REVIEWS AND SYNTHESES

Trends in the state of nature and their implications for human well-being

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Abstract

Two major international initiatives – the Convention on Biological Diversity's target to reduce the rate of biodiversity loss by 2010, and the Millennium Ecosystem Assessment – raise the profile of ecological data on the changing state of nature and its implications for human well-being. This paper is intended to provide a broad overview of current knowledge of these issues. Information on changes in the status of species, size of populations, and extent and condition of habitats is patchy, with little data available for many of the taxa, regions and habitats of greatest importance to the delivery of ecosystem services. However, what we do know strongly suggests that, while exceptions exist, the changes currently underway are for the most part negative, anthropogenic in origin, ominously large and accelerating. The impacts of these changes on human society are idiosyncratic and patchily understood, but for the most part also appear to be negative and substantial. Forecasting future changes is limited by our poor understanding of the cascading impacts of change within communities, of threshold effects, of interactions between the drivers of change, and of linkages between the state of nature and human well-being. In assessing future science needs, we not only see a strong role for ecological data and theory, but also believe that much closer collaboration with social and earth system scientists is essential if ecology is to have a strong bearing on policy makers.

INTRODUCTION

Growing concerns about declines in wild populations and the places they live, and about the consequences of these losses for human welfare, have recently spawned two major initiatives which bring ecological and other data to bear on high-level decision-making. In September 2002 at the Johannesburg World Summit on Sustainable Development, representatives of 190 countries committed themselves to the central target of the Convention on Biodiversity (CBD), of achieving 'by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national levels as a contribution to poverty alleviation and to the benefit of all life on Earth' (UNEP 2002a). This ambitious agreement represents an important watershed – it is the first time that most of the world's governments have agreed a quantitative target for slowing the loss of nature. However, measuring progress towards the 2010 target and designing policies that will help achieve it will depend on a battery of standardized, regularly repeated and representative measures – of the state of populations and habitats and the benefits they bestow on humanity, as well as the underlying drivers of change, and the impact of interventions aimed at reversing undesirable change (Green *et al.* 2005a). In early 2004, parties to the CBD established a framework for such measures consisting of eight indicators for immediate testing and a further 10 for future development (UNEP 2004). Refining and delivering these measures, and strengthening them by developing additional complementary indicators, will require substantial input from ecologists as well as social and earth system scientists (UNEP 2004; Balmford *et al.* 2005a,b).

The Millennium Ecosystem Assessment (MA), launched in June 2001, similarly hinges on contributions from a large and diverse suite of natural and social scientists (Millennium Ecosystem Assessment 2004). Modelled on the Intergovernmental Panel on Climate Change, the MA aims to provide decision makers and the public alike with a broad scientific evaluation of the consequences of current and projected changes in ecosystems for human well-being, and of policy options for addressing those changes (Reid & Mace 2003; Millennium Ecosystem Assessment 2004; Mooney *et al.* 2004). It therefore has an explicit focus on ecosystem services. It has been designed to meet the needs of existing international conventions (the CBD, the Convention to Combat Desertification and the Wetlands Convention), and is working at multiple scales, from local to global. Several subglobal assessments (e.g. Biggs *et al.* 2004; Bohensky *et al.* 2004; Scholes & Biggs 2004), as well as a conceptual framework document (Millennium Ecosystem Assessment 2003), have already been released. Three global reports, and a synthesis of all the sub-global assessment, are due to be published in 2005, and it is anticipated that the MA process will be repeated thereafter, every 5–10 years.

In the context of these initiatives this paper sets out to sketch a broad overview, aimed at ecologists rather than conservation scientists or policy makers, of what is currently known about present day and projected changes in the status of species, populations and habitats, and how these may impact human welfare. Throughout, we avoid the term 'biodiversity' because we are concerned not just with the variety of living organisms, but with their quantity as well – both are fundamental aspects of the state of the natural world and its impacts on human well-being. Biodiversity, on the other hand, is usually defined in terms of difference rather than amount (although the MA proposes a new, broader definition; Millennium Ecosystem Assessment 2003). In place of biodiversity we use the term 'wild nature' (sometimes abbreviated simply to 'nature') to refer to habitats (and the organisms they contain) which have largely not been converted (at least in the recent past) for human use (Balmford *et al.* 2002). We therefore exclude aspects of nature which persist in cropland or urban areas. The boundaries of wild nature are inevitably imprecise (particularly where habitats that are currently only lightly used have at some stage been heavily impacted by people; and where free-ranging populations occupy semi-natural habitats); nevertheless given its focus on amount as well as variety, and because we suspect it may be more readily understood than biodiversity, we think wild nature is a more helpful term in the present context.

The review is in three main parts. We start off assessing what is known about recent and impending changes in the state of wild nature – what are the overall trends, at the level of species, populations and habitats; how do these patterns vary, taxonomically, spatially and temporally; and why are detailed trends hard to forecast? The second main section then considers the implications of these changes for present and future human well-being, working from general considerations of the benefits derived from natural systems, through to specific examples (both historical and contemporary) of the consequences of the erosion of these systems. We then end by highlighting a number of areas where we think further work (especially ecological research) is needed to better inform both the measurement of global change in the state of nature and the assessment of its consequences for people. Throughout, we do not attempt an exhaustive review of the literature, but instead try to use illustrative examples to highlight both the importance of ongoing losses, and the scientific challenges ahead.

RECENT AND IMPENDING CHANGES IN THE STATE OF WILD NATURE

Three broad themes emerge from considering what is known about trends in the extent of wild populations and habitats. First, although data are patchy, it is clear that humans have brought about substantial changes, especially in the past century, which are largely (although not entirely) negative, and which look set to continue. Second, the extent of these changes varies widely, taxonomically, spatially and temporally. Last, these changes are complex, in several respects; this complexity in turn limits our ability to forecast future changes.

### Changes are substantial and predominantly negative

Although there are major shortfalls in the extent and quality of our knowledge, there is already overwhelming evidence that humans have caused the loss of a great deal of wild nature over the past 50 000 years, and that rates of loss have accelerated sharply over the past century (Mace *et al.* 2005). Information on these losses is of three sorts: data on past and impending extinctions, on population changes and on habitat changes.

Conservation biologists have until recently quantified the impact of people on nature mainly in terms of rates of human-caused extinction and threat (e.g. see Pimm *et al.* 1995). For prehistoric losses, quantifying and establishing the causes of extinctions is extremely difficult. However, the past decade has seen growing (although still disputed) support from harvesting models, analyses of sediments and middens, and improved dating of the timing of human colonization events relative to species disappearance, arguing that overexploitation by human hunters played a large part in the widespread extinctions of the late Quaternary megafauna (Flannery & Roberts 1999; Martin & Steadman 1999; Miller *et al.* 1999; Steadman *et al.* 1999; Holdaway & Jacomb 2000; Alroy 2001; Diamond 2001; Roberts *et al.* 2001; Johnson 2002; Burney *et al.* 2003; for

counterarguments, see Stuart 1991; Brook & Bowman 2002, 2004; Wroe *et al.* 2004). For the more recent past, documented extinctions since 1500 stand at around 800 species (IUCN 2004). As many species probably were and still are being lost before being described by science, this is likely to be a substantial underestimate of the true total. However, within better documented groups (such as birds and mammals), these known losses have been shown to represent a 100–1000-fold increase in extinction rates above background rates in the fossil record (Pimm *et al.* 1995).

What about impending extinctions? Analyses based either on the observed and projected movement of threatened species through the IUCN Red List categories, or on combining the species–area relationship with data on current rates of habitat loss, suggest that a further *c.* 10-fold increase in extinction rates is likely (Reid 1992; Smith *et al.* 1993a,b; Heywood *et al.* 1994; May *et al.* 1995; Pimm *et al.* 1995; Carlton *et al.* 1999; Brook *et al.* 2003). Among extant taxa, *c.* 20% of all species in those groups whose conservation status has been comprehensively (or near-comprehensively) assessed – mammals, birds, amphibians, conifers and cycads – are believed to be threatened with extinction in the near future (IUCN 2004). Moreover, this proportion has increased in recent years (BirdLife International 2004; Butchart *et al.* 2004; IUCN 2004; Stuart *et al.* 2004; Fig. 1). Thus despite uncertainties in current, recent and background rates of loss (Regan *et al.* 2001), it is clear that extinctions have accelerated markedly, and that contemporary extinction rates are at least three orders of magnitude above background (Mace *et al.* 2005).

As species are likely to become ecologically extinct and contribute very little to ecosystem services long before they become biologically extinct, data on trends in population sizes represent an important complement to categorical data on extinct and threatened species (Hughes *et al.* 1997; Balmford *et al.* 2003; Biggs *et al.* 2004; Loh *et al.* 2005). Not surprisingly,
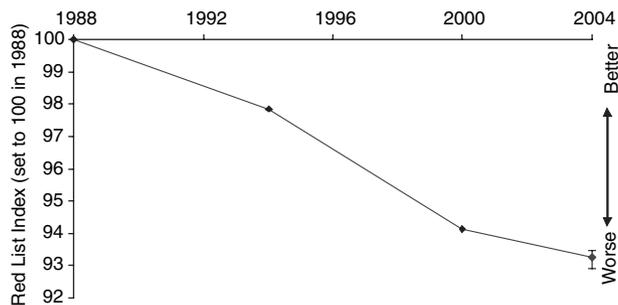
Figure 1 Declining status of the world's birds, as measured by the Red List Index (set to 100 in 1988), which measures changes in the number of species in each Red List category and the number changing categories between successive threat assessments. See Butchart *et al.* (2004) for more details.

quantitative data on population trends extending back more than a few decades are sparse. However, analyses of historical accounts can prove highly informative, suggesting for example, that Caribbean turtle numbers have declined by over 99.9% since 1500 and Australian dugong populations by over 98% in the past century (Jackson 1997, 2001). The taxonomic, geographical and habitat coverage of population monitoring schemes is extremely uneven (see below), but those data that are available show that the past 20–40 years have seen substantial declines in the population size and/or range extent of most groups monitored. Examples include a mean 68% decline in the pre-industrial range extent of 173 declining mammal species (measured at $2° \times 2°$ resolution; Ceballos & Ehrlich 2002); decreases in range size (measured as occupancy of 10 km × 10 km squares) from the 1960s to the 1990s among 54%, 28% and 71% of British birds, vascular plants and butterflies, respectively (Thomas *et al.* 2004a); and mean reductions in population size of over 1100 assorted mammal, bird, reptile, amphibian and fish species of *c.* 38% since 1970 (Loh *et al.* 2005).

Among aquatic organisms, time series data for 936 populations of 157 amphibian species show a near 80% decline since the 1950s (Houlahan *et al.* 2000, 2001; Alford *et al.* 2001); stock assessments by the FAO suggest that three-quarters of harvested fish populations that are monitored are already overexploited or will become so without stringent management intervention (FAO 2000); and analyses of fisheries data indicate that shark numbers in the north-west Atlantic declined by around three-quarters since 1986 alone (Baum *et al.* 2003), and that the recent expansion of fishing into the open oceans was typically associated with population declines of tuna, swordfish and billfish of *c.* 80% in just 5 years (Myers & Worm 2003). Populations of some great whales have increased since the cessation of commercial whaling (International Whaling Commission 2005) but current densities are as yet still a small fraction of pre-harvesting levels (Springer *et al.* 2003).

These declines in populations are broadly mirrored by what is known about recent changes in the extent and condition of natural habitats (Jenkins *et al.* 2003). At a global level, forests represent by far the best studied biome, because of both their commercial importance and their suitability for monitoring via remote-sensing. Recent data for temperate forests suggest that these increased in extent by around 0.1% per year over the period 1990 to 2000, largely because of the abandonment of agriculture in parts of north-east USA (FAO 2001). In contrast, forest cover in tropical regions has continued to decline sharply, with annual loss estimates for the 1990s ranging from 0.4% (for humid forests, Achard *et al.* 2002) to 0.8% (for all tropical forests, FAO 2001). Recent losses have been particularly severe in SE Asia (FAO 2001; Jepson *et al.* 2001; Mayaux *et al.* 2005) and appear to be increasingly impinging on

formally protected areas (Curran *et al.* 2004; DeFries *et al.* 2005; Mayaux *et al.* 2005). Annual rates of loss of mangroves, of considerable importance to human well-being because of their role in onshore protection from storms, and as fish nurseries, may have dropped from *c.* 2% in the 1980s to *c.* 1% in the 1990s (Valiela *et al.* 2001; FAO 2004).

There are generally fewer data available on changes in habitat condition, although these may be more widespread and damaging than changes in habitat extent. However, on coral reefs, where losses typically proceed initially via changes in community composition rather than complete conversion, expert review and meta-analytical techniques have recently generated quantitative estimates of changes in condition. Worldwide, it is estimated that reefs have become 30–80% degraded since pre-human times (Pandolfi *et al.* 2003), while regional meta-analyses of declines in coral cover range from 20–40% since 1965 for the Great Barrier Reef (Bellwood *et al.* 2004), to a mean of 9.2% per year from 1977 to 2001 for the Caribbean (Gardner *et al.* 2003; Côté *et al.* 2005).

However, while human impacts on biodiversity are predominantly negative, it is important to note that the status of some species, populations or habitats has improved under human influence. Besides invasive species (not considered here), and the competitors or prey of declining species (considered briefly below), there are also significant positive examples where species have been brought back from the brink of extinction, alarming declines in populations have been turned around, or natural areas have expanded or been restored from a degraded condition. We briefly consider some examples and some commonalities.

The southern right whale (*Eubalaena australis*) was so heavily exploited in the 19th century that, by the beginning of the 20th century, it had disappeared altogether from much of its former range (Best *et al.* 2001). After almost a century of protection, the global population now exceeds 4000 and is increasing at near its biological maximum, with the species supporting a whale-watching industry which by 1997 was worth over $15 million per year in Argentine Patagonia alone (Rivarola *et al.* 2001). As a terrestrial example, the southern white rhino (*Ceratotherium simum simum*), once widespread in southern Africa, was reduced to 20 animals in a single small area by 1895. Intensive capture and translocation efforts have resulted in recovery to a population of > 10 000 distributed in many areas within its former range, and downlisting of the subspecies from Threatened to Near Threatened (Emslie & Brooks 1999; IUCN 2004). Other examples highlight the importance of active conservation efforts where legal protection of species has not been enough. New Zealand, like many islands, suffered extensive vertebrate extinctions, losing 40% of its terrestrial birds after human settlement with > 40% of the

remainder listed as threatened with extinction, a higher proportion than any other country (Clout 2001). Despite a long history of conservation and an extensive network of nature reserves in New Zealand, populations continued to decline. Active intervention, in the form of eradication of invasive mammals and translocation of threatened species to small off-shore islands, has resulted in dramatic increases in native bird and reptile populations (Atkinson 2001). These efforts were so successful that they have now been extended to areas on the 'mainland' (Saunders & Norton 2001).

Some natural habitats have also shown recent increases in extent or condition. We have already noted the current expansion of temperate forests in NE USA. Abandoned agricultural land is reverting to semi-natural habitat in other industrialized nations too. One particularly useful management tool in the restoration of degraded habitats has been the biological control of invasive species via the introduction of natural enemies from the species native ranges. For instance, the introduction of *Neochetina* weevils has played a key role in the restoration of open waters in Lake Victoria following their infestation by Amazonian water hyacinth (*Eichhornia crassipes*; McFadyen 1998; National Agricultural Research Organisation 2002). There are also some encouraging examples of carefully managed restoration of severely threatened habitat types, such as prairie grasslands in North America, heathland in southern Britain, and Atlantic forest in Brazil (e.g. Forrest *et al.* 2004); importantly, the spatial scale of these initiatives is now increasing. A recurrent theme of many of these success stories seems to be that while benign neglect may occasionally lead to recovery (as in the forests of the NE USA), more often, active management intervention is required to reverse a negative trend. Even protected status is commonly not enough.

These important positive counterexamples notwithstanding, the balance of data on changes in the status of species, populations and habitats provides clear evidence of widespread and continuing anthropogenic declines in the extent and variety of wild nature. However, there are many important gaps in our knowledge (Balmford *et al.* 2005b; Mace *et al.* 2005). Taxonomically, we know very little at global or regional scale about extinctions or population declines in the great majority of groups; key omissions include most plants, nearly all invertebrates, and essentially all microbes. Geographically, while monitoring has long been underway in a handful of temperate regions, there are still very few ongoing schemes for tropical species and biomes. In terms of habitats, there are no global monitoring systems in place for two-thirds of the world's biomes (Jenkins *et al.* 2003), with wetlands, grasslands, and almost all marine habitats being particularly striking omissions. Perhaps of greatest concern is the fact that many of the taxa, regions and habitats about which we know least are those of greatest importance to the sustained delivery of ecosystem

services (Costanza *et al.* 1997; Balmford *et al.* 2003; Jenkins *et al.* 2003). We believe that there is an urgent need to address these data gaps, as well as tackle limitations in existing measures, in order to strengthen our understanding of changes in wild nature and of interventions that might reduce them (Balmford *et al.* 2005a,b).

Changes are varied

Besides being predominantly negative, humanity's impacts on nature vary widely, on at least three dimensions. Taxonomically, it is evident that certain groups are more vulnerable than others: for instance, amphibians as well as freshwater fish and invertebrates generally, are currently more threatened and undergoing steeper rates of population decline than groups such as birds or mammals (Houlahan *et al.* 2000, 2001; Master *et al.* 2000; Alford *et al.* 2001; IUCN 2004; Stuart *et al.* 2004; Loh *et al.* 2005). Within groups, phylogenetically distinct, ancient and species-poor lineages seem consistently to be faring disproportionately badly (e.g. McDowall 1969; Gaston & Blackburn 1997; Russell *et al.* 1999; Purvis *et al.* 2000a; but see Schwartz & Simberloff 2001 for a different pattern among plants). Species with narrow global ranges (for which localized threats can cause global extinction) are typically also more threatened (McKinney 1997; Owens & Bennett 2000; Purvis *et al.* 2000b). Larger-bodied and more specialized species (which generally have more exacting metabolic or ecological requirements) are disproportionately likely to be in trouble, whereas some generalist species are expanding their ranges (Bennett & Owens 1997; McKinney 1997; Owens & Bennett 2000; Purvis *et al.* 2000b).

Temporally, two patterns stand out. The first is that, although both on land and at sea pre-industrial human-caused losses were often very substantial (see above), the rate of loss is in general increasing. The second is that the anthropogenic drivers of loss are changing in their relative importance. For example, looking at bird species, extinctions over the past 500 years are roughly equally attributable to invasive species, overexploitation and habitat loss. However, nowadays habitat loss, especially to agriculture, is the biggest problem facing threatened species, and is overwhelmingly the most important for near-threatened species (expected to become threatened in the near future; Fig. 2; BirdLife International 2004; Green *et al.* 2005b). Nevertheless, although they are declining relative to habitat loss, in absolute terms overharvesting (especially of marine fish, and of tropical vertebrates exploited as bushmeat) and invasive aliens (especially exotic pathogens and aquatic species) are increasing as threats (Ricciardi & MacIsaac 2000; Harvell *et al.* 2002; Milner-Gulland & Bennett 2003; Pauly *et al.* 2003; Clavero & Garcia-Bertou 2005). In addition, while not yet reflected in formal threat assessment, accelerating climate change is also forecast to emerge as a major threat to all taxa in the near future (Parmesan & Yohe 2003; Root *et al.* 2003; Williams *et al.* 2003; Thomas *et al.* 2004b).

Last, human impacts vary spatially. Linked in with the importance of introduced aliens, recent extinctions of terrestrial species have been concentrated on islands (Pimm *et al.* 1995). Ongoing changes – in habitat extent and condition, and in population sizes – are more marked in tropical regions (e.g. Loh 2000). Habitat loss in particular, as the greatest current driver of change, has been and looks set to continue to be disproportionately concentrated in endemic-rich parts of the tropics, where areas of dense human settlement and high species richness tend to coincide (Cincotta *et al.* 2000; Balmford *et al.* 2001; Luck *et al.* 2004; Scharlemann *et al.* 2004). As a consequence, impending extinctions are particularly concentrated on tropical island and montane systems (BirdLife International 2004; IUCN 2004). Substantial historical reductions in habitat extent
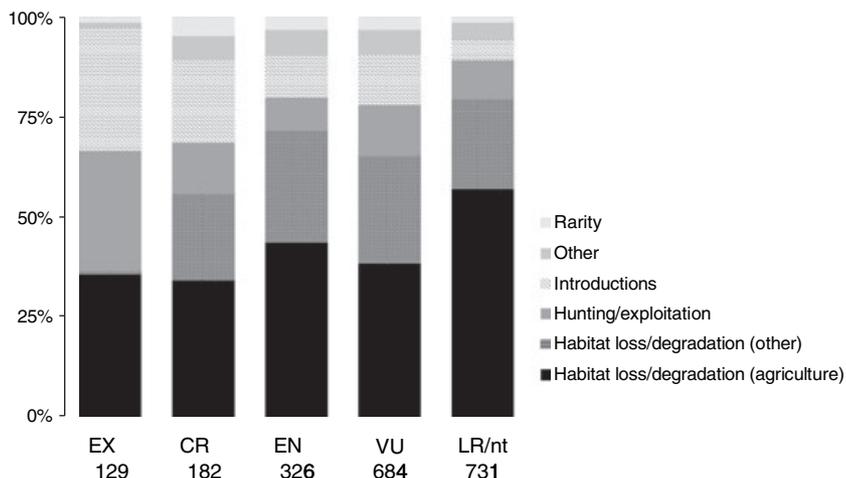
Figure 2 Relative importance of different threats to Extinct (EX), Critically Endangered (CR), Endangered (EN), Vulnerable (VU) and Near-Threatened (LR/nt) bird species; numbers below each column give numbers of species in each threat category. For more details, see BirdLife International (2004) and Green *et al.* (2005b).

have had typically less of an impact in temperate regions, presumably in part because temperate species generally have larger global ranges (Rohde 1992). At present, populations and habitats are expanding in some temperate biomes and regions (Loh 2000; Jenkins *et al.* 2003). Spatial variation in human impacts on freshwater and marine systems are less well documented, although Lake Victoria (impacted by introduced species and siltation from land conversion), the Caribbean basin (affected primarily by overexploitation and siltation), and the freshwater habitats of arid south-western USA (impacted particularly by drainage) stand out as examples of areas where recent losses of species and habitats have been particularly marked (Bruton 1995; Jackson 1997; Seehausen *et al.* 1997; Gardner *et al.* 2003).

Changes are complex

Besides variety, the overriding feature of wild nature is its complexity. Patterns in how nature is being lost are in turn correspondingly complex, in several respects. Species, populations and ecosystems differ not just in their exposure to anthropogenic drivers of changes, but also in their vulnerability to them. One obvious set of reasons is that species differ in their global range size, and in their ecological and physiological resilience to change (see above). However, history can also be important. A potentially useful device here is the concept of extinction filters, whereby prior exposure to a threat may selectively remove those individuals or species which are most vulnerable to it, leaving behind a community which is more resilient to similar threats in future (Balmford 1996). This idea can explain temporal and spatial variation in species vulnerability to repeated natural changes in the past (such as glaciation events, Coope 1994), but it may also shed light on the contemporary and future impact of anthropogenic threats. For example, the current impact of alien invasives appears less marked for those South American taxonomic groups that were involved in the Great American Biotic Interchange of 3 million years ago than for those that were not (Rodríguez 2001). Introduced rats apparently pose less of a threat to island-nesting seabirds on islands with native rats or land crabs which may have selected for resilience to predators (Atkinson 1985). In a similar manner corals may be less likely to bleach in response to rising sea temperatures in areas where they have been repeatedly exposed to temperature stresses in the past (Brown *et al.* 2000; Podesta & Glynn 2001; West & Salm 2003).

Second, complex interactions within communities mean that changes in the abundance of one species will often have other, sometimes broad-ranging effects through a system (Paine & Schindler 2002). The 1998 El Niño-driven drought in northern Borneo, for example, led to a prolonged disruption of fig flowering, causing marked range contrac-

tions of several fig wasp species (Harrison 2000). Many of these failed to recolonize the area after the drought, raising concerns that their disappearance could trigger the loss of the fig species which depend on them for pollination, and in turn the very many species dependent on the fig trees. One of the best-documented examples of a major, human-driven trophic cascade is the switch by north Pacific killer whales to hunting pinnipeds and more recently, sea otters (probably itself prompted by the removal of at last half a million great whales from the region in the 30 years following World War II; Springer *et al.* 2003). The change in killer whale diet has greatly reduced sea otter numbers, allowing the population and grazing pressure of sea urchins to increase, in turn leading to a dramatic decline in kelp density (Estes *et al.* 1998; Fig. 3). Evidence is accumulating of similar, potentially irreversible changes in the food webs of open ocean ecosystems formerly dominated by cod (*Gadhus morua*) and, following sustained overfishing, now dominated by shrimps and snow crabs (Frank *et al.* 2005). In Australia, the deliberate introduction of highly flammable African grasses (such as gamba grass, *Andropogon gayanus*) to native woody savannas has also introduced frequent, very intense fires (Rossiter *et al.* 2003); as elsewhere (D'Antonio & Vitousek 1992), changes in the fire regime in turn reduce native tree and shrub cover, thereby accelerating the invasion of fire-tolerant aliens and resulting in a wholesale ecosystem shift from woody vegetation to open grassland.

These latter examples illustrate a third aspect of complexity. It is becoming clear that often, ecosystems do not respond linearly to external changes but instead do so in a stepwise manner. Thus cumulative biotic or abiotic pressures which at first appear to have little effect may lead to quite sudden and unpredictable changes once thresholds are crossed (Scheffer *et al.* 2001; Folke *et al.* 2004). Such thresholds may be lower in species-poor systems with little redundancy in their representation of functional groups, or whose component species exhibit only a limited range of responses to external challenges (Folke *et al.* 2004). Consequently, as anthropogenic impacts simplify systems and reduce their resilience to change, major regime shifts – some of them effectively irreversible – may become more frequent. Examples have now been documented from all major biomes (Scheffer *et al.* 2001; Folke *et al.* 2004). One particularly well-studied case concerns the sudden switch in 1983 from coral to algal domination of Jamaican reef systems. This followed several centuries of overfishing of herbivores, which left the control of algal cover almost entirely dependent on a single species of sea urchin, whose populations collapsed when exposed to a species-specific pathogen (Hughes 1994; Jackson 1997). As a result, Jamaica's reefs shifted (apparently irreversibly) to a new low diversity, algal-dominated state with very limited capacity to support fisheries (McManus *et al.* 2000; Bellwood
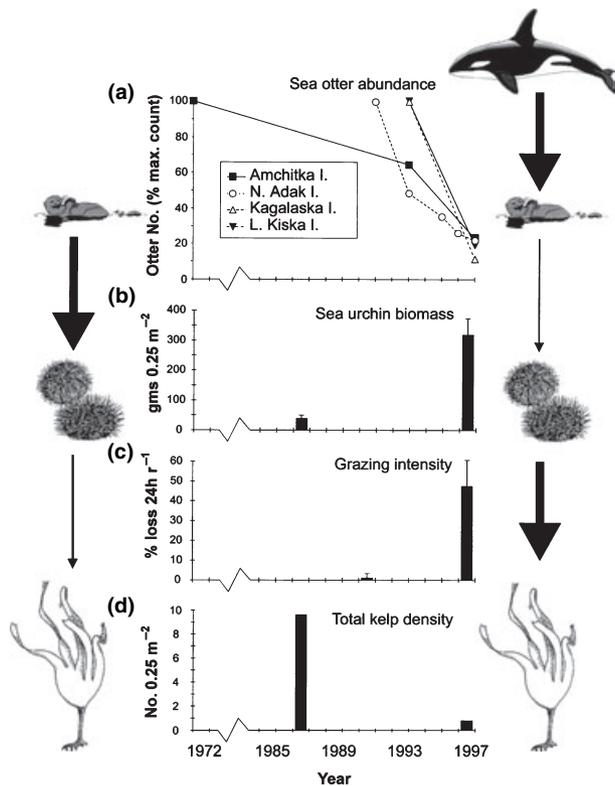
Figure 3 Human-driven trophic cascade in the Aleutian islands, illustrated by declining sea otter abundance (a) and associated increase in sea urchin biomass (b), grazing intensity (c) and reduction in kelp density (from Estes *et al.* 1998). The decline in sea otters was most likely driven by a change in killer whale behaviour from hunting pinnipeds to hunting sea otters [itself probably part of a wider megafaunal collapse in the northern Pacific (Springer *et al.* 2003)], and is associated in a switch from a system dominated by sea otter predation of urchins (left-hand drawings) to one dominated by killer whale predation of sea otters and urchin grazing of kelp (right-hand drawings). Reprinted with permission from Estes *et al.* (1998), *Science*, **282**, 473–476. Copyright 1998 AAAS.

et al. 2004). Given their potential importance, much more work is needed on regime shifts, and especially on how reversible they are, where thresholds lie, and how to detect their approach.

Last, community dynamics as well as socio-economic interactions mean that threats themselves rarely operate in isolation (Ehrlich & Holdren 1971; Myers 1995). There are now numerous examples of synergistic effects between different drivers of change. For instance, there is growing evidence of synergistic effects of increased UV-B exposure, acidification and pathogens on declining amphibian populations (Kiesecker & Blaustein 1995; Long *et al.* 1995; Stuart *et al.* 2004), and between the effects of logging, forest fragmentation and fire in tropical forests (Cochrane *et al.*

1999; Cochrane 2003). In the UK, data on butterflies show that the impact of climate change is more severe when transformation of their habitats blocks the ability of species to shift their ranges and so remain within their preferred climatic envelopes (Hill *et al.* 1999; Warren *et al.* 2001; Thomas *et al.* 2004b). In Hawai'i, it is anticipated that climate change will allow the spread of introduced avian malaria into those few high altitude refuges where endemic forest birds have so far persisted (Benning *et al.* 2002). Experimental plots replicating observed changes in Californian grassland diversity suggest that as species richness declines, community resistance to an invading alien plant, yellow starthistle, will also decrease (Zavaleta & Hulvey 2004). These examples are all mediated via species and communities themselves, but human-mediated interactions are also emerging. For example, long-term data from Ghana indicate that interannual variation in the rate of decline of mammal populations in nature reserves, driven by bushmeat hunting, can be predicted from changes in per capita availability of marine fish as a protein source for people (Brashares *et al.* 2004). When fish availability decreased, hunting increased and wildlife declines accelerated – suggesting a direct link between overexploitation on land and at sea.

What can we predict about future change?

Interactions among species, and among threats, nonlinearities, and the emergence of as yet unforeseen drivers of change all mean that forecasting future changes in the state of wild nature is extremely difficult. Nevertheless, some broad-brush projections are possible (for further discussion see UNEP 2002b; Jenkins 2003; Mace *et al.* 2005). Extrapolation from current trends suggests that both the amount and variability of nature will continue to decline over much of the planet. Decreases in many narrowly distributed species, coupled with increases in a small number of cosmopolitan species, will lead to increasing homogenization of the biota (McKinney & Lockwood 1999). These general trends may be offset in some developed countries by agricultural abandonment and, in some instances, ambitious restoration programmes, which may lead to increases in the extent of some habitats and their associated populations (Sutherland 2002, 2004; Rounsevell *et al.* 2005). In contrast, clearance of natural habitats, reductions of populations, and the associated loss of populations and indeed species, look set to persist and even accelerate across much of the tropics, and across many if not most aquatic systems. Particularly vulnerable areas include cloud forests, coral reefs and mangroves (all threatened by the synergistic effects of climate change and habitat clearance), all but the very largest blocks of tropical forest, and most freshwater habitats. Particularly vulnerable taxa include large marine species and

large-bodied tropical vertebrates (both already threatened by overharvesting), and many freshwater groups (threatened by the continuing conversion and degradation of their habitats).

IMPLICATIONS OF CHANGES IN WILD NATURE FOR HUMAN WELL-BEING

Why should people be concerned about the widespread and accelerating loss of populations, species, and habitats? There are of course fundamental moral reasons, frequently expressed in religious or spiritual terms, or in terms of the rights of non-voting species. Here, however, we concern ourselves with more prosaic reasons for concern, which have attracted considerable attention from ecologists and economists over the past decade. While their findings highlight the very substantial gaps still remaining in our understanding of the links between changes in the state of nature and human well-being, several generalities nevertheless emerge. Studies at a suite of scales, from experimental microcosms, through field measurements of particular services, to economic assessments of multiple services, together show that the benefits people derive from nature are diverse, complex and frequently substantial, yet are also generally non-marketed and thus vulnerable to market-driven economic activities. Historical and contemporary case studies confirm these general insights, and provide important illustrations of the range and magnitude of the economic, political and cultural consequences of losing wild nature. By contrast, a handful of recent examples show that timely quantification of the importance of natural systems for people can act as an important catalyst for conservation action.

General considerations

Work across a broad range of scales suggests that the consequences for the delivery of ecosystem services and thus for human well-being of the erosion of wild nature are poorly understood and complex, but are likely on the whole to be both negative and substantial. At the fine scale a growing number of experimental studies have explored whether diversity, *per se*, contributes to ecosystem function (Loreau *et al.* 2001, 2002). Most of these studies have focused on plants and many have shown positive (although asymptotic) effects of diversity on primary production and nutrient retention. Their relevance to the noisy world of natural ecosystems is far from clear, not least because it is difficult to disentangle whether the effects are caused by general diversity or particularly influential species. Just which species will be influential in which ecosystems, at what scales, and at what times remains an open empirical question (Loreau *et al.* 2001). New theory, together with experimental and comparative studies may yet contribute to general principles, or to the recognition of key functional types, relating diversity to ecosystem function (Naeem & Wright 2003). However we should not be surprised if the connections are idiosyncratic, varying in different ecosystems in different places. In contrast to this rather unclear picture, there is consensus that more diverse ecosystems are more likely to contain species that will cope with changing environments helping to maintain the stability of ecosystem processes (Grime 1998; Loreau *et al.* 2001).

Reviewing larger-scale field data on three sets of services illustrates further the complex linkages between human well-being and the state of nature. Among the most frequently studied (yet perhaps least straightforward) are the hydrological services associated with natural forests (for reviews, see Chomitz & Kumari 1998; Giambelluca 2002; Dudley & Stolton 2003; Hamilton & Cassells 2003; Bruijnzeel 2004). Contrary to the popular perception that removing forest cover will usually reduce water yield, the bulk of empirical studies suggest the opposite: that by reducing losses through evapotranspiration, forest clearance typically increases total water yield. However, this generality masks important complexities. For instance, forest conversion often reduces the absorptive capacity of underlying soils, increasing peak season run-off, and (depending on how the loss of infiltration compares with the reduction in evapotranspiration), potentially reducing dry season flows (for a worked example of these combined impacts on hydroelectric power production, see Guo *et al.* 2000). Moreover certain forest types – such as cloud forests, which intercept fog and often use little water themselves – can increase both dry season and total water yield (Becker 1999). The role of forests in reducing sedimentation and the risk of downstream flooding is similarly complex, with marked benefits of forest retention at small scales in steep areas, which become progressively diluted downstream and at basin-wide scales. Less equivocal is the contribution of forests to maintaining water quality. Forests are widely regarded as the most reliable land cover for catchments providing clean drinking water (Hamilton & Cassells 2003), and indeed at least one-third of the world's largest cities depend for their water supply on forest protected areas (Dudley *et al.* 2003).

Complexity also characterizes a second, widely discussed set of benefits – those associated with nature-based tourism. On the one hand, tourism is currently the world's fastest growing industry, with nature-based tourism considered its fastest-growing sector (Davenport *et al.* 2002). Across southern Africa, nature-based tourism has recently been estimated to generate roughly the same revenue as agriculture, fisheries and forestry combined (Scholes & Biggs 2004), and to be growing much more rapidly. On the other hand, scope for nature-based tourism in more remote areas with less charismatic species or scenery is likely to be much

more limited (McClanahan 1999; Davenport *et al.* 2002). Moreover, the economic benefits of nature-based tourism accrue mostly at national or international rather than local scales (Bookbinder *et al.* 1998; Walpole & Goodwin 2000; Kiss 2004), and are highly sensitive to periods of political instability (e.g. Butynski & Kalima 1998).

A third set of services which have attracted growing attention centre around linkages between wild nature and human health (for recent reviews, see Aguirre *et al.* 2002; Chivian 2002; Patz *et al.* 2004). Besides disruptions to the provision of healthy drinking water (see above), the diverse concerns here include the decreasing availability (as a result of habitat loss and overexploitation) of wild-harvested medicines; the loss of species that may contain as yet undiscovered drugs; the apparently negative effects of reduced contact with nature on people's mental and physical health and recovery from illness (Ulrich 1984; Frumkin 2001; Katcher 2002); increases in population sizes of reservoir and vector species and in people's exposure to them, through a combination of reductions in predator numbers and habitat fragmentation; and increased exposure to novel diseases because of greatly increased trade in wildlife. Analyses of emerging infectious diseases of major public concern, from SARS and Lyme disease to HIV/ AIDS, suggest that reasons for their emergence may often lie in anthropogenic changes to the natural environment (Bell *et al.* 2004; Patz *et al.* 2004).

These examples deal with just three of a much larger set of ecosystem services (Daily 1997). Synthesizing data across all services and extrapolating to regional and global scales suggests that the combined, gross value of the services provided by wild nature is vast. One widely cited synthesis of small-scale studies has estimated the global value of ecosystem services at very roughly $38 trillion ($10^{12}$) per year (in US$2000; Costanza *et al.* 1997) – more than global GDP. This analysis has been criticized for its extrapolation from the margin to the globe, and its reliance on a globally unrepresentative data set, but regional studies provide estimates which, although lower, are broadly similar in scale (Pimentel *et al.* 1997; Turpie *et al.* 2003). Most of these benefits are non-marketed and public. In contrast, habitat conversion or overexploitation, which generally increases
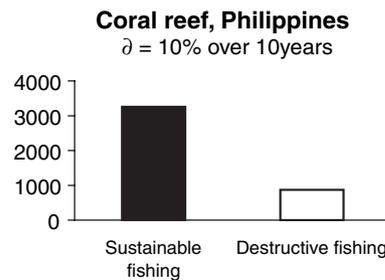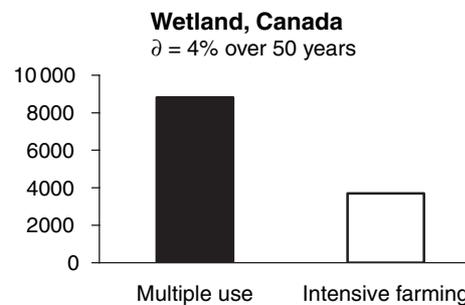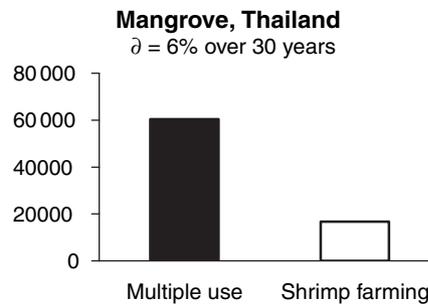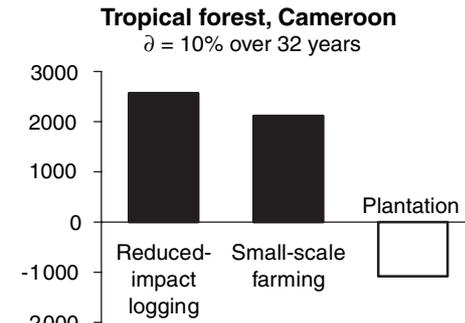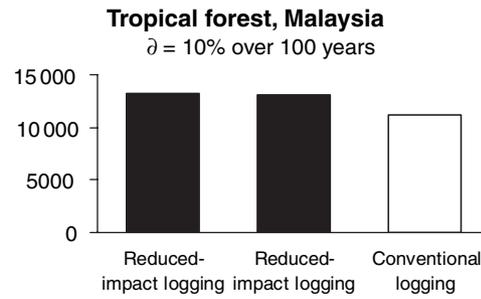
Figure 4 Results of five studies examining the marginal benefits of retaining and converting natural habitats, expressed as Net Present Values (in 2000 US$ ha^{-1}) calculated using the discount rates (∂) and time horizons presented. Values of measured goods and services delivered when habitats are relatively intact and when converted are plotted as black and white columns respectively. For case study sources and further details, see Balmford *et al.* (2002). Redrawn with permission from Balmford *et al.* (2002), *Science*, **397**, 950–953. Copyright 2002 AAAS.

the flow of marketed, private goods, typically makes narrow economic sense (Balmford *et al.* 2002; Turner *et al.* 2003; Turpie *et al.* 2003). However, the few case studies available suggest that those private gains achieved by conversion are typically outweighed by the loss of public benefits, so that in overall, societal terms, conversion of remaining intact habitat rarely makes net economic sense (Fig. 4; Balmford *et al.* 2002; van Beukering *et al.* 2003; Turner *et al.* 2003).

### Historical and contemporary examples

Large-scale economic arguments such as these can be persuasive, but perhaps more immediately compelling are examples that link losses of nature to documented declines in human well-being. At one extreme, these include studies suggesting that the decline and in some cases even the collapse of several ancient civilizations was associated with the overexploitation of biological resources. Among the more fully documented are the decline of the Maori, and the Rapanui of Easter Island, but other suggested examples include the collapse of successive Mesopotamian empires, of the Mayan civilization and even of ancient Greece (Deevey *et al.* 1979; Flenley & King 1984; van Andel *et al.* 1990; Ponting 1991; Flannery 1994; Redman 1999; for a recent review, see Diamond 2005).

On a more contemporary timescale, numerous studies confirm the variety and the magnitude of the consequences of losing wild nature for human well-being. For example, the early 1990s collapse of the Newfoundland cod fishery has cost tens of thousands of jobs, as well as at least $2B in income support and re-training (Commission for Environmental Cooperation 2001). Even a decade after ground-fishing was suspended, there is little evidence of stock recovery. More recently, the largely deliberate burning in 1997 of *c.* 50 000 km^2 of Indonesian vegetation (itself only *c.* 60% of the total area burnt from 1997 to 1998) affected around 70 million people (Schweithelm & Glover 1999). Some 12 million required health care and overall economic costs, through lost timber and non-timber forest products, lost agriculture, reduced health, increased CO_2 emissions, lost industrial production, and lost tourism revenues, have been conservatively estimated to run to $4.5 billion (Ruitenbeek 1999; Schweithelm *et al.* 1999). Most recently, the 95% decline since the mid-1990s of the *Gyps* vulture populations of the Indian subcontinent (a result of accidental poisoning by a veterinary drug, Green *et al.* 2004; Oaks *et al.* 2004; Shultz *et al.* 2004) is reported to have led to increases in the prevalence of rabies and plague, severe financial hardship for traditional bone and hide collectors, and even to deep divisions in the Parsi religion about how to dispose of their dead now that the traditional laying-out of corpses in Towers of Silence is no longer effective (Trivedi 2001).

The power of quantifying benefits

While these examples are sobering, more encouraging are a growing number of cases where the timely quantification of ecosystem services (or of disservices associated with ecosystem disruption) has helped trigger promising conservation interventions. We consider three.

The remaining forests of western Ecuador are among the biologically richest yet most threatened habitats on earth (Myers *et al.* 2000). Until 1995 attempts to encourage local peasant communities to conserve one important remnant cloud forest, in the 68 km^2 Loma Alta watershed, proved unsuccessful, despite secure land tenure arrangements and knowledge of the area's global importance for species conservation (Becker 1999; Becker *et al.* 2005). However, a joint initiative between NGOs and the local community succeeded in involving villagers in collecting data on differences in fog (garúa) interception between intact cloud forest and areas that had been cleared for fields and pasture. Losses in water yield were substantial (Fig. 5), and because water is sufficiently limiting that it is sold (for around $0.003/l), researchers and community members were able to calculate that the previous two decades of cloud forest clearance were now costing Loma Alta residents a mean of $640/household/year, in lost water alone. Catalysed by this finding, and with continued NGO support, the community subsequently established a *c.* 30 km^2 ecological reserve, where deforestation has been completely curtailed (for details, see Becker 1999; Becker *et al.* 2005).
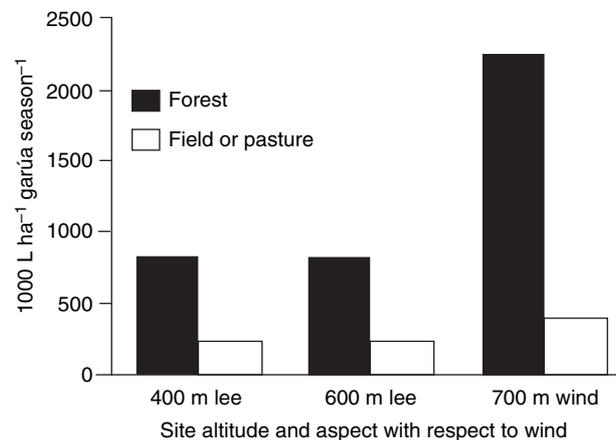
Figure 5 Seasonal interception of fog (garúa) from intact cloud forest and areas cleared for pasture or fields at three different combinations of altitude and aspect at Loma Alta, Ecuador. Water loss due to deforestation can be estimated as the difference between the paired columns; even if only 10% of this difference in drip-fall becomes available to villagers, two decades of forest clearance cost Loma Alta residents a mean of $640/household/year in lost water. See Becker (1999) for more details. Redrawn with permission from Becker (1999).

In South Africa, quantification of a disservice arising from the spread of alien trees has resulted in what is probably the largest single conservation intervention in the developing world. In this case, data gathered over decades showed that exotic trees that have invaded from forestry plantations (chiefly *Acacia* and *Pinus*) not only pose a major threat to native species by encroaching into natural habitats, but also severely reduce streamflows, with serious impacts for economic growth and human well-being (van Wilgen *et al.* 1998). In response to this evidence, in 1995 the South African government established its Working for Water Programme. With an annual budget currently around $70 million, this simultaneously increases water availability more cost-effectively than by dam-building, employs over 20 000 workers, and addresses a major driver of biodiversity change (van Wilgen *et al.* 2002; Görgens & van Wilgen 2004; Working for Water 2004).

Last, in Madagascar, a recent assessment by international and Malagasy economists concluded that continued upland deforestation by an estimated 50 000 slash-and-burn farmers leads to increased siltation and reduced water flows to > 2 500 000 downstream rice farmers (Carret & Loyer 2003). Comparing the total costs of conservation with a conservative estimate of its economic benefits (focusing on hydrological, tourism and existence values), the report's authors concluded that expanding current conservation efforts made sound economic sense. These findings are believed to have played a pivotal role in the Malagasy government's 2003 decision to triple the size of Madagascar's network of protected forests (J.-C. Carret and J.-P. Paddack, personal communication). Given their policy impact, we believe that there is a pressing need for many more locally relevant case studies such as these.

What can we predict about future well-being?

Clearly, our ability to forecast where, when and by how much changes in wild nature will impact human well-being is limited – we have too few data even on current losses, our knowledge of the dynamics of future change is patchy, and our understanding of the complex linkages between natural systems, service provision and human well-being is as yet rudimentary (see below). Future surprises are very likely. However, some more concrete inferences are also possible.

In the broadest terms, the available evidence clearly indicates that predicted future losses of wild nature will erode human well-being considerably. More specifically, the continued clearance of large areas of tropical forest will add substantially to global CO_2 levels, thereby accelerating global climate change (Houghton *et al.* 2001). The continued loss of cloud and other upland forests will reduce the quality and availability of water supplied to domestic consumers, industry and hydroelectric schemes in dozens of the world's

largest cities (Dudley *et al.* 2003). The loss of mangroves and coral reefs through destructive fishing, habitat conversion and climate change will both reduce inshore fisheries and result in increased storm- and flood-related damage to coastal settlements (Mumby *et al.* 2004; Anon 2005). And the continued overexploitation of marine fisheries worldwide, and of bushmeat in many areas of the tropics, will lead to a reduction in the availability of wild-caught animal protein, with serious consequences in many countries for food security and hence for human health (Fa *et al.* 2003; Pauly *et al.* 2003).

One last, overarching consideration is that areas where wild nature is being lost most rapidly are often affected by the erosion of many ecological services simultaneously (Scholes & Biggs 2004). Given that these are typically areas of high poverty and dense human settlement, it is unsurprising that they are often also characterized by marked social conflict (Scholes & Biggs 2004). With continued losses of wild populations and habitats in these areas, and their consequences for the provision of ecosystem services, we may expect such conflict to worsen (Homer-Dixon 1999).

SCIENCE NEEDS

It is evident that much more work is needed on trends in the state of nature and the consequences for people. While our limited knowledge should by no means be taken as an excuse for inaction, we believe that sharpening our understanding will yield more focused policy interventions, at all levels. This review has raised five areas which we think stand out as being in particular need of greatly increased attention from the scientific community.

First, our knowledge of current rates of change in the sizes of populations and habitats is very patchy. This is particularly worrisome given that some of the greatest gaps are concerned with those aspects of wild nature of greatest importance for the delivery of ecosystem services. We believe there is a pressing need for developing novel techniques using ground-truthed remote sensing to quantify changes in the condition of key habitats (e.g. see Thompson *et al.* 2005), and for extending promising meta-analytical approaches for using existing data on population and habitat trends (e.g. Côté *et al.* 2005; Loh *et al.* 2005).

Second, our ability to predict future changes in the state of nature is hampered by our ignorance about trophic and other cascades within communities, about the generality and nature of threshold effects, and crucially, about where thresholds may lie and how to detect their approach.

Third, input is needed from a broad range of social and natural scientists to improve our understanding of how current drivers of change are likely to vary over time, and

how they may (or may not) respond to policy interventions. What interactions can we expect among different drivers, at biological, geophysical or social levels? What interventions work best, under which sorts of circumstances? And can we improve our ability to detect potential new drivers and threats?

Last, we suggest two ways in which to improve our theoretical and empirical understanding of how, when and where specific changes in the quantity and quality of wild nature will affect human livelihoods. On the one hand, we believe there is a pressing need to develop models describing the linkages between the state of nature, the delivery of ecosystem services, human well-being and the underlying drivers of ecosystem change. Like early models of global climate change and its forcing, these may initially be crude and inaccurate. However, explicit models of complex systems are of enormous value even when wrong because they drive development and testing that lead to more accurate and useful models that can provide valuable insights into the likely consequences of different policy alternatives.

Finally, we argue that there is a considerable need for local field studies quantifying the impacts on human well-being of changes in the size or composition of populations and habitats. Monitoring of service delivery is very limited, and quantitative studies focusing on the consequences of change are few and far between. However, as the examples from Ecuador, South Africa and Madagascar illustrate, such studies can not only improve our general understanding of ecosystem services, but can act as triggers for practical attempts to slow the loss of nature.

Much of this work is ecological in nature, but a great deal of input is also needed from social and earth system scientists (see also du Toit *et al.* 2004; Balmford *et al.* 2005a). This level of interdisciplinary collaboration will not be easy to achieve. However, the MA, and the stated commitment of the world's governments to the 2010 target of reducing biodiversity loss, underscore the importance of ecologists and other scientists working closely with these and related initiatives.

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