

## BIODIVERSITY AND INFECTIOUS DISEASE: WHY WE NEED NATURE

ANDREW P. DOBSON

### *Preface*

The large leather bible hit the congressional committee room table with a crash that commanded the attention of congressmen, their aides, and the press assembled for the Endangered Species Act hearings. 'Extinction is a sin – We are destroying God's creation', announced the President of Christians for the Environment. This produced a nervous shuffling in seats. Congressmen unmoved by economic or scientific arguments were plainly disconcerted by this sharp reminder that our moral responsibility to other species puts parts of their constituency in blunt conflict with each other. The rest of us breathed a little more easily. The current US Congress, curiously immune to economic and scientific arguments, has a visceral response to the Old Testament. Here I will expand on this testimony and outline the broader economic, scientific and ethical arguments for 'Why we need nature'.

### *Biodiversity as Food-Webs*

One of the first things we learn about in school nature classes is food chains. My five-year-old son can happily arrange krill, fish, big fish, and sharks into a logical hierarchy of producers and consumers. Ecologists and economists have long been fascinated with the mathematical properties of simplified food webs (Dunne, 2005). The Italian mathematician, Vito Volterra, initially examined the properties of the simplest one predator and one prey food web in the 1920s (Volterra, 1926). His stimulus was the worry that his daughter would marry a fisherman. When he created a mathematical model of the interactions between fisherman and fish he realized that

that even this simple model had a pathological tendency to undergo sustained cycles of abundance of predators (fisherman) and prey (fish). While this was an unsuccessful deterrent to his daughter's marriage, it catalyzed a massive expansion in mathematical interest in the properties of ecological systems. This early work of Volterra and Lotka (Lotka, 1923) advanced our understanding of consumer-resource relationships considerably beyond Malthus, whose worries about the geometric and arithmetic rates of increase of consumer and resource are but a sub-set of this broad and complex set of problems. The mathematical study of predator-prey systems is at the heart of many natural processes; lions chasing zebra, insects eating plants and each-other, right through to how the immune system interacts with viral and other pathogens that invade our bodies (May, 2001; Nowak and May, 1991). These problems rapidly become more complex as we increase the numbers of species that interact as hierarchical networks of consumer and resource species within a food web (Cohen, 1989; Cohen *et al.*, 1990; Cohen *et al.*, 2003; Dunne *et al.*, 2002).

*'There Ain't Have Been Some Clever Geezers...'*

To understand the scientific complexity of the problem we have to compare ecology and the other life sciences to physics and chemistry. One way to do this is to reduce these sciences to the level of the numbers of different particles they consider, the spatial and temporal scales at which those particles interact, and the complexity, or non-linearity, of these interactions. In their purest form physics and chemistry consider limited numbers of particles interacting at either extremely small or rapid scales, or at huge scales over rapid timescales. The sheer magnitude of these scales creates a mystical awe. Ironically this masks their lack of utility to any aspect of human health or well being! In contrast, biologists consider interactions between large numbers of particles of different types (molecules, cells, species) embedded in a complex hierarchy of webs, where processes occur at timescales from seconds and minutes to millennia. Because many of the species involved are cute, charismatic, or pests, and studied at scales closer to fish-tanks and fields, there is less mystical awe in the study of their interactions.

When we convert forest or savannas to agricultural land we simplify the local food webs and focus on cultivating a handful of domesticated species as resources. This simplification reduces our potential to benefit from the services supplied by the natural web. How we value nature is

intimately linked with understanding the trade-offs between agriculture, trade and nature (Arrow *et al.*, 1995; Balmford *et al.*, 2002; Costanza, 1991). Inherently asking the question ‘Do we need Nature?’ assumes we can realistically compare the long-term value of natural habitats, whose benefits are diffusely appreciated by a variety of people, with the instantaneous and focused annual yields of agriculture, timber products, or golf course revenues. Some of the problems associated with this calculation boil down to simply not knowing if the land is worth more as agricultural land or natural habitat (Balmford *et al.*, 2002). If we focus on a single service or product we will always underestimate its natural value. If we try and completely enumerate its value, we run the risk of exaggeration. Even if we could undertake these calculations, we’d then need to quantify the dependence of the modified habitat on services produced by the natural habitat (Dobson, 2005b).

In the absence of a comprehensive pricing of nature’s services, then the natural habitat will appear to be worth less than when converted to agricultural land. This creates further pressure to convert all of the land to agriculture. As an example, consider an area of land containing a patch of woodland or prairie – this could range in size from a small farm, to many hundreds of square miles, the Amazon basin, or the Serengeti. If we convert the forest or savanna to agricultural land (or a golf course), its economic value will be determined by the quality and quantity of products and services produced, minus the cost of converting the land. In contrast, if we leave the land in an undisturbed state it will have an economic value determined by a complex calculation that sums the resources people remove from it for food or fiber, plus the added value we obtain as it cleanses the surrounding air and water. We may also have to add its value as a sink for greenhouse gases. Finally we must include a more complex value determined by the pleasure people receive from spending time there, or even simply knowing it is there. Alternatively, we could convert a proportion of the land to agriculture and leave the rest as forest. This may be particularly sensible if the agricultural land is dependent upon the forest for services such as a constant water supply, or a source of pollinators that ensure crop fertility (Figure 1, see page 407).

Determining the proportion of land to convert and the proportion to leave available for other species is the central problem of natural resource management. Unfortunately the less we value Nature then the smaller the proportion of land that will be kept set aside for other species. Many international conservation treaties recommend leaving ten percent of the

land as set aside for Nature. Their logic stems from the well-known 'species-area' relationship discovered by Robert MacArthur and E.O. Wilson in the 1960s (MacArthur and Wilson, 1963; MacArthur and Wilson, 1967); this relationship suggests that each successive 90% loss in habitat dooms 50% of remaining species to local extinction. From a purely utilitarian perspective, the amount of biodiversity we save is one answer to the question 'Will this level of biodiversity be sufficient to supply all the necessary services we are used to receiving from Nature?'

Unfortunately, the benefits of maintaining biodiversity are most sharply appreciated in their absence! This usually occurs when we notice a decline in air or water quality, reductions in crop pollination rates, or increased pest and disease outbreaks. We are then stuck with the problem of either replacing 'Nature's services' with a technological fix, or of trying to restore the natural habitat. Both are likely to be expensive; in the case of restoration the significant current costs may not be met by future discounted potential benefits (Dobson, 2005b; Dobson *et al.*, 1997; Simberloff *et al.*, 1998). Restoration also assumes we know enough about ecosystem functioning to put food-webs back together (Bradshaw, 1983; Bradshaw, 1984). This illustrates one of the deepest scientific ironies of the 21st Century: while we know much about the structure of atoms and of the universe, we have only the most rudimentary understanding of the structure of salt-marshes, forests, or even the soil beneath our crops.

### *Reasons to be Careful... Part 3*

When land is converted from natural habitat, different species will go extinct at different rates (Seabloom *et al.*, 2002; Tilman *et al.*, 1994). Species are lost as their habitats are converted to agricultural land, as we exploit them for food, or as they are out-competed for space and resources by a suite of invasive plants and animals that are the camp followers of human expansion (Crawley, 1986; Soulé, 1986). We are thus seeing a transformation from a world of tropical forests, tigers, orchids and pandas, to one of weeds, mosquitoes, goats, and sparrows. This sequential loss of biodiversity means that the economic services will be lost at different rates. Services that are predominantly supplied by species with large area requirements, rare species, or species with specialist habitat requirements, will be lost more rapidly than those mediated by species that can persist in a handful of soil, or those able to rapidly adapt to the suburban environment (Dobson *et al.*, 2006; Jenkins, 2003; Kremen,

2005). In some cases agricultural or weedy species may replace some of the ecosystem services performed by the original native species. In general, the services provided by species at the top of the food chain will be lost more rapidly than those provided by those at the base of the web (Dobson *et al.*, 2006; Loreau *et al.*, 2001). This creates a hierarchical loss of natural services, initially the aesthetic benefits will decline, orchids and pandas will become rare, and tigers and other predators will disappear locally (Figure 2, see page 408). Except in areas that are strongly dependent upon ecotourism, this will have only a limited impact on the local economy. It will create problems, the loss of predators will cause the species they prey upon to increase in abundance and become pests (Duffy, 2003). In turn this will lead to an increase in thorny, inedible vegetation that encourages the now abundant deer, rabbits and insects to feed upon crops. The increased contact of these species with humans and domestic livestock increases the potential for disease transmission. Laws such as the Endangered Species Act in the United States can prevent this cascade of events. While focusing attention on individual species, the law seeks to protect entire functioning food webs (Carroll *et al.*, 1996; Eisner *et al.*, 1995; Mann and Plummer, 1995).

### *Biodiversity and Infectious Diseases*

A central question in the field of biodiversity and conservation biology is whether increased diversity of host species tends to either buffer or amplify disease outbreaks (Dobson, 2004; Dobson, 2005a). In the simplest case the potential for disease outbreaks will be determined by the magnitude of  $R_0$  – this number is formerly defined as the number of secondary infections produced by the initial infectious individual introduced into a population of susceptible hosts (Anderson, 1982; Anderson and May, 1986; Dietz, 1993).

We can think of  $R_0$  as a heuristic mathematical device that allows us to examine the biological conditions that lead to an outbreak; quantifying the relative contribution of the ecological factors that determine the magnitude of  $R_0$  considerably focuses our understanding of how different pathogens might be controlled. In cases where increases in species diversity lead to increases in the number of contacts between infected individuals and potentially susceptible hosts, increased host diversity will always lead to increased values of  $R_0$  and a greater potential for disease outbreaks (Figure 3, see page 409). In contrast, where increases in inter-spe-

cific transmission lead to reductions in within-species transmission, then it is possible for increased host species diversity to lead to reductions in  $R_0$ . This will be the case for vector-transmitted pathogens such as malaria, yellow fever, dengue fever and Lyme disease (Dobson, 2004). On one hand, increased host diversity will lead to increases in the resources available to the vector population (e.g., more blood meals). However, as most vectors take a finite number of blood meals per lifetime, this will lead to an increased proportion of bites wasted on hosts that may be less viable resources for the pathogen (Figure 3, page 409). Whether or not the pathogens are buffered or amplified by the increased host diversity will depend on whether increases in the size of the vector population are sufficient to compensate for the 'wasted bites' on less viable hosts. Ecologists have called this reduction in disease risk as host species diversity increases 'the dilution effect' (LoGuidice *et al.*, 2003; Schmidt and Ostfeld, 2001). In a world where global climate change may lead to range expansion of vector transmitted pathogens from the tropics into the sub-tropics and temperate zones, the dilution effect creates an important utilitarian argument for conserving biological diversity (particularly vertebrates) – as long as these species are present in abundance, the biting rate of mosquitoes on humans should be reduced.

### *Rinderpest in the Serengeti*

As a final example of the role that infectious diseases can play in modifying the structure of complex ecosystems, let us consider the impact that a single introduced pathogen has had on species that live in the African savanna; an ecosystem where a large proportion of the human population are highly dependent upon a range of ecosystem services to supply most of their food and economic well-being (Homewood and Rodgers, 1991). The savannas of East Africa support a large pastoralist population, their herds often share grazing habitat with wild antelope species, and the millions of ecotourists that visit the region each year provide the major input into the local economy. Yet the region also provides perhaps the best example of a pathogen completely modifying the structure of a food web: the introduction of the rinderpest virus into sub-Saharan Africa in the 1890s (Branagan and Hammond, 1965; Plowright, 1982). Rinderpest is a morbillivirus that infects hoofed animals: cattle, wild buffalo, wildebeest, giraffe, and other large antelope. It is closely related to both canine distemper (CDV) and measles, two of the com-

monest diseases of humans and their domestic dogs; the recent evolution of these three pathogens is intimately entwined with domestication of dogs and cattle, this created the opportunities for the pathogen to establish in new host species, where a few mutations allowed it to differentiate itself from rinderpest, which is the ancestral main trunk of the morbillivirus tree (Barrett, 1987). The split between the three pathogens is so recent (<5000 years) that there is still strong cross immunity between them; inoculation of dogs with rinderpest vaccine will protect them against distemper. This again raises interesting questions about how we classify pathogens in food webs where they may fail to establish a dependence upon a host, but stimulate an immunological response that allows the host to protect itself against invasion by a potentially lethal natural enemy.

Rinderpest caused one of the largest pandemics in recorded history, it took 10 years to spread from the Horn of Africa to the Cape of Good Hope, during this time it reduced the abundance of many ungulate / artiodactyl species by as much as 80% (Plowright, 1982). This in turn produced a transient glut of food for decomposers and scavengers, such as vultures and jackals, however, this quickly led to a massive reduction in food supply for the predators that relied on wildebeest and other game for food. The removal of the ungulates changed the grazing intensity on both shrubs and grasses. This seems to have allowed some tree species to undergo a pulse of recruitment, thus many of the fever trees that create woodlands in damper areas of the savanna seem consist mainly of individual trees that are now just over a hundred years old (Dobson, 1995; Dobson and Crawley, 1994; Prins and Weyerhaeuser, 1987). In contrast, reduced levels of grass grazing led to an increased fire frequency, which prevented the establishment of miombo bushland that had previously covered the savanna. This in turn modified the habitat for many of the predators that require thicker bush coverage to successfully attack their prey.

The development of a vaccine for rinderpest in the 1950s allowed these processes to be reversed (Dobson, 1995; Plowright and Taylor, 1967). There is an instructive irony here: the presence of rinderpest in wildlife was blamed as the major reason why it had proved almost impossible to establish large-scale cattle ranches in East Africa. The rinderpest vaccine was largely developed to help the cattle industry, it was only ever applied to cattle, but this in turn led to its disappearance from wildlife. Thus cattle had been the reservoir and the repeated epidemics observed in wildlife were in response to constant spillovers from cattle. Rinderpest

vaccination has successfully eradicated the disease from most parts of Africa, except in times of civil unrest, when declines in vaccination coverage allow it to resurge. The impact on wildlife has been spectacular: in the Serengeti, wildebeest numbers have grown from around 250,000 to over 1.5 million; buffalo have appeared in areas where they previously unrecorded, and lion and hyena numbers have increased dramatically in response to the enhanced food supply (Sinclair, 1979). This observation strengthens our contention that predators are less effective than pathogens in regulating host abundance. The numbers of some species have declined, for example there are fewer Thompson's gazelles perhaps because of more competition for grassland forage, but more likely because of increased predation pressure from the more numerous hyenas. African wild dogs have also declined since widescale rinderpest vaccination allowed their prey to increase in abundance; this may be primarily due to competition with hyenas, though there may also be increased risk of infectious disease, particularly distemper (Creel and Creel, 1996; Dobson and Hudson, 1986). In the absence of rinderpest, it may be that wild dogs (and other carnivores such as lions), no longer acquire cross-immunity to distemper. The increased wildebeest abundance has reduced the excess of dried grass during the dry season; this has in turn led to a reduction in fire frequency, which has allowed the miombo bushland to return to some areas of the Serengeti (Sinclair and Arcese, 1995; Sinclair and Norton-Griffiths, 1979).

The key points to take from this example is that while the biomass of the rinderpest virus in the Serengeti was always less than 10 kg, the virus had an impact on the abundance and dynamics of nearly all of the dominant plant and animal species in the system – even those which it did not infect. It strengthens the notion that indirect effects may be as important in shaping species abundance and web linkages as are direct interactions. It also reinforces the earlier comments that pathogens may be as powerful as predators in regulating abundance and distribution of free-living species in natural ecosystems. Finally the rinderpest epidemic illustrates the importance of considering not just infectious diseases of humans when we examine the epidemiology of future human well-being. The pastoralist population of East Africa was heavily impacted by the great rinderpest epidemic, as their herds died, the pastoralists either starved, or changed lifestyles and changed from pastoralists to farmers who settled and permanently farmed the same area for crops. In the absence of wildlife, tsetse flies switched to feeding on humans and created a major



epidemic of sleeping sickness (Rogers and Randolph 1988); a vivid illustration of the dilution effect described above. The recovery of wildlife, itself a direct consequence of the control of rinderpest in livestock, led to the huge expansion of tourism which provides most of the financial input into the local economy.

### *Outro*

My friend's Bible again crashes on the congressional committee room table, 'Extinction is a sin!'. We can now add that the changes in land use that create endangered species also create bell-ringers for the decline of a variety of economic goods and services that will become increasingly limiting. This creates a final irony. The most vociferous critics of environmental protection implicitly assume humans and their domestic livestock will be amongst the last species to go extinct. This opinion is inherent in the belief that human existence is independent of the welfare of other species. It is a dangerous form of naivety. Our dependence upon other species makes it highly unlikely that humans will be the last species left alive on the planet. The simplest bet is that we will go extinct about halfway down the list. With a bit of luck, and a deeper understanding of food webs, our technological skills may delay this inevitable demise. This is less naïve, but still assumes we can develop replacements for the services provided by biodiversity. The alternative is to conserve a significant amount of biodiversity and explicitly acknowledge that Nature has a value beyond our current ethical, economic and scientific understanding. Ultimately, our greatest need from Nature may be the challenge it still presents to human creativity. This is both beyond value and essential to our long-term health and economic and spiritual welfare.

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