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Biodiversity and extinction: losing the common and the widespread

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I Introduction

Species-level conservation activities tend to be focused on those species that are highly threatened with global or regional extinction in the near future. This is broadly logical, if one of the principal goals is to retain as great a proportion of the composition of original species assemblages as possible, within the severe constraints of available conservation resources. In the main, those species which have a high likelihood of rapidly becoming regionally or globally extinct also have small total population sizes and/or restricted geographic ranges within the appropriate region or worldwide (Gaston, 1994; 2003). That is, the importance of each individual organism to the persistence of the species is on average high, and/or there is limited spatial spreading of risk, increasing the vulnerability of the species to guite localized threats.

While the importance of protecting threatened species and reducing rates of extinction is widely accepted, concerns have repeatedly been raised about the relative significance of this component of species-level conservation (as well as about the relative role of species-level activities in conservation at large; Mace et al., 1998). The merits have variously been championed and debated of alternatively or also focusing conservation attention on, for

example, keystone species (eg, Simberloff, 1998; Kotliar, 2000; Rosell et al., 2005), umbrella species (eg, Simberloff, 1998; Caro and O'Doherty, 1999; Andelman and Fagan, 2000; Caro, 2003; Roberge and Angelstam, 2004; Bifolchi and Lode, 2005; Rowland et al., 2006), flagship species (eg, Simberloff, 1998; Andelman and Fagan, 2000; Williams et al., 2000; Bowen-Jones and Entwistle, 2002; Caro et al., 2004), and indicator species (eg, Simberloff, 1998; Snaith and Beazley, 2002; King and Beazley, 2005; Maes and van Dyck, 2005; Bani et al., 2006). The principal rationale is that such foci may in the long run serve to retain more biodiversity than simply concentrating on those species that have the greatest likelihood of being lost in the short term. In a similar vein, and at first sight perhaps rather perversely, a further issue coming to the fore is the importance of the conservation of presently still quite common and widespread species, the very antithesis of those that principally feature on existing lists of priority species for conservation.

Common and widespread species are arguably of significant conservation concern for three linked reasons. First, a number of species that are presently highly threatened or have recently become extinct could previously have been described as common and

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widespread. Second, there is growing evidence that large numbers of presently still common and widespread species are undergoing massive declines, with major ramifications for ecosystem functions and services, and potentially for many other species. Third, the processes that underlie these declines seem likely to intensify in many regions in the future. In this paper we selectively review each of these three issues.

II The past

Although it is far from inevitable under all forms of speciation, classically species are held to originate with rather small population sizes and small geographic ranges, subsequently to increase in numbers and distribution, and then to decline to extinction (Gaston, 2003). Many species doubtless become extinct very rapidly after speciation, and may not undergo any significant phase of population growth and spread. For those that do persist for any reasonable length of time, there has been much discussion of the forms taken by the temporal trajectories of overall population and geographic range size, how simply these forms can be characterized, how widely they generalize, and what their implications might be (eg, Willis, 1922; Jablonski, 1987; Gaston, 1998; 2003; Gaston and Chown, 1999; Webb and Gaston, 2000). All of these issues are extremely difficult to address empirically in any detail, given constraints on available data and particularly those which can be derived from the fossil record. Nonetheless, even those species that at some point in their lifespan do become extremely abundant and widespread also become rare and highly restricted on the trajectory to their extinction.

Understanding of the natural dynamics of species' ranges might therefore lead us to expect a suite of species to be currently highly threatened with extinction, that many species will have in recent times gone extinct, or that some of these species were previously common and widespread. However, from a conservation perspective, crucial facts are that (i) the majority of species are in this state not

because of the natural evolutionary dynamics of abundances and distributions, but as a direct or indirect consequence of human activities (very few recent global extinctions appear to have occurred other than as a consequence of human activities; for cases of hurricanes causing severe decline or extinction of small-island endemics, see Macouzet and Escalante Pliego, 2001, and Williamson, 1989, respectively), and (ii) when compared with the geological record current rates of decline and global extinction are greater than would otherwise be expected outside of mass extinction events (Lawton and May, 1995; Pimm et al., 1995; 2006).

How long human impacts have been such major determinants of the persistence of species continues to be debated. That virtually all of the continents lost the majority of large-bodied terrestrial animals (and many others) broadly around the time when humans first colonized and spread across those land masses is widely agreed. Rather more contentious are how synchronous were the two sets of events, whether humans could have driven these species to extinction, whether they actually did so and, if so, how (eg, Martin, 2001; Roberts et al., 2001; Brook and Bowman, 2002; 2004; Barnosky et al., 2004; Cardillo et al., 2004; Lyons et al., 2004; Miller et al., 2005). Nonetheless, it seems highly likely that humans played an important role in the extinction of at least a proportion of these species, many of which, because of their large body masses and hence large area requirements, would have been extremely widely distributed (within higher taxa, increases in the minimum geographic range sizes of species with body mass have been well documented; eg, Brown and Maurer, 1987; Gaston and Blackburn, 2000; Gaston, 2003).

Much of the debate concerning megafaunal extinctions has focused on whether at that time humans were capable of hunting such species to extinction, or at least to the point where their extinction was almost inevitable. Perhaps ironically, many of the best documented examples of previously common and widespread species being driven

extinct or to a highly threatened status concern more recent cases in which overexploitation has undoubtedly played a major role. In the terrestrial realm these include, for example, lesser prairie-chicken Tympanuchus pallidicinctus (total population may have declined by 97% since the 1800s, 20,000 individuals at present; BirdLife International, 2006), passenger pigeon Ectopistes migratorius (3-5 billion individuals before significant human impact, extinct in early 1900s; Schorger, 1955), chinchillas Chinchilla spp. (Jiménez, 1996); eastern spotted skunk Spilogale putorius (Gompper and Hackett, 2005), North American bison Bison bison (30 million individuals in early 1800s, 210,000 at present; Isenberg, 2000), blackbuck Antilope cervicapra (4 million individuals in the 1800s, 80,000 in 1947, 8000 in 1964; Nowak, 1991), and African elephant Loxodonta africana (1.3 million individuals in late 1970s, 660,000 at present; Nowak, 1991; Blanc et al., 2003). With the dramatic declines of such species have gone some of the great wildlife spectacles of Earth.

Fisheries and whaling have similarly been responsible for great declines in a variety of previously common and widespread species in the marine realm including, for example, Atlantic cod *Gadus morhua*, green turtle *Chelonia mydas*, dugong *Dugong dugon*, and northern right whale *Eubalaena glacialis* (eg, Jackson *et al.*, 2001; Jackson and Sala, 2001; Roman and Palumbi, 2003). The scale of many of these declines has only recently become apparent, through the careful examination of the accounts of early travellers (eg, Saenz-Arroyo *et al.*, 2006).

In addition to overexploitation, the three other major drivers of threat and extinction are habitat loss and degradation, the introduction of alien species, and extinction cascades; these constitute Diamond's (1984) 'evil quartet'. Habitat loss often acted in combination with overexploitation in some of the examples of declines of common and widespread species listed above. However, in isolation it is likely to have accounted for many more such

declines, given the massive changes in land cover that humans have wrought. For example, Klein Goldewijk (2001) estimates that, compared with their extent before significant human disturbance, forest/woodland has declined in area by 29%, steppe/savanna/ grassland by 49%, shrubland by 74%, and tundra/hot desert/ice desert by 14%. Although more abundant and widely distributed species have been argued to have broader niches than less abundant and more narrowly distributed species (eg, Brown, 1984), there is rather limited evidence that this is so, and a substantial amount to the contrary (Gaston, 2003). Thus, abundant and widely distributed species are not per se any better able to cope with changes in land cover by exploiting the replacement cover (predominantly agricultural). Unfortunately, however, given the lack of commercial interest in many of the individual species concerned, the declines associated with habitat loss and degradation are much more poorly documented than some of those associated with overexploitation, and in many cases one can only speculate on the impacts. For example, it is evident that vast areas of natural forest have been cleared both regionally and globally (Williams, 2003), and even where some of these areas have ultimately been replaced with plantations these have greatly impoverished species richness (eg, Aratrakorn et al., 2006; Peh et al., 2006; Raman, 2006). Most obviously, such activities must at least have led to reductions in the abundance and distribution of many previously common and widespread tree species.

Turning to a vertebrate group, Gaston et al. (2003) estimate that as a consequence of changes in land cover alone, the global number of individual breeding birds may have declined by at least between a fifth and a quarter since the advent of extensive agriculture. This estimate ignores the effects of habitat degradation within a given land cover type, and thus could be extremely conservative. Given that species-abundance distributions (the frequency distribution of species with different levels of abundance) are invariably

strongly right-skewed, with most individuals belonging to a small proportion of species (Gaston and Blackburn, 2000), this suggests that previously common and widespread species, particularly associated with those land covers that have experienced the greatest loss of extent, may have undergone enormous declines. The skew exhibited by species-abundance distributions, in which large numbers of species have few individuals and a small number of species account for the majority of individuals, is evidenced by the fact that, although threatened species presently comprise 12% of the extant species of birds, they have been estimated to comprise only 0.06% of the overall global total number of individual birds (Gaston and Blackburn, 2003). Of course, some of those species that have been evolutionarily predisposed, or have adapted, to those forms of land cover that have increased will likely have become common and widespread when they were not previously so. In particular, many species that benefited from agriculture will historically have increased in abundance and expanded their distributions.

In a fascinating exercise, Maroo and Yalden (2000) estimated the change in the abundance structure of the non-volant mammal assemblage of Britain between the Mesolithic period (c. 7000 years ago, when the region was largely covered by woodland) and the present. Their figures suggest a decline in the total numbers of individuals of native species of approximately 60%, that 26 out of 30 of these species declined, and that the populations of the three most abundant species in the Mesolithic, common shrew *Sorex araneus*, bank vole *Clethrionomys glareolus* and wood mouse *Apodemus sylvaticus* decreased by 70%, 80%, and 30%, respectively.

The impacts of changes in land use can be extremely rapid, particularly where at times species naturally become concentrated into smaller areas. The Rocky Mountain grasshopper *Melanoplus spretus* is a notable example (Lockwood and DeBrey, 1990; Chapco and Litzenberger, 2004; Lockwood, 2004).

During outbreaks it may have numbered perhaps 15 trillion individuals, and was distributed across much of the western USA between the Mississippi and the Rocky Mountains, destroying crops over vast areas and devastating plains farming communities. However, at other times it was largely restricted in relatively small (though still large in absolute terms) numbers to the valley bottoms of the Rocky Mountain region. which experienced dramatic expansion in agricultural activity in 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.

If well-documented examples of declines in common and widespread species as a consequence of habitat destruction are scarce, those that may have taken place as a result of the introduction of alien species or extinction cascades are yet more so. Perhaps the bestdocumented such decline as a consequence of an alien species is that of the American chestnut Castanea dentata. Originally distributed abundantly across much of eastern North America, and greatly increasing in abundance as a consequence of its ability to grow rapidly and outcompete other hardwood trees in areas that had been logged, it subsequently was nearly destroyed throughout most of its native range by two accidentally introduced pathogens, root rot Phytophthora cinnamoni and chestnut blight Cryphonectria parasitica, and virtually all known natural populations remain infected by the latter (Elton, 1958; Anagnostakis, 2001). Harper (1977: 493) observes: 'This is probably the largest single change in any natural plant population that has ever been recorded by man.' Troublingly, a number of other abundant American tree species are presently experiencing problems from introduced pathogens (von Broembsen, 1989; Flannery, 2001; Rizzo et al., 2002; Lovett et al., 2006).

Evidence of extinction cascades resulting in declines in common and widespread species is scarce. Although never common, the black-footed ferret Mustela nigripes was formerly very widespread, distributed across the entire Great Plains region from Texas and Arizona to Alberta and Saskatchewan (Schreiber et al., 1989). It declined dramatically to near extinction following the colonization of North America by Europeans, largely because its main prey species, the black-tailed prairie dog Cynomys ludovicianus, was subjected to an eradication programme, which resulted in a 98% decline in the prairie dog population by the late twentieth century (Barko, 1997). Many of the common and widespread species that have declined to extinction or to the point of being highly threatened will have had speciesspecific parasites that will also have suffered such declines. The most frequently cited example is that of the passenger pigeon and its louse Columbicola extinctus which was thought to have become extinct before or at the same time as its host (Stork and Lval. 1993), but subsequently found to have persisted on other hosts (Clayton and Price, 1999). Outright extinction of the host species is not a necessary precondition for the extinction of a host-specific parasite. Indeed, when host populations become small the persistence of parasites is less likely for simple population dynamic reasons. Thus, previously common and abundant host species may have lost associated specialist parasites to extinction when those hosts have declined, even if the hosts have persisted. Also, population reductions across a broad taxonomic host group can lead to declines in more hostgeneralist parasites. Previously widespread North American Anodonta mussels are in severe decline across much of their former ranges, partly as a result of declines in many native fish species, which are hosts for a parasitic stage in the life cycle of the mussels (Mock et al., 2004). Based on measures of mean host specificity, Koh et al. (2004) estimate that across selected groups 200 species have become extinct and 6300 species are endangered because of coevolved interspecific interactions with hosts that are currently listed as endangered.

The purposeful control and eradication of pests and parasites and their vectors has also resulted in the decline of previously common and widespread species. Perhaps the bestknown example is the smallpox virus Variola major. Estimated to have killed many millions of people in the twentieth century, and giving rise to an essentially incurable disease once contracted, vaccination campaigns eliminated it, and it is thought to exist now only as laboratory cultures. The many other examples include successful eradication programmes for Texas Cattle Fever (concerning the vector Boophilus annulatus and the parasite Babesia bigemina) in the USA, American screwworm Cochliomyia hominovorax in North America, the hookworms Ancylostoma duodenale and Necator americanus in the USA, Trypanosoma equiperdum in North America, Hypoderma spp. in Great Britain, Echinococcus granulosus in Iceland, Cyprus, Tasmania, New Zealand and the Falkland Islands, and ongoing eradication programmes for tropical bont tick Amblyomma variegatum in the Caribbean, guinea worm Dracunculus medinensis globally, river blindness Onchocersiasis globally, lymphatic filariasis (Wuchereria bancrofti and Brugia malayi) globally, chagas disease (Trypanosoma cruzi and triatomid bugs) in Central and South America, and trypanosomiasis and tsetse fly Glossina spp. in Africa (Bowman, 2006).

For many previously common and wide-spread species that are now highly threatened or extinct as a consequence of human activities, the precise reasons for their decline remain difficult to establish, and are sometimes hotly disputed. Examples include the Carolina parakeet *Conuropsis carolinensis* (extinct in the 1930s; for discussion, see Snyder, 2004). In some cases the causes of decline may have been relatively straightforward, but impossible to ascertain due to a lack of relevant data. In others, the causes may have been complex, and genuinely difficult to disentangle post hoc.

It is not necessary that species be abundant and widespread to have significant consequences for ecosystem structure and functioning. However, it is difficult to conceive of abundant and widespread species that do not have such consequences. Thus, in marked contrast to the majority of threatened and recently extinct species, their declines and losses (often to the point of ecological extinction, if not absolute extinction) have had major impacts on ecosystems (Ellison et al., 2005). The most widely discussed examples both in terrestrial and marine systems typically concern the consequences of (i) the huge reductions in herbivory and associated changes in nutrient cycling that have occurred with the declines in large-bodied and previously extremely abundant primary consumers; and (ii) the declines and losses of top predators (often previously widespread), the direct impacts on populations of large herbivores and meso-predators, and the indirect impacts on the prey of mesopredators (eg. Jackson and Sala, 2001: Jackson et al., 2001; Terborgh et al., 2001; Springer et al., 2003; Myers and Worm, 2005).

III The present

Marked declines in common and widespread species have not ended. Rather, there is ample and troubling evidence that they are ongoing for many groups of organisms. Indeed, a great many species once held to be extremely abundant may increasingly no longer be so. Here we highlight evidence of declines for species in three selected higher taxa (for other examples, see Carrier and Beebee, 2003; Poole and Downing, 2004; Pergams and Nyberg, 2005; Lehtinen and Skinner, 2006) – insects, fish and birds.

1 Insects

Large-scale changes in the abundances and range sizes of insects are poorly documented, and many could be occurring essentially unobserved. A few pieces of evidence suggest that in some regions at least this may indeed be so. In Europe, where insect

recording systems are best developed, there is evidence of long-term declines, particularly in moths and butterflies, likely principally as a consequence of habitat and climate change (eg, Cowley et al., 1999; León-Cortés et al., 1999; 2000; Conrad et al., 2002; 2004; Thomas et al., 2004; Swaay et al., 2006). For example, Conrad et al. (2006) document declines in the abundances of two-thirds of 337 widespread and common species of moths in Britain over a 35-year period, with a fifth of the species declining by more than 30% per decade. Declines in insect abundance have been implicated as causal factors in the losses of many farmland bird populations (Benton et al., 2002), and in some cases insect declines are at least partly a consequence of larval foodplant decline (eg, common blue butterfly Polyommatus icarus and its foodplant Lotus corniculatus; León-Cortés et al., 1999).

Particular concerns have been expressed about the future of otherwise abundant and widespread insect species which, like the Rocky Mountain grasshopper, are naturally concentrated for periods into much smaller areas. The monarch butterfly Danaus plexippus is one such species; by late summer spread over much of North America, individuals migrate south to overwinter in huge aggregations in small patches of forest in Mexico and California (Scott, 1986). In Mexico, which holds the largest proportion of overwintering individuals, this forest has been markedly degraded principally through logging (Brower et al., 2002), and in addition is likely to become increasingly unsuitable under climate change (Oberhauser and Peterson, 2003).

2 Fish

Almost by definition, a substantial part of the fishing industry targets abundant species for exploitation. The 1950s and 1960s saw a huge increase in global fishing effort, fuelled in large part by its industrialization, which gave rise to rapid increases in catches. The first major stock collapse was that of the Peruvian anchoveta *Engraulis ringens* in 1971–72. This was accompanied by declining catches

elsewhere, which accelerated in the late 1980s and early 1990s when cod Gadus morhua stocks off New England and eastern Canada collapsed (Pauly et al., 2002). Global fishing effort nonetheless continued to expand, such that by the mid-1990s a high proportion of stocks had collapsed or were being exploited beyond sustainability (Grainger and Garcia, 1996). Reported world fisheries landings have been declining slowly since the late 1980s by about 0.7 million tonnes per annum (Watson and Pauly, 2001; Pauly et al., 2002). With declines of fisheries stocks in shallow waters, increasing emphasis has been directed toward deep-water stocks. which comprise species whose life histories render them even less robust to such impacts (Roberts, 2002: Morat et al., 2006).

The impacts of fisheries have not simply been on the relatively few target species that account for the bulk of landings. Large predatory species, many of which have historically had large geographic ranges, have particularly experienced marked population declines (Myers and Worm, 2005), as have other large vertebrate species that are subject to incidental take or bycatch (Lewison *et al.*, 2004). For example, Casey and Myers (1998) document the range wide decline of the barndoor skate *Raja laevis*, a previously widely distributed species depleted by trawl fisheries targeted on smaller fish.

3 Birds

The best empirical evidence for ongoing declines of common and widespread species is for birds. Concern has particularly been raised about three groups of species. The first are long-distance migrants breeding in temperate regions (Terborgh, 1989; Holmes and Sherry, 2001; Faaborg, 2002; Lloyd-Evans and Atwood, 2004; Sanderson *et al.*, 2006; G.H. Thomas *et al.*, 2006). Many such species have been suffering substantial population losses as a consequence of habitat loss and degradation or environmental change, in some cases on the breeding grounds, in many others on the wintering grounds, and sometimes on

both. Particularly problematic may be where the wintering grounds are much more restricted than the breeding grounds, making the species both vulnerable to the loss of suitable habitat in this smaller area and resulting in individuals potentially being redistributed at much lower density on the breeding grounds. Remsen (1995) calculates, on the basis of minimum estimates of the rate of destruction of tropical forest of 76,000 km² yr¹ and a breeding bird density of 1900 km², that 144.4 million individual birds may be lost annually as a consequence. This figure would be greatly increased if migrants were to be included.

Significant concern also exists over bird species that exploit agricultural habitats across much of Europe and North America, although these declines may also be taking place in other regions. Many such species presumably benefited originally from the expansion of such habitats (see above), and became common and widespread (they include some of the regionally most abundant species), but are now in decline as a consequence of the intensification of agricultural activities and the resultant paucity of available resources (eg, Fuller et al., 1995; Murphy, 2003; BirdLife International, 2004; Gregory et al., 2004; Newton, 2004; Eaton et al., 2006). Indeed, across Europe declines are more marked in those regions where such activities are most intense, and less so elsewhere (eg, Donald et al., 2001).

Albatrosses and petrels constitute a third group of birds of which a number of species are experiencing marked declines in abundance. While few of these species have especially large global populations and their breeding grounds are typically restricted, many of them have large overall geographic ranges with individuals foraging over huge distances. This accentuates the likelihood of individuals foraging in areas subject to commercial fishing operations, increasing the likelihood of death as bycatch, with even low levels of such mortality having major impacts on the populations of such long-lived birds (eg, Gales et al., 1998; Nel et al., 2002; BirdLife International, 2004).

4 Measuring rates of decline

The criteria associated with the present IUCN Red List Categories for the threat of extinction faced by species include observed, estimated, inferred or suspected decline rates (IUCN, 2001). As such, the recent observed declines in some common and widespread species have triggered a global or regional threat listing, or would do so if the criteria were employed (Conrad et al., 2006; http://www.iucnredlist.org/). Such cases have sometimes proven very contentious. The listing is triggered because if the decline continued at the same rate then the species concerned would become extinct in the near future, and it therefore conforms to the precautionary principle. At the same time, in many cases it seems unlikely that the rate will be sustained as the species concerned become more scarce, and thus unlikely that they do actually have a high likelihood of extinction in the near future. This begs important questions as to the relative importance that should be placed on depletions of the abundances and distributions of species and on the extinction risks that they face.

IV The future

The lessons of recent and more distant history teach that initially common and widespread species can be massively depleted by human activities, even when those species are not themselves being directly exploited. Projected levels and patterns of global environmental change suggest that this will continue to be the case, with many of the pressures that these species have faced being predicted to increase rather than ease in their intensity (Cardillo *et al.*, 2004; Scholze *et al.*, 2006; Lewis, 2006; Thuiller *et al.*, 2006).

Under the four scenarios used in the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment, 2005), agricultural land is predicted by 2050 to extend over 107–124% of its 2000 coverage, forest/woodland over 97–106%, steppe/savanna/grassland over 84–92%, scrubland over 60–88%, and tundra/hot desert/ice

desert over 96-97%. Projected future loss of, for example, grasslands in Alaska may threaten the integrity of migration routes between calving and wintering areas for the caribou Rangifer tarandus population of an estimated one million animals (Ricketts et al., 1999). Formerly abundant grassland birds such as bobolink Polichonyx oryzivorus and lark bunting Calamospiza melanocorys are undergoing consistent long-term declines across much of North America, predicted to continue as a result of agricultural intensification (Sauer et al., 1997; White et al., 2000). The ability of previously common and widespread species to respond to future changes in land cover as a direct consequence of human activities will be further complicated by changes engendered by systematic alterations in climate, and the rate at which they can track changing conditions (Hill et al., 2002; Menendez et al., 2006).

Evidence is growing that changes in land cover are likely to be accompanied by the ongoing homogenization of biotas, and processes in which native species are replaced by a relatively small set of alien species (McKinney and Lockwood, 1999; Olden and Poff, 2003; Clergeau et al., 2006; Olden and Rooney, 2006). Attention has thus focused on how some common and widespread species will become yet more common and widespread (eg, the global geographic range of the house sparrow Passer domesticus has continued to spread in recent years; Summers-Smith, 1988; 1990). However, perhaps more significant will be the declines and extirpations of many naturally previously common and widespread species, with attendant repercussions for numerous ecosystem functions and services, and potentially for many other species.

The relative paucity of information on past declines in common and widespread species, but evidence that these have often been marked highlights the importance of documenting future changes in their distribution and population status (León-Cortés *et al.*, 1999; C.D. Thomas *et al.*, 2006). Information on changes in population levels and range extent will inevitably be of higher quality in

species with restricted ranges and hence more tractable for distributional studies and wholesale population trend assessment. This suggests that, as in the past, future declines in more widespread species may be overlooked because in practice a full assessment across their geographic range is difficult to achieve. We believe that conservation tools to identify and alleviate declines in common and widespread species should emerge that complement those already in place that focus on rare and restricted range species.

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