Red-lists and hot-spots - questioning the role of rare species strategies in biodiversity management

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Abstract

There is a broad consensus to protect biodiversity and the primary motivation is to secure life-sustaining systems of the biosphere. However in practice biodiversity is not well defined and many policies are confused. Despite general acknowledgement that ecosystem processes are driven by common species, conservation is in practice focused entirely on rare species through measures like the Endangered Species Act, Red Lists and protection of biodiversity hot-spots. In contrast, management of genetic biodiversity of common species has largely been neglected. There are very many truly rare species: They represent 25-45% of all species, while functionally or numerically dominant species are relatively few in numbers in both species-rich and species-poor ecosystems. Reviewing experimental research on biodiversity and ecosystem function show no evidence that the many rare species are important to ecosystem structure and function. In contrast, there is growing evidence for the importance of genetic biodiversity at population level, both as a prerequisite for evolutionary modifications in response to environmental changes and as a fundamental component of local adaptation of species. It would thus seem that management activities should be redirected towards functionally dominant species of ecosystems and moved to the level of populations rather than species. Sustaining ecosystem functions by relevant management of common species, will also be beneficial to the rare species, and may be the most cost-effective way to protect them.

Keywords: species diversity, genetic diversity, keystone species, Red Lists, biodiversity conservation

Introduction

Experimental research on biodiversity has during the last decades produced an impressive amount of research that indicates that there is a positive relationship between biodiversity and ecosystem function (reviewed by Loreau et *al.* 2001; Hooper et *al.* 2005; Balvanera et *al.* 2006; Cardinale et *al.* 2007 and many others). During the same period of time, and as a consequence of a large political endeavour to protect biodiversity, the IUCN (World Conservation Union) and national Red Lists of Threatened Species have become major tools in biodiversity management, and are used to set priorities for conservation in many countries (Simberloff 1998; Miller et *al.* 2006; Gaston & Fuller 2007). Superficially, the scientific support for a general role of biodiversity in ecosystem function and the focus on protecting endangered species make a perfect fit, and this impression is possibly caused by the habit of politicians, managers and scientists alike to talk about “biodiversity” as some kind of holistic entity, or a parameter reflecting all types of non-human life (Ridder 2008).

When politicians and activists speak of “biodiversity” it often seems that it is “Mother Nature” as such they seek to protect. The underlying motives can vary from the protection of certain ecosystem services to existence values, beauty, recreation or all of the above and more motives associated with a “good” or “natural” state of nature. To all these motives it seems that “biodiversity” provides a more “scientific” measure. The trouble is that a concept can barely be described as scientific unless it has a clear definition and unless there is agreement about how it is to be measured. On closer inspection the concept of biodiversity is far from clear and we will start by discussing some possible definitions each of which would presumably have a different relationship with threatened species or with ecosystem services.

One possible measure – and apparently the most popular – is simply the total number of species found. As we will discuss in detail presently, this measure has some shortcomings.

One of the problems with this is that there are very large numbers of extremely rare organisms. These are so numerous as to make the total number both arbitrary and uncertain since at any given time, and in any given ecosystem there will be a very large number of species that have not yet been discovered. If most of the organisms are extremely rare, it is furthermore unlikely that they play a critical role for the ecosystem. Also the number of species says nothing about the frequency distribution. Say there are 100 species in an ecosystem then surely there is a difference if they each account for 1% of the total number of individuals or if there is one species that accounts for 90%, ten species for say one percent each while 90 are so rare they have a share insignificantly above zero. Intuitively we might consider the former more diverse since the chance that two randomly chosen intervals are of the same species is lower. Simpsons index formalizes this concept in the index $S = 1 - \Sigma(P_i)^2$ where P_i is the share of all individuals belonging to species i.

Most common species	Other species	Number of species	Simpsons Index
100%	0%	2	0
50%	50%	2	0,5
1/3	1/3 each	3	0,67
50%	50 and ~0 % resp.	3	0,5
1%	1% each	100	0,99
95%	0,05% each all rest	100	0,10

Table 1 shows some values for the various indices: In rows 1-2 there are two species. With two species the maximum for Simpson’s index is 0,5 and this value applies to the case when both species have an equal number of individuals so that they account for half the population each. If one of the species is dominant and has a share that approaches 100% while the other is rare and approaches 0% then Simpsons index is (close to) 0. Similarly if there are three species then the maximum diversity according to Simpsons index is 0.67 and occurs if all three species have the same population size. If however two of the three have (close to) 50% each while the third has an insignificant number then Simpsons index is again 0.5 – the same as for two species. This illustrates a big difference between Simpsons index and N the number of species. The number of species increases a lot while Simpsons index is unchanged if there are– to take the extreme case- a number of species with just one member so that their population share is insignificant. An ecosystem with 100 species would of course count as very diverse by then simple measure N. Whether or not the diversity would be high according to Simpsons Index would depend on whether there was one dominant species or equal population shares for all the species.

The measure discussed so far is a measure of species diversity, but the same general principle applies to measures of genetic diversity; counting the number of genes (alleles) is mostly irrelevant while most measures of genetic diversity takes frequencies into account (REFs). One point should be amply clear: the simple measure of species count is not unproblematic nor natural. There are several others (e.g. Shannon, Simpson, Weitzman) that each describe the diversity in slightly different ways. It cannot be sufficiently underlined that the fact we have no universally accepted measure of species diversity is quite serious. It means that it is hard to research and to draw policy conclusions concerning how important “biodiversity” of species is for “ecosystem services” (which again is not well defined) or more generally for welfare. Moreover, diversity of species is merely the top of the ice-berg, as the largest part of the biological diversity is truly found within species; being genetic variation within diploid individuals, genetic variation among individuals of a population, and genetic variation among populations.

It is against this background that arguments in support of the view that loss of rare species would cause major ecosystem shifts are weird. This because any approach of valuing diversity in a more sophisticated way than through a direct count of the number of species, will show that a rare species will contribute extremely poorly to the total diversity at genetic or species level in any ecosystem. The relevance of the opinion of a tight relationship between species diversity and ecosystem functioning has also been seriously questioned (Loreau et *al.* 2001; Srivastava & Vellend 2005). This applies in particular to the practice of extrapolating results from studies of an extremely small proportion (~0.1%) of an ecosystem's diversity of species up to ecosystem or even global scale effects (e.g. Worm et *al.* 2006). Thus, if true that most ecosystem functions are upheld by a few dominant species or by assemblages of common species (see below), the focus on threatened species in conservation practice (through red-listing) may be a serious mistake, which risks distracting both resources and initiatives from measures that are more promising.

Reviews have emphasized the importance of common species in maintaining ecosystem functions (Gaston & Fuller 2007; Ridder 2008), and have suggested a shift in focus from species-extinctions to population trends for assessments of the status of nature (Luck et *al.* 2003; Balmford et *al.* 2003). In this review we examine in more detail the evidence for a role for rare species in contributing to ecosystem functions, in light of the fact that rare species make up a considerable part of the total number of species and thus in commonly used praxis may contribute significantly to proxy estimates of biodiversity. The red-listing conservation strategy is contrasted against a focus on common species and the genetic diversity of these species that contribute fundamental functions to ecosystems.

The challenge of managing – and measuring - biodiversity

Monitoring provides a basis for both decisions and evaluations of management measures. Biodiversity is costly to monitor and requires involvement of taxonomic expertise. In accordance with the Rio agreement, Sweden has made a huge effort to count all species present in the country and the list currently includs 61,000 species (Gärdenfors et *al.* 2003), with some 33,000 species being metazoan. However, there is a substantial number of unrecognized/unidentified species and it is estimated to take 20 years of taxonomic work at a cost of €130 millions to include all these (Ronqvist & Gärdenfors 2003). For example, 89 new species of marine meiofauna (17 new for science) were found during a 10-day inventory in a small marine area at the Swedish westcoast (the Kosterfjord) during 2007. As a proper management of all species, including the rare ones, requires monitoring the occurrences over time and space to assess changes and trends, it is fairly obvious that for most ecosystems this is simply not feasible.

Motives to protect species diversity

Ethical and aesthetic arguments may be invoked to justify the protection of all species alike. In reality some species get attention and protection because they are beautiful or "emblematic" in some other way (tigers, falcons, polar bears) but more frequently policy makers refer to the importance of biodiversity for upholding ecosystem function and sustainability. Although a main target of biodiversity protection is to prevent loss of ecosystem functions, rare species are given priority over populations of common species in conservation through being included or potentially included in the IUCN or national Red Lists

(Milner-Gulland et *al.* 2006; Miller *et al. 2*006; Fontaine et *al.* 2007). Furthermore, it has been suggested that the 25 areas with the richest numbers of endemic species should be prioritized for global conservation (Myers et *al.* 2000, Myers 2003).

A reason for focusing on rare species is of course that a lost species can never be replaced by exactly the same biological entity. However, can this argument be used to give priority to save species instead of saving ecosystem functions on which our society depends, as do the rare species?

Rare species are common

One definition of truly rare species is that these are encountered no more than one time (singletons) or two times (doubletons) during extensive taxonomic inventories including 10,000-100,000 specimens. Such species will classify at least as “vulnerable” and more probably as “endangered” or “critically endangered” following the criteria of the IUPN Red List and/or on national red lists. The total number of singletons and doubletons in any ecosystem is, however, surprisingly high, an observation that was made more than 60 years ago (e.g. Brown 2001, Magurran & Henderson 2003). In ambitious taxonomic inventories of different areas, biotopes and taxa, rare singletons and doubletons represent a substantial part (25-45%) of the total number of species (Fig. 1). If counting moths in Ohio, trees in Peru or marine coral reef molluscs in New Caledonia, a large share of all species found are truly rare and will appear just once or twice among thousands of specimens. It may indeed be surprising that the number of rare species is so high, and also that patterns are so similar among taxa and ecosystems, but despite this pattern being known for decades it still lacks a simple explanation (McGill et *al.* 2007, Pueyo et *al.* 2007).

It is unlikely that rarity in one place is simply a consequence of low-density distributions. For example, the European database covering all multicellular animal species recorded in Europe show that 36% of the 130,000 species are only found in one of 68 countries (Fontaine et *al.* 2007), and the number of endemic plant species in the world is estimated to be in the range 22-62% of all plant species (Pitman & Jorgensen 2002). Hence, the overall pattern appears similar at different geographic scales, and is likely not a consequence of anthropogenic extinctions as it is found in pristine environments as well. This suggests that the large majority of rare species are rare owing to natural circumstances.

Are Red Lists covering the bulk part of rare species of ecosystems? The national Swedish Red-List, an example of an ambitious list, reports 3% of all known marine species and 12% of terrestrial and freshwater species as vulnerable, endangered or critically endangered. Among the 130,000 species of multicellular non-marine animals listed in the Fauna Europaea database, only 0.4% is on the IUCN Red-List (Fontaine et *al.* 2007). The IUCN Red List contains 41,415 species which is 2.8% of the 1.5 millions of named species in the world. Clearly, a minimum estimate of rare species should be at least a magnitude larger than the number of species included on current Red Lists. (If the true number of species on earth is 20 millions, Wilson 2003, the number of red-listed species should probably be counted in millions.) Thus Red Lists are surprisingly incomplete and certainly not informative enough to guide policy concerning most rare and endangered species of ecosystems.

...while common species are rare

In contrast, but less often highlighted (but see Gaston & Fuller 2007), is the observation that the common species of any ecosystem are relatively few in numbers. Indeed, of 127,000 specimens distributed over 2738 species of tropical marine molluscs only less than 1% had a total count of 1000 individuals or more (Bouchet et *al.* 2002). Similarly, an inventory of Atlantic marine invertebrate species sampled over 101 sites west Norway showed that only 2.2% of the species were present at half the number of sites or more (Ellingsen & Gray 2002), and similar trends are found in tropical lagoon species (Schlacker et *al.* 1998) as well as in tropical forest trees (Pitman et *al.* 2001). That common species are both few and easy to find, suggests that monitoring of these species is much more reliable and inexpensive than monitoring high numbers of species that each of them are hard to find.

Biodiversity and ecosystem function

The hypothesis that increased biodiversity improves ecosystem function has been critically assessed using several hundreds of manipulative experiments. Almost all studies of how biodiversity affect ecosystem functions use the number of species as a proxy for biodiversity (e.g. Balvanera et *al.* 2006 list 446 studies and 393 of these use species numbers, 30 use species eveness or diversity, while only 23 used functional diversity). In contrast, no more than a handful of studies have addressed the effect of genetic biodiversity on ecosystem functions (e.g. Hughes & Stachowicz 2004: Reusch et *al.* 2005; Gamfeldt et *al.* 2005).

Many experimental studies have suggested a positive relationship between species diversity (species number) and ecosystem functions, such as, productivity, nitrogen uptake, resistance towards introductions etc. (see e.g. Tilman et *al.* 1997, and reviews by Loreau et *al.* 2001; Hooper et *al.* 2005; Duffy *et al. 2*007). Examining one ecosystem function at a time, the overall conclusion is, somewhat surprising, that there is only a weak positive relationship. Perhaps on the other hand, we should not be so surprised since monocultures may arise and in fact be planted exactly because that one species is so productive in some particular way.

Summarising the result of 446 experiments the average effect size of species diversity on ecosystem function was no more than 0.10 and ranged widely among individual studies (-2.71 to 2.39) (Balvanera et *al.* 2006). Notably, no overall effect was found for dominant ecosystems such as grassland, freshwater, marine and forest ecosystems, while overall significant effects were found in ruderal/salt marsh, bacterial, crop/successional and soil ecosystems. Lacking an overall effect for grassland ecosystems are supported by earlier reviews of grassland biodiversity showing that moderate plant diversity give more productive ecosystems than either species-poor or species-rich systems (Huston 1997; Hodgson *et al. 2*005). However, recent studies have suggested that if multiple ecosystem functions are considered simultaneously, the relationship between overall ecosystem functioning and species diversity becomes stronger (Hector & Bagchi 2007; Gamfeldt et *al.* 2008). (Which is less surprising since different species are likely to be crucial to different functions in the ecosystem.)

The mechanisms behind the positive relationship between species biodiversity and ecosystem function, when present, are not completely understood, but several studies suggest that this is largely a "sampling" effect (Houston 1997; Loreau et *al.* 2001; Bunker et *al.* 2005; Cardinale et *al.* 2006; Duffy *et al. 2*007), although a recent metaanalysis considered this a premature conclusion drawn from experimental studies of too short duration to allow for complementary effects among species (Cardinale et *al.* 2007; Fargione et *al.* 2007). Nevertheless, if among all species present in an ecosystem (or an experiment), some are superior in providing the particular function (or functions) measured, random removal of species will result in a positive relationship between species number and ecosystem function, as the more species that remains in the ecosystem, the larger is the chance that a particular species that contribute substantially to the measured ecosystem function is still present. However, random extinction of species is less likely in nature, and non-random removal studies get completely different results to those where species are removed or added at random (Raffaelli 2004). Both modeling and empirical studies show that non-random removal of dominant species renders dramatic losses of ecosystem effects while removal of less common or rare species do not affect ecosystem functions (Smith & Knapp 2003; Solan et *al.* 2004).

Interestingly, a full-scale comparison of carbon fluxes in two large marine ecosystems, the Baltic Sea and the North Sea, supports the view that major ecosystem functions can be upheld by very few species, if these are a non-random sample of a larger species-pool. The Baltic and North Sea ecosystems are geographically adjacent and very similar with respect to climate, physical environment (except salinity) and type of organisms present, while differing radically in species richness; the Baltic Sea contains only about 10% of the marine species present in the North Sea due to a much lower salinity (3-10‰ in the Baltic, >25‰ in the North Sea). (The Baltic Sea contains some freshwater species not present in the North Sea, but they are coastal and of minor importance for the overall productivity of the ecosystem.) Despite the different magnitudes of biodiversity the overall productivity measured as carbon flux is of very similar sizes in the two seas (Elmgren & Hill, 1997 and references there in). However, in the northern most part of the Baltic Sea, the Bothnian Bay, carbon flux drops owing to a loss of a dominant filter feeder, the blue mussel. Hence a tenfold increase in species richness does not affect main ecosystem functions, while loss of one particular species results in a profound functional reduction.

Which species contribute to ecosystem function and sustainability?

Extensive experimental data from grassland ecosystems show that it is the most common species of plants that essentially determine the properties of grassland ecosystems and that these properties are independent of species diversity, and furthermore, that the many rare species that contributes substantially to biodiversity do not contribute to ecosystem function (reviewed by Grime 1998; Geider et *al.* 2001). Loss of rare species in a grassland ecosystem was also compensated by the production of common species that replaced the rare ones, and a three-fold loss of uncommon and rare species did not at all affect ecosystem productivity (Smith and Knapp, 2003). Moreover, rare species go extinct first when grasslands are subject to chronic nitrogen addition (Clark & Tilman 2008). An observation supporting earlier conclusions from marine benthic communities, where it has been observed that contaminated areas first loose the rare species (Gray 1979). Another way of saying this is perhaps that the loss of rare species is an indicator or early sign of loss.

A recent modelling study, evaluating the effect of non-random species removal from a natural marine ecosystem, showed that the extinction of rare species did not affect bioturbation (a central function of benthic habitats), while the extinction of a very common and rather large species (a brittle star) had a huge effect (Solan et *al.* 2004). In this study, rare species had no compensatory effect even if they were allowed to increase and replace more common species that went extinct, as the risk of extinction of a rare species was larger owing to a small population size and being under similar threats as the dominant species (if part of the same functional group).

Although rare species do not replace common species when they are lost (Smith & Knapp 2003; Solan et *al.* 2004), less rare species, often denoted “uncommon species” or “minor species” might contribute to ecosystem functions if they possess unique functional characteristics, or if they resist environmental changes that remove dominant species (Walker et *al.* 1999; Bellwood et *al.* 2006; Zavaleta & Hulvey 2007).

On a more general basis, it has been questioned if it is species loss *per se*, or the mechanism causing the loss of species (e.g. habitat loss, overexploitation, pollution) that impact ecosystem function the most (Srivastava & Vellend, 2005). No doubt, habitat loss etc. will cause more loss of ecosystem functions than loss of the rare species. It also seems extremely unlikely that rare species will act as insurance species upon loss of more common species, following habitat destruction. At least this would apply to each one of the rare species individually. It is still possible that the total number of rare species harbours some variation that could have value in the face of environmental change.

The importance of ecosystem dominants

At any given position in time and space, a minor number of species accounts for most of the ecosystem functions. These functions are essential both for the maintenance of the ecosystem itself, and for the production of services that are indispensable for human societies. These species are naturally dominant either by their high numbers (e.g. primary and secondary producers, species controlling parasites), or by their function (e.g. pollinators and top-predators). A third group is species that provide habitats for other species, and these may sometimes as well be important primary or secondary producers (e.g. trees, corals). If a dominant species becomes locally or globally rare, through overexploitation, habitat loss or otherwise, they can no longer contribute important functions to the ecosystem (Luck et *al.* 2003; Gaston & Fuller 2007). Oak, for example, is no longer a dominant species in many parts of NW Europe where it was once a major forest-building tree. Another example is wolf, which is locally depleted (or extinct) to population sizes of no ecosystem importance, while still abundant enough to contribute to regulation of herbivore species in other areas. Functionally dominant species might well be termed keystone species, (keystone species are species that “exert influences on the associated assemblage, often including numerous indirect effects, out of proportion to the keystone’s abundance or biomass”, Paine 1995), but species being dominant through numbers or biomass might have similarly important impacts on fundamental ecosystem processes without being traditional keystones. Dominant species are thus a broader category than keystone species, and one and the same ecosystem will always include at least some dominant species.

Today many dominant species are loosing their role as important motors of essential ecosystem functions. Atlantic cod is an excellent example, but a number of other predatory fishes, marine mammals, herbivorous fishes of coral reefs, predatory birds, terrestrial predatory and herbivorous mammals, coral species, sea grasses, mangrove species, etc. etc. have diminishing populations with dramatic local or sometimes global effects on ecosystem functions. The decline in pollinating insects in fruit-districts in China is a frightening example of how the disappearance of a key function of an ecosystem requires costly compensation (hand-pollination) (Partap et *al.* 2001).

In exceptional cases, dominant species may instead explode in numbers to become pests, for example, if introduced to non-indigenous areas, or if a regulating mechanism has been removed, such as the mass occurrence of sea-urchins after removal of predatory coral fishes (Bellwood et *al.* 2004). Of course, management of dominant species must include regulation of undesired population increases in competitive species.

Sometimes it is not single species but a group of functionally similar species that provide an ecosystem service. With the loss of one or a group of dominant species involved in the same function, a fundamental ecosystem service may be more or less completely lost (Bellwood et *al.* 2004). A salient example is the role algal-grazing fish species have on natural recovery of coral reefs. Following the 1998 coral bleaching, algal growth on dead corals prevented coral recruitment, but if herbivorous fishes were present (rescued from overexploitation by nature reserves) the algae were removed and coral recovery was extensive (Hughes et *al.* 2007).

Although we have less knowledge about population structures of habitat-forming species, it seems likely that genetically distinct local populations of corals, mangrove species, tropical trees and bushes, are seriously threatened by extinction or already lost. To provide continued ecosystem functions, all these species and local populations need urgent protection in large enough populations. Red-listing is not generally an accurate measure to handle this type of biodiversity threat as most of these species will not be included on Red Lists until they are close to local or global extinction. Indeed, numerous dominant species that lack proper management are not present on Red Lists (because they are still not rare enough), and consequently, they are not highlighted as objects for biodiversity protection measures (Gaston & Fuller 2007). This is a most essential point to raise and a fundamental difference between focusing conservation on threatened species, or focusing on the components of ecosystem that have a <u>quantitative</u> impact on maintenance of ecosystem functions.

It is important to stress that it is generally not presence or absence (living or extinct) that is of interest, but commonness or rarity. That is, the properties of a species are tightly linked to its functional dominance, either by being numerous or by being common enough to play an important functional role in an ecosystem. Hence, as highlighted in earlier studies (Luck et *al.* 2003; Gaston & Fuller 2007) an important target of management is to preserve population sizes and distributions of such a species to secure continued output of ecosystem functions in required quantities. Secondly, and somewhat more complex, the genetic (intraspecific) biodiversity of species is crucial to the maintenance of functions over spatial and temporal scales.

The importance of genetic biodiversity

Preserving large enough population sizes of dominant species is essential to secure necessary quantities of important ecosystem functions, but population sizes are also critical to prevent loss of genetic components of biodiversity. In the first place, both total and local population sizes of species need to be large enough to prevent stochastic loss of genetic variation. Moreover, the genetic structure of most species is heterogeneous over the species' distribution, and this includes genetic adaptation of populations to local environments. A notable example is the populations of marine species inhabiting the Baltic Sea. The Atlantic cod population of the Baltic Sea, for example, has a distinct reproductive season and different egg buoyancy in the Baltic Sea and very little genetic exchange with cod populations outside its area of residence (Nielsen et *al.* 2003). The maintenance of a local cod stock is critical not only for an important cod fishery, but as well for a number of ecosystem functions of the Baltic Sea (Fig 2 and references therein). The genetic biodiversity of cod is truly critical to its role as a functionally dominant species. Recent research shows that Atlantic cod is divided into often small and local stocks, such as in Norwegian fjords where populations only 60 km apart are genetically distinct (Knutsen et *al.* 2003). Hence, even if cod as a species is not endangered, its contribution to ecosystem function in an area is in many places depending on the presence of a locally adapted population. Loss of the local population may lead to long-term loss of an essential ecosystem function, even if cod populations in other areas do fine, as is illustrated by the loss of the Newfoundland stock more than a decade ago.

The mixing of hundreds of locally spawning stocks of sockeye salmon in the Bristol Bay, Alaska, is a remarkably example of when biodiversity at the genetic level provide the foundation for a sustainable fishery (Hilborn et *al.* 2003), and most likely for additional ecosystem functions. Each of the local stocks has specific adaptations to its local spawning environment in, for example, life-history traits. As a consequence of climate variation, some stocks are more successful in some years and others in other years, and the mixed composition of the exploited population in the bay is hence buffered against extreme events by its complexity at the genetic level. Sterner (2007) however shows how unobserved genetic diversity of cod actually can serve as a cause for extinction of substocks, see also Svedäng et al 2010).

The cod and salmon examples illustrate the importance of between-population genetic variation for maintaining ecosystem functions of substantial economic and ecological importance. Quite obviously, a substantial drop or a complete loss of a local population of a dominant species will be much more serious to the ecosystem functions than loss of a rare endemic species of the same area. Even if a local population of a dominant species can in principle be re-established, this might take long time, as locally important traits must evolve *de novo*. Worst-case scenario is that the ecosystem might have shifted into another state with negative feedback mechanisms that prevent reestablishment of a dominant population (Folke et *al.* 2004; Österblom et *al.* 2007).

The maintenance of genetic variation within species is probably the most important insurance to future environmental changes. The potential to adapt to new conditions by natural selection is directly proportional to the content of genetic variation of populations (Futuyma 2005), and large populations will be better prepared to meet global changes in temperature, pH, precipitation etc. than small, simply because the former contain more genetic variation. In addition, a species living in a heterogeneous environment with local populations containing genetically different adaptive traits will increase its chance to survival compared to a genetically homogeneous species.

Earlier conservation genetics focused on the genetic content of endangered species and loss of genetic variation owing to genetic drift in small populations and increased risks of inbreeding. A new concern that is even more important to large than to small populations is the consequences of harvesting selection. For species in which human exploitation is a dominant adult mortality factor genetic variation can be radically shifted towards loss of important traits (Kuparinen & Merilä 2007).

Relatively few experimental studies have directly addressed the relationship between biodiversity at the genetic level and ecosystem function, but results this far suggest a strong positive relationship between within-population genetic variation and primary production, nutrient uptake, associated biodiversity of habitat-forming species, resilience towards species loss and species invasions, resistance to perturbations, and larval recruitment (Booth & Grime 2003; Hughes & Stachowicz 2004; Reusch et *al.* 2005; Gamfeldt et *al.* 2005; Crutsinger et *al.* 2006; Johnson et *al.* 2006; Gamfeldt and Källström 2007; Crutsinger et *al.* 2008, and see review by Hughes et al. 2008). Hence, genetic variation within species, and in particularly, within species with fundamental ecosystem roles, is vital to maintain ecosystem functions over both space and time. The current ignorance of intraspecific biodiversity of common species in conservation is a serious problem, along with the ignorance of protecting large enough population sizes of ecosystem dominant species.

Conclusions and a new perspective of biodiversity management

Protecting all biodiversity is an unattainable target, and a focus on red-listed species that represents but a tiny fraction of all rare species is a futile effort to try to halt the current loss of thousands of species. Instead, the priority of biodiversity protection must be to maintain critical ecosystem functions. The recent introduction of an Ecosystem Approach in management, further elaborated in the twelve Manilla Principles (CBD 2007), reflects a partly new policy of the Convention of Biological Diversity (CBD) that emphasizes the importance of conserving ecosystem functions rather than individual species. However, as ecosystem functions are the result of individual species, or more precisely, local populations of species, we need to spot the species and populations of these that are most critical to ecosystem functions (here termed "dominant species"), and identify how we can secure their capacity to contribute to ecosystem functions, mainly by protecting population sizes and genetic variation including local adaptations. Perhaps, shifting the focus to functional groups instead of populations and species, would be an alternative strategy (Hughes et *al.* 2005). A caveat, however, is that functional biodiversity seems almost as weakly linked to ecosystem function as species numbers (Balvanera et *al.* 2006). Incomplete knowledge about what species are functionally important for specific situations, may additionally weaken management solely based on functional groups, as is illustrated by a dramatic example of coral reef recovery where the effect of 43 species of herbivorous fishes were completely overshadowed by the effect of one species earlier not considered as a herbivore (Bellwood et *al.* 2006). Moreover, focusing on functional groups will completely loose track on the genetic components of biodiversity.

Simberloff (1998) concludes that neither management of endangered species, nor management of whole ecosystems is likely to be successful, as management of single-species sometimes results in conflicting needs of measures and ecosystem management tend to focus on landscapes and processes while risk the loss of the components (species and populations). Indeed, he suggests management of keystone species as an alternative. Through cascading effects this will be an effective way of protection, and it will furthermore generate an understanding of ecosystem properties that would help in taking additional conservation measures. This suggestion is interesting, but needs to be extended to cover all main functions of an ecosystem, and hence protection of all functionally dominant species needs to be included.

If we focus on protection of populations of dominant species, will we then risk the loss of rare species? As rare species are completely reliant on ecosystem functions provided by the dominant species, maintaining vivid populations of the latter will provide a more comprehensive protection of rare species than measures directed towards rare species one at a time, and thus there is no conflict between preserving ecosystem functions and protecting rare species. This points perhaps to the importance of an open-minded and eclectic approach. At the end of the day, human preferences are fundamental. There is no readily available scientific basis for protecting all threatened species but if there is an opinion in favour of affording special protection to a few (emblematic) species then so be it. If we in addition include some element of analysis into the foundations for ecosystem services we will appreciate that we also need to care about genetic diversity among the dominant or large species. The fact that multiple approaches compete may be disturbing to some but surely we must be open to any source of interest since the environment as a whole needs more not less protection. This however is also the reason why we cannot afford to waste resources in endeavors that lack scientific and policy relevance.

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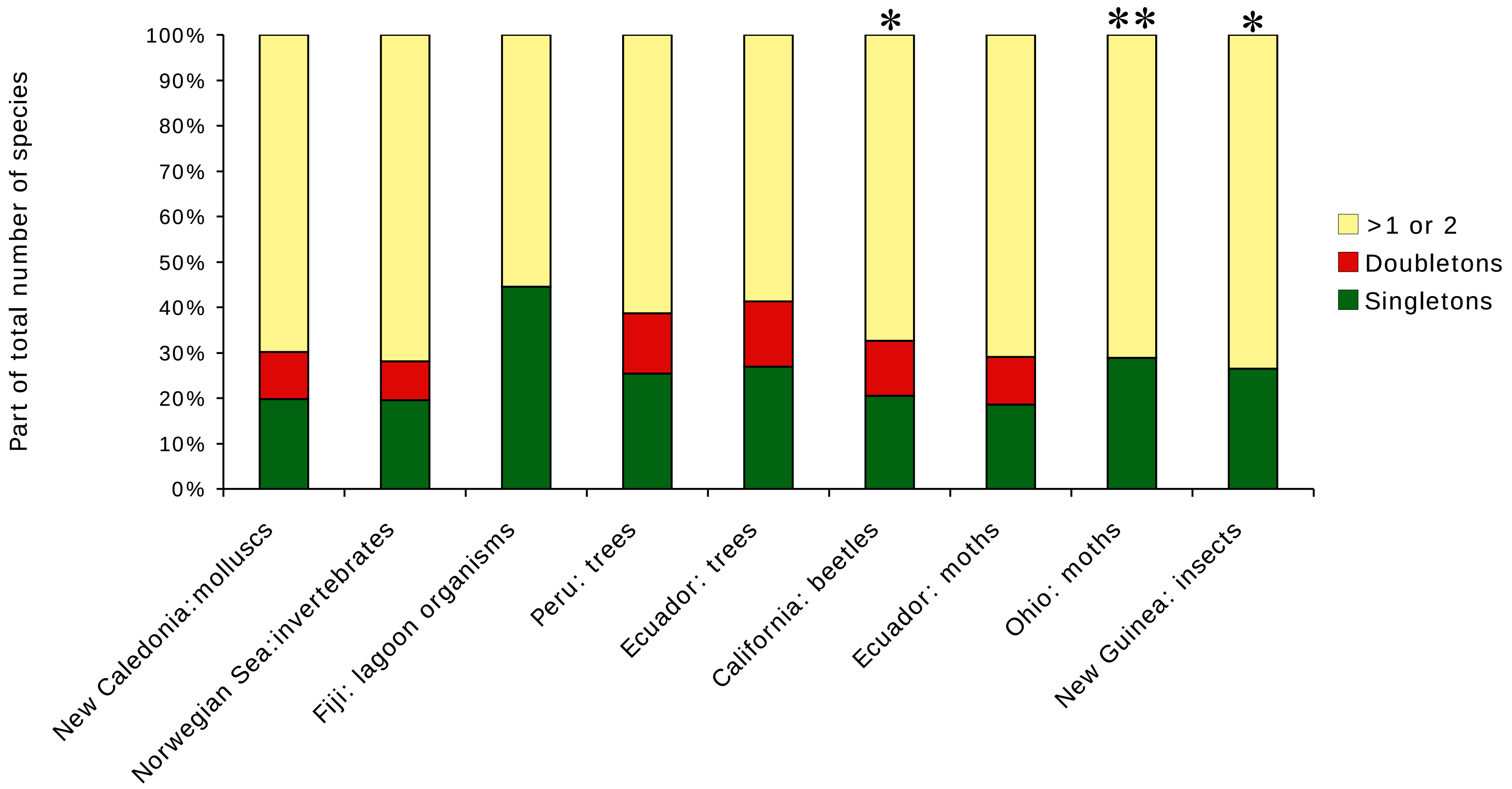
Figure legends

Fig. 1 The occurrence of singletons (species observed only one time) and doubletons (species observed only two times) in comprehensive taxonomic inventories of various organisms and habitats. The inventories are all large-scale including on average 42,700 specimens (range 8,300-127,600) and with the exception of the studies marked with an asterix (*) an average of 35.3 sites were included in each study (range 14-101). One study (**) included resampling of the same site 50 times. Data from Bouchet et al. 2002; Ellingsen and Gray 2002, Schlacher et al. 1998, Pitman et al. 2001, Caterino 2007, Hill et al. 2006, Summerville and Crist 2005, Novotnhy and Basset 2000.

Fig. 2. Cascade effects of overexploitation (fishing) and habitat contamination (eutrophication) on ecosystem functions linked to one population (Eastern Baltic) of a functionally dominant species (Atlantic cod). Several of the links have high experimental support while some are tentative but yet not fully supported by experiments. Species/group effects are in bold frames. Data from Österblom et al. 2001, 2006, and Nilsson et al. 2004. The figure is modified from Bernes 2005.

Fig 1.



Part of total number of species
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
*
**
*
>1 or 2
Doubletons
Singletons
New Caledonia:molluscs
Norwegian Sea:invertebrates
Fiji: lagoon organisms
Peru: trees
Ecuador: trees
California: beetles
Ecuador: moths
Ohio: moths
New Guinea: insects

Fig. 2