

Ecological Consequences of Extinction

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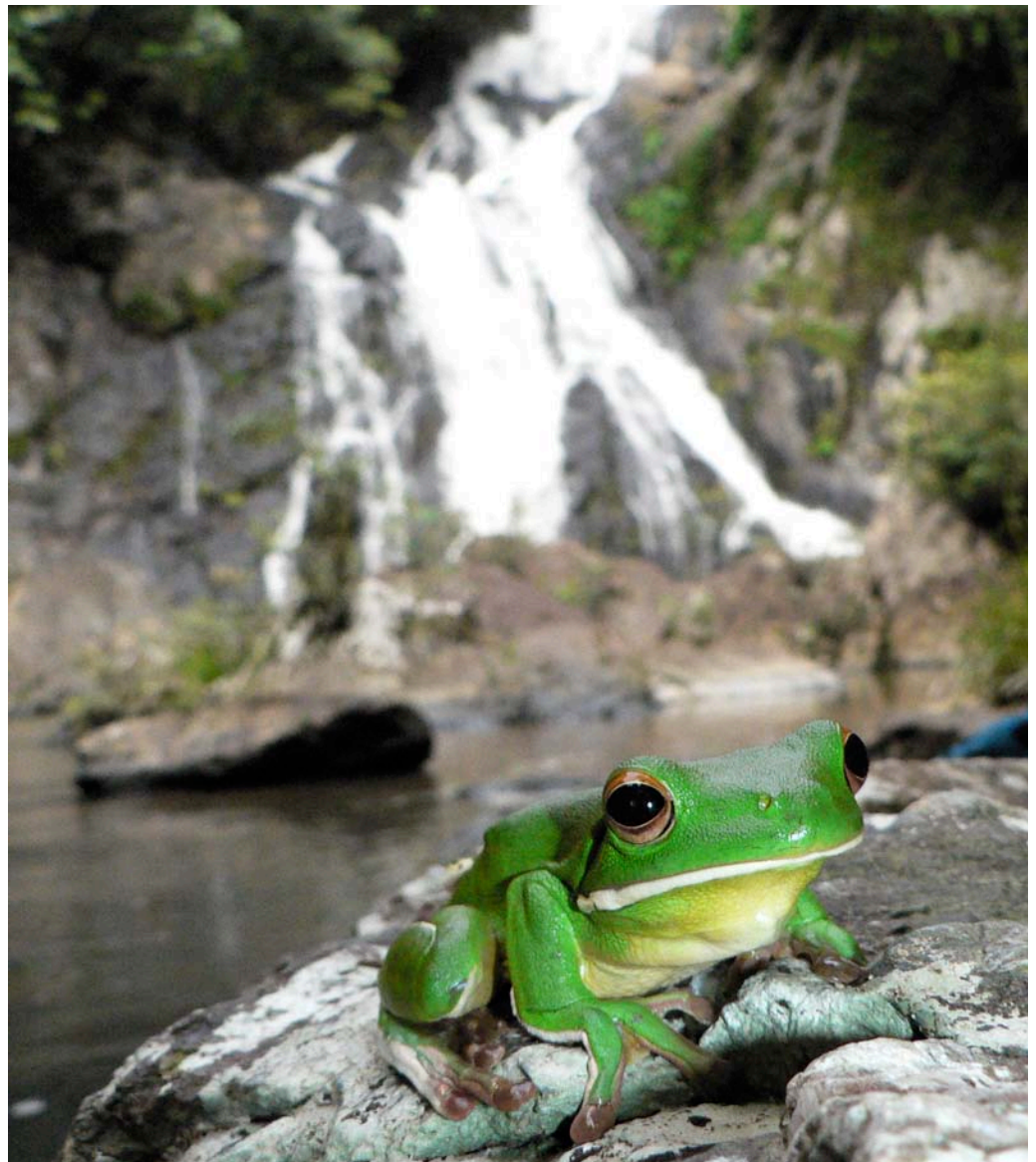
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Madhu Rao and Trond Larsen

Introduction

Extinction is a natural process, but it is occurring at an unnaturally rapid rate as a consequence of human activities. Humans have caused the extinction of between 5–20% of the species in many groups of organisms, and current rates of extinction are estimated to be 100–1,000 times greater than pre-human rates (Lawton and May, 1995; Pimm et al., 1995). Overall, accelerated extinctions of species and loss of *biodiversity* are no longer disputed issues in the scientific community. Although much effort has gone into quantifying the rates of biodiversity loss for particular animal and plant groups, the impact of such losses on ecosystems is less clear, especially when many different kinds of plants and animals are simultaneously lost (Raffaelli, 2004). In a review of the ecosystem consequences of bird declines, Şekercioğlu et al. (2004), report that 21% of all bird species are currently threatened or near threatened by extinction, and 6.5% are *functionally or ecologically extinct*. Their projections indicate that by 2100, 6–14% of all bird species will actually be extinct, and 7–25% (28–56% on oceanic islands) will be functionally extinct. These extinctions are likely to disrupt important ecosystem processes such as decomposition, pollination, and seed dispersal.

Evidence from observational and experimental studies suggests that species extinctions are likely to have far-reaching consequences including further cascading extinctions, disruptions of *ecosystem services*, and the spread of disease (Terborgh et al. 2001; Şekercioğlu et al., 2004; Larsen et al. 2005). Ironically, the accelerating effects of human activities on biodiversity can have direct consequences for ecosystem goods and services that support human activities and life (Daily, 1997; Chapin et al., 2000). These services include the maintenance of soil fertility, climate regulation, natural pest control, and the provision of goods such as food, timber and fresh water.

Biodiversity and Ecosystem Function

Some of the first ideas on how biodiversity affects the way ecosystems function are attributable to Darwin and Wallace, who stated that a diverse mixture of plants should be more productive than a monoculture (Darwin and Wallace, 1858; Darwin, 1859). They also suggested the underlying biological mechanism: because coexisting species differ ecologically, loss of a species could result in vacant *niche-space* and consequent disruption of ecosystem processes maintained by that niche. Darwin and Wallace's early hypothesis predicts that intact, diverse communities are generally more stable and function better than less diverse communities. This hypothesis has provided the basis for much of the later ecological research that will be addressed in this synthesis.

Influence of Community Structure on Ecosystem Function

Several components of biodiversity are relevant to *ecosystem function*, including:

- 1) the number of species present (*species richness*);
- 2) their relative abundances (*species evenness*);
- 3) the particular species present (*species composition*);
- 4) the interactions among species (*non-additive effects*); and
- 5) the temporal and spatial variation in these properties of community structure (Symstad et al., 2003).

In addition to their effect on ecosystem function, changes in these components of biodiversity influence the *resilience* and *resistance* of ecosystems to environmental change (Chapin et al., 2000).

Species richness is important for ecosystem functioning for

several reasons, including higher complementarity of species' differing ecological roles. Several studies have used experimental species assemblages in an attempt to isolate the inherent role of species richness for ecosystem functioning, such as rates of *primary productivity*, nutrient retention, and decomposition of organic matter (Tilman et al., 1996). Many of these studies seek to identify whether species richness is important for function independently of other biodiversity components such as species composition.

Changes in the *relative abundance* of species (or species evenness) are more frequent than species loss and can have significant consequences for ecosystem function long before a species is actually threatened by extinction. The concept of ecological extinction refers to the, "Reduction of a species to such low abundance that, although it is still present in the community, it no longer interacts significantly with other species," (Estes et al., 1989). The implications of reduced species abundance for trophic interactions are discussed in the

final section of this synthesis.

Because species differ ecologically, the identity of species present in a community (species composition) can strongly influence ecosystem functions. For example, particular species can have strong effects on ecosystem processes by directly mediating energy and material fluxes or by altering abiotic conditions that regulate the rates of these processes (Hooper and Vitousek, 1997). Keystone species are examples of species with large effects on ecosystem process and function.

Species interactions, including mutualisms, trophic interactions (predation, parasitism, and herbivory) and competition may affect ecosystem processes directly by modifying resource-use efficiency and pathways of energy and material flow (de Ruiter et al., 1995) or indirectly by modifying the relative abundances of species (Power et al., 1996). Thus the disruption of species interactions through the loss of species can lead to many types of ecosystem effects.



The effects from some species interactions can impact entire ecosystems. Pollination, a mutualism between plants and pollinators, is considered an ecosystem service Source: S. Spector

Diversity-Function Relationships and Hypotheses

Although several aspects of biological communities influence ecosystem function, the majority of research has focused on the role of species richness, sometimes also referred to as *diversity*. There are many types of ecosystem functions and processes that can be influenced by species richness, including productivity, decomposition rates, *nutrient cycling*, and resistance and resilience to perturbations, disease, and *species invasions*.

The diversity-stability hypothesis (MacArthur, 1955) introduced the idea that increasing the number of trophically interacting species in an ecological community should increase the collective ability of member populations to maintain their abundances following disturbance. The hypothesis predicts that ecological communities will improve in energetic efficiency (or productivity), and in the ability to recover from disturbance, as the number of species in the system increases. Conversely, removing any species from a food web will enhance the susceptibility of the system to disruption via perturbation. MacArthur based this hypothesis on the premise that energy flow in complex food webs (meaning those featuring the greatest number of interspecific links or ‘connectance’) will be least disrupted by disturbance because alternative pathways for energy flow are available. Another hypothesis proposes that ecosystem resistance — the ability of a system to absorb changes in abundances of some species without drastically changing ecosystem performance (e.g., biomass production) — can decline as species are lost, even if system performance appears outwardly unaffected, with potentially sudden and drastic consequences as some threshold is passed (Ehrlich and Ehrlich, 1981). This hypothesis likens species in an ecosystem to rivets holding an airplane together — the removal of rivets beyond some threshold number may cause the airplane, or the ecosystem, to suddenly and catastrophically collapse.

Diversity-function relationships are usually plotted with species richness as the independent variable and a measure of ecosystem function as the dependent variable. This relation-

ship can take many forms. Sometimes no relationship or an idiosyncratic (or unpredictable) relationship is observed. This relationship would be expected, for example, in communities featuring *higher-order interactions* (Lawton, 1994). However, the majority of studies have found a positive but saturating relationship between richness and function, such that ecosystem function approaches its maximum level at some intermediate level of species richness (Schwartz et al., 2000). One explanation for this relationship is based on the ecosystem redundancy hypothesis (Walker, 1992), which proposes that there is some degree of functional redundancy in the roles species play in the ecosystem. At the heart of this concept is the idea that species are segregated into functional groups; those within the same group are predicted to be more expendable in terms of ecosystem function if the remaining species can maintain the same functional role. However, from a functional standpoint, many species may be less expendable than they appear. The insurance hypothesis suggests that even in systems, which appear to show saturation of function at low levels of richness, maintaining high levels of species richness provides long-term insurance to buffer against the disruption of function in response to future environmental change and fluctuation (Yachi and Loreau, 1999).

Other studies have found a positive, linear relationship between richness and function, suggesting that all species, even rare ones, are required to maintain healthy levels of ecosystem function (Johnson et al., 1996). More recently, studies looking specifically at the effects of extinctions have found a positive curvilinear relationship where function increases slowly at low levels of richness and more rapidly at the highest levels of species richness and does not saturate at all (Zavaleta and Hulvey, 2004; Larsen et al., 2005). In these cases, initial extinctions lead to large functional loss, as has been observed in several systems, particularly those with large animal consumers (Duffy, 2003). This type of relationship provides a greater challenge because it suggests that to maintain ecosystem function, it is not only important to conserve the full set of species, but also to protect the most sensitive species that are lost first with disturbance.

Assembly Experiments and Diversity-Function Mechanisms

Studies examining the ecological consequences of extinction can be broadly classified as comparative/observational or experimental (Schwartz et al., 2000). Observational research simply measures changes in biodiversity and associated function, and may or may not make comparisons with other observations of other systems. This helps to describe the complex relationships between extinctions or abundance changes and ecosystem function, but cannot usually address mechanisms. Most experimental studies have sought to isolate the relationship between species richness and ecosystem function by constructing randomly assembled communities (known as *assembly experiments*). Consequently, many of these experimental studies are not designed to address the effects of extinctions, but instead often attempt to identify the mechanisms driving the relationship between species richness and function. However, another recently proposed method uses removal experiments to examine the effects of extinction by actively removing species from naturally assembled communities (Diaz et al., 2003).

Although assembly experiments do not usually examine extinctions, they are briefly addressed here because they have increased our understanding of the mechanisms by which species diversity can be important for ecosystem processes. These experiments have demonstrated that at least three distinct mechanisms contribute to the positive effect of species diversity on ecosystem functions (Chapin et al., 1997; Tilman et al., 1997a,b; Loreau, 1998a,b).

The two primary proposed mechanisms are the *sampling effect* model and the resource use complementarity or *niche differentiation* model. According to the sampling effect model, as species richness increases, so does the probability of including a dominant competitor that will contribute disproportionately to ecosystem function (Tilman et al., 1997b). According to the niche differentiation or resource complementarity model, interspecific niche differences lead to complementarity and higher overall efficiency (usually in resource use),

causing an increase in ecosystem function. A good example is when several species of plants with different root lengths are able to maximize the use of nutrients available at different soil depths. The relative functional contribution of sampling effects and resource use complementarity have been widely debated (Wardle et al., 1997; Hector, 1998; Loreau, 1998b). Pacala and Tilman (2001) discuss how plant communities in the short-term can usually be characterized by the sampling effect, while over the longer term, interspecific competition and niche differentiation take over, preventing the dominance of fast growing species. A third model predicts that the frequency of *facilitative interactions* between species will increase as the number of species itself increases (Chapin et al., 2000). Facilitative interactions can increase ecosystem function if certain species interact directly or indirectly with other species in a way that increases that species' efficiency within its niche (Jonsson and Malmqvist, 2003). All three mechanisms are supported by the general rule that communities represented by many species contain a greater range of species traits than do species-poor communities.

Because of greater experimental tractability, a large proportion of assembly experiments have focused on grassland plants or laboratory aquatic microbial systems, with less attention given to how changing animal diversity may influence ecosystem processes (Duffy, 2002). Many experimental plant studies have shown that ecosystem functions such as annual rates of primary productivity, community respiration, disease or drought resistance, decomposition, and nutrient and water retention, increase with increasing plant species richness, but often saturate at a relatively low number of species (Naeem et al., 1994, Tilman et al., 1996; Hector et al., 1999). Other communities such as microbes, fungi, and arthropods also exhibit increased ecosystem function at higher levels of species richness (Didham et al., 1998; Chapin et al., 2000; Jonsson and Malmqvist, 2000; Wolters et al., 2000). Despite the generally observed positive trend, the form of the richness-function relationship is variable, and a few studies find no relationship between increased ecosystem diversity and function or stability (Pfisterer and Schmid, 2002; Schaffers, 2002). It is now becoming clear that the specific form of the diversi-

ty-function relationship depends on many factors that vary across a large range of ecological functions, scales, and systems, and also depends on other components of biodiversity and extinction order (Huston et al., 2000; Symstad et al., 2003).

Patterns of Non-Random Species Loss

Contrary to the assumptions of many assembly experiments, the sequence of species loss from a community under human pressure is not random but is determined by traits of organisms (Duffy, 2003). General principles of population biology as well as empirical evidence, confirm that extinction risk in both plants and animals is exacerbated by factors such as rarity, small population size, small geographical range size, slow population growth and specialized ecological habits (Didham et al., 1998; Pimm et al., 1988; Purvis et al., 2000; Duffy, 2003; Şekercioğlu et al. 2004). Şekercioğlu et al (2004) show a very strong positive correlation between bird specialization and extinction-proneness (Figure 1b in Şekercioğlu et al. 2004).

In both terrestrial and aquatic systems, large animals and higher trophic levels have been found to be highly vulnerable to extinction (Diamond, 1982; Redford, 1992; Didham et al., 1998; Pauly et al., 1998; Terborgh, 1988; Purvis et al., 2000; Alroy, 2001; Cardillo and Bromham, 2001; Jackson et al., 2001; Myers and Worm, 2003; Şekercioğlu et al., 2004). These studies have shown that two distinct processes tend to make large species especially vulnerable. First, large animals and those high in the food chain tend to be associated with the aforementioned demographic risk factors of small population size and slow population growth, making them more sensitive to disturbances such as habitat destruction (Pimm et al., 1988). Şekercioğlu et al. (2004) show that different avian functional groups have large differences in extinction-proneness, possibly leading to community disassembly. Although most research has focused on *consumers*, large invertebrate species and plant species can also be more sensitive, perhaps due to higher area and resource requirements (Duarte, 2000; Larsen et al., 2005). Second, large vertebrates (both predators and herbivores) are often selectively targeted by human hunting, and commonness does not necessarily confer pro-

tection. This is supported by evidence of mass extinctions of formerly abundant Pleistocene megafauna, which closely followed human arrival on continents and islands throughout the world, and by the decline or extinction of the bison, great auk, and passenger pigeon more recently (Diamond, 1982; Alroy, 2001).

A frequently reported threat that ultimately results in the non-random loss of species is human hunting. Intensive hunting has led to substantial reductions in the abundance of certain target species in both terrestrial and aquatic ecosystems (e.g., Redford, 1992; Myers and Worm, 2003). This has also caused changes in the structure and species composition within communities (Greenstreet and Hall, 1996). In general, as would be expected from classic foraging models, hunters in tropical forest regions primarily target large-bodied species (Peres, 1990; Bodmer, 1995). Large-bodied species provide hunters with a greater return on investment in weapons and ammunition. In the sea, relentless fishing pressure throughout the oceans has systematically depleted top predators, and then shifted to the next most valuable (usually the next largest) animals, a phenomenon known as ‘fishing down the food web’ (Pauly et al., 1998). Evidence for the parallel phenomenon on land is less well-documented, but there are reports of how extirpations of large, preferred species has led to increased hunting pressures on smaller, less-preferred taxa. In general, the responses of predator populations in aquatic and terrestrial systems to human harvesting seem to follow similar patterns, with removal of the largest-sized fauna from the system, ultimately, leading to dominance by smaller-bodied fauna. Sustained and uncontrolled harvesting will lead to a gradual decline in the body size spectrum of the animal population, and an increase in the biomass of small and mid-sized species as a proportion of the overall community (Rice and Gislason, 1996; Peres, 2000).

Consequences of Non-Random Species Loss

The order in which species go extinct can have dramatic consequences for ecological function (Petchey, 2000; Ostfeld and LoGiudice, 2003; Zavaleta and Hulvey, 2004). These conse-

quences will largely depend on two different types of species-specific traits: 1) Response traits that determine sensitivity to disturbance; and 2) Effect traits that determine the functional contribution of a species (Lavorel and Garnier, 2002; Naeem and Wright, 2003). If response and effect traits are independent, the order of species loss from communities will be random with respect to functional importance. However, if these traits are correlated, the relationship between richness and ecosystem function can be strongly modified (Larsen et al., 2005). For example, as described previously, several studies have found that large species, especially vertebrate consumers, are more extinction-prone. Many large species also have disproportionately strong impacts on ecosystem structure and functioning by influencing processes such as predation, selective grazing, seed predation, seed dispersal, nutrient regeneration, disturbance, and bioengineering activities (Owen and Smith, 1987; Redford, 1992; Terborgh et al., 1999; Jackson et al., 2001 and refs. therein; Duffy, 2002;). Consequently, the initial loss of sensitive species can cause a rapid and drastic decline in ecosystem function not predicted by models based on random species assembly. These results have been observed for mammals, birds, insects, and plants, where the most functionally important species (such as keystone species described below) are also the most extinction-prone (Petchey and Gaston, 2002; Zavaleta and Hulvey, 2004).

However, the opposite trend can occur if the most extinction-prone species do not strongly influence ecosystem functioning. This has been observed in some systems, particularly for plants, in which rare species, due to their low abundance, do not interact strongly in the ecosystem and are especially sensitive to disturbance (Wilsey and Polley, 2004). Although rarity is often associated with extinction-proneness, rare species can also be functionally important; other studies show that extinction-prone rare plants can be disproportionately important for maintaining invasion resistance (Lyons and Schwartz, 2001; Zavaleta and Hulvey, 2004).

In addition to species traits, the functional consequences of extinctions can be strongly influenced by how the remaining biological community responds following species loss. For

example, remaining species may maintain the same level of function if they are functionally redundant with the species that were lost (Walker, 1992). Remaining species can also alter their behavior to compensate for the roles played by the lost species. *Density compensation* can occur, frequently as a result of relaxation of competition in a less diverse community, whereby remaining species increase in abundance following species loss. In some cases, density compensation may act as a buffering mechanism to maintain ecosystem function (Lawton and Brown, 1993; Tilman and Downing, 1994; Ruesink and Srivastava, 2001).

Keystone Species

The keystone species concept has been the focus of scientific interest since its introduction by Robert T. Paine (Mills et al., 1993; Paine, 1966; Power et al., 1996; Navarrette and Menge, 1996; Kotliar, 2000). A keystone species is defined as one whose impact on its community or ecosystem is not only large, but disproportionately large relative to its abundance (Power et al., 1996). By definition, keystone species differ from dominant species in that their effects are significantly greater than would be predicted from their abundance. Given their importance in the community, loss of keystone species is expected to have major consequences for ecosystem structure and function. Identifying keystone species becomes essential to understanding how their loss will affect ecosystems. Ambiguity in the use of the term keystone, and the lack of an operational definition, led to initial criticism of its continued application in research and policy contexts (Mills et al., 1993) and was later followed by clarification of the concept (Power et al., 1996).

Several case studies of keystone species reviewed by Bond (1993), Mills et al., (1993) and Menge et al., (1994) make the following generalizations. First, keystone species occur in all of the world's major ecosystems. Second, keystone species are often, but not always of high trophic status (e.g. predators). For example, certain plant species may be keystone resources for pollinators or dispersers if they flower or fruit in times of scarcity (e.g. Terborgh, 1986). Third, keystone spe-

cies influence communities through mechanisms that include consumption, competition, mutualism, dispersal, pollination, disease, and by modifying habitats and abiotic factors (as “keystone modifiers”) (Bond, 1993; Mills et al., 1993). Keystone modifiers include ecosystem engineers such as beavers, which inundate forests and meadows (Naiman et al., 1988; Lawton and Jones, 1993; Pollock et al., 1995); and gophers and leaf cutter ants, whose tunnels pipe water through hillslopes (Elmes, 1991).

Knowledge of keystone species is clearly important, as conserving them is necessary for maintaining intact communities and ecosystems. The following sections outline some of the challenges in identifying keystone species (Power et al., 1996).

Keystone Species Versus Keystone Guilds

Although the clearest application of the keystone concept is to single species, identifying “keystone guilds” may be relevant to scientific understanding and management (Brown and Heske, 1990; Power, 1990). This term refers to groups of species that are known to have impacts that are disproportionately large relative to their collective biomass.

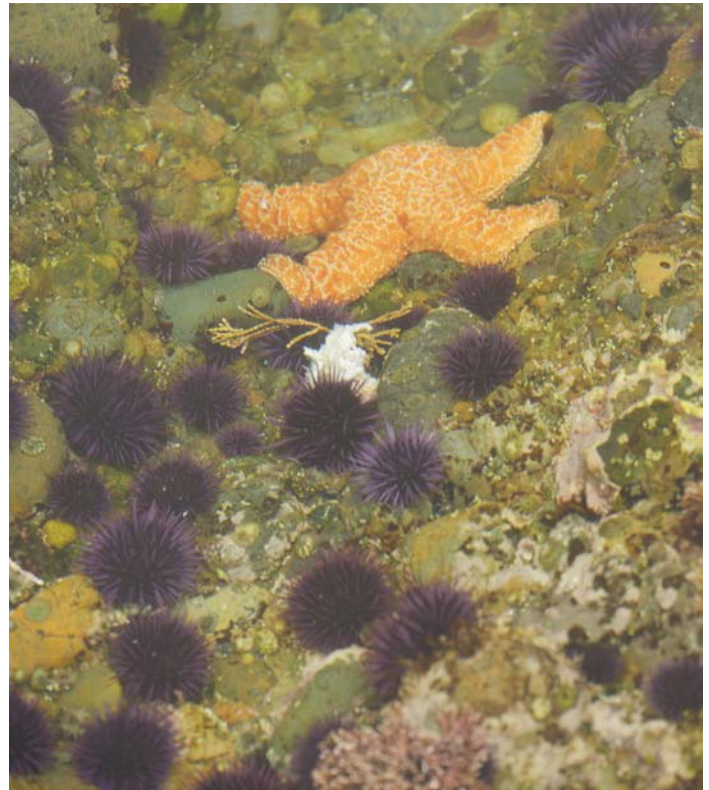
Time Scale

It is often a challenge to assess the impacts of species loss or abundance changes because the consequences can manifest themselves at different time scales. For example, the full impact of top predator removal from tropical forest ecosystems takes decades to centuries to become apparent, and considerably longer to ripple through different elements of the community (Terborgh, 1986; Dirzo and Miranda, 1991; Jackson et al., 2001).

Context Dependence

An increasing body of evidence suggests that keystone status is context-dependent. That is, keystone species are not neces-

sarily dominant controlling agents in all parts of their range or at all times. Some taxa play keystone roles only under certain conditions. For example, the keystone starfish species *Pisaster ochraceus* occupies an unambiguous keystone role on wave-exposed rocky headlands (Menge et al., 1994). In more wave-sheltered habitats, however, the impact of *Pisaster* predation may be weak or nonexistent.



Some starfish act as keystone species. Source: K. Frey

Overall, the keystone species concept shows how the loss of a species with low abundance may have surprisingly dramatic effects. In addition, the concept implies that focusing conservation concerns on a single species may be problematic since other species (keystone) may be unknowingly influencing its abundance. For further discussion on the utility of the keystone species concept as outlined in Power et al (1996), see Hurlbert (1997) and Kotliar (2000).

Table 1. Potential impacts of the loss of species at different trophic levels

Trophic Interaction	References
Predation: Loss of predators leads to an increase in herbivore densities and generally reduces primary productivity	Estes and Palmisano, 1978; Leigh et al., 1993; McLaren and Peterson, 1994; Terborgh and Wright, 1994; Estes and Duggins, 1995; Terborgh et al., 2001
Predation: Loss of predators leads to <i>mesopredator</i> release and increased levels of predation by mesopredators on their prey	Palomares et al., 1995; Ostfeld et al., 1996; Crooks and Soulé, 1999; Terborgh et al., 1999
Frugivory: Loss of frugivores frequently decreases plant regeneration through reduced seed dispersal, increased seed predation, and reduced seedling recruitment	Dirzo and Miranda, 1991; Redford, 1992; Hamann and Curio, 1999; Andresen, 1999; Ganzhorn et al., 1999; Wright et al., 2000
Herbivory: Loss of herbivores increases the density of seedlings and consequently plant regeneration	Dirzo and Miranda, 1991; Redford, 1992; Hamann and Curio, 1999; Andresen, 1999; Ganzhorn et al., 1999; Wright et al., 2000
Pollination: Loss of pollinators reduces seed and fruit set; causes erratic pollination service (fewer visits, mixed pollen loads, etc.); lowers crop yields; leads to reproduction by clonal growth; negative consequences for fig tree reproduction and further cascading effects on frugivorous birds and bats.	Janzen, 1974; Cox, 1983; Terborgh, 1986; Cropper and Calder, 1990; Cox et al., 1991; Thomson et al., 1991; Johnson and Bond, 1992; O'Toole, 1993; Steiner, 1993; Compton et al., 1994; Kearns and Inouye, 1997; Allen-Wardell et al., 1998; Kremen et al., 2002

Trophic Interactions

Loss of species results in the disruption of trophic interactions, which has consequences for ecosystem structure and function. A brief summary of the potential impacts of the loss of species at different trophic levels is provided in the following section, with the main points summarized in Table 1.

Loss of Predators

Ecological consequences of the loss of predators can be broadly classified into two categories: i) Increased herbivory due to higher densities of herbivorous prey following the loss of their predators; and ii) Increased densities of smaller predators known as mesopredators.

i. Increased herbivory

There is considerable evidence to suggest that the removal of top predators results in increased herbivory, and ultimately affects primary productivity. McLaren and Peterson (1994) investigated tree growth in Isle Royale National Park in Michigan, U.S.A. They found that plant growth rates were regulated by cycles in animal density, and trees increased in primary productivity only when released from herbivory due to predation by wolves on herbivores. It has also been shown that sea otters can have a profound effect on the structure of marine communities by controlling densities of herbivorous sea urchin populations, which feed on kelp beds. Absence of sea otters resulted in high densities of sea urchins, increased herbivory, and depletion of kelp beds (Estes and Palmisano, 1978; Estes and Duggins, 1995; Estes et al., 1998).

ii. Mesopredator release

Loss of predators may also lead to increased densities of smaller predators, a phenomenon known as 'mesopredator release' (Soulé et al., 1988). This release has been implicated in the decline and extinction of prey species (Soulé et al., 1988; Palomares et al., 1995; Sovada et al., 1995; Rogers et al., 1998; Crooks and Soulé, 1999). Crooks and Soulé (1999) describe a study of urban habitat fragments in coastal southern California. They test the hypothesis that the decline of the most common large predator (coyote) would result in the ecologi-

cal release of mesopredators, both native (striped skunk, raccoon, grey fox) and exotic (domestic cat, opossum), and that increased predation by these mesopredators would result in higher mortality and local extinction rates of scrub-breeding birds. They found that bird species diversity decreased with total mesopredator abundance and was higher in fragments where coyotes were either present or more abundant. Other examples of direct and indirect effects of predator loss are given in Table 2.

Loss of Herbivores and Frugivores

There is a large body of research documenting the important role played by mammals and large birds in herbivory, seed dispersal, and seed predation (Redford, 1992). In Mexico, Dirzo and Miranda (1991) compared two tropical forests, one with a full complement of large mammals (peccaries, deer and tapir) and another in which these species had been extirpated by hunters. A striking differences between the two forests exists; the hunted forest was typified by seedling carpets, piles of uneaten rotting fruits and seeds, and herbs and seedlings undamaged by mammalian herbivores — phenomena much less evident in the non-hunted forest. Similarly, in central Panama, a study by Wright et al. (2000) showed that poachers reduce the abundance of herbivorous mammals, which in turn alters seed dispersal, seed predation, and seedling recruitment for two palms (*Attalea butyraceae* and *Astrocaryum standleyanum*).

Hamann and Curio (1999) assessed the potential impact of frugivore extirpations on forest regeneration in a wet tropical rainforest ecosystem in the Philippine islands. They found that dispersers of late-successional tree species were mostly endangered species including hornbills and fruit pigeons. Late-successional tree species were most specialized with respect to dispersers and could therefore be susceptible to extirpation following the loss of their dispersers due to overhunting.

In a comprehensive review, Şekercioğlu et al. (2004) present a general framework for characterizing the ecological and societal consequences of biodiversity loss and apply it to the global avifauna. The table in Appendix 1 describes

the ecological and economical contributions of avian functional groups and the consequences of their loss. The unique study is perhaps the first to provide a rigorous and comprehensive understanding of the ecosystem consequences of bird declines. The major findings suggested that 21% of bird species are currently extinction-prone and 6.5% are functionally extinct contributing negligibly to ecosystem processes. Their projections indicate that by 2100, 6–14% of all bird species will be extinct, and 7–25% will be functionally extinct.

A number of studies have highlighted the role of primates in forest regeneration. A study in a rainforest in southeastern Peru by Andresen (1999) showed a complex web of interactions among seed dispersers, seed predators, and secondary dispersers that influence the fate of seeds. The study documented the significance of primates for seed dispersal by showing that spider monkeys (*Ateles paniscus*) and howler monkeys (*Alouatta seniculus*) dispersed the seeds of 71 and 14 plant species respectively. In a dry deciduous forest in Madagascar, Chapman and Onderdonk (1999) assess the potential importance of primates as seed dispersers in tropical forests and evaluate the possible consequences of hunting primates for recruitment in tropical tree communities. They use a case study in the Kibale National Park, Uganda to show that disrupting the complex interactions among primates and fruiting trees can have negative and possibly cascading effects on ecosystem processes.

Loss of Pollinators

Many authors have documented exclusive mutualisms between plant species and their pollinators, and highlighted the potential consequences of disruptions of mutualisms for plant regeneration and food crop yields (Cox et al., 1991; Compton et al., 1994; Allen-Wardell et al., 1998). Pollinator loss can affect plants in several ways, including loss of, or reduced, seed set (Kearns and Inouye, 1997). In addition, a scarcity of pollinators may affect a plant's mating system, resulting in the production of less vigorous offspring. This is because in the absence of pollinators, a higher percentage of seeds may be set through *self-pollination*, decreasing *heterozygosity* and in-

creasing the expression of deleterious traits associated with *inbreeding*. On a broader scale, loss of pollinators or disruption of pollination systems may cause reduced seed and fruit production and ultimately, plant extinction. Any of these events will affect the organisms that consume seeds, fruits, or plants, or that use plants for nest construction. The plants most at risk from the loss of a pollinator are those that are *dioecious* and self-incompatible, those that have a single pollinator, and those that propagate only by seeds.

Bond (1994) developed a vulnerability index to rank the threat of extinction of a plant species due to the loss of pollinator or disperser mutualisms. The index assesses the vulnerability of a species by considering the following variables: the number of pollinator and disperser species needed, the level of *vegetative propagation*, whether the species is self-compatible, and whether the species depends on seedling recruitment. Analysis of case studies suggests that plants often compensate for high risk in one of the three categories by low risk in another. For example, self-incompatible plants with rare specialist pollinators often propagate vegetatively. Many of the species that appear vulnerable have compensatory mechanisms that buffer them in part from pollinator failure: the bird-pollinated species can be pollinated by beetles, and the dioecious ones can be wind pollinated (Bond, 1994). Some systems, including elements of the Cape flora in South Africa and lowland tropical rain forests, lack compensatory traits and the risk of plant extinction from failed mutualisms is high.

There is widespread concern regarding the potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields (Allen-Wardell et al., 1998; Kremen et al., 2002). Approximately 30% of human food is derived from bee-pollinated crops (O'Toole, 1993) and thousands of wild plants depend on the services of bees for seed and fruit formation. Managed and feral European honey bees, throughout the United States and some European countries, are experiencing major population declines due to introduced parasitic mites, pesticide misuse, bad weather, or threats from Africanized honey bees (Matheson et al., 1996). Worldwide, nearly 200 species of wild vertebrate pollinators

may be on the verge of extinction along with an untold number of invertebrate pollinators (Matheson et al., 1996). These declines are expected to have consequences that are both ecologically and economically significant, with serious implications for natural and agricultural systems.

Flying foxes (*Chiroptera: Pteropodidae*) are known to be of extraordinary ecological and economic importance throughout the forests of the old World tropics, but are seriously threatened by overexploitation. Many species appear to be in severe decline and several species are already extinct. A study by Fujita and Tuttle (1991) showed that at least 289 plant species rely to varying degrees on large populations of flying foxes for propagation. These plants, in addition to their many ecological contributions, produce some 448 economically valuable products. Additional evidence for the significance of flying foxes as pollinators is found in Cox et al. (1991) and Elmqvist et al. (1992).

There are several examples of extirpations of animal partners in reproductive mutualisms, but very few of subsequent plant extinctions. For example, the oil-collecting bee pollinator of a rare fynbos shrub *Ixianthes*, has become locally extirpated but the plant still sprouts and is not immediately threatened with extinction (Steiner, 1993). In Hawaii, extinction of native bird pollinators resulted in a change of pollinators for the *Freycinetia arborea*, but not extinction (Cox, 1983). Memmott et al. (2004) explored probable patterns of extinction in two large networks of plants and flower visitors by simulating the removal of pollinators and consequent loss of the plants that depend upon them for reproduction. Plant species diversity declined most rapidly with preferential removal of the most-linked or most generalized pollinators as compared to the least-linked or most specialized pollinators. However, both pollination networks were relatively tolerant to loss of component species. Overall, the evidence for functional declines associated with the loss of pollinators is mixed. Systems with *redundancy* in which pollinator species can interact with a single plant may tolerate declines, while other plant species in non-redundant systems may go extinct and crop yields may decline.

Table 2. Examples of documented trophic cascades (adapted from Pace et al., 1999)

Ecosystem	Cascade	Effect	References
<i>Marine</i>			
Open ocean	Salmon-zooplankton-phytoplankton	Twofold higher phytoplankton when salmon are abundant	Shiomoto, et al., 1997
Coastal	Whales-otter-urchins-kelp	Increased predation by whales on otters leads to increased urchin grazing and up to ten times fewer kelp	Estes et al., 1998
<i>Freshwater</i>			
Streams	Fish-invertebrates-periphyton	Production of periphyton affected (six-fold) by predation of invertebrate populations	Huryn, 1998
Shallow lake	Fish-zooplankton-phytoplankton	Significant changes in fish populations due to mortality lead to shifts in zooplankton size structure and corresponding strong effects on phytoplankton	Jeppesen et al., 1998
<i>Terrestrial</i>			
Tropical forest	Beetles-ants-insects-Piper plants	Beetles prey upon ants that remove herbivorous insects that consume plants; more foliage consumed in the presence of beetles	Letourneau and Dyer, 1998b
Boreal forest	Wolves-moose-balsam fir	Wolf predation controlled moose densities which in turn influenced primary productivity	McLaren and Peterson, 1994

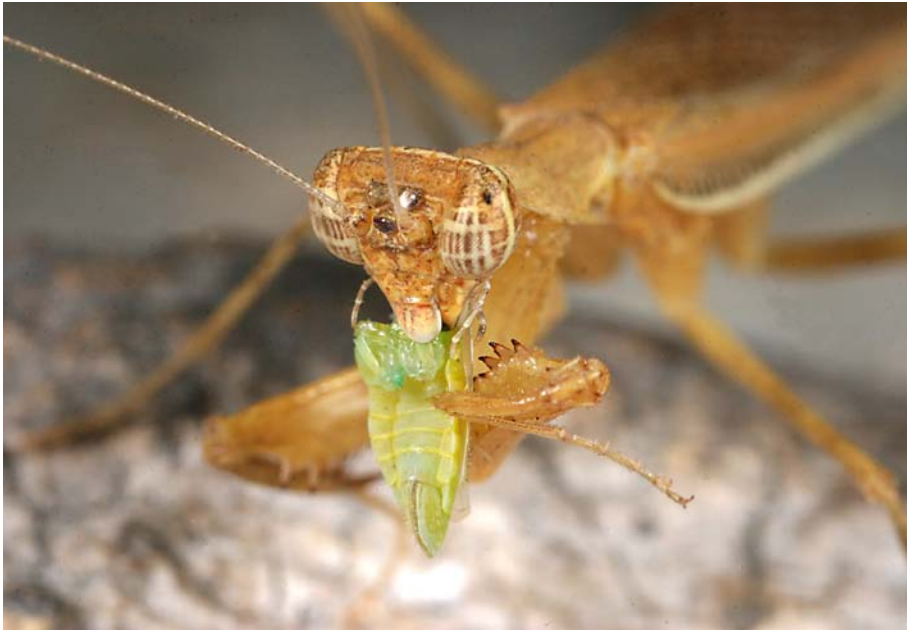
Weak Interactors

‘Strong interactors’ are similar to keystone species, and usually have disproportionately large effects on the rest of the ecosystem. As described in the previous section, the loss of strong interactors can cause dramatic changes in communities (Paine, 1969; Estes and Palmisano, 1978; Menge et al., 1994; Power et al., 1996). Experiments indicate that in many communities only a few species will have such strong effects, whereas most will have weak effects owing to small per capita effects and/or low abundance (Power et al., 1996; Paine, 1992; McGrady-Steed et al., 1997; Berlow, 1999). Alarmingly, some studies have shown that even the extinction of these ‘weak’ interactors could significantly alter natural communities because they play important stabilizing or ‘noise-dampening’ roles (Navarrete and Menge, 1996; Bengtsson et al., 1997; McGrady-Steed et al., 1997; McCann et al., 1998). Using a simple rocky-intertidal food web as a model system, Berlow (1999) showed that weak interactors play an impor-

tant, but unappreciated role in maintaining landscape-scale diversity if their effects on species abundances are strongly context-dependent, or highly variable over space and time. Overall, these studies indicate that even though strong interactors clearly play important functional roles, it is important not to overlook the non-obvious stabilizing effects of some weak interactors.

Trophic Cascades

All of the above changes in communities that follow species loss, especially changes in trophic interactions, can lead to extended cascading effects throughout ecosystems due to species interactions. Trophic cascades result in inverse patterns in abundance or biomass across more than one trophic link in a food web (Carpenter and Kitchell, 1998). For a three-level food chain, abundant top predators result in lower abundances of mid-level herbivores and higher abundance of basal producers. In this case, removing a top predator would result in a greater abundance of consumers and fewer pro-



Abundance changes of organisms on one trophic level has repercussions on other trophic levels. Source: S. Spector

ducers. Global extinction of a species or local extirpation of a population can result in disruptions of trophic cascades leading to dramatic shifts in community composition, structure, and function.

The ‘trophic cascade’ concept arose from the observations and experiments of field ecologists who observed the powerful effects of predators in the marine intertidal zone (Paine, 1980) and in lakes (Shapiro et al., 1975). Estes et al., (1989) provide a classic example of a trophic cascade in the sea otter–urchin–kelp interaction of coastal North America. Otters stabilize a system of abundant kelp forests by reducing urchin grazing. Removal of otters shifts the system to urchin dominance with substantial reductions in kelp coverage and productivity. Studies have documented trophic cascades in diverse ecosystems such as streams, lakes, marine intertidal zone, terrestrial and marine ecosystems including fields, soils, forests, and the open ocean. Table 2 provides a non-exhaustive summary of documented trophic cascades.

There may be a number of mechanisms suppressing cascades but recent studies have emphasized the importance of omnivores. Omnivory by top predators and mid-level consumers

can exert strong regulation of other trophic levels in ways not predicted by cascading trophic interactions. In Costa Rican lowland streams, electric enclosures were used to limit access by fish and shrimp to benthic communities. Increases in the number of insects in these enclosures did not lead to a significant reduction in algae, contrary to expectations based on cascading interactions (Pringle and Hamazaki, 1998). Similar results were observed when fish were excluded from areas of Venezuelan streams (Flecker, 1996). In these cases, the top predators are omnivores that consume both insects and algae thereby precluding the potential for cascades. Recent work has shown that higher predator diversity can dampen the magnitude of trophic cascades (Finke and Denno, 2004).

Overall, there appears to be much evidence for cascading effects of species loss from diverse ecosystems. Given accelerated human alteration of ecosystems, increased management of species and ecosystems may become necessary to either prevent cascading effects or remedy the disruption of cascades responsible for maintaining ecosystem structure and function.

Species Co-extinctions

The term “co-extinction” has been used to describe the process of the loss of parasitic insects with the loss of their hosts (Stork and Lyal, 1993). The concept has been expanded to describe the demise of a broader array of interacting species including predators with their prey and specialist herbivores with their host plants (Koh et al., 2004a). Koh et al. (2004b) define co-extinction as the loss of a species (the affiliate) upon the loss of another (the host).

Larval host plant specificity was an important ecological determinant of butterfly extirpations in Singapore (Koh et al., 2004a). The authors indicate that the number of locally ex-

tinct butterfly species is expected to increase exponentially with that of extinct host plants. Further, butterflies may go extinct sooner than their host plants when the declines, and not necessarily extinctions, of certain host plants (e.g., long-lived tree species) reduce butterflies to below their *minimum viable populations* (see section on ecological extinctions below). Although the loss of butterflies may result in declines of flowering plants that need these butterflies for pollination, the reverse is more likely to be true, whereby the loss of host plants drives butterfly extinctions. This is because caterpillars are often more dependent on plants for food than plants are on adult butterflies as generic pollinators (Ehrlich and Raven, 1964, Corlett, 2004).

Koh et al. (2004b) use a model to examine the relationship between co-extinction levels (proportion of species extinct) of affiliates and their hosts across a wide range of co-evolved interspecific systems: pollinating *Ficus* wasps and *Ficus*, parasites and their hosts, butterflies and their larval host plants, and ant butterflies and their host ants. They estimate that 6,300 affiliate species are “co-endangered” with host species currently listed as endangered, thus calling for a need to increase current extinction estimates by taking species co-extinctions into account. Species co-extinction is a manifestation of the interconnectedness of organisms in complex ecosystems. The loss of species through co-extinction represents the loss of irreplaceable evolutionary and co-evolutionary history (Nee and May, 1997; Purvis et al., 2000).

Ecological Extinctions

Extinction is irreversible. However, human activities influence the relative abundances of species more frequently than they cause extinction. Species abundance distributions warrant increased attention, because they usually respond more rapidly to human activities than do changes in species richness, and because they can have important consequences for ecosystems long before a species is threatened by extinction (Chapin et al., 2000; Wilsey and Potvin, 2000; Smith and Knapp, 2003). Estes et al. (1989) defined ecological extinction as the reduction of a species to such low abundance that, although it is still

present in the community, it no longer interacts significantly with other species. Very little is currently known about the prevalence of ecological extinctions, which can often be difficult to measure empirically.

It has been suggested that vertebrate populations which meet demographic and genetic criteria for viability (i.e., they occur at minimum viable population (MVP) size) could still be so sparse that they no longer interact as intensely as they previously did when they occurred at higher densities (Conner, 1988; Redford and Feinsinger, 2001). For example, if populations of seed-dispersing primates were maintained only at MVP levels, total numbers of seeds dispersed might decline abruptly and vegetation dynamics would be affected by a reduction (not extinction) of the primate population (Redford and Feinsinger, 2001). In other words, even if a species is not locally or globally extinct, a reduction in population size could initiate cascading effects. According to Redford and Feinsinger (2001): if the population of species A no longer maintains interactions with species B to Z due to a reduction in the population size of species A, the cascading effects that result will be indistinguishable from those where species A has gone completely extinct.

Redford and Feinsinger (2001) examine the impacts of population reduction of a target species due to harvesting and present two models of species interaction in forests with demographically viable but ecologically extinct animal populations. In the uniform model, a reduction in consumer population either by harvesting or another phenomenon reduces the population by 50%. All else being equal, this should simply lead to a 50% reduction in use, on average, across the resources used by the population, i.e. the response is uniform. The population displays the same pattern of relative selectivity as before, and even the least preferred class of resource still has its share of users. Reduction in population density has only quantitative but not qualitative effects. However, available ecological data do not support the assumption that individuals within a population will respond in a homogeneous fashion irrespective of that population's density. Evidence suggests that changes in animal population density appear to

have qualitative as well as quantitative effects through either one or both of two mechanisms: 1) Individuals that make up the consumer population are not identical. Every animal's choices may differ consistently from those of others. 2) An individual may change its choices as a direct or indirect result of the density of competitors of the same species.

According to the differential model, substantial reductions in animal population density will rarely, if ever, result in uniform reduction in interactions across the various classes of foods. Instead, depending on which particular individuals disappear and take their unique diet-related traits with them, some kinds of food may be consumed nearly as frequently as previously (when the population is at a higher density) while others will scarcely be consumed at all. For example, less preferred resources may be passed over by surviving foragers. If the different classes of resources are different species, then population dynamics of species less preferred by consumers might change dramatically, with resulting cascading effects.

The concept of ecological extinctions has been applied to terrestrial as well as marine settings. A study by Şekercioğlu et al. (2004) found 7% of birds being ecologically extinct whereas 1% were actually extinct (Figure 1a in Şekercioğlu et al., 2004). A study by Novaro et al. (2000) concludes that native large-bodied prey species (guanacos, *Lama guanicoe*, and rheas, *Pterocnemia pennata*) are ecologically extinct as prey and a source of carrion for native carnivores in northwestern Patagonia and likely throughout Argentine Patagonia. The geographical ranges and densities of native prey species have been greatly reduced due to hunting, habitat degradation, and competition with introduced livestock and wild exotic species. This is likely to lead to reductions in abundance and/or extinctions of native carnivores. In two different systems, Larsen et al. (2005) found that human landscape alteration strongly reduced bee and dung beetle abundance. Reduced abundance of bees was associated with lower pollination estimates for crops and reduced abundance of dung beetles was associated with disruption of estimated dung burial and associated functions such as seed dispersal.

Summary

Human domination of Earth's ecosystems is accelerating the extinction of species and is significantly changing the structure and dynamics of biological communities worldwide. Within this context, a relevant and pragmatic question that arises is the extent to which this loss of biodiversity matters and whether stability, productivity, and other aspects of the functioning of both managed and natural ecosystems are dependent on biodiversity. This synthesis attempts to provide a brief overview of the consequences of biodiversity loss to ecosystem functions and processes, focusing on evidence from field experiments, mechanistic theory, and quantitative field observations. Overall, increasing research and understanding of the ecological consequences of species loss has led to the emergence of generalities relevant for conservation planning and management.

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Glossary

Assembly experiments: experiments that are used to examine the functional relationship between species richness and ecosystem function using artificially assembled communities within controlled environments.

Biodiversity: the variety of life on Earth at all its levels, from genes to ecosystems, and the ecological and evolutionary processes that sustain it.

Consumers: organisms that ingest other organisms or organic matter in a food chain.

Density compensation: an inverse relation between population density and species richness; differences in species richness result in compensatory changes in the abundance of populations. For example, loss of one species could result in an increase in the population density of remaining species.

Dioecious: a dioecious plant has unisexual flowers or functionally equivalent structures of both sexes occurring on different individuals.

Diversity: use of the term diversity has led to some confusion, since diversity sometimes refers to the number of species, but more often refers to a measure combining species richness and evenness (the degree to which species in a community are equally abundant).

Ecosystem function: the term “ecosystem functioning” refers to the biogeochemical processes particular to a system, such as photosynthesis, decomposition, and nitrogen fixation

Ecosystem services: defined as the processes and conditions of natural ecosystems that support human activity and sustain human life. Such services include the maintenance of soil fertility, climate regulation and natural pest control, and provide flows of ecosystem goods such as food, timber and fresh water. They also provide intangible benefits such as aesthetic and cultural values.

Extinction: the global extinction of a species refers to the irreversible loss of all populations (and thus individuals) of the species across its entire range. At a smaller spatial scale, a species is considered locally extinct if there are no populations within a particular geographical area or site, a phenomenon that is also known as extirpation. Unlike global extinction, local extinction or extirpation is theoretically considered to be a reversible phenomenon. The reversibility of local extinctions is influenced by many factors including whether the population of individuals is open (individuals from extant populations in other locations could potentially recolonize) or closed (the population is isolated such that it is not possible for new individuals to recolonize). Ecological extinctions are a separate phenomena, whereby a population is reduced to a low enough level at which the species can no longer maintain its functional role in the ecosystem.

Facilitative interactions: interactions in which certain species interact directly or indirectly with other species in a way that

increases species’ efficiency within its niche.

Functional or ecological extinction: the concept of ecological extinction refers to the, “Reduction of a species to such low abundance that, although it is still present in the community, it no longer interacts significantly with other species,” (Estes et al. 1989).

Heterozygosity: a measure of the genetic diversity in a population, as measured by the number of heterozygous loci across individuals.

Higher-order interactions: refers to any non-additivity of the per capita interaction terms describing different species effects on the per capita growth rate of a focus species (Case and Bender 1981); has also been used to describe a functional change in the interaction of two species caused by a third species (Wootton 1993). These functional changes cannot be extrapolated from the dynamics of single species or species pairs in isolation.

Inbreeding: the mating of individuals who are more closely related than by chance alone.

Keystone guilds: a guild is defined as a group of species that exploit the same class of environmental resources in a similar way. This term groups together species that overlap significantly in their niche requirements without regard to taxonomic position. For example, in Brown and Heske’s study (1990), seeds constituted the primary food for three groups of granivores—rodents (*Dipodomys* sp., *Perognathus* sp., and *Peromyscus* sp.), harvester ants (*Pogonomyrmex* sp.) and various species of birds. The three groups of granivores together constitute a guild.

Mesopredator release: the process by which smaller predators known as mesopredators increase in abundance following the loss of top predators that control their densities; the process of mesopredator release leads to a decrease in the population density of small prey species.

Minimum viable populations: the smallest isolated population size that has a specified percent chance of remaining extant for a specified period of time in the face of foreseeable demographic, genetic, and environmental stochasticities, plus natural catastrophes. (Meffe and Carroll 1994)

Niche space: definitions of niche emphasize either an organism's individual characteristics or its relationships within a community. An alternative definition of niche involves arbitrary subdivisions grouping similar species, sometimes called 'habitat' or 'trophic' niches. Grinnell (1917) defined it as all the sites where organisms of a species can live (where conditions are suitable for life). Elton (1927) described the niche as the function performed by the species in the community of which it is a member. Hutchinson (1957) defined a niche as a region (n-dimensional hypervolume) in a multi-dimensional space of environmental factors that affect the welfare of a species.

Nutrient cycling: the processes by which elements are extracted from their mineral, aquatic, or atmospheric sources or recycled from their organic forms, converting them to the ionic form in which biotic uptake occurs and ultimately returning them to the atmosphere, water, or soil (taken from the Millenium Ecosystem Assessment Glossary).

Primary productivity: rate at which new plant biomass is formed by photosynthesis.

Redundancy: refers to a state of being redundant i.e. exceeding what is necessary.

Resilience: ecosystem resilience measured as a rate of change refers to the amount of time taken for an ecosystem that has been displaced from equilibrium returns to it. It is also defined as how fast a variable that has been displaced from equilibrium returns to it (Pimm 1991). Holling (1973) defines resilience to be how large a range of conditions will lead to a system returning to equilibrium. In his definition, highly resilient systems will almost always return to equilibrium,

whatever happens to them; systems that are not resilient will often be fundamentally changed after a perturbation, perhaps by losing species or by moving to a new equilibrium involving very different species' densities.

Resistance: measures the consequences when a variable is permanently changed: how much do other variables change as a consequence? If the consequent changes are small, the system is relatively resistant. Resistance is measured as a ratio of a variable before and after the change. (Pimm 1991).

Self-pollination: transfer of pollen from the anther to the stigma of the same flower.

Species invasions: the introduction of species beyond their native ranges. There are many examples of disastrous invasions by such species that has resulted in losses of native species, changes in community structure and function, and even alterations of the physical structure of the system. Not all species invasions result in disaster (Meffe and Carroll 1994).

Succession: the natural, sequential change of species composition of a community in a given area.

Vegetative propagation: a process of asexual reproduction by which new plant individuals arise without the production of seeds or spores.

Appendix I

Ecological and Economical Contributions of Avian Functional Groups (From Şekercioğlu et al. 2004. Proceedings of the National Academy of Sciences 101 [52]: 10842-18047. Copyright 2004 National Academy of Sciences, U.S.A).

Functional group	Ecological process	Ecosystem service and economical benefits	Negative consequences of loss of functional group
Frugivores	Seed dispersal (1–4)	Removal of seeds from parent tree (5–8); escape from seed predators (9,10); improved germination (11,12); increased economical yield (13–16); increased gene flow (17–19); recolonization and restoration of disturbed ecosystems (20–24)	Disruption of dispersal mutualisms (25–27); reduced seed removal (28); clumping of seeds under parent tree (29); increased seed predation (10); reduced recruitment (28,30); reduced gene flow (31,32) and germination (12,33,34); reduction (35,36) or extinction (37–40) of dependent species
Nectarivores	Pollination (3,41,42)	Outbreeding of dependent (42–44) and/or economically important species (14,45)	Pollinator limitation (45,46); inbreeding and reduced fruit yield (47–52); evolutionary consequences (41,45,53); extinction (37,54)
Scavengers	Consumption of carrion (55)	Removal of carcasses (56,57); leading other scavengers to carcasses (55); nutrient recycling; sanitation (56,57)	Slower decomposition (55); increases in carcasses (56,57); increases in undesirable species (56,57); disease outbreaks (56,57); changes in cultural practices (56,58)
Insectivores	Predation on invertebrates	Control of insect populations (59–65); reduced plant damage (62,66,67); alternative to pesticides (68–70)	Loss of natural pest control (68,69); pest outbreaks (59,61,71); crop losses (62); trophic cascades (72)
Piscivores	Predation on fishes and invertebrates Production of guano	Controlling unwanted species (73); nutrient deposition around rookeries (74–78); soil formation in polar environments (79); indicators of fish stocks (80); environmental monitors (81)	Loss of guano and associated nutrients (82); impoverishment of associated communities (83); loss of socioeconomic resources (84) and environmental monitors (81); trophic cascades (73,85)
Raptors	Predation on vertebrates	Regulation of rodent populations (86,87) secondary dispersal (88)	Rodent pest outbreaks (89); trophic cascades (72,90,91); indirect effects (92)
All species	Miscellaneous	Environmental monitoring (93,94); indirect effects (88,95–101); bird-watching tourism (102–104); reduction of agricultural residue (105); cultural and economic uses (106)	Losses of socioeconomic resources (102,107) and environmental monitors (108); unpredictable consequences (96)

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