Commonness, population depletion and conservation biology

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Species conservation practice, as opposed to principle, generally emphasizes species at risk of imminent extinction. This results in priority lists principally of those with small populations and/or geographical ranges. However, recent work emphasizes the importance of common species to ecosystems. Even relatively small proportional declines in their abundance can result in large absolute losses of individuals and biomass, occurrences significantly disrupting ecosystem structure, function and services. Here, we argue that combined with evidence of dramatic declines in once common species, this suggests the need to pay more attention to such depletions. Complementing the focus on extinction risk, we highlight important implications for conservation, including the need to identify, monitor and alleviate significant depletion events.

Priority species

Judgements about extinction risk are key drivers of global conservation priority setting and action at the species level. Those species at greatest risk of being lost in the near future, and the areas in which they are still found, are widely recognized to be targets for conservation investment. Indeed, high extinction risk typifies the most iconic species of biological conservation (e.g. giant sequoia *Sequoiadendron giganteum*; leatherback turtle *Dermochelys coriacea*; California condor *Gymnogyps californianus*; giant panda *Ailuropoda melanoleuca*; and blue whale *Balaenoptera musculus*), and many iconic places for conservation are typically rich in threatened species (e.g. the Himalayas, Brazilian Atlantic forest, the Andes and Madagascar) [1].

Although it has repeatedly been observed that it is far from the sole approach (other approaches include focussing on keystone, umbrella, flagship or indicator species [2–4]), the use of extinction risk to set conservation priorities has considerable logical support. Attempts to retain species that are at higher risk of extinction will serve to reduce overall species loss resulting from past, present, and potentially future, environmental change [5]; reduce the loss of evolutionary novelty [6]; and are in keeping with the notion that conservation is a crisis oriented discipline [7,8].

Although many rare species are not at high risk of imminent extinction, threatened species are typically rare (i.e. having small global populations and/or restricted distributions) [9]. Thus, in practice, species level conservation is concerned principally with rare species. The common species, those with large numbers of individuals compared with other species in the same taxonomic group, receive much less attention. Although we do not wish to imply a conflict between approaches based on threatened and common species, recent work in two fields suggests an urgent need to reduce this disparity. First, it is becoming increasingly apparent that common species are fundamental to the structure of most assemblages and ecosystems. Second, the collation of historical records has revealed that many previously naturally common species have undergone substantial declines, typically without becoming threatened with imminent extinction.

Here, we argue that in addition to threatened species, conservation biologists need to pay more attention to the depletion of common species, and that so doing has several important implications, including the need to identify, monitor and alleviate significant depletion events.

Common species shape the world

To a first approximation, it is common species that shape the world around us. They form much of its structure, function and service provision, to the point that we routinely distinguish different kinds of assemblage, habitat and ecosystem on the basis of the identities of common species they contain or that form their characteristic structure. Indeed, what have variously been termed 'dominant', 'foundation' or 'structural' species, are frequently, although not exclusively, common (for definitions, see [10]).

Although rare species can also have influential roles, this ecological importance of common species almost inevitably follows from their two foremost characteristics. The first is that they are indeed common, and that even relatively small proportional reductions in their abundance can remove a large number of individuals from assemblages and can impact across large geographical areas, because these species are typically also widespread [11]. The second is that commonness is itself rare. Thus, the few most abundant species usually account for most individuals in an assemblage and often a large proportion of the biomass and function, and the most widespread species account for most occurrence records (Box 1). Because of the extremely right-skewed nature of species-abundance, species-biomass and species-range size distributions, these contributions are particularly marked [12].

There has been much discussion, albeit inevitably often based on rather anecdotal evidence, of the profound ecosystem consequences that can follow historical depletion of common species. Indeed, severe depletion of the populations of, for example, American chestnut *Castanea dentata*, Rocky

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Box 1. Common species contribute a disproportionately large number of individuals and biomass to assemblages

Data on the breeding avifauna of Britain reveal that the assemblage is structured primarily by common and widespread species [44]. The contribution to total number of individuals (black line) and biomass (grey line) is greatest for the most common species, which diminishes rapidly as rarer species are added (Figure Ia). The 25% most abundant species in the assemblage (the upper quartile) comprise 95.02% of all breeding individuals and 87.64% of all breeding biomass, conversely the 25% least abundant species comprise 0.01% of all breeding individuals and 0.06% of all breeding bird biomass. A weaker, albeit still marked, pattern is apparent for range size (Figure Ib), with the 25% most widespread species comprising 59.8% of all 10×10 km resolution occurrence records [45] during the breeding season, whereas the 25% most restricted species comprise just 0.91% of all occurrence records. A consequence of this characteristic of assemblages is that the loss of individuals, biomass and geographic range coverage that results from a given proportional decline is greater in common species than in rare ones.

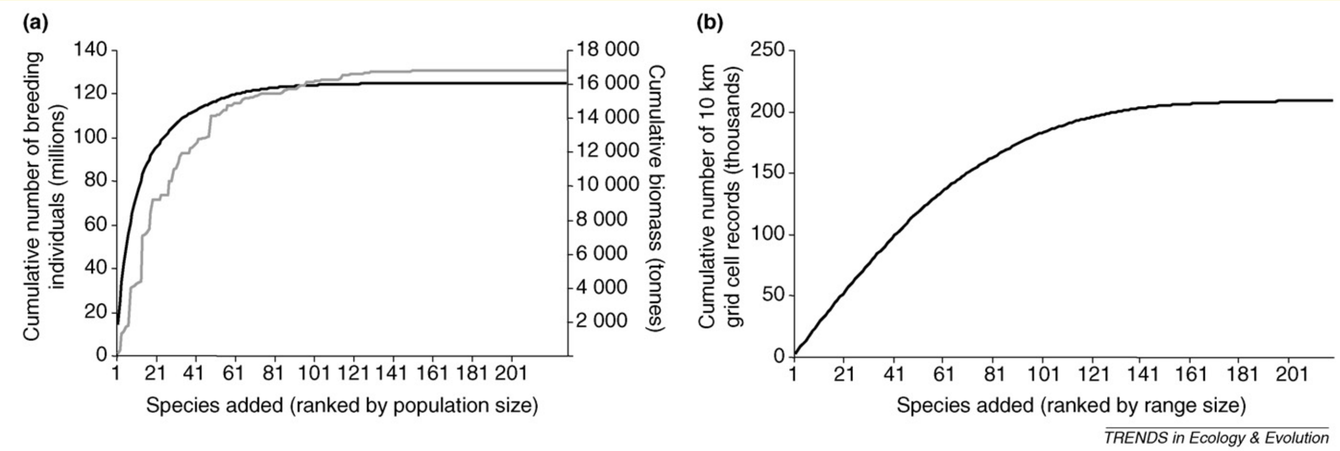

Figure I. Cumulative contribution of progressively rarer species to **(a)** total number of individuals and biomass, and **(b)** occurrence records, for birds in Britain.

Mountain grasshopper *Melanoplus spretus*, salmon *Oncorhynchus* spp., passenger pigeon *Ectopistes migratorius*, black-tailed prairie dog *Cynomys ludovicianus* and bison *Bison bison* have arguably reshaped several terrestrial and freshwater ecosystems in North America [10,13,14]. Likewise, coastal marine ecosystems over much of North and Central America, including coral reefs, kelp forests, sea grass beds and estuarine habitats, have been reshaped by the loss of most populations of formerly abundant species, including corals, oysters and vertebrate grazers [15].

Research on the relationship between biodiversity and ecosystem function has begun increasingly to focus on the role of species identity rather than simply species richness [16–20]. Dominant species are generally agreed to contribute disproportionately to ecosystem function [16,21]. For example (i) total loss and reductions in density of the dominant plant species in an experimental native prairie tallgrass plot reduced productivity, whereas equivalent loss of rare species had no short term effect [22]; (ii) simulations show that levels of sediment bioturbation are disproportionately influenced by abundant species of marine benthic invertebrates [18]; (iii) natural declines and experimental removal of a common detrital-feeding riverine fish increased downstream transport of organic carbon and increased primary production and respiration [23]; and (iv) experimental changes in the abundance of dominant grassland plant species variously increased and decreased susceptibility to invasion [24,25].

The importance of common species extends to the geographical structuring of assemblages. Recent analyses have shown that, counter to much previous assumption, common rather than rare species are the principal drivers of spatial variation in species richness, and of relationships between species richness and environmental variables [26–28]. Indeed, increasingly it seems likely that common species are disproportionately influential in shaping many macroecological patterns.

Depleting the common

The conservation importance of naturally common species would perhaps be of only passing interest if such species tended to remain relatively unscathed by human activities. However, anthropogenic threats have impacted common species for millennia [29]. Even in the past few centuries, all four of Diamond's [30] 'evil quartet' of major drivers of threat and extinction (overexploitation, habitat loss and depletion, introduction of alien species, extinction cascades) have reduced the abundances and range sizes of previously common species. In some cases this has led to high levels of threat or extinction, but in others relatively small proportional declines have resulted in the loss of large numbers of individuals.

Overexploitation has resulted in enormous declines in the abundances of many previously common species, perhaps most notably through logging, hunting and fishing. Indeed, these activities are, to a large extent, founded on the population depletion of such species, although they are often not explicitly couched in these terms. Examples include depletions of many commercially exploited trees and marine fish (Box 2). Such losses of common species are often expressed in units that obscure the scale of population depletion. For example, deforestation is principally expressed in terms of area logged or volume of timber extracted, and landings of marine fishes are usually expressed in terms of biomass, rather than loss of individuals.

Box 2. Case studies of population depletion of previously common species

Rocky Mountain grasshopper *Melanoplus spretus*

During outbreaks, this species might have numbered perhaps 15 trillion individuals, and was distributed across much of the western USA between the Mississippi and the Rocky Mountains, it destroyed crops over vast areas and devastated plains farming communities [46]. However, at other times, it was largely restricted in relatively small (although still large in absolute terms) numbers to the valley bottoms of the Rocky Mountain region, which experienced dramatic expansion in agricultural activity during the late 1800s, particularly stock raising and the growing of forage crops, which would, in short order, have destroyed much of the breeding habitat required by the species. In the space of just a few years, the Rocky Mountain grasshopper went from being one of the most serious agricultural pests in North America to extinction.

Peruvian anchoveta *Engraulis ringens*

The principal direct consumer of planktonic production in the coastal waters of Peru, more than 10 million tonnes of this pelagic fish species were harvested in some years before the stock collapsed in 1972. The collapse was apparently brought about by a combination of the level of exploitation and natural population variability in the Peruvian upwelling system. The decline persisted into the mid-1980s, when the stock began a period of increase towards its earlier levels before collapsing again during the late 1990s.

Passenger pigeon *Ectopistes migratorius*

Arguably, at one time perhaps the most numerous bird on earth, this species was distributed across much of North America, west to the Great Plains and from southern Canada to the northern Mississippi. During autumn and winter, it was nomadic, forming vast flocks that searched for masting trees. However, by the early 1900s, it was extinct in the wild, in large part from overexploitation, with habitat loss as a potential contributing factor [47]. 'The loss of the passenger pigeon must have had profound ramifications for forest ecosystems, altering the lives of predators and prey, shifting and changing the pathways of nutrients and energy in ways we will never know' [14].

Saiga *Saiga tatarica*

This species once occurred abundantly in the steppe grasslands and semi-arid desert habitat of southern Russia and Central Asia. Since the break up of the former USSR uncontrolled illegal hunting for horns and meat has led to a catastrophic fall in numbers from over a million to a few tens of thousands, and to highly skewed sex ratios that are resulting in reproductive collapse, with most remaining individuals in Kazakhstan [48,49]. It is listed as 'Critically Endangered' by IUCN.

Habitat loss and degradation have also usually resulted in substantial depletion of previously common species, although again seldom couched in these terms. Thus, the loss, since before significant human disturbance, of 29% of the area of forest and woodland, 49% of steppe, savanna and grassland, 74% of shrubland, and 14% of tundra, hot desert and ice desert, much of which is ongoing [31], directly reflects the depletion of many once common species, and inevitably resulted in the severe depletion of many others that occurred within these environments [32]. Recent attention has focussed on losses of common species of birds as a consequence of losses of tropical forest, temperate grasslands and the intensity of modern agricultural practices [33].

Depletions of common species as a consequence of the introduction of alien species are being increasingly documented. Perhaps the starkest example concerns the American chestnut. Historically common and widely distributed across much of eastern North America, it became yet more abundant following the onset of anthropogenic habitat transformation owing to its rapid establishment in previously logged areas. However, its fortunes rapidly reversed and the species was brought to the brink of extinction across much of its former range by two introduced pathogens, root rot *Phytophthora cinnamoni* and chestnut blight *Cryphonectria parasitica* [34]. Knock-on effects on ecosystem function included reduction in leaf processing and consumption rates, and decreasing growth rates and adult body mass in macroinvertebrate stream shredder communities, because fast-decaying and nutritious American chestnut leaves originally provided the main inputs into forested headwater streams [10].

Finally, some previously common species have been seriously depleted as a consequence of extinction cascades. The most obvious examples are parasites. *Columbicola extinctus*, the louse of the passenger pigeon, was thought to have become extinct before or contemporaneously with its host. Although it has subsequently been found on other hosts, its numbers must have been greatly diminished by the loss of one that is estimated to have numbered formerly in the billions [35].

Of course, threatening processes can impact common species in rather different ways. They might result in persistence of local populations at much reduced abundances (e.g. some forms of overexploitation), entire loss of local populations (e.g. outright habitat destruction), or some combination of the two [36]. In practice, however, as the overall abundance of a species declines, these two outcomes tend to become more closely linked, with the dependencies between the population dynamics of local populations meaning that reductions in their abundances lead to declining occupancy [11].

Formal analyses are urgently required to determine which intrinsic or extrinsic traits tend to be most strongly associated with significant declines of common species, and which might therefore help identify those species at greatest risk. Although the answer doubtless depends on the form of the threatening process, obvious contenders include that (i) they are heavily exploited (e.g. many tree and fish species); (ii) they occur in habitats that are being lost; (iii) abundances are naturally highly variable through time (e.g. some insect and smaller fish species); (iv) they have low population growth rates; and (v) individuals aggregate into relatively small areas at key points in their life cycle (e.g. many migratory species or those breeding in confined areas). The last of these appears to be a surprisingly frequent trait among common species, particularly in temperate regions with marked seasonal fluctuations in resource availability.

The road to extinction

Dramatic impacts on ecosystem function can follow from depletions of common species without necessarily threatening the global persistence of those species in the short term. Nonetheless, the many documented examples of previously common species that are now listed as threatened with extinction (e.g. big-leaved mahogany *Swietenia* *macrophylla*, American burying beetle *Nicrophorus americanus*, Atlantic cod *Gadus morhua*, white-rumped vulture *Gyps bengalensis*, harbour porpoise *Phocoena phocoena*, saiga antelope *Saiga tatarica* and European bison *Bison bonasus*), or have actually been driven to extinction (e.g. Rocky Mountain grasshopper, passenger pigeon and Carolina parakeet *Conuropsis carolinensis*) indicate that rapid slippage of a common species to rarity or even extinction is not as unlikely as it might seem. Elton [37] observed that 'The argument that a species is in no danger because it is very common is a complete fallacy; but is very often brought forward quite honestly, especially by people who have a financial interest in destroying the animals'.

Although there are many examples of previously common species now threatened with extinction, few data exist on the form of such temporal trajectories. High rates of global population decline can, however, trigger the listing of a species as threatened with extinction in the near future using the criteria used by many national and international conservation agencies [4]. Some previously common species have been listed in this way (e.g. Atlantic cod, Atlantic halibut *Hippoglossus hippoglossus*, haddock *Melanogrammus aeglefinus* and common skate *Dipturus batis*), and we suspect that many others, particularly from habitats that have experienced severe reductions in extent, could similarly be listed. The approach is precautionary, based on the presumption that the decline will continue. Much debate seems, however, to result from a belief that in many such instances this is unlikely to be the case, with the decline being anticipated to become shallower or cease at low population levels. Indeed, many direct anthropogenic threats are probably density dependent or at least spatially variable, such that the rate of decline decreases as the species becomes rarer (and 'commercially extinct'). However, there is also the possibility that the human value attached to rarity will lead to continuing exploitation at previously uneconomic levels [38]. Whichever mechanism prevails, population depletions remain marked, and are shared by many other previously or still common species, even when the rates are insufficient, have not been adequately documented or are now too distant in the past, to trigger a threat listing on the basis of extinction risk, or concern taxa whose risk of extinction has yet to be evaluated.

Implications

A need to pay increased conservation attention to common species has several significant implications, including the need to identify, monitor and alleviate significant depletion events.

Listing of population depletion

Given the importance of common species for natural ecosystem structure and function, it would seem sensible for conservation to identify not only those (typically rare) species that are at the greatest risk of extinction, but also those that are suffering marked population depletions (Box 3). Indeed, one might envisage a categorization of species based on their level of population depletion that in some ways mirrors the existing IUCN (The World Conservation Union) approach to threat listing (http://www.iucnredlist.org/). This would entail paying more attention to the status and dynamics of many of the more common species than is typically done at present. However, there are far fewer common species than rare ones, and the range of parameters pertinent to depletion listing would be smaller than that considered during threat listing (which can include population size, range size, number of subpopulations, fragmentation of range and declines in population size, range size, habitat or number of subpopulations [4]). The key parameters would be some estimate of the absolute and proportional levels of decline in numbers of individuals. Key issues in listing of population depletion would include how to distinguish between systematic depletion and natural abundance fluctuations, particularly when trying to detect relatively small proportional declines, and the baseline against

Box 3. Extinction and depletion in conservation biology

From a starting point at **(a)** in Figure I, loss of species and individuals from an assemblage, if unchecked, ultimately result in assemblage extinction at **(b)**. The trajectory toward assemblage extinction can be described as a tradeoff between loss of species (extinction) and loss of individuals (depletion). Effective conservation depends on achieving some balance between these two processes to optimize species richness and ecosystem biomass at any point between (a) and (b), represented by the broken line. Disproportionate loss of species is commonplace **(d)** for example through habitat fragmentation that results disproportionately in the extinction of species with small ranges, habitat degradation that leads to the loss of specialists, and invasive species that displace poor competitors. These problems will be exacerbated in areas where little effective protection of rare species is achieved. Overexploitation, by contrast, will result in disproportionate loss of individuals, which leads to drastic changes in biomass, assemblage structure and ecosystem function, but causes species extinctions relatively rarely **(c)**. Effective protection of rare species, such as that achieved through modern conservation programmes in western Europe and in the USA, will further diminish the rate of species extinctions, whereas relatively little conservation investment is devoted to more widespread species, often outside protected areas, and which show smaller proportional declines. Thus, because of the emphasis on preventing extinctions, much modern conservation practice results in a trajectory biased toward (d).

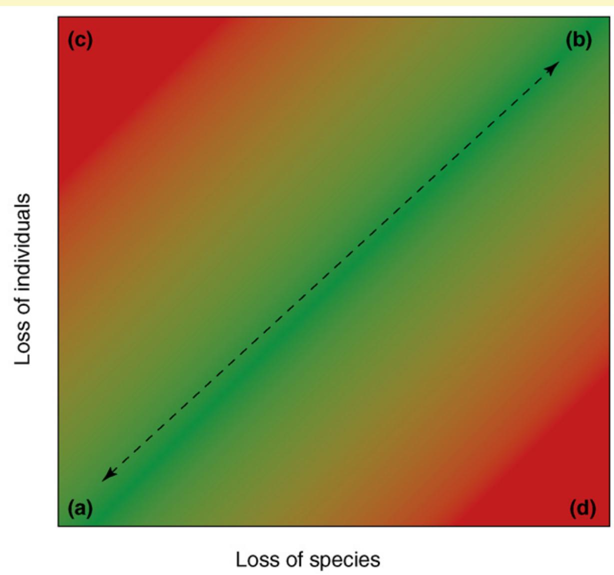

Figure I. Extinction and depletion in conservation biology.

which to measure population depletions (particularly for species in habitats that are products of human activities; e.g. farmland). Both are also challenges in threat listing.

Biodiversity indicators

At present, species based indicators of the state of biodiversity tend to be heavily biased against common species. Some, such as the Red List Indices are solely concerned with threatened, and therefore predominantly rare, species [39]. Others, such as the Living Planet Index are based on abundance, but weight equally a given proportional change in the abundance of common and rare species, even though the former might involve numbers of individuals several orders of magnitude higher than the latter [40]. The bird indicators presently used in the UK and Europe are constructed in a similar way and although they tend to concentrate on the more common species, this set of species is broadly defined to include all those that can be effectively monitored using standard field methods and generalized schemes [41].

It would also seem sensible to use indicators that reflect overall levels of loss of individuals, and thus that are disproportionately influenced by the depletion of the populations of common species. Indeed, one might argue that existing demand for such indicators is evidenced by the fact that the trends in those that weight species equally have on occasion been incorrectly observed as demonstrating overall changes in abundance.

Protected areas and wider landscapes

Finally, paying attention to population depletions as well as risks of extinction might change perceptions of the justifications for, and the relative emphasis to be placed on, establishing and maintaining protected areas and on schemes to improve the environmental quality of the wider landscape matrix. Protected areas lie at the heart of many regional and global conservation strategies, and their establishment and maintenance absorbs the bulk of the global conservation budget [42]. Although they have been argued to serve the purposes both of capturing a sample of biodiversity, and of separating or buffering this sample from external pressures, the focal species (as opposed to other biodiversity features) of the sample tend to be rare and threatened. Common species doubtless gain important conservation benefit from protected areas, but only small proportions of individuals are typically covered, and in isolation this will seldom be sufficient to maintain their common status.

Schemes to improve the environmental quality of the wider landscape matrix (e.g. agri-environment schemes, urban greenspace planning) will be essential to maintaining naturally common species in this state. In this context, common species are likely to respond well to schemes that chiefly focus on developing the overall capacity of the landscape to maintain populations, on reducing the proportion of productivity that flows to the human population and on maintaining and building ecosystem function and services. Indeed, one might argue that the state of populations of naturally common species might provide a valuable indicator of the success of such schemes, which inevitably constitutes a daunting challenge given the scale of the human enterprise [43].

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