

Understanding ecosystem dynamics for conservation of biota

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Summary

1. Ecosystems have higher-order emerging properties that can affect the conservation of species. We identify some of these properties in order to facilitate a better understanding of them.
2. Nonlinear, indirect effects of food web interactions among species can produce counterintuitive changes in populations.
3. Species differ in their roles and linkages with other species in the system. These roles are a property of the system. Such differences in roles influence how we conserve individual species.
4. Ecosystems operate at a multitude of interacting spatial and temporal scales, which together structure the system and affect the dynamics of individual populations.
5. Disturbance also structures an ecosystem, producing both long-term slow changes and sudden shifts in ecosystem dynamics.
6. Ecosystems therefore can have multiple states, determined both by disturbance regimes and biotic interactions. Conservation should recognize a possible multiplicity of natural states while avoiding aberrant (human-induced) states.
7. Ecosystem processes are influenced by the composition of the biota they contain. Disturbances to the biota can distort processes and functions, which in turn can endanger individual species.
8. The goal of ecosystem conservation is the long-term persistence of the biota in the system. There are two paradigms: community-based conservation (CBC) and protected area conservation. Both have their advantages but neither is sufficient to protect the biota on its own.
9. CBC is required to conserve the majority of the world's biota not included in protected areas. However, current CBC methods favour a few idiosyncratic species, distort the species complex, and ignore the majority. More comprehensive methods are required for this approach to meet the goal of ecosystem conservation.
10. Protected areas are essential to conserve species unable to coexist with humans. They also function as ecological baselines to monitor the effects of humans on their own ecosystems.
11. However, protected areas suffer from loss of habitat through attrition of critical areas. Thus, renewal (addition) of habitat is required in order to achieve the long-term persistence of biota in functioning ecosystems. Identification of minimum habitat areas and restoration of ecosystems become two major priorities for future research.

Key-words: disturbance, ecosystem conservation, keystones, multiple states, restoration.

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Introduction

FROM SPECIES TO ECOSYSTEMS

Conservation threats to species are usually stated in terms of habitat loss (Griffith *et al.* 1989; Sutherland 1998; Kerr & Deguise 2004), overharvesting and overpredation (Caughley 1994; Sinclair *et al.* 1998). However, population declines often occur through a combination of factors, derived from complex interactions between environment and biota, which together overwhelm the ability of a species to withstand them (Czech, Krausman & Devers 2000). Thus, complex ecosystem dynamics often dictate the fate of individual species. Natural ecosystem complexity arises from factors such as nonlinear biotic interactions, evolutionary history and assembly history of species, and often-unpredictable environmental disturbance. As a consequence of these interactions ecosystems exhibit derived behaviour, or emerging properties that would not necessarily be predicted from the study of single species populations. However, conservation of individual species may sometimes benefit from an understanding of these ecosystem properties. For example, the placement of artificial waterholes in Hwangi Park, Zimbabwe, Kruger Park, South Africa and the Sahel of northern Africa at first seemed a sensible strategy to benefit particular ungulate species searching for water. However, these waterholes differed substantially from the natural water regimes of the region and, in the longer term, they had complex and unwanted ecosystem effects (Sinclair & Fryxell 1985; Harrington *et al.* 1999; du Toit, Rogers & Biggs 2003).

The immediate causes of population declines, while requiring urgent attention, may themselves be a result of higher-order ecosystem processes. For example, the Vancouver Island marmot *Marmota vancouverensis* is Canada's only endangered mammal. Three decades ago it existed in alpine habitats at a relatively stable 200–300 animals. Around 1989 it began a steady decline so that by 2004 there were only 20 animals left in the wild (A. Bryant pers. comm.). Observers noted that predators (wolves *Canis lupus* and golden eagles *Aquila chrysaetos*) were consuming an increasing proportion of the population as marmot numbers declined, thus having a destabilizing effect, and one might conclude they were the cause of the decline. However, the dynamics of predation (Pech, Sinclair & Newsome 1995) suggest otherwise: with such low numbers of marmots, predation impacts were due to chance 'by-catch' of predators dependent on other prey; that is, inverse density-dependent predation of marmots is the *consequence* of low numbers rather than its original cause. Recent evidence (Hebda, McDadi & Mazzuchi 2004) suggests that a progressive loss of alpine habitat since the Pleistocene could have reduced marmot numbers to a threshold where predators took over. Thus, efforts to counteract predation would only address the final stage in this process and not the ultimate cause, namely climate change and habitat loss.

The purpose of this paper is to examine some case histories to illustrate how an understanding of historical legacy, community interactions and disturbance at different scales might benefit conservation. In particular we select examples where we can learn from unintended or undesirable outcomes. We start with relatively simple systems and build to complex and large-scale systems. We end by examining some difficult ecosystem problems that arise from our current conservation approaches; these problems should dictate future research directions.

Food webs and intertrophic interactions

Much of the study of population dynamics focuses on the more predictable roles of predation and competition in limiting numbers. Some indirect interactions that result from these processes are also predictable, particularly those that are linear along a food chain producing cascades (Palomares *et al.* 1995). However, nonlinear effects that percolate through the food web (Billick & Case 1994; Wootton 1994) can produce surprising outcomes. We provide two examples.

The Channel Islands off the California coast are home to two coexisting and endemic small carnivores, the island fox *Urocyon littoralis* and spotted skunk *Spilogale gracilis amphiala*. Several decades ago feral pigs became established and sufficiently numerous to provide prey for golden eagles, which took up residence there for the first time in 1992, and these have subsequently increased in number. Consequently, eagle predation on foxes, as secondary prey, has driven fox numbers down. Skunks have increased, being nocturnal and therefore less subject to predation by eagles, and have now been released from interspecific competition with foxes (Roemer, Donlan & Courchamp 2002). This has exacerbated conservation efforts for the more restricted fox.

In western North America many oligotrophic lakes contain the opossum shrimp *Mysis relicta*, a favourite food of kokanee salmon *Onchorhynchus nerka*. Flathead Lake in Montana, USA, contained these salmon, which supported a sizeable population of the iconic bald eagle *Haliaeetus leucocephalus*. However, Flathead Lake did not contain the opossum shrimp. Therefore, in the late 1960s managers introduced the indigenous shrimp so as to obtain more salmon (for fishermen) and indirectly more eagles. The shrimps took nearly two decades to increase, but when they did in 1985, numbers of both salmon and eagles, instead of increasing as predicted, collapsed almost to zero (Fig. 1). It transpired that the shrimp were more successful competitors for the cladoceran food of the salmon while for unknown reasons they were not in this case food for the salmon (Spencer, McClelland & Stanford 1991). In both of these examples ecosystem disturbances through introduction of a new species resulted in unpredicted outcomes due to indirect food web interactions, with perverse results for conservation.

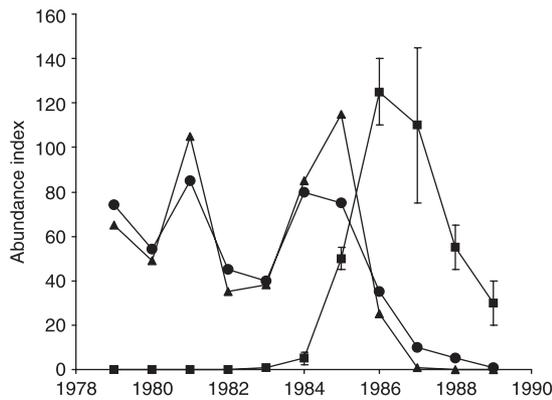


Fig. 1. In Flathead Lake, Montana, the abundance of kokanee salmon (triangles), and bald eagles (circles), that feed on salmon, declined contrary to expectation, when opossum shrimps (squares) increased (Vertical lines 1 SE) (redrawn from Spencer *et al.* 1991).

Community features and conservation strategy

KEYSTONE SPECIES

Not all species within a community have equal functional roles. This is obvious from the frequency distribution of abundances where generally there are a few abundant species and many rare ones (e.g. Magurran 2004). These differences are evident in analyses of food webs (Polis & Winemiller 1996) and interaction strengths (Menge *et al.* 1994; Berlow 1999; Goldberg *et al.* 1999). Paine (1966, 1980) formalized a component of this inequality with his definition of a 'Keystone species', which is one whose functional role is disproportionately greater than its abundance. Problems with methods for identifying keystones and for the measurement of their impact (Power *et al.* 1996) have led some authors to abandon the concept (Hurlbert 1997). However, common sense dictates that we recognize species differences – a few structure the ecosystem, whereas most are of lesser consequence – because these differences influence conservation strategy.

The classic example of a keystone species, the Pacific sea otter *Enhydra lutris*, was demonstrated when 99% of the population was removed for the fur trade in the 1800s. Removal of otters led to a rapid increase in sea urchins (prey of otters), with a resultant loss of giant kelp stands with their inshore fish communities, and formation of sea urchin-dominated grazing lawns of small algae (Estes & Duggins 1995). In another example, the migratory wildebeest *Connochaetes taurinus* population structures the entire Serengeti ecosystem in East Africa. A major perturbation to the population over a century ago through the impacts of an exotic viral disease, rinderpest, caused reverberations that continue to ripple through the system, and illustrate the keystone role of the wildebeest (Sinclair 2003). Wildebeest determine the abundance and diversity of the large mammal community by affecting competition, predation and complex indirect effects (Sinclair &

Norton-Griffiths 1979; Sinclair & Arcese 1995). Recent work has detected the impact of wildebeest in less obvious components of the system: they determine both the physical structure and the species composition of grasses and herbs of the Serengeti plains, perennially grazed swards of low stature (< 30 cm) supporting many dicots (*c.* 70 species) compared with only 15 species in ungrazed swards. The bird community is also affected by grazing due to changes in grass height that determine nest sites, mode of feeding and food availability. Of the eight commonest bird species feeding in the grass layer of grazed sites, only one became more abundant in ungrazed sites whereas all others were reduced by 50–80% (A. Sinclair unpublished data). This example also highlights the important role of behaviour, in this case migration, in affecting the greater ecosystem.

The wildebeest migration depends on a single river, the Mara, the only permanently flowing river in the Serengeti ecosystem. If it were to cease flowing (for example, in 2001 there were plans to redirect the flow of water from the Mara upstream of Serengeti to other rivers) the majority of animals would very likely die, with consequent changes in the whole ecosystem. The conservation consequences from the loss of wildebeest as a keystone species would be disproportionately greater than those due to the loss of black rhino *Diceros bicornis* and wild dog *Lycaon pictus*, both of which have occurred with little impact on the system. In this example knowledge of the ecosystem did allow direct and immediate action by UNESCO to prevent the water diversion.

Keystone species can also have counterintuitive effects. Bell miners *Manorina melanophrys* are dominant territorial insectivorous birds feeding on psyllids (plant sucking Homoptera) in Australian eucalypt forests. Where bell miners occur trees appear unhealthy, the foliage infested with these insects. When bell miners were removed 11 other insectivore bird species moved in, fed on the psyllids and within 4 months eradicated the infestation (Loyn *et al.* 1983). Interspecific territoriality by the miners maintained their food supply but reduced the diversity of competing predators.

OVERPREDATION

Top predators can increase the diversity of prey species through intermediate disturbance effects (Connell 1978). However, predators can also have the opposite effect and reduce diversity of prey. Thus, lizards in the Caribbean reduce the diversity of their spider prey species by feeding preferentially on rare species, causing local extinction of spiders (Spiller & Schoener 1998). Such effects arise because rare species are secondary prey, essentially bycatch for predators that depend on more common prey (Sinclair *et al.* 1998), as mentioned for the Vancouver Island marmot. It is, of course, the rare species that attract the attention of conservationists.

If indigenous predators can threaten rare species, then one should expect the effects of exotic predators to be even more marked. This is clearly demonstrated where exotic predators such as red fox *Vulpes vulpes* in Australia, stoats *Mustela erminea* in New Zealand and a plethora of other species on islands in the Pacific and Indian oceans, supported by exotic prey or carrion, have caused the extinction of numerous marsupial mammals, birds and invertebrates (Serena 1994; Atkinson 2001).

The concept of bycatch stems from human predation, particularly fisheries harvests. Many fish species are caught as bycatch in fisheries that focus on more abundant species. The latter can be maintained while the bycatch species decline, either because they are easier to catch or because they have a lower intrinsic rate of increase (Hilborn *et al.* 2003). In the Atlantic, both common skates *Raja batis* and barndoor skates *Raja laevis* were brought to the verge of extinction because of bycatch (Brander 1981; Casey & Myers 1998), and shark numbers have declined by over 50% in the past 15 years due to bycatch in the swordfish and tuna fisheries (Baum *et al.* 2003).

In general, the dynamics of predation, whether by natural predators or by humans, affect prey species differently depending on the role that prey play in the system, their abundance and their intrinsic adaptations (Courchamp, Langlais & Sugihara 1999, 2000). Furthermore, a prey species' role can change depending on both the community of other species and the physical attributes of the ecosystem. In British Columbia moose *Alces alces* are primary prey for wolves, which in turn are driving mountain caribou *Rangifer tarandus* to extinction (Seip 1992; Wittmer, Sinclair & McLellan 2005); but in the nearby Banff ecosystem moose are secondary prey that are being exterminated by wolves dependent primarily on elk *Cervus elaphus*. In essence, conservation action to counter the effects of predation depends on whether the prey is primary or secondary. The physical structure of the system can affect the impact of predation. Thus, in Australia predators can drive native marsupials to extinction when the latter live in small habitat patches with little cover, but cannot do so in large patches with dense cover (Sinclair *et al.* 1998).

COEVOLVED ASSOCIATIONS

A species may not be a keystone, yet can be essential to the survival of other species if it has closely evolved associations with those species. Many tropical flowers have special adaptations to attract specific insect pollinators. In Hawaii, a whole group of plants, *Hibiscadelphus*, have become extinct, or nearly extinct, after the extinction of their honeycreeper pollinators. On Mauritius, the tree *Calvaria major* almost went extinct following the extinction of the large flightless pigeon, the dodo *Raphus cucullatus* that ate the seeds and promoted their germination, probably by cleaning the

fruit (Temple 1977; Traveset 1998). Such coevolved associations have important flow-on effects on ecosystem dynamics.

New Zealand is relatively depauperate in animal pollinators, allowing the evolution of some unusual coevolved associations (Webb & Kelly 1993). One such association involves the rare dioecious obligate root parasite of forest trees, *Dactylanthus taylorii*, which produces strongly scented brownish flowers on the forest floor. This species has adaptations for pollination by short-tailed bats *Mystacina* spp., which in the total absence of terrestrial mammals forage on the forest floor like rodents. Multiple threats such as limited pollination of *Dactylanthus* due to declining bat populations (Ecroyd 1996), and severe herbivory by the exotic brush-tailed possum *Trichosurus vulpecula*, feral pig *Sus scrofa* and rats *Rattus* spp. have put the plant in serious decline.

Even common species can be threatened if there is a coevolved association with a vulnerable species. For example, pollination limitation is becoming increasingly evident in mainland New Zealand flora compared with that on offshore islands (Montgomery, Kelly & Ladley 2001; Anderson 2003; Kelly, Ladley & Robertson 2004) and the decline in avian pollinators appears to be the main cause. Thus, the mistletoe *Peraxilla tetrapetala* is showing declining pollination rates (Ladley & Kelly 1995; Robertson *et al.* 1999; Kelly *et al.* 2004). This plant is pollinated by the bellbird *Anthornis melanura*, an endemic honeyeater, whose numbers, originally assumed to be stable, are now thought to be declining (Murphy & Kelly 2001). In general, these plant species were not themselves under threat until the species that they depended upon declined. Thus, the conservation needs of one species must take into account the requirements of other species. Prior knowledge of such obligatory associations in the ecosystem would allow conservationists to predict threats to survival of species, and expedite action earlier for both the common and rare partners in associations.

LONG DISTANCE AND LONG TIME-SCALE CONNECTIONS

Although population declines can often be attributed to immediate proximate causes such as predation and habitat loss, ultimately large scale, remote causes may underlie these events. Such fundamental causes only become apparent when the large-scale ecosystem is considered. Thus, in North America the brown-headed cowbird *Molothrus ater* is a nest parasite of many small passerines. Its population is increasing and it has caused the decline of at least two species, Least Bell's vireo *Vireo bellii* and the black-capped vireo *V. atricapillus* (Smith *et al.* 2000). The ultimate cause is due to events more than a century ago (Rothstein 1994). This cowbird's original range lies in forests of the American north-east where it prefers open areas for foraging. Expansion of open land through agriculture across North America allowed the cowbird to spread into new

areas, and parasitize species that have few adaptive traits to counter it. Both large-scale and long-term events underlie the spread of this nest parasite.

Prior to the arrival of humans in New Zealand (around the year 1300), vast numbers of small burrowing petrels and shearwaters (described as billions) roosted and nested on the forest floors of the mainland as well as outer islands (Worthy & Holdaway 2002). These numbers were sufficiently great that they provided considerable nutrient inputs to the ecosystem, which at that time was more than 85% forest; in effect, these allochthonous inputs fertilized much of the terrestrial system, equivalent to superphosphate-fertilized pastoral soils (Hawke *et al.* 1999), maintaining a rich invertebrate fauna, and higher vertebrates dependent upon it. The arrival of the Pacific rat (or kiore) *Rattus exulans*, until recently considered an ineffective, innocuous predator, is now thought to have caused the catastrophic decline of the seabirds within a century, and with them the associated invertebrates, lizards and terrestrial birds. The demise of the many species of endemic ratites, collectively known as the moa, may have arisen more from the reduction in nutrient flow, and hence food supply, than from human predation (Atkinson & Cameron 1993; Cooper *et al.* 1993; Worthy & Holdaway 2002). Furthermore, kiore selectively depredate seeds and seedlings of forest plants so that the composition of the forest flora is now considerably different from that before they arrived (Campbell & Atkinson 1999). The kiore is, thus, a novel keystone species, radically changing the New Zealand forest ecosystem. Its effects, however, are more noticeable through large-scale and long distance nutrient dynamics between marine and terrestrial ecosystems; furthermore, these effects were only detected from palaeontological data. From a conservation perspective we see that present day studies of kiore on mainland New Zealand provide few clues to these ecosystem effects, unless they are compared with rat-free islands over long time-scales.

The recent collapse of the Canadian arctic grazing ecosystem has occurred through subsidies to snow geese *Chen caerulescens* on winter feeding grounds as far away as southern USA resulting in overpopulation, overgrazing and a new ecosystem state in the Arctic. Jefferies, Rockwell & Abraham (2004) point out that conservation action on the distant wintering grounds, rather than on the disturbed Arctic swards, is what is required. This brings us to multiple states.

Multiple states

Communities can exist in different combinations of species abundances under the *same* environmental conditions. These multiple states within an ecosystem are detected when a perturbation radically alters the abundance of many species in the community, which then do not return to their original abundance when the perturbation is removed (Holling 1973; Sinclair 1989; Knowlton 1992; Beisner, Haydon & Cuddington

2003). Changes in state are characterized by nonlinear dynamics between trophic levels, exhibiting initial slow change followed by fast, catastrophic change (May 1977; Scheffer *et al.* 2001). Usually changes in state result from nonlinear top-down effects of predators, although they can also result from changes in competitive interactions among species. We present three examples where a change of state has resulted in undesirable outcomes.

In the semiarid regions of the Negev–Sinai in Israel and Egypt, and in the Sahel of Africa, a shrub and herb layer acts as a blanket on the soil, retaining moisture and heat overnight. During the day thermal upcurrents carry moisture from both the soil and transpiring plants to upper levels where it condenses as rain. This supplies the plants and soil, completing a positive feedback self-sustaining system when in an undisturbed state. In contrast, overgrazing by livestock leaves a denuded soil surface, higher surface albedo and a cooling at night. There are fewer thermals, and these carry less moisture. Thus, overgrazed areas have much lower precipitation, and this is also a positive feedback (Otterman 1974; Sinclair & Fryxell 1985). The vegetated state switches to the denuded one through the disturbance of overgrazing, i.e. there is a threshold level of disturbance (grazing) where one state switches to another. A similar positive feedback switch in vegetation state occurs in Niger where overgrazing has altered vegetation structure leading to reduced water retention, increased soil loss and further vegetation loss. The system is now locked into this reduced state (Wu, Thurow & Whisenant 2000).

Some ecosystem states are meta-stable; that is, a disturbance is needed to maintain the new state, but to shift back to the original state requires a reduction of the disturbance to a far lower level than that precipitating the new state. This implies an hysteresis effect. For example, livestock have grazed the grasslands of Inner Mongolia for centuries. However, in recent decades (1948–67) livestock numbers increased steadily and once they reached a particular density Brandt's vole *Microtus brandti*, which prefers very short grass, suddenly increased to high abundance through much more frequent eruptions (Fig. 2). Similar changes in the state of grasslands are occurring throughout central Asia, particularly on the Tibetan Plateau (Jiang *et al.* 1999). In Inner Mongolia, Brandt's voles now maintain an even lower grass sward height where they outcompete the livestock. Ideally, livestock numbers should now be reduced so that grass can regrow to a level unsuitable for voles. One social consequence of this change in ecosystem state, which makes itself felt far from the original disturbance, is that Beijing now experiences much more frequent dust storms (Zhang *et al.* 2003).

The effect of top-down disturbance resulting in a change in state can also be seen with the overharvesting of marine fish stocks. A particularly clear case has occurred off Nova Scotia where the benthic fish community has switched suddenly, over an extremely large area, to a

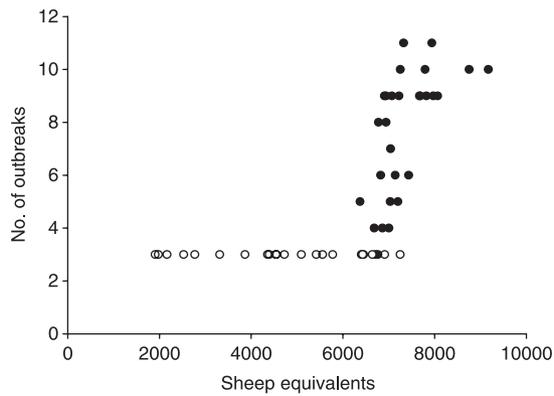


Fig. 2. The frequency of Brandt's vole outbreaks in Inner Mongolia increased rapidly from a baseline level of about three per year to 10 per year once grazing impacts from livestock reduced the grass layer to a sufficiently low level. Open circles taken from the Statistical Yearbook of Inner Mongolia with a mean value for outbreaks 1948–67; closed circles are annual data. From data in Zhang *et al.* (2003) supplied by R. Pech (pers. comm.).

pelagic community as a result of overharvesting, especially of Atlantic cod *Gadus morhua*. This change in ecosystem state has been exacerbated by decadal variability in water temperature in the north-west Atlantic (Choi *et al.* 2004).

In general, these examples illustrate that ecosystems need not change linearly with disturbance, that there are thresholds for change, and that more than one state can occur under a given set of climatic conditions. This is not to say that multiple states always occur, or are even commonplace in ecosystems. Indeed, good examples are rare, a few known from lakes, rivers, coral reefs, grasslands and forests (Knowlton 1992; Milchunas & Lauenroth 1995; Scheffer 1998; Augustine, Frelich & Jordan 1998; Dent, Cumming & Carpenter 2002).

Disturbance

Factors such as fire, floods, droughts, hurricanes and herbivory act both to structure ecosystems and to change them (Sutherland 1998). These disturbances are characterized by intensity, frequency and extent (scale). Moderate levels of herbivore disturbance may reduce the effect of dominant competitors [the classic intermediate disturbance hypothesis of Connell (1978)] thereby increasing the species diversity of an ecosystem. Moderate degrees of burning in savannas can reverse succession or maintain a 'fire disclimax', increase heterogeneity of the landscape, improve resilience as a buffer to other disturbances and also increase diversity (Williams, Whelan & Gill 1994). Persistent disturbances, such as hurricanes, over the past 14 000 years are thought to structure some tropical forests (Bush & Colinvaux 1994).

However, disturbances that are too frequent or too extreme can radically alter an ecosystem, changing it to a different state. Persistent overgrazing can result in denudation, as mentioned earlier for semiarid areas

(Wu *et al.* 2000), or in a change from grassland to woodland, as in savanna areas (Walker *et al.* 1981). Other forms of human overdisturbance are often the underlying cause for invasions of exotic species that can take over and maintain new states (Vitousek *et al.* 1996). In the forests of the Annamite range of Laos, south-east Asia, shifting agriculture has been the norm, probably for centuries: patches of forest are clear cut, burnt to release nutrients, planted with crops for 2–3 years, then left to regrow for 20–30 years while the villagers move on to new areas. However, some villagers have now become sedentary, and overcropping covering many years has so depleted soil nutrients that the invasive grass *Imperata cylindrica*, has taken over whole mountainsides. The forest cannot regenerate, these areas are no longer productive for humans and rodent outbreaks are now prevalent (W. Robichaud, G. Singleton pers. comm.).

More rarely, single extreme natural disturbances can change ecosystem states: the 'Wahine' storm of 1968 destroyed the beds of aquatic macrophytes in Lake Ellesmere in the South Island of New Zealand, and the physical change in the lake sediments has prevented their return. The resident population of black swans *Cygnus atratus* numbered 40 000–80 000 in the 1950s and 1960s. They used the weed beds for food and to raise young. Mortality from the storm itself, starvation and reduced breeding because of a lack of suitable habitat, rapidly reduced the population to < 10 000 in subsequent years and they have never returned to their original numbers (Fig. 3) (Bucknell 1969; Williams 1979; New Zealand Acclimatization Society and New Zealand Fish & Game Council unpublished reports, with permission).

Earthquakes are another form of disturbance that can cause sudden effects in an ecosystem with long-term consequences. Botswana in southern Africa is so flat that even minor tectonic shifts can change the direction of river flows (Cooke 1980; Shaw 1985). The Savuti

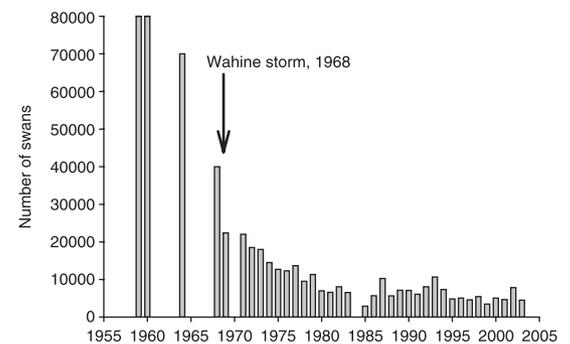


Fig. 3. The number of black swans on Lake Ellesmere, New Zealand, collapsed following a severe storm event (the 'Wahine' storm). Numbers have never recovered due to changes in the sediments and vegetation of the lake. Data from Bucknell (1969), Williams (1979), O'Donnell (1985); and annual reports of the New Zealand Acclimatization Society (1965–90) and the New Zealand Fish & Game Council (1991–2003).

River is a side channel from the Kwando/Linyanti river system that flows into the Zambezi. The Savuti was dry from the 1860s to the 1950s. In 1956 the channel started flowing due to a tectonic shift and continued to flow, with floods in 1979, until 1983 when just as suddenly it stopped. The channel has been dry since then, and now both the Kwando and Linyanti are drying, exacerbated by climate change and human use. The Savuti was used extensively by large numbers of ungulate species in the dry season. When the river dried, it altered the ecology of a large region, with ungulate migration patterns changing to other areas on the Linyanti (M. Vanderwalle personal communication). In New Zealand, earthquake disturbances are relatively frequent and their ecosystem effects can be of a lower intensity, but widespread. Landslides resulting from earthquakes cause sudden catastrophic mortality of forest trees that is scale-dependent and has important effects on forest dynamics: multiple small patches have high mortality resulting in a mosaic of different aged stands in the forest (Allen, Bellingham & Wiser 1999).

Climatic and temperature changes in physical oceanic conditions, as occurred suddenly in the north Pacific in the late 1970s, appear to have long-term ecosystem consequences. In the north Pacific the complex of fish species changed after the regime shift and it appears the new fish community cannot provide sufficient quality food for the Steller's sea lion *Eurometopias jubatus*. In the mid-1970s this sea lion population had been increasing and was about 250 000. It dropped rapidly to 100 000 by 1990, and 50 000 by 2000 (Trites & Donnelly 2003). It is possible, though not yet established, that killer whales *Orcinus orca* are exacerbating the decline through predation on sea lions at these low numbers (Springer *et al.* 2003).

Scale effects

Ecosystems function at multiple scales, small scales affecting large scales and vice versa. The Serengeti wildebeest migration covers the entire ecosystem of 25 000 km². Wildebeest move several hundred kilometres to the short grass plains in the wet season because these plains support the most nutritious grasses in the system (Fryxell 1995; Murray 1995). Dung beetles, of which there are some 80 species, rapidly bury faeces (within a few minutes) and hence expedite nutrient cycling on these plains. They promote the high-quality nutrition of the grasses, producing a positive feedback (Foster 1993). Dung beetles can only function when the soil is damp, so they have a negligible effect on returning nutrients to the soil in the dry season when wildebeest are in woodland areas. Thus, the very local scale functions of the beetles influence the large-scale movements of the ungulates.

Giant pandas *Ailuropoda melanoleuca* in China feed on a very restricted diet of a few bamboo species, in particular of the genus *Fargesia*. Several of these species flower synchronously over large areas with a period of

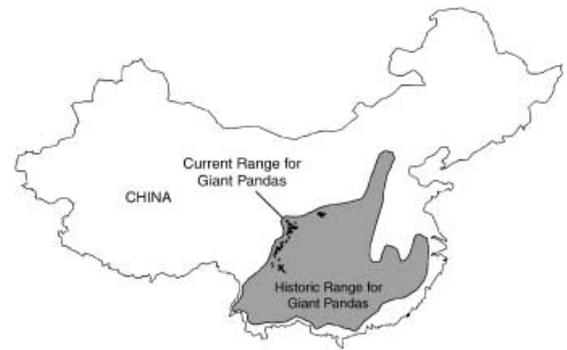


Fig. 4. The current and historical range of the giant panda in China. Present-day protected areas are confined to a small region that does not represent the range of the panda's natural food supply. Adapted from World Wildlife Fund: (http://archive.panda.org/about_wwf/what_we_do/species/what_we_do/flagship_species/).

about 70 years, the last flowering being in the mid-1970s (Schaller *et al.* 1985, 1989). After flowering, the plants die and large areas of lower-elevation bamboo, required by pandas for three-quarters of the year, become unavailable. The current range of pandas is now so restricted (Fig. 4) that they have become vulnerable to the large-scale die-off of their food plants: panda conservation areas were not sufficiently spread over their historical range to fall outside the area of bamboo die-off, severely limiting the panda's ability to recover from natural fluctuations in its food supply. Conservation plans have redesigned reserve networks by connecting isolated patches so that animals can search a wider area (Sutherland 1998).

Large-scale temporal patterns are also important in ecosystem dynamics. There is increasing evidence that complex ecosystem processes are influenced by multi-year fluctuations in climate such as the North Atlantic Oscillation and the southern and northern Pacific oscillations (Post & Stenseth 1998; Bradley & Ormerod 2001; Coulson *et al.* 2001). The classic snowshoe hare *Lepus americanus* cycle of North America is synchronized spatially by decadal weather events (Sinclair & Gosline 1997; Haydon & Steen 1997). This cycle of numbers then influences the rest of the ecosystem (Krebs, Boutin & Boonstra 2001). Synchrony is enhanced by environmental correlation across sites and reduced by dispersal between sites (Kendall *et al.* 2000). In the context of long-term conservation, spatial and temporal synchronies are of particular concern when a species is rare because of its increased probability of extinction.

Systems may oscillate at even greater time-scales. For example, the savanna vegetation of the Serengeti goes through oscillations of abundance and species composition with a period of 90 years (Sinclair 1995). Long-lived species may produce difficulties for conservation planning: conservation benefits only accrue over a long time-scale if the longevity of many tree species is taken into account, for example. Thus, conservation needs to plan on the same time-scales.

Human-induced changes in climate can be considered very long-term, persistent disturbance. Global climate change is now having measurable effects on ecosystems, altering community composition by shifting species ranges differentially towards the poles, higher in altitude [especially in the tropics (Pounds, Fogden & Campbell 1999), and away from the tropics (Lawton 1995; Schneider & Root 2002; Parmesan & Yohe 2003)]. In Britain, birds and other groups are breeding earlier. Changes in community structure mean that species will experience changes in food supply and predation rates (Crick *et al.* 1997).

Climate change has been proposed as a cause of desertification in the Sahel of Africa (Le Houerou 1996). However, the climate data are equivocal, and it is more likely that overgrazing creates ecosystem vulnerability to occasional low rainfall years, precipitating a rapid change to a denuded state (Wu *et al.* 2000). Indeed, climate change might have its greatest effects by increasing the fragility and decreasing the resilience of human-stressed ecosystems: increased climatic variance can push the adaptations of biota beyond their tolerance limits, resulting in a change in ecosystem state (Kareiva, Kingsolver & Huey 1993; Hellmann 2002). One example is the possible irreversible changes in the ecosystem of the Southern Ocean affecting primary production, krill recruitment and the recovery of whale populations due to oscillations in the extent of sea ice (de la Mare 1997) putatively through climate change (Broecker 1987).

In general, ecosystem processes at different spatial and temporal scales, including disturbance and long-term trends, must be considered as part of any conservation strategy for the ecosystem in which a threatened species exists. Such processes operate at larger scales than we have traditionally planned for.

Ecosystem processes

We now broaden our considerations still further. Ecosystem processes include a variety of different factors such as hydrology, biogeochemical cycles, energy flow, pollution buffering and resilience to disturbance. Their study is well established (e.g. Schulze & Mooney 1993; Kinzig, Pacala & Tilman 2001; Loreau, Naeem & Inchausti 2002). The distortion of such processes can lead to unwanted ecosystem effects and threats to individual species. For example, Australia before European settlement was largely covered in eucalypt woodland. In the past century agriculture has removed nearly all of this woodland, especially in Western Australia. Originally eucalypts kept groundwater levels down through transpiration processes. Once the trees were removed, groundwater levels rose, water evaporated at the soil surface and saline deposits made the soil unsuitable not only for crops but also for native biota. Now large areas of Australia have a major problem with salinization of soil and groundwater upwelling, with a resultant decline in agricultural productivity. In

response to this ecological (and economic) problem, Australia has had to adopt the expensive policy of revegetation (Hobbs 1993; McFarlane, George & Farrington 1993).

The function of biota in creating resilience to disturbance is the subject of much current interest. The thesis is that the great diversity of nature provides a safety net against catastrophic change while simultaneously maintaining ecosystem processes (Ehrlich & Mooney 1983; Walker 1992, 1995; Tilman 1999). Although there have been useful laboratory and field experiments involving a few species demonstrating what might occur if species are lost, evidence is very difficult to obtain for near complete ecosystems (Naeem & Li 1997; Tilman *et al.* 1997; Naeem 1998; Kareiva & Levin 2003). However, disturbed systems provide some useful indicators.

Intact eucalypt forest in Australia supports many species of coexisting endemic honeyeaters. In contrast, the noisy miner *Manorina melanocephala*, the geographical replacement to the bell miner mentioned above, dominates the bird community in fragmented forest in which an open canopy has developed through a combination of logging, persistent livestock grazing and agriculture. The noisy miner aggressively excludes most of the smaller honeyeaters. Consequently, exposed trees suffer chronic infestations of psyllids, die-back of their main limbs, and death. In essence, exposed trees are no longer viable due to the dearth of insectivorous birds (Landsberg 1988; Clarke *et al.* 1995; Grey, Clarke & Loyn 1997, 1998).

In another example, reef-building corals *Monastrea* spp. host dynamic, multispecies communities of dinoflagellates *Symbiodinium* spp. These corals exhibit 'bleaching', a loss of photosynthetic ability, as a consequence of abnormally high irradiance and seawater temperature. However, corals with a more diverse community of symbiont dinoflagellates are better able to withstand these stresses and exhibit less bleaching (Rowan *et al.* 1997). Thus, it may be that synergistic effects of species assemblages contribute to ecosystem resilience, especially where mutualisms occur. Such interactions are particularly apparent between plants and soil organisms. Thus, southern beech trees *Nothofagus* in New Zealand, and pine trees *Pinus* globally, require mycorrhizae for establishment (Wardle 2002; Wardle *et al.* 2004). Much still needs to be done to determine whether such synergisms are a common feature of ecosystems and if so to elucidate the mechanisms for them. Nevertheless, these examples show that where ecosystem processes have been ignored or distorted they can lead to perverse effects for both communities and individual species: Conservation needs to learn by these mistakes because species could be threatened through a change in the integrity of the biota as a whole (Schwartz *et al.* 2000; Hector *et al.* 2001).

Ecosystem conservation

The primary goal of ecosystem conservation is the long-term persistence of the whole biota in a fully

functioning state. There are two paradigms for the conservation of ecosystems, community-based conservation (CBC) (Hulme & Murphree 2001) and protected area conservation (PAC) (Brandon, Redford & Sanderson 1998; Bruner *et al.* 2001). Although often treated as alternative and competing strategies, these two paradigms address different needs and neither is sufficient alone to represent all fully functioning ecosystems.

COMMUNITY-BASED CONSERVATION

Currently, protected areas cover less than 10% of the global terrestrial surface and it is unlikely this value will increase much more. Thus, from standard species-area relationships something less than 50% of the terrestrial biota will ever be found in protected areas. Furthermore, many protected areas are not large enough to maintain viable populations in isolation from the surrounding matrix. Therefore, if we are to ensure the persistence of the other half of the biota we must look to human-dominated ecosystems, that is we employ CBC.

However, as currently practised, CBC has some fundamental problems that work against conserving fully functioning ecosystems. First, CBC favours only those species that are either useful to or tolerant of humans, and the latter are often those least in need of protection. Other species that are detrimental to humans, such as large carnivores, are often excluded. Secondly, the focus of CBC relies on species providing some value, usually economic value, so as to advance human welfare. Yet even with 'useful' species, where economic value has been assessed, it rarely exceeds 10% of the potential agricultural value. Thus, there is a strong incentive to replace the few useful wild species with domestic species (Bond 2001; Emerton 2001).

Thirdly, and as a consequence of the above, the vast majority of the biota has no assessed economic value at the margin, and hence little conservation effort is spent on them. Despite some global attempts at evaluation (Moran, Pearce & Wendelaar 1997; James, Gaston & Balmford 2001), local communities have yet to devise methods for determining the value of individual species (Sedjo 2000; Simpson 2000). For example, ecosystems depend to a great extent on the microbial biota of the soil and their linkages with the above-soil community (Wardle 2002; Wardle *et al.* 2004). Yet such microbes are so little known, and so little valued, that CBC does not consider their conservation (and to our knowledge has not done so anywhere in the world). Nevertheless, where studies have been conducted, as in the logging of British Columbia forests, microbe types are lost from the soil where human impacts are large (Axelrod *et al.* 2002). Thus, microbes are sensitive to disturbance and such sensitivity likely affects ecosystem function through loss of critical species.

Fourthly, human-dominated systems, i.e. those where CBC must be practised, result in a distorted

biota that may not be sustainable in the long term. The population declines of common bird species in Britain, attributed both to a decline of insect food due to changes in agriculture (Fuller *et al.* 1995; Krebs *et al.* 1999; Chamberlain *et al.* 2000; Robinson *et al.* 2004), and to an increase in predation (Tapper, Potts & Brockless 1996), are a reflection of this distortion of the biota. Society is forced to subsidize the ecosystem by provision of insect food and reduction of predators (e.g. for the grey partridge *Perdix perdix*; Aebischer 1997). In short, if CBC is to contribute to long-term sustainability of the biota it must put ecosystem processes first, taking a more holistic, less idiosyncratic view.

PROTECTED AREA CONSERVATION

Although we recognize that humans are an integral part of ecosystems, many species simply cannot coexist with humans. Protected areas therefore must conserve those species. Obvious examples of such species are large carnivores, large ungulates such as elephants, those that require intact ecosystems such as interior forest species (many birds, large primates) or species that require fragile ecosystems such as wetlands (many plants, insects, amphibians) or undisturbed breeding sites. For example, the Wood Buffalo National Park in northern Canada is the only location in the world that can provide the endangered whooping crane *Grus americana* with an area in which the species can breed naturally.

One of the most compelling reasons for PAC, from the point of view of ecosystem dynamics, is the need to provide ecosystem baselines undisturbed by humans (Arcese & Sinclair 1997; Sinclair 1998). The rationale is that in order to understand the impacts humans are having on ecosystems we need 'control' areas where human interference is kept to a minimum. There are two aspects to this.

First, society has little long-term institutional memory to detect slow change caused by humans in ecosystems. For example, a mere 10 thousand years ago the holarctic tundra and boreal forest ecosystems were dominated by megaherbivores such as mammoths. Europe was the scene of large-scale animal migrations. These species evidently interacted with humans, and yet society has no memory of these events. In New Zealand, forests were dominated by a dozen species of large ratites, the moas, and much of the ecosystem was adapted to their impacts. They died out only a few hundred years ago, with some perhaps persisting to the 1800s, but little remains of their presence in the oral history of the Maori people (Worthy & Holdaway 2002). In another example, present-day Scotland is a well-known tourist destination, the scenic attraction being the mountainous, treeless heather moors. The general public rarely appreciates that the moorland is an artefact of human destruction of the original pine forests. A few thousand years ago Scotland was covered in forests similar to

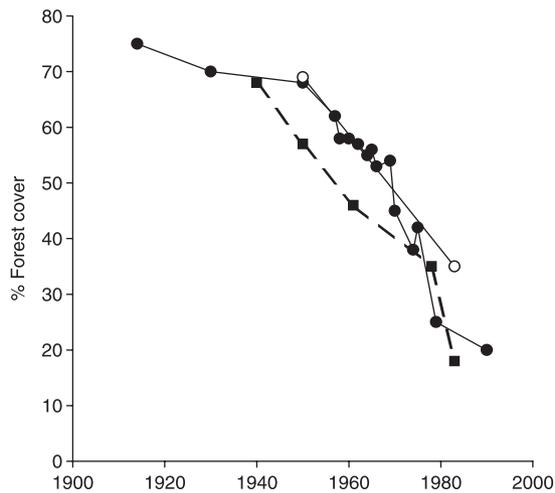


Fig. 5. Loss of tropical forest habitat illustrates the accelerating decline of natural habitat in most global ecosystems. Examples are from Thailand (closed circles), Costa Rica (squares) and Madagascar (open circles). Data from Sinclair *et al.* (1995).

those found in Norway and Sweden today. Even 200 years ago, extensive forests still remained, but they were eventually cleared for sheep farming (Yalden 1999; Smout 2003). In general, slow ecosystem change caused by humans goes unnoticed and unremembered unless we have baselines as a reference point. They become both society's ecosystem memory and society's insurance against wholesale ecosystem collapse.

Secondly, baselines allow us to distinguish between natural or long-term disturbance and local human impacts, in order to predict the potential outcomes of current and future disturbance events. Without such baselines we can misinterpret causes of change. The great famines of northern Africa in the past 30 years have been ascribed to unfortunate and unavoidable droughts. However, other evidence on long-term overgrazing, which we discussed earlier, suggests that this might actually have been the cause of the famine. An area in Mali of some 1000 km² had been set aside as a cattle ranch in 1968. It supported a modest number of cattle but excluded the activities of the local nomadic peoples. During the famine of 1973, originally blamed on drought, this cattle ranch remained green, covered in meter-high grass with healthy cattle. It experienced the same rainfall as the surrounding famine-stricken nomadic areas, which exhibited a bare sandy soil with no herb layer. This ranch acted as the baseline to demonstrate that rainfall was adequate to produce good plant growth and grazing, and that a drought did not prevail. It showed instead that long-term persistent overgrazing caused the ecosystem to become sensitive to small changes in rainfall, which then precipitated the famine (Sinclair & Fryxell 1985). In essence, the baseline highlighted a change in ecosystem function, namely the resilience of the system to fluctuations in climate.

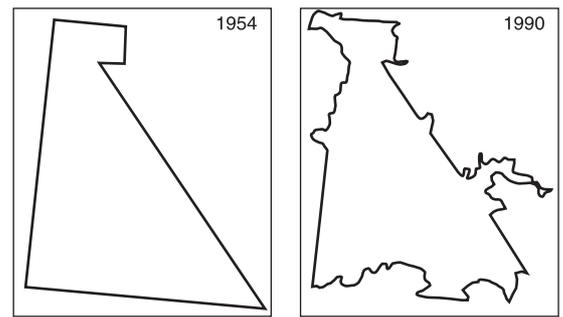


Fig. 6. The boundaries of Strathcona Park on Vancouver Island, British Columbia, have been eroded between its establishment in 1954 and 1990 due to requirements of the logging industry for mature trees in the valley bottoms. The addition comprises nival habitat (rock and ice) only. Redrawn from maps in Husband (1993).

DO PROTECTED AREAS ACHIEVE ECOSYSTEM CONSERVATION?

In most biomes there is a continuing, even accelerating, loss of habitat, this being especially marked in tropical forests (Fig. 5) (Sinclair *et al.* 1995). Demarcation of protected areas is the main method of ensuring the persistence of representative portions of the biota, the assumption being that the rate of loss due to human exploitation within the reserve is zero. (For this point we are putting aside the additional effects of faunal collapse due to fragmentation of habitats.) there is accumulating evidence that even protected areas experience continuing attrition due to human encroachment. Figure 6 illustrates how the boundaries of Strathcona Park on Vancouver Island, British Columbia, originally demarcated in 1954, have been gradually eaten away by successive governments giving in to demands of the logging industry: the excised parts in the 1990 map were all valley bottoms with mature forest. Each excision was treated as a compromise between the demands of industry and the demands of conservation. Obviously sequential compromise will result in eventual reduction to a size where the reserve ceases to protect representative biota. Sequential compromise occurs primarily because of the lack of institutional memory that we discuss above. Figure 6 provides an illustration of a general process that is evident in most protected areas of the world, including the high profile Serengeti National Park (Sinclair *et al.* 1995). Attrition occurs not just from legislated boundary changes, but also from the informal or illegal inroads of human activities such as tree cutting, burning and exploitation of dominant or keystone plants and animals.

As there appears to be a continuing attrition of protected areas, we cannot rely on their mere presence to achieve the long-term persistence of the biota. At some point we must decide on the minimum area necessary to maintain the biota *in perpetuity*, the 'habitat minimum'. This area can only be maintained by adding to protected areas at the same rate that they are eroding.

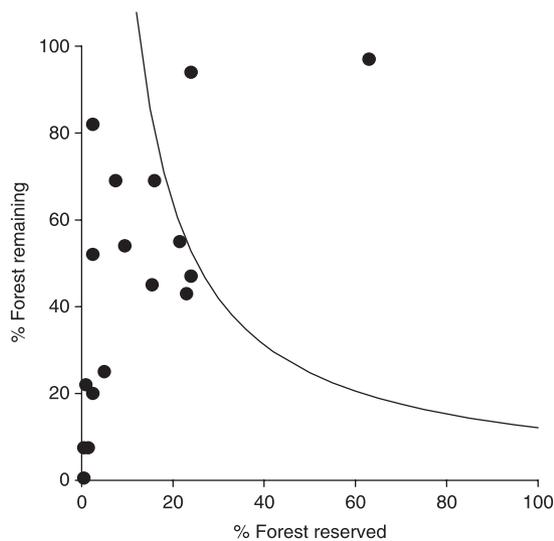


Fig. 7. Proportion of tropical forest protected in reserves compared with the proportion of original forest still present in the country, for 17 South-east Asian and Pacific countries. The line assumes a 'habitat minimum' for protection of 12% of the original extent (WCED 1987). The proportion that should be protected increases until all must be reserved if only 12% remains (from Sinclair *et al.* 1995).

In essence, this requires a policy of 'habitat renewal', that is addition of new habitat, in order to achieve a minimum area of habitat protection (Sinclair *et al.* 1995; Dobson, Bradshaw & Baker 1997).

There have been some attempts to place a figure on this 'habitat minimum'. The Brundtland Report (WCED 1987) mentioned 12% of the original area. However, this is an arbitrary figure and chosen proportions will differ with habitat type. Nevertheless, taking the 12% value as a convenient point we compare it with the proportion of lowland tropical forests remaining in countries of South-east Asia and the south Pacific (Fig. 7). Only two countries protect an amount of forest greater than 12% of the original extent. Several countries have almost no habitat left.

Current evidence therefore suggests that sequential attrition of protected areas works against the ideal of conserving biota in ecosystems in the long term. Furthermore, habitat renewal is already necessary in many parts of the globe to counteract the effects of such attrition.

Emerging properties of ecosystems and their consequences for conservation

To synthesize our understanding of ecosystems: there are certain properties that derive from complex interactions of species with each other and their environment. We have examined some of these higher-order emerging properties including the disproportionate effects of some species in structuring the community (keystone effects), the direction of control within trophic levels, the way ecosystems respond to disturbance, and the complex interaction of different scales

of disturbance. These, in turn, result in changes to the species composition of a community, changes to ecosystem function, and multiple states, the sudden switch from one community to another because of thresholds to disturbance. All of these features result from the types of species in a community and how they respond to disturbance.

One of the important features of ecosystem dynamics is the possibility that such emerging properties result in unexpected outcomes for conservation. For example, whether a species is a keystone or not depends on the ecosystem in which it lives, and so its effects are a property of the system: the migratory wildebeest population in Serengeti is a keystone, but the sympatric resident population in Serengeti and other populations in different systems are not. keystones are thus an emergent property. The roles of such species, their behaviour and how they respond to dynamic systems should be taken into account in conservation planning (Sutherland 1998; Mace 2004).

Whether top-down processes control an ecosystem depends not just on the type of predators present but also on both the community of prey species and the features of the ecosystem itself – the physical and temporal changes. These can be complex: large ungulate species in Serengeti are bottom-up controlled, but they support a suite of predators that control small prey species. Prey size and the community of both predators and prey determine the direction of control, which is an ecosystem feature (Sinclair, Mduma & Brashares 2003). From a conservation perspective both keystones and the direction of control determine the presence or absence of other species.

Thus, the combination of species that comprise the community determines the persistence of individual species. As species have differing biological attributes that predispose them to the risk of extinction (Purvis *et al.* 2000), emerging properties that affect community composition also affect the probability that vulnerable species are included. The community also determines ecosystem function and distortions of the community can change the stability properties of that system, as we illustrated in the Australian honeyeater example.

Disturbance is a major external driver in ecosystem dynamics, and its influence may derive locally or from long distance or long time-scale connections. For example, the profound changes in the nutrient dynamics of New Zealand forests (many centuries ago over vast areas), described earlier, precipitated a radically altered community state and resulted in widespread and numerous extinctions.

Ecosystems are not static. They oscillate at various frequencies and so conservation planning should accommodate such changes at the appropriate scale. The marked changes in vegetation observed over the past century in Serengeti, Yellowstone and other protected areas should be considered in this context as part of the natural ecosystem process. However, human-induced change can cause undesirable disruptions.

Climate change, for example, is now seen to be affecting the vulnerability of systems by decreasing their ability to tolerate other natural changes, i.e. ecosystems could become more fragile and less resilient to human interference. Related to this aspect is the property of thresholds of disturbance: if these thresholds are exceeded through human interference then new ecosystem states appear that might have detrimental consequences, as discussed for Inner Mongolia (Zhang *et al.* 2003). Changes in state could lead to changes in species composition and so further threaten vulnerable species. For example, in Kruger Park changes in water distribution through placement of artificial waterholes has led to changes in the ungulate community, and indirectly to increased predation on vulnerable species such as roan antelope (Harrington *et al.* 1999).

Thresholds result in multiple states. There are three points related to these: first, multiple states are an emerging property of ecosystems. Second, conservation paradigms should be able to accommodate more than one state in nature. For example, Serengeti supports two vegetation states, grassland maintained by elephants, and woodland in the same area that supports elephants but is not determined by them, and the two states switch over time (Dublin, Sinclair & McGlade 1990). Third, we should avoid becoming trapped, perhaps permanently, in aberrant states due to excessive human disturbance, as we have discussed above for Australian eucalypt ecosystems.

Ultimately, therefore, it is the ecosystem that needs to be conserved for the protection of individual species. Conservation of ecosystems must incorporate the effects of major natural disturbances such as earthquakes, fires, floods and storms, and the consequences of natural changes in state. Such changes lead to changes in the level of threat to species through changes in community composition. Equally, conservation would benefit from knowing where thresholds to human disturbance occur, so as to avoid such thresholds and to allow recovery from disturbance. To do this requires standardized measures of the state of ecosystems and their disturbances, and these must be monitored over long time periods to act as baselines (Green *et al.* 2005).

The future: reconstituting ecosystems

It follows from our discussion of protected areas that they do not conserve biota in the long term. They merely buy time due to the slower rate of loss within them compared with outside. This time should be used to implement habitat renewal; this concept therefore becomes a major conservation objective for the future (Townes & Ballantine 1993; Dobson *et al.* 1997). In countries where there is insufficient habitat remaining, or where habitats have long been altered by human use (for example, in most of Europe), reconstitution of ecosystems as baselines (to as 'natural' a state as possible) should be a top priority. Studies of species loss from ecosystems suggest that ecosystem function and structure

change slowly at first, but suddenly unravel when dominant or keystone species (with their dependent species) drop out. Therefore, in reconstituting an ecosystem is it possible that the biota could do the opposite of unravelling if a few key species are initially introduced or if exotic predators or competitors are removed? Would species self-establish once the basic structure is in place? If so, restoration would be considerably easier than if all species had to be artificially established. Perhaps such a concept could be termed 'ravelling up'. Research to address these questions should become a priority.

Reconstituting ecosystems will be particularly important in the future as climate change alters local environments. It is likely that species, particularly plants and other sedentary biota, will need to be moved to new locations if they are to be conserved in the long term. Predicting (by modelling) where new protected areas should be located, and determining which species will need assistance to establish, will be an important component of restoration research. Identifying and acquiring these new areas should be a priority for conservation.

Conclusions

Ecosystem dynamics involving the interaction of communities with the external environment can result in complex higher-order system behaviour ('emerging properties') that can affect the persistence of endangered species. Such properties can arise from nonlinear interactions in food webs, the changing roles of species within communities, and the direction of control in the trophic dynamics. In turn these interactions can result in multiple states. Ecosystems are always changing through both long-term continuous change as well as sudden shifts. Some degree of disturbance structures a system including determining species composition, but excessive disturbance, particularly from human exploitation, can produce unwanted results. Much of our current understanding of ecosystem dynamics comes from examples with such undesirable consequences; the study of pathology in ecosystems, as in medicine, provides as much insight for conservation as the study of undisturbed systems.

Ecosystem conservation should therefore take into account the complex, nonlinear interactions and processes that determine the dynamics of the system. The two approaches of CBC and PAC have different advantages, and both are required in different contexts. However, both have shortcomings that must be addressed if the goal of long-term persistence of the biota is to be achieved. In particular, habitat renewal is essential if protected areas are to be maintained in the long term, so research in this area is a priority for the future of ecosystems.

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