

## Key Topics in Conservation Biology

# Dedication

This book celebrates the move of Oxford's WildCRU to its own centre, Tubney House, and is thus dedicated to the memory of Miles and Briony Blackwell and to the Trustees of the Tubney Trust who made this possible.

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(whose members commented on drafts of every chapter)

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*When I was a boy of fourteen, my father was so ignorant I could hardly stand to have the old man around. But when I got to be twenty-one, I was astonished at how much he had learned in seven years.*

**(Mark Twain, 'Old Times on the Mississippi', *Atlantic Monthly*, 1874)**

# Key Topics in Conservation Biology

Edited by

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# Preface

*It's easy to think that as a result of the extinction of the dodo we are now sadder and wiser, but there's a lot of evidence to suggest that we are merely sadder and better informed.*

**(Douglas Adams and Mark Carwardine, *Last Chance To See*, 1990.)**

## Why bother?

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It seems only fair to the reader, at the start of any book, to explain why the trouble was taken to write it. In the case of *Key Topics in Conservation Biology*, the question has answers at two different levels – the first explains why the topic itself is rivetingly relevant for everyone who gives even a jot, not just about Nature, but about the future of the human enterprise worldwide (and surely that makes it relevant to just about everybody), whereas the second explains why we tackled it in this particular way – an answer which reveals, unusually, that in this case the process is almost as interesting as the product.

At the first level, the reason why the key topics of wildlife conservation are relevant are not only because we are in the midst of an extinction crisis, but also because countless species not yet facing extinction, and their

habitats, are nonetheless facing grave change (almost always for the worse), invariably due ultimately to the hand of Man and often with consequences that also affect people. The extinction crisis itself is the topic of the first essay, by Pimm, Dickman and Cardillo, so there is no need to repeat the detail here. Similarly, issues such as bushmeat, hunting, pest control, agriculture and other forms of conflict are each the topic of other essays, as are such issues as infectious disease, invasive species and climate change. Again, other than drawing attention to the breadth of these topics, our purpose here is not to summarize these essays, but rather to direct the reader to them.

Like medicine, conservation biology is a mission-driven science. Physicians take it for granted that we all care about saving and extending human lives. Thus motivated, they study the pathology of ill health and practice methods to prevent or minimize it. Although

death is an inevitable part of life, we deem a high number of premature deaths – from disease or accident – to be a particular concern. Likewise, conservation biology is about biodiversity loss and the methods to minimize it. Essays in this collection introduce some of the tools of this trade – spanning the ingenious gadgetry reviewed by Ellwood, Wilson & Addison, through the computer models explained by Boyce, Rushton & Lynam, to the institutional structures described by Cobb, Ginsberg & Thompsen. Others introduce the biological framework within which the natural environment can be understood, for example through the genetics (Geffen, Luikart & Waples) and the spatial organization (Akçakaya, Mills & Doncaster) of populations.

Why should we care about the loss of biodiversity? It is conventional to couch the answer in terms of economics, ethics and aesthetics (which, with the neologism of American spelling, can catchily be labelled the ‘three e’s’). These three resonate with the elements of triple bottom-line accounting (economics, environment and social responsibility) that has rightly become fashionable in reporting the impacts of corporations, and are also the basis of accounting in any conservation debate. Both trios emphasize that costs and benefits are measured in many different, and often awkwardly incommensurate currencies. You might value a species on the basis of its direct market worth, or its indirect value (e.g. in persuading people to go on holiday to watch it – calculated by so-called hedonic valuation), or in more abstract terms by the value you put on its existence (fuzzily quantified by so-called contingent valuation). The revelation of 50 years of conservation biology is that every issue is complicated, and every solution must be interdisciplinary – biology is a necessary component, but not a sufficient one, for understanding and thus solving conservation problems. This reality, which makes clear that there is a ‘human dimension’ to every conservation issue, and that this dimension is generally unavoidably central to the solution, reverberates through every essay in this book – it is the

entire topic of the essay on environmental economics by Pearce, Hecht & Vorheis, and a central message of the concluding overview in Macdonald, Collins & Wrangham’s postscript. In short, whether or not an individual happens to realize it, or to be interested in biodiversity, everybody’s life is affected by, and affects its conservation.

Turning to the more nuts-and-bolts question of how, and why, we produced this book the way we have, the answer lies in the invitation, in 2000, to create a module in Conservation Biology within the University of Oxford’s Master of Science course entitled *Integrative Biology*, which is organized by the University’s Department of Zoology. Believing that there was little merit in cajoling lecturers to prepare, and then compelling students to listen to, lectures that rehearsed conventional material that could more efficiently be gleaned from textbooks, we decided instead to organize the course as a series of workshops at which front-line specialists of international standing led discussions on their experiences at the cutting-edge of conservation. These sessions took the form of day-long Think Tanks, in which not only the Masters students and our invited guests, but also researchers from the Wildlife Conservation Research Unit pitched in together. Rather than wearisome essays, the course assignments involved snappy thought-pieces on emergent issues – the key topics in wildlife conservation. The formula was so energizing – flatteringly, the students repeatedly voted it their favorite module – that we thought to develop the approach as a book. Close to the front of our minds, and it was a thought that found favor with many of our visiting speakers, was a growing disquiet that the very welcome rise to prominence of conservation biology was tainted by an occasional and unwelcome tendency towards bluster! Specifically, our Think Tank sessions became vigilant to such refrains as ‘it is really important that we study ... such and such’, to which the probing chorus of ‘why?’ sometimes revealed that although the topic might indeed be interesting, it was less



obvious why it was operationally important. The notion grew, therefore, of assembling teams to write the essays that now comprise this book, and of selecting for each team a trio of renowned authors, each with a different perspective, and urging them to work together on the difficult task of stripping down to the essentials the issues that really are important in their topic. It is for that reason that the working title of this book has been 'Conservation Without Crap' – although the proposal that this should be the cover title was one from which the publisher politely demurred.

Because discussion had been such a prominent strength of the workshops that had catalysed this book, we sought to emulate this by subjecting each essay to the equivalent of a roomful of discussants. Not only did all the authors review each other's essays, but all members of the Wildlife Conservation Research Unit reviewed them too. The result was that most essays received over a dozen reviews, and went through many drafts in response. In conversation amongst the authors it emerged that a surprising number of our sons and daughters were biology students, and who more critical than an offspring to savage that which flows from the parental pen! Therefore, with something of a family feel, we assembled the Student Panel (listed on preliminary p.ii of this book) to cast a critical consumer's eye over each essay (although we hope these essays will fascinate, inform and entertain a wide readership from the loftiest authority to the aspirant Sixth Former, from interested layman to policy-maker to naturalist, our imagined modal reader might well be a Masters student). Each essay represents a hill – a vantage point from which a particular trio of specialists views the conservation landscape. Having been assaulted by the assembled army of over 70 reviewers, almost all the authors commented that the toughest comments to deal with came from the Student Panel – tellingly, perhaps their views of the hills were unencumbered by the baggage that older reviewers had accumulated while climbing them – who as yet know nothing of things

like the Research Assessment Exercise (RAE) and why it matters, or does not (for any readers also fortunate enough to be in this position, the RAE is a performance indicator that encourages scientists in the pursuit of a high score rather than of wisdom or usefulness). One of the most inescapable realizations drawn from the process of producing these essays, and something perhaps felt most keenly by the five of us reading the comments of our offspring, is just how radically the conservation landscape has changed in just one professional generation. As a practical aside, a lesson that might assist editors and authors as they recruit reviewers: as we five fathers watched our offspring toil over early drafts of these essays during the 2004 Christmas vacation, we also learnt how fiercely one cares about the quality of a script that presents to one's children the subject to which we have devoted our lives! Anyway, the quality of the final essays owes much to the diligent reviews not only of the authorial team and the Student Panel but equally to the following members of the Wildlife Conservation Research Unit: Christina Buesching, Ruthi Brandt, Zeke Davidson, Harriet Davies-Mostert, Carlos Driscoll, Hannah Dugdale, Adam Dutton, Paul Johnson, Jan Kamler, Kerry Kilshaw, Steven Gregory, Lauren Harrington, Donna Harris, Jorgelina Marino, Fiona Mathews, Tom Moorhouse, Inigo Montes, Jed Murdoch, Deborah Randall, Greg Rasmussen, Lucy Tallents, Hernan Vargas, Nobby Yamaguchi and Zinta Zommers.

Finally, each essay in this collection is intended to stand alone, but the collection as a whole is more than the sum of its parts, together introducing the nature of the problem, the framework in which it can be understood, some tools that can be used in the quest for solutions, and various of the issues that are topical. As such, it has no pretensions to compendiousness – there are many more than 18 key topics in wildlife conservation – nor even balance (although they drift variously over every type of organism, most of the authors have greater expertise in animals than in plants, and most specialize in vertebrates).

Nonetheless, this collection of essays does give a representative insight across the landscape of conservation. Just as it was spawned by days of debate between a diverse assemblage of people in our discussion groups, we hope that *Key*

*Topics in Conservation Biology* will be the catalyst for countless fruitful discussions amongst those to whom it will fall to deliver the solutions that are required if Nature is to survive as more than a poor shadow of its former glory.

*Truths would you teach, and save a sinking land?*

*All fear, none aid you, and few understand.*

**(Alexander Pope, in *Essay on Man*, 1994.)**

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# The pathology of biodiversity loss: the practice of conservation

Chris R. Dickman, Stuart L. Pimm and Marcel Cardillo

*Don't it always seem to go, that you don't know what you've got 'til it's gone . . . They paved paradise and put up a parking lot*

(Joni Mitchell, *Big Yellow Taxi*, Siquomb Publishing Co. 1969.)

## Introduction – what is biodiversity?

In this essay we start with the definitions of biodiversity and the problems of measuring it. These problems are significant, but not so insurmountable that we cannot quantify the timing and geographical distribution of biodiversity loss. We show that the loss of biodiversity is now hundreds to thousands of times faster than it should be because of human actions involving a variety of mechanisms. Some places, however, are very much more vulnerable to biodiversity loss than others; i.e. biodiversity loss is variable geographically.

Over the past 25 years the concept of biodiversity has been studied, reviewed and debated passionately by increasing numbers of scientists and resource managers, and has exploded into the public consciousness so pervasively that it underpins national agendas in many parts of the world. A search for the term on Internet websites yields far more hits than for many icons of popular culture (Norse

& Carlton 2003). So, what is biodiversity, why is it so important, and why has it become 'mainstream' only recently?

The term 'biodiversity' is commonly used to connote the 'variety of life', or 'God's Creation' to some, whereas others have proposed that it encompasses nothing less than the 'irreducible complexity of the totality of life' (Williams et al. 1994).

People have studied the variety of life for millennia, as hunter-gatherers harvesting food and other products of the natural world for their immediate survival, as settlers in agro-economies, as curiosity-driven natural historians, and as bio-prospectors who seek new medicines and genetic improvements for agriculture. Studies of biodiversity are clearly not new. They have, however, become more urgent owing to concern that life's variety is being eroded by human activity. Warnings of impending 'extinction cascades' or 'biodiversity crises' are becoming increasingly common. In the current climate, 'biodiversity' appears to be moving beyond being a neutral term to one that additionally conveys emotion and value. Indeed, for some authors 'biodiversity'

and 'nature conservation' are interchangeable (Bowman 1993).

Our definition of biodiversity is that provided by Elliott Norse for a report produced for the US Congress Office of Technology Assessment (OTA 1987): 'Biological diversity refers to the variety and variability among living organisms and the ecological complexes in which they occur... (T)he term encompasses different ecosystems, species, genes...'

This three-part definition 'genes, species, ecosystems' – along with their evolutionary and ecological histories – produces a comprehensive value-free definition. It is also a **practical** one. We can measure the numbers of species and map their distributions. Maps of different ecosystems – forests or grasslands, for example, have been familiar for 100 years or more. Although more difficult, we can sometimes quantify the variety within a species. The diversity of genetic varieties of crop plants is one example.

This three-part definition forms the core of the ideas in UNEP's (United Nations Environment Programme) Convention on Biodiversity (signed by 150 government leaders at the 1992 Rio Earth Summit; SCBD 2005) and the Global Biodiversity Assessment (Heywood 1995). As one might expect, the easy-to-measure numbers of species provide these documents with most of their examples.

Equally, scientists wish to make the meaning of biodiversity more complex. The term sometimes means not just species and their genes, but the evolutionary history they represent and the ecological communities and processes that they create. Several authors have argued that 'biodiversity' should also include behavioural, ecological, physiological and life-form variation between individual organisms of the same species (e.g. Soulé 1991; Reich et al. 2003).

Biodiversity is thus a multifaceted concept that we can measure in a variety of ways, though no single measure can capture all of its aspects (Purvis & Hector 2000). For practical purposes, we need a surrogate measure that allows biodiversity to be assessed effectively and that identifies major patterns and changes.

In practice, the measures most commonly used are simple counts of species (species richness) or counts that are weighted by the relative abundances and representation of species (species diversity) in samples. Species-based assessments have several advantages over possible alternatives. The primary one is that species are usually easier to count than genes, ecological interactions or other processes (Gaston 1996). Use of species measures can also be problematic.

First, species boundaries are sometimes difficult to define, especially in sibling taxa and in small, cryptic species that are morphologically conservative. Resolution of species is usually possible if small portions of the genome are characterized, but this adds cost and time to any assessment of biodiversity.

Second, even for conspicuous, well-differentiated species, taxonomists have described relatively few of the likely total. Taxonomists have named just over one and a half million species, but estimates of the total number of insects alone vary from 10 million to 100 million (Stork 1998; May 2000). Discoveries of 'extremophile' organisms deep in the soil profile, in underground lakes and around oceanic vents with no access to sunlight suggest further that much life remains to be inventoried. Despite such stocktaking problems, species remain the primary currency of biodiversity measurement, and lists of threatened species provide triggers for conservation action at local, national and international levels (Heywood, 1995; Burgess 2001).

An alternative approach, gaining in popularity, is to use measures of phylogenetic or phenotypic disparity among species. The philosophy underlying this approach is that it is preferable to conserve, for example, a member of a monotypic genus with no close living relatives than a species with numerous members of the same genus, because loss of the first species represents the loss of a far greater amount of unique evolutionary history. Phylogenetic diversity (PD) quantifies evolutionary history by measuring the summed lengths of the phylogenetic branches that separate species, either in terms of time since separation or the amount of evo-

lutionary divergence (Faith 1992). This relies, of course, on availability of phylogenetic information, which is still non-existent for the great majority of species. The approach also represents an interesting value judgment. In diametric opposition one might argue that a large genus represents a lineage that is producing many new species and is thus one that merits priority for its evolutionary dynamism.

### Measuring the loss of biodiversity

Most of this essay will be about species loss, for the practical reasons already noted. At least two major research efforts take exception to this emphasis. The first, mounted by scientists at the World Wildlife Fund (WWF), categorizes global ecosystems, then produces more finely divided continental **ecoregions** and assesses the threats to them. The second is from Paul Ehrlich's group at the Centre for Conservation Biology at Stanford University, California. If present trends continue, although many species may be saved in protected areas, these survivors will merely be remnants of their once geographically extensive and genetically diverse selves. The emphasis, they argue, should be on measuring the loss of local populations, for the 'services' biodiversity provide depend on what is present locally. (We shall return to this idea at the essay's end.)

### The loss of ecosystems

The WWF has classified terrestrial ecosystems into 825 ecoregions, has another 500 for freshwater ecosystems and is working on classifying marine ecosystems (Ricketts et al. 1999; see <http://www.worldwildlife.org/science/ecoregions.cfm>). As an example, the first ecoregion listed for South America is the forest type dominated by *Araucaria* ('monkey puzzle') trees. They occur in the coastal mountains of Brazil, extending

into northern Argentina. Of an original area of c.200,000 km<sup>2</sup>, only c.13% remains.

As this example illustrates, one can immediately rank ecoregions by the fraction of their former extent that remains. Those with the least fraction remaining represent priorities for conservation action. How do such priorities match those based on species? Ecosystems such as tropical dry forests, deserts, tundra, temperate grasslands, lakes, polar seas and mangroves all contain characteristic species. Although conservation justifiably prioritizes tropical moist forests because they hold such a large fraction of the world's species (see below), a comprehensive strategy should also save distinctive ecosystems. Ecoregions also house distinctive ecological and evolutionary phenomena – they are, in part, defined by them. Given that we know such a small fraction of the world's species, it is at least possible that ecoregions provide a better clue to where distinctive species live than areas defined only on what we know about the few well-known taxa such as birds.

### The loss of within-species variety

Other estimates of biodiversity loss focus on populations. Populations supply genetic diversity, because different populations across a species' range will differ to varying degrees in their genetic composition. Thus, as populations disappear locally, genes may become globally extinct. Hughes et al. (1997) defined population diversity as the number of populations on the planet. They estimated that an average species consists of 220 populations, suggesting that there may be more than 2 billion populations globally, of which 160 million populations (8%) are lost each decade. This is a much higher rate than the loss of species (below) because many populations are often lost before the species itself expires. Large areas of North America and Europe, for example, have lost almost all their large birds and mammals.

An obvious example is our own species. While our numbers are expanding rapidly, our cultural diversity – as measured by the number of languages that we speak – is shrinking rapidly. Few languages spoken by fewer than 500,000 people are taught to children on contact with western culture. That means that about 90% of the world's > 6000 present languages will disappear in a generation or so (Pimm 2000).

At issue here is a matter of scale. Although much of the concern over the loss of biodiversity focuses on the global loss of species, most of the benefits conferred by biodiversity arise from large numbers of local populations of species (Hughes et al. 1997). An obvious example is the loss of forests that provide protection to a town's watershed. Although no species might become extinct globally, the forest trees provide a local service in preventing the soil erosion that would follow if the forests were cleared. Even if a species is not in danger of global extinction, it is 'ecologically extinct' if it has disappeared from most of its former distribution, and hence no longer performs any ecological role there.

### **The loss of species: what should we expect?**

The arguments for measuring biodiversity as populations or ecosystems are compelling, but so too are measures of species numbers. That generations to come might not experience 'lions and tigers and bears, Oh my!' (Wizard of Oz) probably motivates public opinion in a direct way that the loss of (say) *Araucaria* forest does not. (Of course, species will continue to go extinct precisely because they lose their habitats.) Yet, how can we make sensible statements about species loss, if we do not know how many species there are?

We cannot estimate how many extinctions there are per year without making extravagant guesses from better known species groups. Absolute estimates of the numbers of extinctions must be extrapolated from the 100,000 well-

known species to the one and a half million described species, to the likely grand total of a few to tens of millions of species (May 2000). Statements of how many species become extinct per year, or per day, can vary 100-fold because of uncertainties about total numbers of species (Pimm et al. 1995).

We can derive more confident **relative** estimates of extinction rates using the proportions of species that become extinct over time (Pimm et al. 1995). Such estimates beg the obvious question: are these proportions, which are based inevitably on well-known species, typical of the great majority of species groups that are not well-known? They are likely to be so if extinction rates in widely different groups and regions are broadly similar.

There is another way in which we must make estimates of extinctions relative. Extinctions have always been a part of Earth's history, so we scale any claims of massive extinctions now or in the future to past extinctions. The fossil data suggest that species last for one to a few million years except for the major upheavals, such as the one that eliminated dinosaurs (but not birds) at the end of the Cretaceous Period.

These background rates of extinction derive from the abundant and widespread species that dominate the fossil record (Pimm et al. 1995). Species most prone to current extinction are rare and local, so fossil data may still underestimate past extinction rates.

Recent work supplements these assessments of fossils by using the rapidly expanding knowledge of speciation rates based on molecular estimates of the evolutionary divergence of species. The argument has two parts. The first is that speciation and extinction rates cannot be very different. Were the latter higher than the former, the variety of life would have shrunk. If speciation rates were higher, we would often observe very 'bushy' evolutionary trees. There are some – that for human female mitochondrial DNA is an example – showing that all variation arose recently and in Africa. Such examples are rare, however.

The second part of the argument is that we can date some speciation events from well-timed geological events. They can be old, such as the division of the Caribbean from the Pacific, when the Panamanian land bridge was formed, or very recent, such as the isolation of populations on mountain tops as the last glaciation retreated. From these events, we can produce a time-calibrated scale of molecular divergence and so predict the time when other species diverged. It is this process that estimates the divergence of the human line from the chimpanzee line at a few million years ago.

These estimates now include a wide variety of species, including those that are rare and local (Pimm 2001). Molecular estimates are broadly compatible with the fossil data in suggesting a benchmark value for species longevity of a million years (perhaps more). It follows, that each year about one in a million species will expire from natural causes. Any more than that indicts human actions as responsible for their cause.

Box 1.1 presents several case studies demonstrating that current rates of extinction exceed the background rate by orders of magnitude. These examples demonstrate that extinctions can take place quickly, over large areas, in a wide variety of habitats, and involve very different kinds of species. In the next section we ask the obvious questions of what (if any) are the common patterns in what causes extinctions and which species and places are most vulnerable.

### Causes of biodiversity loss

In his overview of recent extinctions, Diamond (1989) succinctly described four processes – the ‘Evil Quartet’ – that exterminate species. They are (i) habitat destruction, (ii) overexploitation, (iii) introduced species and (iv) secondary extinctions – the loss of a species that follows from the extermination of another species.

### Habitat loss

Habitat loss through destruction and fragmentation is the predominant cause of extinction (WCMC 1992). On land, perhaps three-quarters of all well-known species live in tropical moist forests. Within the past 100 years (and often much less), human actions have shrunk these forests by half (Pimm 2001). The rates of deforestation are probably increasing. Other ecosystems are also shrinking, some, such as prairies and some tropical drywoodlands, at rates faster than tropical moist forests.

Habitat loss also has a significant impact on oceanic and freshwater habitats, with human activities such as damaging fishing techniques, exploitation, pollution and coastal development threatening 58% of the world’s coral reefs (Bryant et al. 1998). Riverine habitats are similarly affected through extensive physical modifications such as damming and channelling. The seas cover more than two-thirds of the planet’s surface yet only 250,000 to 300,000 marine species have been described, compared with more than one million on land. As on land, the peak of marine biodiversity lies in the tropics. Coral reefs account for almost 100,000 of these species, perhaps as much as 40% of the world’s marine fishes, yet comprise just 0.2% of the ocean surfaces (Roberts et al. 2000). Although damage to coral reefs is important for the loss of species, by area, trawling does the greatest physical damage to ocean ecosystems. These effects occur across larger areas of the planet than tropical deforestation and involve even greater, more frequent disturbances. Watling & Norse (1998) estimated that  $15 \times 10^6 \text{ km}^2$  of the world’s sea floor is ploughed each year by bottom trawling. Almost all the world’s fisheries are concentrated in the  $30 \times 10^6 \text{ km}^2$  of nutrient-rich waters that are on the continental shelf, plus a few upwellings. On average, the ocean floor of these productive waters is trawled every 2 years. In reality, although a few areas escape trawling, others may be trawled five or even 50 times a year. Regrowth of animals is slow,



**Box 1.1** Case histories*Freshwater mussels*

In North American freshwater mussels, approximately 21 out of 297 species have become extinct since 1900 owing to habitat modification (Williams et al. 1992). Divide the number of extinctions (21) into the regional total (297) and multiplying it by the number of years over which the extinctions have occurred (c.100). That is, there have been 21 extinctions per 297 species in 100 years. Extrapolated to a million species, this regional rate is approximately 714 extinctions per million species per year – compared with the expectation of a single extinction per million species per year. Of course, we have selected these mussels as a special case of rapid extinction.

We can also generate a conservative estimate of **global** extinction rates, by supposing that these were the **only** freshwater mussel extinctions worldwide. By dividing the known extinctions per year by the worldwide total of species of freshwater mussels (c.1000), the global extinction rate of freshwater mussels over the past 100 years is approximately 200 extinctions per year per million species.

*Freshwater fish*

Of the approximately 950 species of freshwater fish in the USA, Canada and Mexico, 40 have become extinct in the past 100 years (Miller et al. 1989). The northern lakes, southern streams, wetlands and desert springs are very different habitats, but all have lost species. The arid region of south-western North America has lost most species, mainly from physical habitat changes and introduced species at springs, which are highly sensitive to disturbance. Some 50 species of Cyprinidae are threatened, including 14 species that inhabit spring systems in Nevada and 14 species in the Colorado River system. Impoundments, ground-water extraction, channelization and irrigation schemes appear to be contributory factors in 18 extinctions. Of 488 species of freshwater fish in south-eastern USA, four have become extinct and 80 more are threatened. Increasing development and chemical alteration of Appalachian and Cumberland mountain streams pose serious threats to many species (Miller et al. 1989).

*Australian mammals*

Australia and its surrounding islands are home to a unique mammal fauna: 85% of species are endemic, and it is the only region with all three major divisions of mammals (marsupials, monotremes and placentals) extant. Australian mammals have suffered two recent waves of extinction. The first was the ‘megafauna’ extinction event in the late Pleistocene between 50,000 and 10,000 years ago, when at least 20 genera of Australian mammals were lost. This wave of extinction has been attributed to ice-age climate change (Main 1978) and to human impact (Martin 1984; Flannery 1994). Some evidence suggests that the timing of megafaunal extinctions corresponds more closely with the arrival and spread of humans, around 50,000 years ago, than with the period of most extreme aridity around the Last Glacial Maximum 20,000 years ago (Miller et al. 1999; Roberts et al. 2001). The human overkill hypothesis is widely, but not universally, accepted (Wroe et al. 2004).

The second wave of Australian mammal extinctions began with European settlement in the late eighteenth century. Twenty-two mammal species have become extinct in that period, more than on any other continent (Australian Terrestrial Biodiversity Assessment 2002). A further eight species persist in tiny populations on offshore islands but are extinct in mainland Australia or Tasmania. If we include these eight species in the calculation, the recent rate of extinction of Australian terrestrial mammals is around 1400 species per million per year – twice that of the North American mussels. Of the Australian mammal species remaining, 59 are threatened with extinction (IUCN 2004). There is little doubt that the impacts associated with European settlement are to blame, although scientists debate the exact mechanism. The main causes seem to be habitat clearance for agriculture, habitat degradation by domestic stock and introduced rabbits, predation by introduced cats and foxes, and the breakdown of indigenous land-management regimes. Moreover, it is clear that this wave of extinctions is continuing. Within the past decade, substantial declines in abundance of several mammal species have been recorded in the relatively intact tropical savannas of northern Australia (Woinarski et al. 2001). Around 5 years ago, foxes were introduced into Tasmania and have rapidly established a breeding population, posing severe threats to the native mammal fauna as they have in mainland Australia.



particularly on the outer continental shelf and its slope, where natural storm damage is negligible, and many areas do not even start to recover before they are ploughed again

Sediment pollution from terrestrial run-off, another form of habitat destruction, causes severe reef degradation worldwide. The problem is concentrated in areas with rapid rates of land clearing and high rainfall, which causes swift erosion of exposed soils. Areas worst affected include Southeast Asia, East Africa, the Eastern Pacific and the Caribbean (Bryant et al. 1998), which are also richest in marine biodiversity. It is truly ironic that destruction of the most diverse terrestrial ecosystems – tropical rainforests – is causing the destruction of coral reefs, the most diverse marine system.

### Overexploitation

Overkill results in the hunting of animals and the cutting of plants at rates faster than they can reproduce. Current rates of hunting for ‘bush meat’ are unsustainable in most areas where this activity occurs. (Bush meat is almost any vertebrate, often small ones, but obviously, the larger species are preferred.) Overexploitation occurs both in terrestrial ecosystems – deforestation often results in overharvesting of species such as mahogany, *Swietenia mahoganii* (Oldfield 1984) – and, perhaps more famously, in marine systems. Overfishing has resulted in valuable resources being driven to such low levels that exploitation is no longer sustainable and, in some cases, species have been driven to extinction. For example, since the 1990s, to supply a growing international market, many sharks are declining and are unable to recover due to their low reproduction rates (Manire & Gruber 1990; Waters 1992).

### Introduced species

The translocation of alien species to new environments has caused mass extinctions of endemic faunas and floras, especially on islands

where the biota were naïve to the effects of the invaders. Rats, rabbits, goats, pigs and predators such as cats have been among the most widely translocated and destructive of alien species (see Chapter 13).

### Secondary extinctions

Finally, ‘chains of extinction’ (or ‘extinction cascades’) describe situations where the loss of one species causes the extinction of others that depend on it. For example, a specialized parasite would disappear if its specific host became extinct, as would plant species that lost their specific pollinators or seed dispersers. Other changes can be quite complicated. Once a species is lost, the species that fed upon, were fed upon, benefited or competed with that species will be affected. In turn, these species will affect yet other species. Food-web theory suggests that the pattern of secondary extinction may be quite complicated and thus difficult to predict (Pimm 1991). It also predicts that following the removal of particular species – often called ‘keystones’ – that the community of species that remain may change dramatically.

### Which species are vulnerable?

#### Quantifying extinction risk

To understand which species are particularly vulnerable to these causes of extinction, we can obviously examine the characteristics of species that have already become extinct. It also makes sense to study those that we deem more or less close to extinction to glean insights from them.

Unfortunately, the information needed to do this is available for only a small fraction of the world’s taxa, and estimates of extinction probability are usually little more than guesswork. The most comprehensive attempt to quantify extinction risk for large numbers of species is the Red List, compiled by the International Union for

**Box 1.2** The IUCN Red List categories and criteria*Categories*

The general aim of the Red List categories is to 'provide an explicit, objective framework for classifying the broadest range of species according to extinction risk' (IUCN 2004). Species categorized as Vulnerable, Endangered or Critically Endangered are grouped as 'Threatened'.

*Extinct*: there is no reasonable doubt that the last individual of this taxon has died.

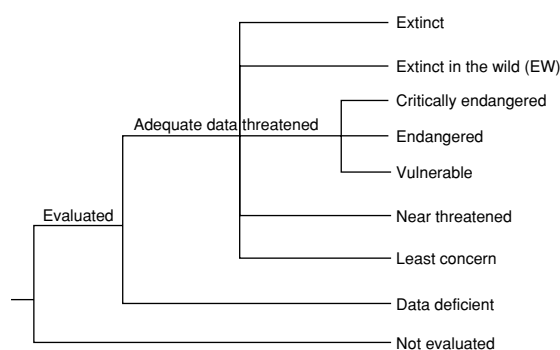
*Extinct in the Wild*: the taxon is known to survive only in captivity or cultivation.

*Critically Endangered*: the taxon faces an extremely high risk of extinction in the wild. *Endangered*: the taxon faces a very high risk of extinction in the wild.

*Vulnerable*: the taxon faces a high risk of extinction in the wild.

*Near Threatened*: the taxon is close to being threatened in the near future.

*Least Concern*: the taxon is not at risk.

*Criteria*

The five Red List criteria (A–E), each with several subcriteria, are a set of objective guidelines for the classification of Threatened species (or subspecific taxa) as Vulnerable, Endangered or Critically Endangered. The criteria are based on: observed or estimated population or range reduction (A, B and C), extent of distribution (B and C), total population size (C and D), degree of population fluctuation (B and C) or fragmentation (B), geographical location (D) and quantitative modelling of extinction risk (E).

**A** rapid population or range decline

**B** small distribution and decline or fluctuation

**C** small population and decline

**D** very small or restricted population

**E** quantitative analysis

the Conservation of Nature and Natural Resources (IUCN 2004). Species are evaluated under a common set of quantitative criteria and assigned to one of seven ranked categories (see Box 1.2). Species can be categorized under several criteria, but the highest category specified by any criterion is taken as the species' extinction risk. Species for which too little is known to enable them to be placed in a category are labelled data deficient. To date, the only three major taxa for

which all species have been assessed are birds, mammals and amphibians. Targets for the complete assessment of several other major taxa (reptiles, freshwater fish, sharks, rays and chimaeras, freshwater molluscs and plants) have been set (IUCN 2004). For other groups, however, the number of species currently assessed is a tiny fraction of the known species numbers; for example, fewer than 800 of the several million known insect species appear in the Red List.

### The selectivity of extinction risk

Examining the lists of threatened and recently extinct species shows that by far the most common vulnerability is a small geographical range. Most recent extinctions have been on islands that, by definition, are small. One might think that island species might be unusually vulnerable because they are also ecologically naïve – they have not met the number of predators, for example, present on mainlands. Interestingly, this is not the case: for the same range size, island species are often less likely to be threatened than species on continents (Manne et al. 1999). The explanation is probably the second leading cause of threat – local scarcity. For a given range size, locally scarce species are much more likely to be threatened than species that are locally common. Island species, though geographically restricted, are often unusually common in their small ranges.

The explanation for these major vulnerabilities is obvious: other things being equal, the four major causes of extinction are likely to be greater threats to scarce, geographically restricted species than to common, widespread ones. Habitat destruction, for example, can more easily destroy a species if it has a small range encompassed by that destruction than if it has a larger one.

An unfortunate feature of global human impacts is that they disproportionately affect centres of endemism, where concentrations of geographically restricted species occur. Range-restricted species tend to have lower population densities and higher risks of extinction than widespread species. Myers (1988, 1990) defined these areas, centres of endemism combined with unusual levels of habitat destruction, as 'hotspots'. Species ranges are so concentrated that roughly half of all species on land are found in only 25 'hotspots', occupying only about 10% of the world's land surface. In 2000, approximately 12% of the original habitat of these 25 hotspots remained (Myers et al. 2000), a mere 37% of which is protected in any

way. Sixteen of these hotspots are forests and almost all are tropical forests. As a consequence of these high levels of habitat loss, these 25 hotspots are where the majority of threatened and recently extinct species are to be found.

Other factors are involved in extinction risk and the picture becomes more complex as one looks at smaller sets of species and particular regions. Species with small and declining populations, restricted geographical ranges and large area requirements are likely to be more at risk than common species, but traits such as body size, intrinsic rate of population increase and ecological specialization can all be important (McKinney 1997). Comparative studies of contemporary extinction risk (which typically use the Red List categories as a measure of risk) largely confirm this. In birds, for example, large body size, low fecundity and habitat specialization are associated with high extinction risk (Bennett & Owens 1997; Owens & Bennett 2000). In mammals, species at higher risk tend to be at high trophic levels and have small geographical ranges, low population densities and slow life histories (Purvis et al. 2000b; Cardillo 2003; Cardillo et al. 2004).

It is clear, then, that extinction risk is determined not only by where a species lives and the external conditions it is exposed to, but also by its intrinsic, biological attributes. So far, we know little about whether external or intrinsic risk-promoting factors are more important (Fisher et al. 2003; Cardillo et al., 2004). There is evidence, however, that the two interact to determine extinction risk. In the mammal order Carnivora, there is an interaction between species' biological traits and degree of exposure to human populations. Slow life histories, low population densities and restricted distributions have a more acute influence on extinction risk among species that inhabit regions of high human population (Cardillo et al. 2004). Across mammals generally, body size has important interactive effects: many external and intrinsic factors that affect extinction risk do so more strongly for mammal species of larger size. Moreover, external factors seem to

be more important in determining extinction risk among small species, whereas for large species, both external and intrinsic factors are important (Cardillo et al. 2005).

Intriguingly, there is also evidence that species in small, ancient or distinct lineages are more at risk of extinction than more recently evolved taxa (Johnson et al. 2002). As May (1990) has noted, some of the best-known threatened species, such as giant pandas (*Ailuropoda melanoleuca*) and tuataras (*Sphenodon* spp.), or recently extinct species such as the thylacine (*Thylacinus cynocephalus*), are phylogenetically old and distinct. The actual loss of bird and mammal species results in greater loss of genetic and evolutionary diversity than if extinct species were distributed randomly among higher taxonomic groups (Russell et al. 1988; Purvis et al. 2000a).

### The ecological consequences of biodiversity loss

#### Do extinctions matter?

When species interfere with human endeavours we often suppress their numbers and – in some quarters – celebrate their demise. Such is the case with many carnivorous species such as the thylacine in Tasmania or wolves (*Canis lupus*) and brown bears (*Ursus arctos*) in the UK. Potential competitors or pests such as the passenger pigeon (*Ectopistes migratorius*), and disease organisms such as smallpox, have also been deliberately eliminated. Even when species do not compete with *Homo sapiens*, their passing often elicits little comment; good recent examples include many species of tropical rainforest frogs, small freshwater fish and the spectacular but ill-fated Miss Waldron's red colobus (*Procolobus badius waldroni*) from Ghana. So do extinctions matter?

The answer is in an emphatic 'yes' for a wealth of reasons. The effects of extinctions are obvious and matter profoundly. There are

practical ones about the species itself. Since the invention of bread, housewives may have wished the demise of the mould that spoiled baking. Only in the past 50 years or so have so many of us owed our very lives to *Penicillin* and other antibiotics. Not only are species useful, but so too are the ecosystems of which they are part. Species rarely go extinct as carefully excised members of some ecological community. Most commonly, a hillside is clear-cut, a reef dynamited or a wetland cleared, taking with it species and ecosystem benefits in one fell swoop.

#### Do extinctions matter ecologically?

Playing Devil's Advocate, we might argue that species are rare and often sparsely scattered before they finally expire, so their impact on energy and nutrient flows, use of resources and interactions with other species should be hardly noticeable after they have gone. We could also point to species that contribute little to community function and hence appear to be functionally redundant (Walker 1992). One problem with such arguments is that they often view species as static entities with fixed roles, and do not consider times or places where 'redundant' organisms predominate. One example is the long-haired rat, *Rattus villosissimus*, of central Australia. This distinctive rodent is often invisible at the landscape level for decades at a time, with small populations being clustered around desert oases. After drought-breaking rains its numbers erupt, and migratory hordes sweep across vast areas at speeds of 1–2 km day<sup>-1</sup>; dominating all other small mammals at these times, its burrow systems are used by at least 17 other species of vertebrates, and the excavated soil alters the dynamics of both the soil seed bank and trajectory of plant succession (Dickman 2003a). Despite its usual low profile, the long-haired rat is clearly not 'redundant' in any ecological sense of the word.

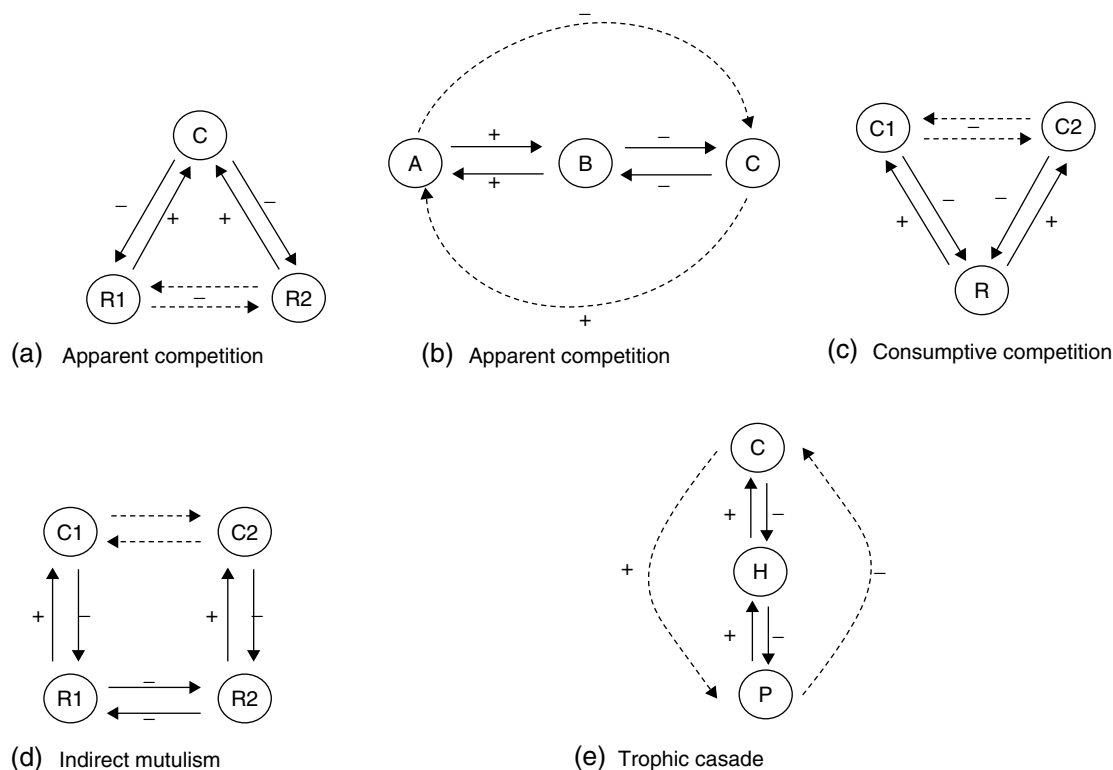
Ecologically, losses of species can have several consequences, and these depend largely on

what the species do. At least three kinds of roles can be distinguished (Kinzig et al. 2001).

In the first instance, species interact with each other directly and indirectly, and influence each other's population sizes, use of resources and evolution. Interactions are sometimes obvious, such as when predators limit populations of their prey, competitively superior species invade the ranges of subordinates, or species depend on each other for provision of resources, as with the fungal and algal partners in lichens. In these one-on-one interactions, loss of one species can either liberate or doom the other. In other situations, interaction pathways occur among suites of species and make the task of

predicting the impacts of a single extinction more difficult (Dickman 2003b). Such indirect interactions include trophic cascades, apparent competition, keystone predation and many others (Fig. 1.1).

As one example, let us consider a special kind of trophic cascade termed 'mesopredator release'. Here, if a top predator suppresses the numbers of a smaller predator, it may indirectly benefit the smaller predator's prey. Loss of the top predator, for example, the coyote (*Canis latrans*), may release mesopredators such as house cats (*Felis catus*), which can then deplete populations of scrub-breeding birds and lizards (Crooks & Soulé 1999). Local extinctions are



**Fig. 1.1** Examples of indirect interactions between species: (a) and (b) depict apparent competition; (c) consumptive competition; (d) indirect mutualism; and (e) trophic cascade. In (b), A, B and C represent species in the same trophic level; in (e), C represents top consumer or predator, H represents herbivore and P represents primary producer. In other interactions, C represents consumer species and R represents resource species. Direct effects between species are shown by solid arrows, indirect effects by broken arrows. Arrow heads show the species affected, and + and - show the direction of the effect. (Redrawn from Dickman, 2003b.)

sometimes followed by bewilderingly diverse effects, such as increases in plant damage following the loss of carnivores (Schmitz et al. 2000), increases in fish populations in the absence of feral horses (Levin et al. 2002) or, most famously, depressed reproductive success in flowering plants when house cats are absent (Darwin 1859). Such effects are often explicable within the framework of indirect interactions.

Second, some species affect their physical environment, and this in turn modulates the resources that are available to others. These species, termed 'ecosystem engineers' by Jones et al. (1994), often have dramatic and powerful effects on the environment, so the consequences of their extinction can be expected to be far-reaching. Two kinds of engineers were defined by Jones et al. (1994): 'autogenic engineers' change the environment via their own physical structures (e.g. corals that form reefs, trees that produce hollows), whereas 'allogenic engineers' change the environment by transforming materials from one state into another (e.g. burrowing animals such as the long-haired rat, noted above) (Fig. 1.2).

Let us consider two examples of the effects of losing engineer species. Firstly, the woylie (*Bettongia penicillata*) is a small (1 kg) marsupial that once occurred over most of southern Australia. Studies in the tiny current range of the species in the continent's far south-west show that individual woylies displace about 4.8 t of soil annually, and contribute significantly to infiltration of water, seed-bank dynamics and dispersal of hypogeal fungi (Garkaklis et al. 2004). Its disappearance from semi-arid habitats has increased rainfall run-off, and hence soil erosion, and appears to slow the establishment and growth of vascular plants. Secondly, the passenger pigeon once occurred in staggeringly large numbers (3–5 billion individuals) in eastern North America, but it was extirpated in the wild by 1900. Huge roosting and nesting aggregations of this species are suspected to have caused breakages of tree branches and limbs, which in turn increased fuel loads on the forest floor and influenced

the frequency and intensity of fires (Ellsworth & McComb 2003). As passenger pigeons consumed vast numbers of red oak (*Quercus rubra*) acorns, the recent expansion of northern red oak forest and decline of white oak *Q. alba* may be further consequences of the pigeon's demise.

A third ecological role performed by species is the provision of 'ecosystem services'. These include fixation of energy and nutrients, cycling of water and minerals, formation of soil, transformation of gases and maintenance of climate. Early ecosystem-level studies suggested that particular species of plants are disproportionately important in fixing energy and matter (Waring 1989), so we may expect that loss of these species would compromise one or more ecosystem services (Ehrlich & Ehrlich 1992). Intriguingly, some research indicates that only a few species – perhaps a dozen – are needed to perform geochemical services, but key services such as primary productivity and uptake of CO<sub>2</sub> diminish with declining species richness (Naeem et al. 1995; Schlöpfer et al. 2005).

Extinctions do not always have immediate or detectable effects, especially if the species lack strong engineering or keystone credentials. However, if losses are cumulative, ecosystem functioning may decline gradually until the system collapses. This scenario has been popularized as the 'rivet hypothesis' (Ehrlich & Ehrlich 1981), which likens species to rivets supporting an aircraft wing. Loss of just one or two rivets may increase only slightly the chance that the wing will fail, but catastrophe occurs when the next rivet is lost and the aircraft crashes. There is little, if any, evidence that collapse occurs catastrophically, but examples of progressive (and sometimes rapid) loss of ecological function abound.

Historical overexploitation of fisheries provides a good example. In many parts of the world, as readily exploited species of fish and shellfish have declined in catches, they have been replaced sequentially by ecologically similar species, thus delaying the onset of obvious system failure. However, as replacement species have themselves become progressively overfished (the last 'rivets'), coastal ecosystems have