit from considering the roles of long-missing species in maintaining desired processes or populations. For example, plant restoration efforts in California do not often consider the complications to them posed by the relative absence of top predators and omnivores like wolves and bears. It has been suggested that regeneration of California's endemic deciduous oaks (e.g., *Quercus lobata, Q. douglasii, Q. kelloggii*) might have declined in the last century because of high rodent populations in the absence of high predator densities (Adams and Weitkamp 1992). By considering past species losses and their effects, ecologists can set more realistic baselines of historical change, make predictions for future changes, and ultimately have a better chance to reverse disassembly by restoring processes long missing from ecosystems.

Should We Do Conservation Differently Because of Community Disassembly?

We argue that community disassembly is a real, and useful, concept for conservation practice. It emphasizes the ordered nature of species losses from a given locale or ecosystem type and provides some rules of thumb about the likely order of species loss. Selection of indicator species could reflect these rules of thumb, as could prioritization of species for protective measures that remedy range contractions, as well as deter outright extinction. The disassembly concept also emphasizes the mechanism of cascading extinctions through the ecosystem consequences of initial species losses. It thereby provides not only stronger rationale for preventing early species losses in relatively intact assemblages but also a conceptual tool for considering what kinds of management interventions in incomplete assemblages could stem ecosystem change and follow-on extirpations or extinctions. The disassembly literature underscores that community assembly is a different process, not a mirror to species loss order, and that assembly should therefore not guide understanding of species vulnerability.

Finally, an emergent understanding that vulnerability and contribution to functioning are positively correlated in classes of species with particular characteristics argues for shifting conservation priorities toward these species. Not only are they most likely to be under threat and underrepresented globally, but they are also most likely, as they decline, to trigger changes that threaten other native taxa. Debate over whether to prioritize species conservation action based on species' vulnerability or species' functional contributions could be partly resolved by the recognition that some of the same species characteristics underlie both criteria, and that a key functional contribution of species with these characteristics can be the maintenance of ecosystem processes that prevent further species losses.

Acknowledgments

One of the authors (E.Z.) was supported by the A. W. Mellon Foundation. The authors thank Kris Hulvey, Kevin Cullinen, Bill Schlesinger, and an anonymous reviewer for improving the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

References

Adams, T.E. & H.W. Weitkamp. 1992. Gophers love oak—To death. *Calif. Agric.* **46:** 27–29.

Anonymous. 1993. *Is It Food? Workshop Proceedings 93-01.* University of Alaska Sea Grant. Fairbanks.

Balmford, A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends Ecol. Evol.* **11:** 193–196.

Balvanera, P., C. Kremen & M. Martinez-Ramos. 2005. Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecol. Appl.* **15:** 360–375.

Balvanera, P., B.A. Pfisterer, N. Buchmann, *et al*. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* **9:** 1146–1156.

Beckerman, A.P., M. Uriarte & J.O. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc. Natl. Acad. Sci.USA* **94:** 10735–10738.

Beissinger, S.R. 2000. Ecological mechanisms of extinction. *Proc. Natl. Acad. Sci.USA* **97:** 11688–11689.

Belyea, L.R. & J. Lancaster. 1999. Rules within a contingent ecology. *Oikos* **86:** 402–416.

Bennett, P.M. & F.P.I. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. B Biol. Sci.* **264:** 401–408.

Berger, J., B.P. Stacey, L. Bellis & P.M. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.* **11:** 947–960.

Beyer, H.L., H.E. Merrill, N. Varley & S.M. Boyce. 2007. Willow on yellowstone's northern range: evidence for a trophic cascade? *Ecol. Appl.* **17:** 1563–1571.

Bielby, J., A.A. Cunningham & A. Purvis. 2006. Taxonomic selectivity in amphibians: ignorance, geography or biology? *Anim. Conserv.* **9:** 135–143.

Blackburn, T.M. & J.K. Gaston. 2002. Extrinsic factors and the population sizes of threatened birds. *Ecol. Lett.* **5:** 568–576.

Blockstein, D.E. 1998. Letter to the editor. *Science* **279:** 1831.

Bolger, D.T., C.A. Alberts & E.M. Soule. 1991. Occurrence patterns of bird species in habitat fragments—Sampling, extinction, and nested species subsets. *Am. Nat.* **137:** 155–166.

Bond, W.J. & E.J. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* **20:** 387–394.

Bossuyt, B. & O. Honnay. 2006. Interactions between plant life span, seed dispersal capacity and fecundity determine metapopulation viability in a dynamic landscape. *Landscape Ecol.* **21:** 1195–1205.

Bracken, M.E.S., E.S. Friberg, C.A. Gonzalez-Dorantes & L.S. Williams. 2008. Functional consequences of realistic biodiversity changes in a marine ecosystem. *Proc. Natl. Acad. Sci. USA* **105:** 924–928.

Bridgham, S.D., A.C. Johnston, J. Pastor & K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate-change—An outline of an approach to predict climate-change impact. *Bioscience* **45:** 262–274.

Bunker, D.E., F. DeClerck, C.J. Bradford, *et al*. 2005. Species loss and aboveground carbon storage in a tropical forest. *Science* **310:** 1029–1031.

Buzas, M.A. & J.S. Culver. 1998. Assembly, disassembly, and balance in marine paleocommunities. *Palaios* **13:** 263–275.

Cardillo, M. & L. Bromham. 2001. Body size and risk of extinction in Australian mammals. *Conserv. Biol.* **15:** 1435–1440.

Cardillo, M., M.G. Mace, E.K. Jones, *et al*. 2005. Multiple causes of high extinction risk in large mammal species. *Science* **309:** 1239–1241.

Carlton, J.T. 1993. Neoxtinctions of marine invertebrates. *Am. Zool.* **33:** 499–509.

Chan, K.M.A., R.M. Shaw, R.D. Cameron, *et al*. 2006. Conservation planning for ecosystem services. *PLoS Biol.* **4:** 2138–2152.

Chapin, F.S. 1997. Biotic control over the functioning of ecosystems. *Science* **277:** 500–504.

Chapin, F.S., S.E. Zavaleta, T.V. Eviner, *et al*. 2000. Consequences of changing biodiversity. *Nature* **405:** 234–242.

Chase, J.M. 2003. Community assembly: When should history matter? *Oecologia* **136:** 489–498.

Cook, R.R. & I. Hanski. 1995. On expected lifetimes of small-bodied and large-bodied species of birds on islands. *Am. Nat.* **145:** 307–315.

Cooper, N., J. Bielby, H.G. Thomas & A. Purvis. 2008. Macroecology and extinction risk correlates of frogs. *Global Ecol. Biogeogr.* **17:** 211–221.

Council, N.R. 2003. *Decline of the Stellar Sea Lion in Alaskan Waters*. Washington, DC.

Darwin, C. 1859. *On the Origin of Species by Natural Selection*. Murray. London.

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* **45:** 137–159.

Dennis, R.L.H., G.J. Hodgson, R. Grenyer, *et al*. 2004. Host plants and butterfly biology. Do host-plant strategies drive butterfly status? *Ecol. Entomol.* **29:** 12–26.

Diamond, J.M. 1984. "Normal" extinctions of isolated populations. In *Extinctions*. M.H. Nitecki, Ed. University of Chicago Press. Chicago.

Driscoll, D.A. & T. Weir. 2005. Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conserv. Biol.* **19:** 182–194.

Dobson, A., D. Lodge, J. Alder, *et al*. 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* **87:** 1915–1924.

Duffy, J.E. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* **99:** 201–219.

Duffy, J.E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* **6:** 680–687.

Dulvy, N.K. & D.J. Reynolds. 2002. Predicting extinction vulnerability in skates. *Conserv. Biol.* **16:** 440–450.

Dulvy, N.K., Y. Sadovy & D.J. Reynolds. 2003. Extinction vulnerability in marine populations. *Fish Fish.* **4:** 25–64.

Duncan, R.P. & R.J. Young. 2000. Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology* **1:** 3048–3061.

Duncan, R.P., M.T. Blackburn & H.T. Worthy. 2002. Prehistoric bird extinctinons and human hunting. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **269:** 517–521.

Ellison, A.M., S.M. Bank, D.B. Clinton, *et al*. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **9:** 479–486.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen. London.

Estes, J.A. & O.D. Duggins. 1995. Sea otters and kelp forests in Alaska—Generality and variation in a community ecological paradigm. *Ecol. Monogr.* **65:** 75–100.

Estes, J.A., T.M. Tinker, M.T. Williams & F.D. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282:** 473–476.

Feeley, K.J. & W.J. Terborgh. 2005. Elevated densities of herbivores (Alouatta seniculus) affect soil nutrient concentrations and tree growth on islands in Lago Guri, Venezuela. *Ecology* **86:** 116–124.

Feeley, K.J. & W.J. Terborgh. 2006. Habitat fragmentation and effects of herbivore (howler monkey) abundances on bird species richness. *Ecology* **87:** 144–150.

Feeley, K.J.T., W. Gillespie, J.D. Lebbin & S.H. Walter. 2007. Species characteristics associated with extinction vulnerability and nestedness rankings of birds in tropical forest fragments. *Anim. Conserv.* **10:** 493–501.

Foufopoulos, J. & R.A. Ives. 1999. Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *Am. Nat.* **153:** 1–25.

Fox, B.J. 1987. Species assembly and the evolution of community structure. *Evol. Ecol.* **1:** 201–213.

Freville, H., K. McConway, M. Dodd & J. Silvertown. 2007. Prediction of extinction in plants: interaction of extrinsic threats and life history traits. *Ecology* **88:** 2662–2672.

Gage, G.S., D.M. Brooke, E.R.M. Symonds & D. Wege. 2004. Ecological correlates of the threat of extinction in neotropical bird species. *Anim. Conserv.* **7:** 161–168.

Gonzalez, A. & J.E. Chaneton. 2002. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol.* **71:** 594–602.

Gunderson, L.H. & S.C. Holling, Eds. 2002. *Panarchy: Understanding Transformations in Human and Natural Systems*. Island Press. Washington, DC.

Hartnett, D.C. & T.W.G. Wilson. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* **80:** 1187–1195.

Hassan, R., R. Scholes & N. Ash, Eds. 2005. *Ecosystems and Human Well-Being: Current State and Trends, Volume. Findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment*. Island Press. Washington, DC.

Hastings, A., E.J. Byers, A.J. Crooks, *et al*. 2007. Ecosystem engineering in space and time. *Ecol. Lett.* **10:** 153–164.

Hector, A., J. Joshi, P.S. Lawler, *et al*. 2001. Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia* **129:** 624–628.

Henle, K., F.K. Davies, M. Kleyer, *et al*. 2004. Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.* **13:** 207–251.

Hero, J.M., E.S. Williams & E.W. Magnusson. 2005. Ecological traits of declining amphibians in upland areas of eastern Australia. *J. Zool.* **267:** 221–232.

Hobbs, R.J. & A.H. Mooney. 1995. Spatial and temporal variability in California annual grassland—Results from a long-term study. *J. Veg. Sci.* **6:** 43–56.

Hooper, D.U., S.F.I. Chapin, J.J. Ewel, *et al*. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr* **75:** 3–35.

Hutchins, H.E. & M.R. Lanner. 1982. The central role of clark nutcracker in the dispersal and establishment of whitebark pine. *Oecologia* **55:** 192–201.

Jennings, S., R.P.S. Greenstreet & D.J. Reynolds. 1999a. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J Anim. Ecol.* **68:** 617–627.

Jennings, A.E., F.W. Manley, B. MacLean & T.J. Andrews. 1998. Marine evidence for the last glacial advance across eastern Hudson Strait, eastern Canadian Arctic. *J. Quart. Science* **13:** 501–514.

Jennings, S., D.J. Reynolds & C.V.N. Polunin. 1999b. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conserv. Biol.* **13:** 1466–1475.

Jetz, W., S.D. Wilcove & P.A. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* **5:** e157.

Jiguet, F., S.A. Gadot, R. Julliard, *et al*. 2007. Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biol.* **13:** 1672–1684.

Johnson, C.N. 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **269:** 2221–2227.

Jones, H.P., R.B. Tershy, S.E. Zavaleta, *et al*. 2008. Severity of the effects of invasive rats on seabirds: a global review. *Conserv. Biol.* **22:** 16–26.

Keane, A., M.D. Brooke & P.J.K. McGowan. 2005. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). *Biol. Conserv.* **126:** 216–233.

Kiessling, W. & M. Aberhan. 2007. Geographical distribution and extinction risk: lessons from Triassic-Jurassic marine benthic organisms. *J. Biogeogr.* **34:** 1473–1489.

Larsen, T.H., M.N. Williams & C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.* **8:** 538–547.

Laundre, J.W., L. Hernandez & B.K. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Can. J. Zool-Rev. Can. Zool.* **79:** 1401–1409.

Laurance, W.F., E.T. Lovejoy, L.H. Vasconcelos, *et al.* 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* **16:** 605–618.

Lawler, S.P., J.J. Armesto & P. Kareiva. 2001. How relevant to conservation are studies linking biodiversity and ecosystem functioning? In *The Functional Consequences of Biodiversity*. A.P. Kinzig, S.W. Pacala & D. Tilman, Eds.: 294–313. Princeton University Press. Princeton, NJ.

Leach, M.K. & J.T. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* **273:** 1555–1558.

Lehtinen, R.M., B.J. Ramanamanjato & G.J. Raveloarison. 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar. *Biodivers. Conserv.n* **12:** 1357–1370.

Lips, K.R., D.J. Reeve & R.L. Witters. 2003. Ecological traits predicting amphibian population declines in Central America. *Conserv. Biol.* **17:** 1078–1088.

Lomolino, M.V. & R.D. Perault. 2000. Assembly and disassembly of mammal communities in a fragmented temperate rain forest. *Ecology* **81:** 1517–1532.

Loreau, M., S. Naeem & P. Inchausti, Eds. 2002. *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press. New York.

Luck, G.W., C.G. Daily & R.P. Ehrlich. 2003. Population diversity and ecosystem services. *Trends Ecol. Evol.* **18:** 331–336.

Lyons, K.G. & W.M. Schwartz. 2001. Rare species loss alters ecosystem function—Invasion resistance. *Ecol. Lett.* **4:** 358–365.

Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press. Princeton, NJ.

McDonald, K.A. & H.J. Brown. 1992. Using montane mammals to model extinctions due to global change. *Conserv. Biol.* **6:** 409–415.

McIntyre, P.B., E.L. Jones, S.A. Flecker & J.M. Vanni. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. *Proc. Natl. Acad. Sci. USA* **104:** 4461–4466.

Memmott, J., G.P. Craze, M.N. Waser & M. Price. 2007. Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.* **10:** 710–717.

Mikkelson, G.M. 1993. How do food webs fall apart? A study of changes in trophic structure during relaxation on habitat fragments. *Oikos* **67:** 539–547.

Miller, B., G. Ceballos & R. Reading. 1994. The prairie dog and biotic diversity. *Conserv. Biol.* **8:** 677–681.

Mills, L.S., M.E. Soule & F.D. Doak. 1993. The keystone species concept in ecology and conservation. *Bioscience* **43:** 219–224.

Morris, W.F., A.C. Pfister, V.C. Haridas, *et al.* 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89:** 19–25.

Morrow, E.H. & E.T. Pitcher. 2003. Sexual selection and the risk of extinction in birds. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **270:** 1793–1799.

Murray, B.R. & C.G. Hose. 2005. Life-history and ecological correlates of decline and extinction in the endemic Australian frog fauna. *Aust. Ecol.* **30:** 564–571.

O'Grady, J.J., H.D. Reed, W.B. Brook & R. Frankham. 2004. What are the best correlates of predicted extinction risk? *Biol. Conserv.* **118:** 513–520.

Olden, J.D., S.Z. Hogan & M.J. Vander Zanden. 2007. Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecol. Biogeogr.* **16:** 694–701.

Ostfeld, R.S. & K. LoGiudice. 2003. Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology* **84:** 1421–1427.

Owens, I.P.F. & M.P. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl. Acad. Sci.USA* **97:** 757–785.

Paillet, F.L. 2002. Chestnut: history and ecology of a transformed species. *J. Biogeogr.* **29:** 1517–1530.

Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.* **100:** 65–75.

Paine, R.T. & H.T. Suchanek. 1983. Convergence of ecological processes between independently evolved competitive dominants: a tunicate-mussel comparison. *Evolution* **37:** 821–831.

Patterson, B.D. & W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagoes. *Biol. J. Linn. Soc.* **28:** 65–82.

Petchey, O.L., A. Eklöf, C. Borrvall & B. Ebenman. 2008. Trophically unique species are vulnerable to cascading extinction. *Am. Nat.* **171:** 568–579.

Pimm, S.L., L.H. Jones & J. Diamond. 1988. On the Risk of Extinction. *Am. Nat.* **132:** 757–785.

Power, M.E. 1990. Effects of fish in river food webs. *Science* **250:** 811–814.

Power, M.E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* **73:** 1675–1688.

Power, M.E., D. Tilman, A.J. Estes, *et al.* 1996. Challenges in the quest for keystones. *Bioscience* **46:** 609–620.

Purvis, A., M.P. Agapow, L.J. Gittleman & M.G. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. *Science* **288:** 328–330.

Purvis, A., M. Cardillo, R. Grenyer & B. Collen. 2005. Correlates of extinctin risk: phylogeny, biology, threat, and scale. In *Phylogeny and Conservation: Conservation Biology 8*. A. Purvis, J. L. Gittleman & B. Collen, Eds.: 295–316. Cambridge University Press. Cambridge, UK.

Raffaelli, D. 2004. How extinction patterns affect ecosystems. *Science* **306:** 1141–1142.

Reynolds, J.D., K.N. Dulvy, B.N. Goodwin & A.J. Hutchings. 2005a. Biology of extinction risk in marine fishes. *Proc. R. Soc. Lond. B* **272:** 2337–2344.

Reed, R.N. & R. Shine. 2002. Lying in wait for extinction: ecological correlates of conservation status among Australian elapid snakes. *Conserv. Biol.* **16:** 451–461.

Ripple, W.J. & R.L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *For. Ecol. Manage.* **184:** 299–313.

Russell, G.J., M.T. Brooks, M.M. McKinney & G.C. Anderson. 1998. Present and future taxonomic selectivity in bird and mammal extinctions. *Conserv. Biol.* **12:** 1365–1376.

Saavedra, S., F. Reed-Tsochas & B. Uzzi. 2008. Asymmetric disassembly and robustness in declining networks. *Proc. Natl. Acad. Sci. USA* **105:** 16466–16471.

Sakai, A.K., L.W. Wagner & A.L. Mehrhoff. 2002. Patterns of endangerment in the Hawaiian flora. *Syst. Biol.* **51:** 276–302.

Samuels, C.L. & A.J. Drake. 1997. Divergent perspectives on community convergence. *Trends Ecol. Evol.* **12:** 427–432.

Sanders, N.J., J.N. Gotelli, E.N. Heller & M.D. Gordon. 2003. Community disassembly by an invasive species. *Proc. Natl. Acad. Sci. USA* **100:** 2474–2477.

Sandin, S.A., E.J. Smith, E.E. DeMartini, *et al.* 2008. Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE* **3:** e1548.

Schlapfer, F., B.A. Pfisterer & B. Schmid. 2005. Nonrandom species extinction and plant production: implications for ecosystem functioning. *J. Appl. Ecol.* **42:** 13–24.

Schmitz, O.J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* **319:** 952–954.

Schmitz, O.J., P.A. Beckerman & M.K. Obrien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* **78:** 1388–1399.

Schwartz, M.W., A.C. Brigham, D.J. Hoeksema, *et al.* 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122:** 297–305.

Schwartz, M.W. & D. Simberloff. 2001. Taxon size predicts rates of rarity in vascular plants. *Ecol. Lett.* **4:** 464–469.

Simberloff, D. 2003. Community and ecosystem impacts of single-species extinctions. In *The Importance of Species*. P.M. Kareiva & S.A. Levin, Eds.: 221–233. Princeton University Press. Princeton, NJ.

Simberloff, D. & B.V. Holle. 1999. Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions* **1:** 21–32.

Smith, M.D. & K.A. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* **6:** 509–517.

Sodhi, N.S., P.L. Koh, H.S.K. Peh, *et al.* 2008. Correlates of extinction proneness in tropical angiosperms. *Divers. Distrib.* **14:** 1–10.

Solan, M., J.B. Cardinale, L.A. Downing, *et al*. 2004. Extinction and ecosystem function in the marine benthos. *Science* **306:** 1177–1180.

Springer, A.M., A.J. Estes, G.B. van Vliet, *et al*. 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proc. Natl. Acad. Sci. USA* **100:** 12223–12228.

Srivastava, D.S. & M. Vellend. 2005. Biodiversity-ecosystem function research: Is it relevant to conservation? *Annu. Rev. Ecol. Evol. Sys.* **36:** 267–294.

Stachowicz, J.J. 2001. Mutualism, facilitation, and the structure of ecological communities. *Bioscience* **51:** 235–246.

Taylor, B.W., S.A. Flecker & O.R. Hall, Jr. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* **313:** 833–836.

Terborgh, J., K. Feeley, M. Silman, *et al.* 2006. Vegetation dynamics of predator-free land-bridge islands. *J. Ecol.* **94:** 253–263.

Terborgh, J., L. Lopez, V. Percy Nunez, *et al*. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294:** 1923–1926.

Thébault, E., V. Huber & M. Loreau. 2007. Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* **116:** 163–173.

Thompson, J.N. 1998. Rapid evolution as an ecological process. *Trends Ecol. Evol.* **13:** 329–332.

Tilman, D. 1996. Population versus ecosystem stability. *Ecology* **77:** 350–363.

Tilman, D., J. Knops, D. Wedin, *et al*. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277:** 1300–1302.

Tracy, C.R. & L.T. George. 1992. On the determinants of extinction. *Am. Nat.* **139:** 10–122.

Turner, I.M., S.K. Chua, Y.S.J. Ong, *et al*. 1996. A century of plant species loss from an isolated fragment of lowland tropical rain forest. *Conserv. Biol.* **10:** 1229–1244.

Vamosi, J.C. & P.S. Otto. 2002. When looks can kill: the evolution of sexually dimorphic floral display and the extinction of dioecious plants. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **269:** 1187–1194.

Vitousek, P.M., C.M. D'Antonio, L.L. Loope, *et al.* 1997. Introduced species: a significant component of human-caused global change. *N. Z. J. Ecol.* **21:** 1–16.

Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conserv. Biology* **9:** 747–752.

Walker, B., A. Kinzig & J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2:** 95–113.

Walker, K.J. & D.C. Preston. 2006. Ecological predictors of extinction risk in the flora of lowland England, UK. *Biodivers. Conserv.* **15:** 1913–1942.

Wardle, D.A., O. Zackrisson, G. Hornberg & C. Gallet. 1997. The influence of island area on ecosystem properties. *Science* **277:** 1296–1299.

Williams, N.S.G., W.J. Morgan, J.M. Mcdonnell & M.A. McCarthy. 2005. Plant traits and local extinctions in natural grasslands along an urban-rural gradient. *J. Ecol.* **93:** 1203–1213.

Wolf, E.C., J.D. Cooper & T.N. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecol. Appl.* **17:** 1572–1587.

Wright, D.H., D.B. Patterson, M.G. Mikkelson, *et al*. 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia* **113:** 1–20.

Zavaleta, E.S., R.J. Hobbs & H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* **16:** 454–459.

Zavaleta, E.S. & K.B. Hulvey. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invasions. *Science* **306:** 1175–1177.

Zavaleta, E.S. & K.B. Hulvey. 2007. Realistic variation in species composition affects grassland production, resource use and invasion resistance. *Plant Ecol.* **188:** 39–51.