Extinction and the importance of history and dependence in conservation

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ABSTRACT. *Many extinct species have had profound effects on other species through their interactions. In themselves, these interactions or functions are an integral part of biodiversity. The influence of species upon others operates in a variety of ways, independently or synchronously, and includes dispersal, habitat creation and maintenance, provision of nutrients or food resources, and reduction in competition from other species. In particular, large and/or abundant vertebrates that are now extinct or threatened have contributed to extensive environmental heterogeneity. This heterogeneity, or diversity, found in the form of spatial and temporal patches, has generally increased biodiversity. Loss of these vertebrates has major impacts on the species left behind. These impacts range from extinction to various levels of decline.*

*The extinct and extirpated species discussed include the Passenger Pigeon (*Ectopistes migratorius*) , Carolina Parakeet (*Conuropsis caroliniensis*), Dodo (*Raphus cucullatus*), American Bison (*Bison bison*), bears (*Ursus *spp.), Black-tailed Prairie Dog (*Cynomys ludovicianus*), gophers (*Thomomys *spp.), Elephants (*Loxodonta africana*), White Rhinos (*Ceratotherium simum*) and the Pleistocene megafauna including mammoths (*Mammuthus *spp.), horses (*Equus spp.*), camels (*Camelops *spp.), and Ground Sloths (*Nothrotheriops shastense*).*

Affected species discussed are:

*(1) herbs and shrubs including wild grapes (*Vitis *spp.), Sand Cherry (*Prunus pumila*), Miccosukee Gooseberry (*Ribes echinellum*), cabbage family plants (*Lepidium *spp.), pawpaws (*Asimina *spp.), Pokeweed (*Phytolacca americana*), Buffalo Clover (*Trifolium stoloniferum*), Glacier Lily (*Erythronium grandiflorum*), Yellow Sweetvetch (*Hedysarum sulphurescens*), Porsild's Bluegrass (*Poa porsildii*), Asiatic June Grass (*Koeleria asiatica*), Creosote (*Larrea tridentata*), and May Apple (*Podophyllum peltatum*),*

*(2) various trees and larger shrubs including Tambalacoque (*Sideroxylon grandiflorum*), a Palm (*Scheelea rostrata*), Guapinol (*Hymenaea courbaril*), Jicaro Tree (*Crescentia alata*), Yellow Mombin (*Spondias mombin*), American Beech (*Fagus grandifolia*), Critchfield's Spruce (*Picea critchfieldii*), Osage Orange (*Maclura pomifera*), Hercules'-club (*Aralia spinosa*), Honey Locust (*Gleditsia triacanthos*), North American Holly (*Ilex opaca*), and*

*(3) some animals including American Burying Beetle (*Nicrophorus americanus*), California Condor (*Gynogyps californianus*), Black-footed Ferret (*Mustela nigripes*), Mountain Plover (*Charadrius montanus*), Swift Fox (*Vulpes velox*), and Burrowing Owl (*Athene cunicularia*).*

Also highlighted as significantly affected are the heterogeneous prairie, savanna, and parkland ecosystems.

History is important in understanding rarity and protecting a single species often leads to the protection of many species.

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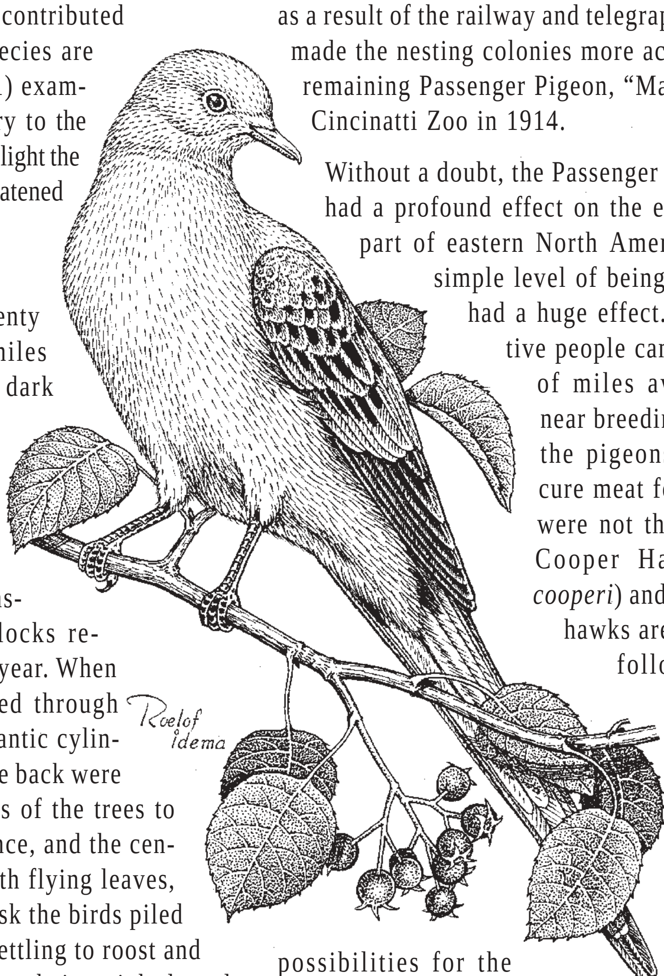
Some species, for a variety of reasons, have profound effects on other species, and the diversity of interactions between species is appropriately recognized as a part of biological diversity (Thompson 1996). Extinction or extirpation of species leads to the decline of other dependent species and biodiversity in all its forms (genetic, species, ecosystem, functional) requires protection. A consideration of historical causes of rarity, including extinction (total loss of a species) and extirpation (regional loss of a species), is valuable in developing hypotheses for research, and for suggesting appropriate actions for conservation of overall biodiversity. Often conservationists need to step back from the mire of current circumstances and peer back into evolutionary history to understand the species "crisis" in its full perspective.

In this paper several examples of extinct, extirpated, or threatened species that have contributed to the current rarity of other species are presented. The objective is to (1) examine the potential value of history to the understanding of rarity, and (2) highlight the frequent importance of a single threatened species to many others.

THE PASSENGER PIGEON

Huge migrating flocks up to twenty miles wide and hundreds of miles long blocked out the sun like dark clouds and often took days to pass by. The droppings fell like hail and left a characteristic odour in the air. They were called Passenger Pigeons because they looked like long passenger trains. The immense flocks remained together for most of the year. When feeding in the forest they rolled through with a deafening roar like a gigantic cylindrical lawnmower. Birds from the back were continually flying up to the tops of the trees to come down in front of the advance, and the center of the cylinder was filled with flying leaves, vegetation, and dust. Then at dusk the birds piled up on top of one another when settling to roost and the noise of limbs breaking under their weight lasted throughout the night. Frequently beneath the roosts, sometimes forty miles long and three miles wide, dung accumulated to a foot deep, and killed the understory vegetation as well as all the trees. Breeding colonies were enormous, and localities changed from year to year depending on the availability of food (primarily mast including beechnuts and acorns from the previous year). One of the larger breeding colonies in Wisconsin in 1871 was 125 miles long and 6-8 miles wide, and was estimated to include well over 100 million adults. Yes, truly, "the Passenger Pigeon (*Ectopistes migratorius*) moved around and nested in such enormous numbers as to confound the senses" (Schorger 1955).

Passenger pigeons occurred throughout much of eastern North America. Only a few centuries ago their population density was 5-6 birds/acre and the total population was 3 to 5 billion. It comprised 25-40% of the total bird population in the U.S. at the time (Schorger 1955), but by the late 1800s, the species was declining, due largely to over-hunting and loss of habitat associated with settlement by Europeans. As numbers declined, social facilitation in food finding was probably seriously compromised. At the same time, the disruption of nesting colonies was increased as a result of the railway and telegraph network, which made the nesting colonies more accessible. The last remaining Passenger Pigeon, "Martha," died in the Cincinatti Zoo in 1914.



Passenger Pigeon, *Ectopistes migratorius, illustrated by Roelof Idema*

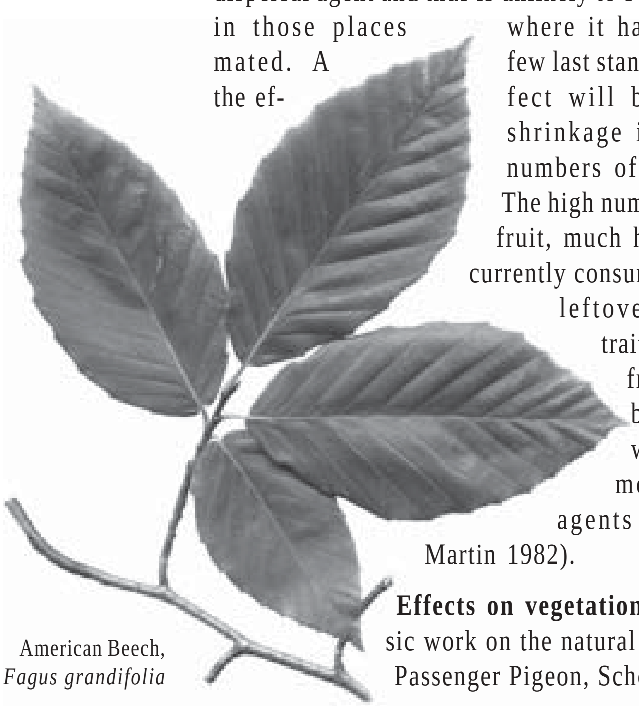
Without a doubt, the Passenger Pigeon must have had a profound effect on the ecology of a large part of eastern North America. On the very simple level of being a food source, it had a huge effect. Hundreds of native people came from hundreds of miles away and located near breeding colonies to use the pigeons as food and to cure meat for later use. They were not the only predators. Cooper Hawks (*Accipiter cooperi*) and a variety of other hawks are reported to have followed the flocks, but the effects extended far beyond the providing of food.

Wasted berries: Consider, for example, the possibilities for the Passenger Pigeon's dispersal of seeds consumed in berries and berry-like fruits. Passenger Pigeons ate many native berries including blueberries, cherries, cranberries, currants, gooseberries, grapes, juneberries, mountain ash, mulberries, raspberries, and strawberries. It seems logical that the extinction of the bird has led to many berries lying on the ground directly under the mother plant—in short, wasted.

For instance, currently in some parts of southern Ontario much of the fruit of wild grapes falls beneath the vines. The only dispersal agents observed are Bohemian Waxwings (*Bombycilla garrulus*) that appear irregularly in eastern North America, Common Starlings (*Sturnus vulgaris*) that were introduced to North America from Europe in 1890, and occasional Robins (*Turdus migratorius*) (personal observation). Black Bears (*Ursus americanus*) also feed on wild grapes to a large extent under certain conditions (Kasbohm et al 1995) but are now extirpated over most of southern Ontario. Passenger Pigeons must have been important dispersal agents in the past; without them, will the range of certain wild berries eventually be reduced?

This appears to be the case for the dune race of the Sand Cherry (Catling and Larson 1997). It is declining around the Great Lakes of eastern North America as a result of selective browsing by dense populations of Eastern White-tailed Deer. If the Cherry were being introduced continually through dispersal of seeds, it could have a chance for survival. However, in some, if not in all, of the productive localities it drops all of its fruit on the sand where it remains without any dispersal. In the past a flock of Passenger Pigeons could have consumed thousands of presently wasted fruits on the dunes in a few minutes and then, only a few hours later, dispersed the seeds by the thousands to isolated and targeted dune systems hundreds of miles away. They would have been attracted to these dunes because of the Cherries growing there and, by the same token, this sandy environment was precisely where the seeds needed to get. Not everything has to be left to speculation. In 1885 Catherine Parr Traill wrote with regard to the Sand Cherries: "so eagerly is the fruit sought by pigeons that it is difficult to obtain any quantity."

Today the Sand Cherry appears to lack a significant dispersal agent and thus is unlikely to be reintroduced in those places where it has been decimated. A few last stands remain, but the effect will be a gradual shrinkage in range and numbers of populations. The high numbers of edible fruit, much higher than is currently consumed, may be a leftover dispersal trait of the Cherry from days gone by when there were many more dispersal agents (Janzen and Martin 1982).



American Beech,
Fagus grandifolia

Effects on vegetation: In his classic work on the natural history of the Passenger Pigeon, Schorger (1955 p. 86) noted that the vegetation that developed on an old pigeon roost differed greatly from that which was present prior to the roost. For example the growth of Pokeweed (*Phytolacca americana*), also frequently called Pigeonberry, was luxuriant. There was also apparently a widespread belief among gatherers of Ginseng (*Panax quinquefolius*) that this plant grew most abundantly at old pigeon roosts. Possibly the decline of the incredible numbers of American Beech trees (*Fagus grandifolia*), which were recorded in all northeastern presettlement surveys, can be partially explained through dispersal and habitat maintenance by Passenger Pigeons. Right now the decline remains an enigma (Cogbill 2000, p. 270), but habitat maintenance could have involved patchy disturbance to overstory, understory, and forest floor by both the Pigeons' behaviour and their droppings. The effects of this patchy disturbance undoubtedly ranged from complete removal of all plant species to differential selection based on levels of disturbance in combination with other factors. Passenger Pigeons have already been implicated as dispersal agents in the rapid Holocene migrations of nut trees (Webb 1986). The composition of eastern North American forests, including both woody and herbaceous species, may have been quite different prior to the extinction of the pigeons.

CAROLINA PARAKEETS

Like Passenger Pigeons, Carolina Parakeets were highly social, gathering to feed in large flocks of hundreds.In presettlement times, this spectacular, green, red, and yellow, hardy parrot was abundant throughout much of the southeastern U.S. Too often they fed on crops and were slaughtered mercilessly. By 1900 they were gone. Coincidentally the last one, like the last Passenger Pigeon, died in the Cincinnati Zoo in 1914. They were sufficiently abundant to have strongly influenced southeastern vegetation.

American Burying Beetle: *Nicrophorus americanus*, one of forty species of insects protected under the U.S. Endangered Species Act, may also have declined as a result of the extinction of the Passenger Pigeon. These beetles, the largest of their group in North America, bury and cure carcasses that then serve as the food resource of their offspring. Passenger Pigeons would certainly have provided an abundance of carcasses of appropriate size to permit optimal reproduction for the Burying Beetle (Amaral et al 1997).

How many other plants and animals of deciduous woodlands, some of which are now rare in at least parts of their range, benefited from the disturbances of Passenger Pigeons? The ecology of woodland herbs is understudied, but many evolved in situations where disturbances to woodlands were greater than they are today and far more complex and diverse. Any eastern

North American woodland herb is a candidate for consideration of the beneficial effects of Passenger Pigeons as well as of a variety of other extinct and extirpated animals (see below).

Some scientists have speculated that the large population of Pigeons may be a relatively recent post-colonial phenomenon, which resulted because indigenous peoples were no longer competing with the birds for nuts. While the population of indigenous people did decline between 1700 and 1900 and there were changes in their food habits (Neumann 1985), this seems unlikely. Many indigenous peoples in this area practiced agriculture and hunted for food so they were not likely to have been major competitors for nuts. The early explorers found Passenger Pigeons extremely abundant and this was prior to the disruptions caused to indigenous lifestyles by colonization. Cartier saw infinite numbers in the mid-1500s and Champlain recorded countless numbers of pigeons on the coast of Maine in 1605. In addition there is evidence that Passenger Pigeons were a regular component of the fauna as far north as Peace River since 8000 B.P. (Driver and Hobson 1992).

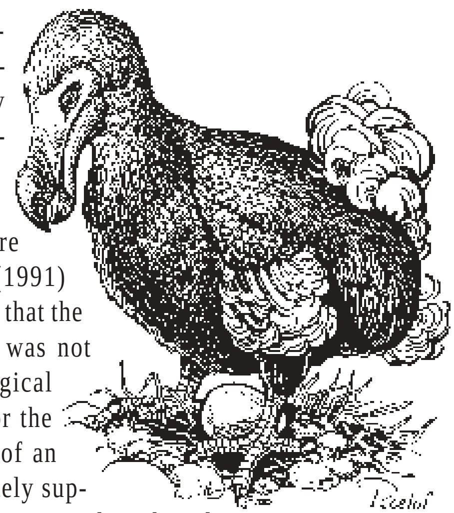
When examining the rarity of a species, scientists should always look at extinct species as only one of the possible causes.

The Miccosukee Gooseberry: Some rare plants are associated with relatively high levels of calcium and soil fertility as well as openness of the woodland canopy in mesic sites where a dense canopy develops in a gap. Many of the rare plants of the southeastern U.S. and the northeast (e.g. Miller 1989) are lime-loving calcicoles. The Miccosukee Gooseberry is one such plant, and currently, it is one of the rarest plants in North America, but it is not clear why. Where it does occur, it is abundant in a number of habitats (personal observation), it is readily pollinated, and it develops ample fruit (Catling et al 1998). It may have been an abundant member of the southeastern Passenger Pigeon species guild only a few centuries ago, and the Pigeons probably acted as dispersal agents for this rare gooseberry At that time the southeastern woodlands would have been more fertile and had higher calcium levels due to the fertilization by huge flocks of both Passenger Pigeons and Carolina Parakeets (*Conuropsis carolinensis*).

Burying Beetle, *Nicrophorus americanus*. Photographed by K. Bolte

BACK TO THE DODO

A classic example of the extinction of one species resulting in the rarity of another is that of the Dodo (*Raphus cucullatus*) and the Tambalacoque tree (*Sideroxylon grandiflorum*, formerly *Calvaria major*) on the island of Mauritius in the western Indian Ocean. It was thought that the seeds of the tree had to pass through the digestive tract of the bird to overcome persistent seed dormancy. In 1681 the huge, flightless bird was extinct, and by 1973 only thirteen very old trees were left because the species had not reproduced for 300 years (Temple 1977).



Dodo Bird, *Raphus cucullatus*, courtesy of Tropical Conservancy

As with other explanations concerning extinct animals, this mutualism has been debated (Owadally 1979, Temple 1979). Other evidence suggested that there had indeed been reproduction over the past 300 years and that there were hundreds of trees left. Witmer (1991) summarized the debate concluding that the Dodo/Tambalacoque relationship was not necessarily an exceptional biological phenomenon, because the need for the seed to pass through the gizzard of an extinct giant bird was not adequately supported. In addition giant tortoises, a giant lizard, and a large-billed parrot, all extinct, may also have been effective dispersal agents of Tambalacoque. The Dodo/Tambalacoque relationship may be no different than hundreds of other non-specific seed dispersal systems. In short the demise of the Dodo may well have been a factor in the rarity of the Tambalacoque tree, but there is insufficient evidence to make it a cause.

This is disturbing because the notion that the seeds of Tambalacoque required treatment by a Dodo's gizzard is a very attractive idea. No wonder it became textbook dogma and has thrived in the ecological literature! This over-entrenched example is instructive in suggesting that one should always consider extinct species as only one of many factors potentially associated with rarity.

AN ASIDE ON THE IMPORTANCE OF DIGESTIVE TREATMENTS

Fruit eaters have long been known to defecate seeds with improved germination and growth as compared with those that have not passed through a digestive system (Ridley 1930). Rates of germination exceeding 50% have been reported following passage through many birds and mammals. However, some of the supporting observations are anecdotal rather than quantitative. There are also some major gaps. For example Willson (1993) noted that "almost no studies of mammalian diets in North America consider the germinability and survivorship of seeds after treatment by the consumer." Furthermore the extent to which treatment by a vertebrate's gastrointestinal system is advantageous is complex from an ecological viewpoint and it requires more study in the case of many species (Willson 1983). Recent studies of declining fruit trees on Mauritius have suggested that the seeds may have required only pulp removal, not digestive treatment, and this could have been done by a number of now-extinct species including various parrots, tortoises, a coconut crab, and a lizard (C. Barlow, personal communication).

The importance of pulp removal or digestive treatment in the current rarity of many species may be extensive. Large flightless, or poorly flying, ground pigeons once existed on other islands of the Indian Ocean, but hundreds of cases of poor germination in the absence of pulp removal or seed abrasion are known from around the world and many have been known for a long time. If only one seed in a million of the North American Holly (*Ilex opaca*) survives by the time the tough seed coat decays (Ives 1923), it may well be dependent on a specific fruit eater. Although some recent comprehensive and quantitative studies support this general effective dispersal of seeds by fruit eaters (Janzen 1981), there is still a need for much more information to provide a better ecological understanding. Interestingly it is not just seeds of fleshy fruits that are dispersed effectively by animals but also small seeds of many herbaceous plants used as forage, in which case the foliage serves as the fruit (Janzen 1984). Additionally the value of the dispersal agent may often be in moving the seeds to the right place, not only in contributing to germination or only moving the seeds.

> *Extinct animals are a very important consideration in the understanding of the form and function of many existing species.*

LOSS OF PREHISTORIC MEGAFAUNA AND THE MAGNITUDE OF EFFECT

Injury to Hercules'-club trees (*Aralia elata*) promotes development of prickles, and these prickles are presumed to be an adaptation to protect the plants from mammalian browsers. During a study of prickle distribution in these trees in the Smoky Mountains of Tennessee, White (1988) did not notice damage to the plants, so that the prickles seemed unnecessary, at least today. He speculated that prickles might represent an adaptation to protect plants from an extinct fauna. He noted the presence of bison and elk in the area until around 1800 and he noted that there was a much richer mammalian fauna several thousand years ago. The fact that morphological features like prickles and certain characteristics of fruit are out of place today was outlined in the classic paper of Janzen and Martin (1982) entitled "Neotropical Anachronisms: the fruits the Gomphotheres ate." The gigantic compound thorns of Honey Locust (*Gleditsia triacanthos*), the thick broad-based thorns on some Central American trees, and the impressive thorns on hawthorns are out of place today and explanations involving monkeys and deer are unconvincing. All one has to do is think in terms of elephants pushing trees over with their foreheads, and five-metre-high giant sloths pulling down branches with their huge curved claws. Considering the examples, extinct animals are a very important consideration in the understanding of the form and function of many existing species.

Another way of interpreting the potential effect of the recently (10-12 000 years before present) extinct Pleistocene megafauna is to look as at a Pleistocene bestiary, and consider both the numbers of different kinds of animals and their sizes. Solely by looking at the giant plant eaters in eastern North America the diversity was incredible. There were large elephant-like mammals (gomphotheres or proboscideans) including the grazing mammoths (*Mammuthus* spp.) and browsing Mastodons (*Mammut americanum*); the browsing and grazing giant sloths (*Eremotherium* and *Megalonyx* spp., and *Glossotherium harlani*); tapirs (*Tapiris* spp.); giant beavers (*Casteroides* spp.); long-nosed and flat-headed peccaries (*Platygonus* and *Mylohyus* spp. respectively); giant deer (*Cervalces* spp.); woodland musk-oxen (*Bootherium* and *Symbos* spp.); and horses (*Equus* spp.) (Anderson 1984). As "giant" suggests, some of these animals were very large and much larger than their living relatives of today. For example, the giant beavers were 2 m long and 1 m high (the size of a modern Black Bear). Preying upon the plant eaters were giant predators such as the Dire Wolf (*Canis diris*), the short-faced bears (*Arctodus* spp.), Lions (*Panthera leo atrox*) and the saber-tooth cats (*Smilodon* and *Homotherium* spp.).

Although climate change may have played a role (e.g. Hayes 1991) in the extinction of all these giants over a very short period at the end of the Pleistocene (10 000 yr B.P.), human hunters (e.g. Martin 1984, Fisher 1984) played a major role, too. The "Clovis" spear points were discovered in abundance with mammoth carcasses on the Llano Estacado (the southernmost high plains) near Clovis, in the state of New Mexico. It is possible that these new hunters (15 000 yr B.P.) developed highly efficient hunting techniques and selected certain species, and thus contributed in a major way to the extinction of these species, but regardless of efficiency, they had the help of dense populations of starving predators (Janzen 1983). There can be little doubt that the loss of the large herbivores had a profound effect on both other species and ecoystems, but was it responsible for a rarity today that has lingered over several thousand years?

Effects on California Condors: Based on discoveries of bones, it is known that California Condors (*Gymnogyps californianus*) were once widespread in the southern parts of North America (north to New England). More recently these very large, vulture-like scavengers became confined to isolated parts of California. Recent radiocarbon dating of bones suggests that they became rare or extirpated over most of their North American range more than 10 000 years ago, coincident with the extinction of megafauna upon which they are presumed to have been largely dependent (Emslie 1987). In pre-settlement times, they did have a broader range which was further reduced due to poisoning by humans (Pimm 2000, Snyder and Snyder 2000).

Plant extinctions and rarity: Plant extinctions at the close of the Pleistocene are undocumented, with the exception of Critchfield's Spruce (*Picea critchfieldii*). The cause of extinction of this wind-dispersed species is unclear (Jackson 1999), but megafaunal interactions have been suggested as a possible cause.

A forest palm (*Scheelea rostrata*), for instance, may have declined in numbers and distribution due to extinction of the gomphotheres (elephant-like mammals) that were previously responsible for dispersing fruits. Now the fruits rot below the parent trees. The few seeds that escape predation (enhanced by concentration) are subject to severe interspecific competition (Janzen and Martin 1982).

In the Pacific lowlands of Costa Rica, another neotropical tree, the Yellow Mombin (*Spondias mombin*) experiences 95% seed predation by beetles in natural forests and is killed by fires in savannas. Recruitment is confined to forest edges that are free of fire for long intervals. The extinct megafauna would have defecated more nuts in sites of high quality for sapling survival (Janzen 1985).

GOMPHOTHERES, TOXODONTS, AND GROUND SLOTHS

Gomphotheres, toxodonts, and ground sloths not only contributed significantly to the dispersal of species they ate but also to the dispersal of species that were distributed as burrs. They also provided open disturbed sites for colonization by plants.

Janzen and Martin (1982) speculated that the Central American neotropical savanna of today, which is patchily browsed by free-ranging livestock, may be more like the habitats that existed for hundreds of thousands of years than like the very young (<10 000 years old) habitats, including certain climax forests, that existed at the time when the first Spanish explorers arrived. Obviously earlier and possibly more relevant reference points are available for protection of biodiversity than the traditional "pre-settlement times."

Jicaro Trees: Remains of central American Pleistocene Horses (*Equus fraternus*) are common in Santa Rosa National Park in Costa Rica, and the effect of contemporary horses suggest that this extinct species must have been a dispersal agent for Jicaro Trees (*Crescentia alata*). Today seedling and saplings of Jicaro Trees are rare where free-ranging wild horses are absent. In these areas the indehiscent fruits lie on the ground and rot in the rainy season, and fermentation of the fruit pulp kills the seeds. In areas inhabited by contemporary Horses (*Equus caballus*), surrogate Pleistocene dispersal agents (Janzen 1982), the range of Jicaro has increased. The recent increase of Jicaro may have, in turn, increased the population of nectarivorous bats that visit the nocturnal flowers (Janzen & Martin 1982), and may also have increased populations of spiny pocket mice (*Liomys salvini*) that avidly harvest seeds from horse dung. The mice cannot themselves open the hard fruits (Janzen 1982).

Howe (1985) suggested that "the megafaunal syndrome must be refined with exclusive and ecologically sound criteria before it can be a useful tool in ecology." Although it has not been refined substantially, it has proven to be a useful tool in ecology. With regard to Howe's criticism, remember that it is the lack of dispersal that is out of place, not the production of billions of viable seeds of which only a tiny fraction reach reproductive maturity. In addition a species may be disadvantaged by one phenomenon but at the same time advantaged by another. Thus when a mutualist partner becomes extinct, the other partner, with its anachronisms, may live on. It may become rare or, for other reasons, it may become common. Since the megafaunal extinctions, the survival of Guapinol (*Hymenaea courbaril*) has been dependent on scatterhoarding Agoutis (*Dasyprocta punctata*), which move the seeds from zones of higher to lower seed and seedling mortality (Hallwachs 1986). The concept that currently surviving plants were originally adapted to extinct megafauna and still reflect those adaptations has been cleverly and convincingly elaborated in a great many more papers than those cited here.

The Mammoth Steppe: A large area of western Yukon and northern Alaska called Beringia was an ice-free refugium during the Wisconsin glaciation, and may have been a grass-dominated steppe (Guthrie 1990). Although this has been debated (e.g. Cwynar and Ritchie 1980, Ritchie and Cwynar 1982), Guthrie (1990) and Zimov et al (1995) claim that the bulk of the evidence supports a productive grassland. This "Mammoth Steppe," which also existed in northern Eurasia, had a remarkable megafauna including mammoths (*Mammuthus* spp.), Steppe Bison (*Bison priscus*), Horses (*Equus caballus*), woolly rhinos (*Coelodonta* spp.), musk oxen (*Ovibos* and *Symbos* spp.), sheep (*Ovis* spp.), camels (*Camelops* spp.), and Saiga Antelope (*Saiga* sp.).

It has been suggested that the extinctions of a few key herbivores by human hunters eliminated the entire mammoth steppe ecosystem. (For more on the keystone herbivore hypothesis, see Owen-Smith 1987). The extinction of the mammoths, Steppe Bison, and woolly rhinos meant lack of soil disturbances and nutrient input. In turn, this resulted in the replacement of nutrient-rich grasses in steppe vegetation by nutrient-poor mosses and sedges in a moss-dominated tundra (Zimov et al 1995, Stone 1998).

If the large herbivores were responsible for the steppe and much of the dry tundra vegetation through trampling and heavy grazing, then it is possible that many restricted species of dry habitats, such as dunes and dry tundra, that are associated with the steppe may have been more widespread prior to extinction of the megafauna. However, species associated with the rich grassland itself may be relatively few (e.g. Lafontaine and Wood 1988). Those associated with grassland may be as much associated with relatively warm preglacial grassland as with mammal-maintained glacial steppe (e.g. Hamilton 1997). Among the relatively large number of currently rare and endemic Beringian plants there are few species, such as the grasses *Koeleria asiatica* and *Poa porsildii*, that may have been an important component of the productive grassland. Possibly the glacial steppe was not as cold as frequently assumed. Alternatively it may be that there is nothing left of the original steppe ecosystem.

RECENT EVENTS

Empty niches? Martin (1969, 1970) stressed that the New World fauna of 1492 A.D. (pre-Columbian times) was not in a natural state because North America had suddenly lost 70% of its large mammals only several thousand years earlier. The megafaunal extinctions left large empty niches in southwestern North America. The large browsers including giant ground sloths, camels, and antelope were gone but evidence of their presence remained. For example, the cactus-dominated communities of the Chihuahuan Desert called Nopaleras, and the characteristics of many of the plant species present, may be understood with reference to the extinct megafauna (Janzen 1986). The Pleistocene mammal extinctions radically altered the dynamics and structure of vegetation in western North America. Interestingly the reintroduction of horses (*Equus caballus*), which were present for many thousands of years in the wild until recently, may have had a beneficial effect on biodiversity. Likewise, in a broad perspective, the feral Burro (*Equus hemionius*) may be viewed as a potentially beneficial native, rather than as a nuisance alien, but what about the browsers?

The extinct Shasta Ground Sloth (*Nothrotherium shastense*) fed on various desert shrubs including Creosote, but this mammal became extinct about 10 000 years ago. If camels were to be introduced (*Cammelulus* to replace the extinct *Camelops*) to reduce the dominance of Creosote Bush (*Larrea tridentata*), also known as "La Governadora" so called "because she dominates," then overall numbers of species might increase. The expansion of Creosote to domination in the southwest following disappearance of major browsers can be compared to the modern invasive aliens that are introduced without controls and dominate ecosystems at the expense of native biodiversity. This example is also instructive in indicating how rarity might be induced indirectly through loss of an interaction causing dominance of one species at the expense of many others. Domination of single species reduces biodiversity, and the extent of domination in various parts of the southwest by Creosote, Sagebrush, Saltbush, Chaparral, or Mesquite and so on could be a result of an unoccupied niche. It has been estimated that 10-20 million camels could occupy this niche in Chihuahua and similar areas which are unsuitable for cattle. The production of protein would not be the only benefit. Numbers of different types of species would doubtless increase as a result of reduced shrub dominance.

Rarity in savannas in relation to fire and megaherbivores. Today the maintenance of biodiversity is often dependent on fire. In the Pleistocene, fire may have played a less important role. In parts of Africa, for instance, which largely escaped the Pleistocene megafaunal extinctions that were characteristic of other continents, Elephants (*Loxodonta africana*) prevent the savanna from becoming dense shrub thickets. Also, White Rhinos (*Ceratotherium simum*) create a mosaic of grass patches, which increases habitat diversity in medium height grasslands (Owen-Smith 1989). Megaherbivores most likely maintained higher diversity than fires in the North American savanna because of the patchiness and continuity of impact. Their effect would also have been less devastating, for example, on insect populations.

Two interesting possibilities emerge from these ideas. Firstly, fire may not be the only advantageous way to manage North American savanna to maintain and promote a wide range of savanna species, many of which are threatened (although it is generally far better than no management). Secondly, the rarity of the North American savanna ecosystem (Nuzzo 1986) and its components may be viewed as related to the absence of megaherbivores as much as to the absence of fire, there being a relatively small time scale difference between which of these one chooses to emphasize. The combined influence of grazing and browsing megaherbivores could lead to structurally and biologically diverse savanna in the complete absence of fire.

Although the comparison is constructive, the situation is more complex than simply comparing herbivores and fire because all herbivores are different and may have subtly but significantly different effects and fire may be regarded as one of the biggest herbivores! With regard to fire, it is also important to note that fire intensity may not be sufficient to prevent encroachment by shrubs in situations where grazers remove the potential fuel. In support of this idea, Owen-Smith (1989) provided an example of a situation in Africa where, once the trend toward woody vegetation was underway, only Elephants could turn it around. As noted by Owen-Smith and many others, the beneficial effects of African Elephants in creating patches for use by other plants and animals extend beyond the savanna to dense evergreen forests. To the contrary Hawthorne and Parren (2000) suggest that only a few plant species (e.g. *Balanites wilsoniana*) are likely to decline in Upper Guinean forests because disturbances by humans more than compensate for lack of elephants.

Other interesting ideas and questions emerge from these observations. Would the caatinga of northeast Brazil and the chaco of northern Argentina be patchy, high-diversity savannas or parklands if a megafauna were re-established? More than 10 000 years ago during the Pleistocene today's extensive prairie region of central North America may have been very limited or non-existent (e.g. Ross 1970, Wells 1970, Wright 1970). If its component species had not been able to originate from herbivore-maintained savanna, which would otherwise (climatically) have been forest, there may have been much less diversity on the prairie than there is today. Despite the frequent reference to "prairie remnants," the central North American prairies may themselves be the remnants of megafaunal-maintained parklands and savannas within a woodland zone (Ross 1970).

Bison and Buffalo Clover. Fifty million Bison (*Bison bison*) roamed over much of North America prior to European colonization, but by 1889 only 541 were left (Walker et al 1975, and Guthrie 1990 for maps). Bison evidently influenced vegetation through a number of concurrent disturbances, such as grazing, trampling, fertilizing, and use of wallows—all of which in certain ways lead to high diversity (e.g. Umbanhowar 1992).

Buffalo Clover (*Trifolium stoloniferum*) was associated with the buffalo, or more correctly Bison, and was once widespread in the Midwest from West Virginia and Kentucky west to Arkansas and Kansas (Bartgis 1985, Campbell et al 1988). It is now extremely rare and occurs in disturbed places along roadsides and trails. It is reported to be sensitive to competition but a vigorous perennial in cultivation. Growing as high as a horse's knees, it was evidently once a community dominant with Cane (*Arundinaria gigantea*) in the Bluegrass region of Kentucky. Early reports suggested that it provided food for Bison and Elk. It may have occurred mostly in the wooded "canebreaks," but also in open places, and it was particularly associated with the "traces" or "buffalo roads" along which large groups of Bison moved between feeding grounds and salt licks.

Although its decline is frequently attributed to the loss of Bison, the mechanism is unclear. Possibly there was a seasonal component of consumption and disturbance in the natural grazing regime. Today, the more continuous disturbance in pastures may promote the alien clovers at the expense of the native species. Perhaps beneficial disturbance at appropriate levels and times was replaced by disturbance that was either too much and too continuous (i.e. pastures) or too little or too infrequent (i.e. woodlands without Bison).

Extirpation of Bears. American Black Bears (*Ursus americanus*) were abundant and widespread in pre-colonial times (e.g. Dickson 1991) occurring in most wooded areas of North America. Grizzly Bears (*Ursus arctos*) were also widespread. Both have been extirpated from large areas of their former range. What has been the effect of this extirpation?

Bears are efficient and major dispersal agents of fruits. They consume up to 200 000 berries in a day and travel a relatively long distance while carrying the seeds in their gut (about 10 km and 1 day respectively; sometimes farther and longer). Present day squirrels, foxes, and mice also disperse fruits but have different, shorter-range patterns of seed dispersal than bears. And of course birds are available, but despite capability of flight, dispersal by birds usually occurs over shorter distances due to shorter periods of seed retention in the digestive system.

Aside from seed dispersal, bears influence vegetation in a variety of ways. Some recent studies have highlighted their importance in digging for edible roots. Mammals are increasingly recognized as significant agents of biopedturbation (soil disturbance by organisms) that contributes to spatial and temporal heterogeneity in ecosystems, but data is still limited (e.g. Whiteford and Kay 1999). Both Grizzly Bears and Black Bears feed on the roots of a number of plants such as Yellow Sweetvetch (*Hedysarum sulphurescens*). In some cases the plants appear to depend on the disturbed digging sites. For example, Yellow Sweetvetch is more productive at bear digging sites, and new robust plants grow from broken roots in excavated holes that also contain hundreds of seedlings (Edge et al 1990). Bears also maintain and improve the fitness of Glacier Lilies (*Erythronium grandiflorum*). Where Grizzly Bears dig the bulbs, plants produce twice as many seeds as do those in adjacent meadows, and the Lilies establish best on bare mineral soil that is largely confined to bear digs (Tardiff and Stanford 1998).

Digging by bears not only reduces competition and creates a new habitat, but it also increases nutrient availability in the soil (Tardiff & Stanford 1998). Bear digging sites may be extensive. One observed in 1824 in Idaho was more than four acres, looked like a plowed field, and had nine Grizzly Bears digging at the same time. Bears are definitely on the list of strong interactors or ecosystem engineers (see Jones et al 1994), but relatively recently their influence has been eliminated over much of North America.

Dogtowns. The burrowing Black-tailed Prairie dog (*Cynomys ludovicianus*) lives in colonies that include hundreds of burrows in areas that range in size from tens to hundreds of hectares (Whicker and Detling 1988). They have been viewed as competitors with cattle for plant forage and have been subjected to extensive poisoning and other eradication programs, which to a degree have been based on misconceptions. In 1919 Prairie Dog colonies covered 40 million hectares (20%) of North American short and mixed grass prairie, and over the past 100 years, the population has declined by 98% (Miller et al 1994).

Through their grazing, burrowing, and fertilizing, they have profound effects on soil and vegetation cover. Areas around burrows are denuded and grazing activities affect the entire area of a colony to a greater or lesser extent. Although plant diversity is sometimes less within colonies (Weltzin et al 1997) than outside, the colonies contribute much to the overall diversity in the grasslands ecosystem. Bison and Pronghorn Antelope (*Antilocapra americana*) preferentially graze within Prairie Dogs towns (Copprock et al 1983, Krueger 1986). Prairie Dogs also significantly constrain the establishment and domination of woody plants and thus could contribute to sustainable livestock production, as well as maintaining habitat (Weltzin et al 1997). The colonies are patches with distinctive ecosystem processes within a grassland

EXTIRPATION OF SEABIRDS AND SEALS IN NEW ZEALAND

Of six species of cabbage family plants (*Lepidium* spp.) found on the coast of New Zealand, one is now extinct and the remainder is threatened with extinction. Explorers between 1760 and 1830 found *Lepidium* to be abundant. Although a number of factors may be involved in their decline, the extirpation of seabirds and seals looms large. These animals contributed to the development of disturbed habitats for colonization, dispersed the seed, and provided nutrient enrichment (Norton et al 1997).

matrix, and they provide an environment essential for certain species of plants and animals.

Not surprisingly their decline has been associated with the changing diversity on prairies and the listing of several closely associated species under the U.S. Endangered Species Act (Miller et al 1994). The eradication of Prairie Dogs has been a major cause of the near extinction of Black-footed Ferrets (*Mustela nigripes*, see Dobson and Lyles 2000) and has been cited as partly responsible for the endangered or threatened status of Mountain Plovers (*Charadrius montanus*), Ferruginous Hawks (*Buteo regalis*), and Swift Foxes (*Vulpes velox*). In the West, decline of Prairie Dogs has also reduced populations of the Burrowing Owl (*Athene cunicularia*), which both nest in the burrows and take advantage of the higher-than-normal densities of mice and insects associated with the colonies (Evans 1982). The Owls (considered endangered in Canada) were already declining due to a variety of factors including the use of toxic chemicals to control grasshoppers; the decline of important "dogtown" habitat increases the danger to these birds. Because approximately170 vertebrate species rely to some degree on Prairies Dog activity for survival—the numbers for insects and plants may be much greater—Prairie Dogs appear to serve as a good modern example of a widely extirpated species, the decline of which has resulted in decline and endangerment of several other species that we know of, and possibly many others that have been inadequately studied.

Stapp (1998) suggested that the characterization of Prairie Dogs as a "keystone species" may be premature. He noted "large gaps" in knowledge of Prairie Dog ecology. Results of many research projects have been published in the last few years and the gaps have closed in favour of recognizing Prairie Dogs as a major keystone species. For example, publications in 1999 indicated that Prairie Dog colonies are associated with higher diversities and abundance of birds, other small mammals, and insects (e.g. Barko et al 1999, Ceballos et al 1999).

The situation with Prairie Dogs has been described as an "ecological train wreck," but the more it is studied the more inadequate this description is. The cost of the poisoning alone has been enormous. The cost of restoring and managing the ecosystem and its components in order to attempt to maintain the species and their interactions therein without prairie dogs, is much greater—even if it could be done. Endangered Species acts have sometimes been criticized for concentrating on species instead of ecosystems, but obviously protecting a single species could lead to the protection of many species and even to protecting an ecosystem.

Of course, Prairie Dogs and Bison are not the only keystone species of the prairie ecosystem. Regional declines in gophers (*Thomomys* spp.) and ground squirrels (*Citellus* spp.) have also influenced many other species, but the effects require more study. Based on what is known, gophers exert enormous influence (Huntly and Inouye 1988) on development of prairie soil, nutrient cycling, and microtopography, and have very substantial effects on other herbivores from grasshoppers to Bison.

Some final examples. Studying the pawpaw shows how genetic variation of a potentially valuable economic plant may be lost, while the example of Osage Orange suggests the possibilities for recovery through human intervention. The large size of eastern North American pawpaw fruits (*Asimina* spp.) makes avian consumption unlikely (Willson 1983) and the fruits have classical traits of mammalian dispersal (sweet pulp, large size, green colour, and falling soon after ripening). Despite these traits, there are few published records of mammals eating pawpaw fruits (Willson 1983), making them a holdover for the benefit of extinct megafauna seem a reasonable possibility. With the megafauna gone, bears, racoons, foxes and coyotes are probably the main dispersal agents, but Black Bears (*Ursus americanus*), which may have been the most important, have been recently extirpated from much of the range of pawpaw. Fragmentation of woodlots and lack of corridors for the remaining raccoons, foxes, and coyotes, suggest that dispersal will become less effective and populations will decline without any replacement. Some species of *Asimina* are already rare and restricted, and even the widespread *Asimina triloba* is rare and local in parts of its range such as southwestern Ontario. This should be a matter of great concern because pawpaw is a potentially valuable native North American crop

IMPACT OF CHESTNUT DECLINE

With up to 300 species of insects dependent on a single species of tree or shrub (Williams 1998), one naturally wonders what the effect of the loss of woody plants has been. For example, how has insect biodiversity been impacted by the loss of the American Chestnut (*Castanea dentata*) from the eastern North American forest?

(Peterson 1990) and loss of genetic variation would eliminate some of the options for crop development.

This model for shrinkage and depletion of range due to association with an extinct herbivore may also apply to such remarkable cases as that of Osage Orange *(Maclura pomifera*), with a native range possibly confined to the Red River area of Texas and Oklahoma where it occurred in rich bottomlands and open prairies. In the late 1800s, before woven and barbed wire fencing were available, this tree was extensively employed as a living fence, especially in the prairies. It was soon growing well throughout much of eastern and midwestern North America from southern Canada southward, and is now spreading from cultivation in some areas far removed from its native range (Smith and Perino 1981). There seems to be little reason for it to be rare but possibly elimination of the optimal combination of conditions is sufficient to tip the scales toward extinction.

HISTORY OF RARE SPECIES AS RELATED TO CONSERVATION

Not considering history leads to inappropriate assumptions and conclusions (Dudley 1999) or wrong impressions may be given, thus leading a user of results to draw the wrong conclusions. For example Box Turtles (*Terrapene carolina*) disperse the yellow fruits (4 cm across) of the woodland herb called May Apple (*Podophyllum peltatum*), and this is information valuable to our understanding of patches and plant populations as well as to dispersal and conservation of Box Turtles (Rust and Roth 1981). But could May Apples have had many other, more important dispersal agents several thousand years ago or even 200 years ago? Is it not appropriate to set the Box Turtle within the context of both past and present dispersal characteristics of May Apples?

Conservation biology is a “crisis-oriented discipline” that draws in all disciplines required to respond effectively, and it “seeks to shape the future,” but practitioners frequently need to step back from the mire of current circumstances to understand them (Meine 1999). Greater interaction is needed between environmental historians and conservation biologists, and temporal scales deserve more attention in defining research questions, interpreting results and making conservation recommendations. Some valuable suggestions for shared inquiry are included in Meine’s discussion.

The concept of protecting biodiversity brings the strict utilitarians and preservationists closer than ever before and the coherent conservation story in conservation biology may be within grasp, but the territory needs to be expanded. The preceding examples of extinct animals are not just a pleasant exploration, but rather an essential education with application. The effect of extinction is a part of environmental history and it should be an operative part of conservation biology, not just an occasional interaction. Environmental history not only seeks to interpret the past, but to understand the present in terms of the past, and thus it contributes to decisions that influence the future.

FOR MORE INFORMATION

This paper was largely distilled from a university lecture course designed to give students an introduction to some of the classic, interesting, and recent literature on extinction and rarity. The subject of keystone species and interactions (see Jones et al 1994 for an introduction) includes many species not touched upon, such as beavers (e.g. Naiman et al 1988) and pocket gophers (Huntly and Inouye 1988). Judging by a table of contents, the subject of anachronisms appears to be very well covered in an upcoming book by C. Barlow. Although this article has concentrated on terrestrial habitats, the loss or decline of a single aquatic species (or species group) or a microscopic organism may have just as many devastating effects on both land and water as loss of the “large” terrestrial species emphasized in this article.

Broad Scope. The I.U.C.N. Red List of Threatened Species (Hilton-Taylor 2000) reveals hundreds of species worldwide that are currently threatened (e.g. Arabian Oryx, Asian Tiger, Haitian Parrot, Black and White Rhinos, among others), and hundreds of other species depend upon these threatened species to a greater or lesser extent. In many cases the extent of interactions is poorly understood. Size of species and abundance have no bearing on their effects. A threatened plant may be the sole food of a threatened insect, for example, and a threatened insect may be the primary pollinator of another threatened plant. How many seeds of currently unrecognized threatened plants are dependent on transport to appropriately disturbed habitats by threatened rhinos, as another example? Threatened species are a time bomb that can only be diffused through decisive, immediate actions of unprecedented scale (Mittermeier 2000). While threats, such as habitat loss or over-hunting, are clear, decline or extinction due to loss of essential interactions is rarely highlighted.

TWO CONCLUSIONS

These last two sections summarize two important conclusions. Firstly, in attempting to understand ecology and rarity, we need to venture into the immediate past and then again even further into the prehistoric past than we normally do. Secondly, in protecting a single species, we protect many species, with substantial benefits to overall biodiversity. Although these conclusions are not startling new discoveries, they have been operationally neglected.

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REFERENCES

Amaral, M., A. Kozol, and T. French. 1997. Conservation status and reintroduction of the endangered American Burying Beetle. *Northeastern Naturalist* 4(3): 121-132.

Anderson, E. 1984. Who's who in the Pleistocene: a mammalian bestiary *in* P.S. Martin and R.G. Klein (eds), Quarternary extinctions, A prehistoric revolution, University of Arizona Press, Tucson, pp. 40-89

Barko, V.A., J.H. Shaw, and D.M. Leslie Jr. 1999. Birds associated with Black-tailed Prairie Dog colonies. *Southwestern Naturalist* 44(4): 484-489.

Bartgis, R.L. 1985. Rediscovery of *Trifolium stoloniferum* Muhl. ex A. Eaton. *Rhodora* 87: 425-429.

Campbell, J.J.N., M. Evans, M.E. Medley, and N.L. Taylor. 1988. Buffalo Clovers in Kentucky (*Trifolium stoloniferum* and *T. reflexum*): historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome number. *Rhodora* 90: 399-418.

Catling, P.M., L. Dumouchel, and V.R. Brownell. 1998. Pollination of the Miccosukee Gooseberry (*Ribes echinellum*). *Castanea* 63(4): 402-407.

Catling, P.M. and B.M.H. Larson. 1997. The decline and current status of Dwarf Cherry, *Prunus pumila* var. *pumila*, on the Canadian shores of the lower Great Lakes. *Canadian Field-Naturalist* 111(2): 187-193.

Ceballos, G., J. Pacheco, and R. List. 1999. Influence of Prairie Dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* 41(2): 161-172.

Cogbill, C.V. 2000. Vegetation of the presettlement forests of northern New England and New York. *Rhodora* 102: 250-276.

Coppock, D.L., J.E. Ellis, J.K. Detling, and M.I. Dyer. 1983. Plant-herbivore interactions in North American mixed-grass prairie II. Responses of bison to modification of vegetation by prairie dogs. *Oecologia* 56: 10-15.

Cwynar, L.C. and J.C. Ritchie. 1980. Arctic steppe-tundra: A Yukon perspective. *Science* 208: 1375-1378.

Dickson, J.G. 1991. Birds and mammals of pre-colonial southern old-growth forests. *Natural Areas Journal* 11(1): 26-33.

Dobson, A. and A. Lyles. 2000. Black-footed Ferret recovery. *Science* 288: 985-988.

Driver, J.C. and K.A. Hobson. 1992. A 10 500-year sequence of bird remains from the southern boreal forest region of western Canada. *Arctic* 45(2): 105-110.

Dudley, J.P. 1999. Coevolutionary implications of an endemic Pleistocene megaherbivore fauna for insular floras of the California Channel Islands. *Conservation Biology* 13(1): 209-210.

Edge, W.D., C. Les-Marcum, and S.L. Olson-Edge. 1990. Distribution and grizzly bear, *Ursus arctos*, use of yellow sweetvetch, *Hedysarum sulphurescens*, in northwestern Montana (U.S.A.) and southeastern British Columbia (Canada). *Canadian Field-Naturalist* 104(3): 435-438.

Emslie, S.D. 1987. Age and diet of fossil California Condors in Grand Canyon, Arizona. *Science* 237: 768-770.

Evans, D. L. 1982. Status reports on twelve raptors. U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report No. 238. 68 pp.

Fisher, D.C. 1984. Taphonic analysis of late Pleistocene mastodon (*Mammut americanum*) occurrences: evidence of butchering by North American Paleo-Indians. *Paleobiology* 10(3): 338-357.

Guthrie, R.D. 1990. Frozen fauna of the Mammoth steppe: the story of Blue Babe. University of Chicago Press. Chicago.

Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae) *in* A. Estrada and T. Fleming (eds). Frugivores and seed dispersal. Dr. W. Junk, Publishers, Dordrecht, pp. 285-304.

Hamilton, K.G.A. 1997. Leafhoppers (Homoptera: Cicadellidae) of the Yukon: dispersal and endemism *in* H.V. Danks and J.A. Downes (eds) Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, pp. 337-375.

Hawthorne, W.D. and M.P.E. Parren. 2000. How important are forest elephants to the survival of woody plant species in Upper Guinean forests. *Journal of Tropical Ecology* 16(1): 133-150.

Hayes, C.V. Jr. 1991. Geoarchaeological and paleohydrological evidence for a Clovis-age drought in North America and its bearing on extinction. *Quaternary Research* 35 (3 part 1): 438-450.

Hilton-Taylor, G. (Compiler) 2000. 2000 IUCN Red List of Threatened Species. IUCN (International Union for Conservation of Nature and Natural Resources), Cambridge, U.K. xviii + 61 pp.

Howe, H.F. 1985. Gomphothere fruits: a critique. *American Naturalist* 125(6): 853-865.

Huntly, N. and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* 38(11): 786-793.

Ives, S.A. 1923. Dissemination of *Ilex opaca*. *Botanical Gazette* 76: 60-77.

Jackson, S.T. 1999. Late quaternary extinction of a tree species in eastern North America. Proceeding of the National Academy of Science, U. S. A. 96(24): 13847-13852.

The loss or decline of a single aquatic species or species group or a microscopic organism may have just as many devastating effects on both land and water as the loss of "large" terrestrial species emphasized in this article.

Janzen, D.H. 1981. *Enterolobium cyclocarpum* seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. *Ecology* 62(3): 593-601.

Janzen, D.H. 1982. Fruit traits, and seed consumption by rodents, of *Crescentia alata* (Bignoniaceae) in Santa Rosa National Park, Costa Rica. *American Journal of Botany* 69(8): 1258-1268.

Janzen, D.H. 1983. The Pleistocene hunters had help. *American Naturalist* 121: 598-599.

Janzen, D.H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* 123: 338-353.

Janzen, D.H. 1985. *Spondias mombin* is culturally deprived in megafauna-free forest. *Journal of Tropical Ecology* 1: 131-155.

Janzen, D.H. 1986. Chihuahuan desert nopaleras: defaunated big