Perspective

Implications of different species concepts for conserving biodiversity

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ABSTRACT

The ~26 definitions of species often yield different numbers of species and disparate groupings, with financial, legal, biological and conservation implications. Using conservation genetic considerations, we demonstrate that different species concepts have a critical bearing on our ability to conserve species. Many species of animals and plants persist as small isolated populations suffering inbreeding depression, loss of genetic diversity, and elevated extinction risks. Such small populations usually can be rescued by restoring gene flow, but substantial genetic drift effects can lead them to be classified as distinct species under the diagnostic phylogenetic species concept. Minimum harm to fitness is done and maximum potential fitness and evolutionary potential benefits accrue when reproductive isolation (pre- and/or post-zygotic) is used as the criterion to define distinct species. For sympatric populations, distinct species are diagnosed by very limited gene flow. For allopatric populations, both minimal gene flow and evidence of reduced reproductive fitness in crosses (or effects predicted from adaptive differentiation among populations and/or fixed chromosomal differences) are required to satisfy conservation issues. Species delineations based upon the biological and differential fitness species concepts meet the above requirements. Conversely, if species are delineated using the diagnostic phylogenetic species concept, genetic rescue of small genetically isolated populations may require crosses between species, with consequent legal and regulatory ramifications that could preclude actions to prevent extinction. Consequently, we conclude that the diagnostic phylogenetic species concept is unsuitable for use in conservation contexts, especially for classifying allopatric populations.

Contents

1. Introduction

There are at least 26 definitions of biological species (see Wilkins, 2009; Hausdorf, 2011). Use of different species concepts to classify species has potential financial, legal, biological and conservation implications (Hey et al., 2003). It leads to much confusion and controversy, and to potential problems of inappropriate delineation of species for conservation purposes. Mace (2004) concluded that 'taxonomists and conservationists need to work together to design some explicit rules to delimit the units included as species for the purposes of conservation planning and assessment.' Thus, there is an urgent need to evaluate the suitability of the different species concepts for conservation purposes.

The three concepts most widely used by the systematic and conservation communities are the biological species concept (BSC; Mayr, 1942, 1963), the evolutionary species concept (ESC; Simpson, 1951, 1961; Wiley, 1978) and the phylogenetic species concept (PSC; Eldredge and Cracraft, 1980; Cracraft, 1997), as defined in Table 1. We also discuss the recently proposed differential fitness species concept (DFSC; Hausdorf, 2011), as it is highly relevant to conservation. This concept is most similar to the BSC, but BSC uses mating isolation and/or sterility to delineate species while DFSC is broader, encompassing any pre- or post-zygotic fitness decrement following attempted crossing.

An alternative to the use of defined species concepts is to rely upon the judgment of taxonomists, sometimes referred to as the taxonomic species concept (TSC; Mayden, 1997). This corresponds to the definition that species are 'whatever a competent taxonomist chooses to call a species' (Wilkins, 2009). This seems to be widely practised, as papers on new species delineations, or revisions usually fail to specify what species concept has been used (see McDade, 1995).

As the literature on species concepts is massive, we can only refer to a sample of references. We favored key references, reviews, recent publications, and studies addressing conservation concerns.

All of the commonly used species concepts suffer from incongruencies with biological reality (Hausdorf, 2011), namely:

1. 'reproductive barriers are often semipermeable to gene flow' (Hey and Pinho, 2012);
2. 'species can differentiate despite ongoing inter-breeding' (sympatric speciation; Papadopulos et al., 2011);
3. 'parallel speciation can occur due to parallel adaptation or recurrent polyploidizations', and
4. 'uniparental organisms are actually organized in units that resemble species of biparental organisms';

In addition, we conclude that:

5. development of reproductive isolation between populations usually accompanies genetic adaption to different environments (via natural selection, as proposed by Darwin (1859)), and/or fixed chromosomal differences (reviewed by Frankham et al., 2011; Sexton et al., 2011; see Supplementary material).

The incongruities indicate that no species concept is without problems. Points 1 and 2 cause severe difficulties for the BSC; furthermore, it does not apply to asexual organisms. For PSC, Points 1, 2 and 3 cause difficulties. Point 3 may cause difficulties for ESC, but ESC copes with the other points. Point 5 partly counters some of the problems, as it makes it feasible to predict reproductive isolations for diagnosing species under BSC and DFSC (see below) (Frankham et al., 2011). A serious concern with PSC is that technological advances (e.g. those lessening DNA sequencing costs) and increased effort lead to increased resolution among lineages, such that even individuals within populations can be diagnosably different (Avise and Ball, 1990; Groves, 2004; Winkler, 2010).

Despite the disparate definitions, species concepts typically indicate that species are cohesive clusters of individuals that have at least partially different evolutionary paths representing different lineages (see Avise and Ball, 1990; Knowlton and Weigt, 1997; de Queiroz, 1998; Hey et al., 2003; Coyne and Orr, 2004; Hausdorf, 2011). The differences among concepts are typically in how far evolutionary population differentiation needs to proceed before the populations should be considered distinct species. All serious concepts recognise that populations inherently incapable of gene exchange are distinct species, while those exhibiting random mating in sympatry are conspecific. However, there are major differences in the treatment of partly diverged allopatric populations capable of gene flow without adverse fitness consequences, or with beneficial consequences. In allopatric populations, especially those with small population sizes, genetic drift and mutation will lead to diagnosably different units that are not intrinsically reproductively isolated (see below) that may be ephemeral under natural patterns of population separation and re-connection. Defining such units as species for conservation purposes may accelerate extinction of broader BSC species rather than preserve adaptive differences (see below).

Scientists working in different disciplines or on disparate major taxa often favor alternative species concepts (Claridge et al., 1997). For example, evolutionary geneticists generally favor BSC (see Noor, 2002; Coyne and Orr, 2004) because it relates to the fitness consequences of gene flow between populations and the process of speciation. In contrast, some taxonomists now favor PSC (Cracraft, 1997; Groves, 2004), because it is considered easier to implement. Use of PSC results in more splitting: it yielded 49% more species than BSC on the same group of organisms (Agapow et al., 2004). In some cases, the groupings according to BSC and PSC were discordant, with PSC species not nested within BSC species, or vice versa. Such inconsistencies can often lead to different management, some resulting in adverse consequences for conservation of biodiversity.

We evaluate methods for defining species from the perspective of conservation biology, advocating that definitions used in conservation biology should maximize conservation benefits. We show, from a population genetics perspective, that current methods for species' delineation often lead to species' classification that is too narrow, or too broad, both of which can compromise the conservation of the taxon's biodiversity. We then recommend use of concepts that are most beneficial for conserving global biodiversity.

2. Minimizing harm and maximizing potential conservation benefits

The ideal species concept for conservation purposes would minimize potential harm and maximize potential benefits, as measured by reproductive fitness and sustaining adaptive evolutionary processes. Loss and fragmentation of habitat stem-

Table 1
Species definition according to different species concepts.

Species concept	Species definition	Reference
Biological (BSC)	'Groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups'	Mayr (1942)
Evolutionary (ESC)	'A species is a lineage of ancestral descent which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate'	Wiley (1978)
Phylogenetic (PSC) (diagnostic)	'A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent'	Cracraft (1983)
Differential fitness (DFSC)	'Species can be defined as groups of individuals that are reciprocally characterized by features that would have negative fitness effects in other groups and that cannot be regularly exchanged between groups upon contact'	Hausdorf (2011)

ming from human population growth is one of the most severe threats to biodiversity (Millennium Ecosystem Assessment, 2005). Fragmentation of populations that were once widely distributed results in small, isolated populations potentially subject to loss of genetic diversity, inbreeding depression and increased risk of extinction (see Allendorf and Luikart, 2006; Frankham et al., 2010). Conservation of these populations often requires re-establishment of gene flow between them (Frankham et al., 2010). Further, it has been proposed that populations be translocated into new habitats to cope with global climate change. For populations with low genetic diversity, the best strategy is often to translocate admixed populations into new habitat (Weeks et al., 2011).

Managers that advocate either the transfer of organisms between fragmented populations or restriction of such transfers need to consider the potential impacts of both outbreeding depression (OD – defined to include any deleterious consequences of crossing on mating preference, pre- or post-zygotic reproductive fitness), and inbreeding depression (ID – defined as the relative reduction of fitness in offspring of related mates compared to matings between unrelated individuals). Thus, definitions and delineations for taxa with fragmented populations should lead to units that simultaneously (a) minimize OD, whilst (b) allowing maximum opportunities to outcross small inbred populations with low genetic diversity to reverse inbreeding depression and loss of genetic diversity (genetic rescue) (Frankham et al., 2010, 2011).

The consequences of different species delineations for six hypothetical populations are illustrated in Fig. 1. Too broad a delineation of species in case 1 leads to a high risk of OD when populations a and b are crossed. Over splitting in case 2, as a result

of large genetic drift effects in small populations (see below), classifies the small $a4$ population as a distinct species, without any populations within its species that can be used to rescue it genetically or reinforce it demographically. This means that splitting, sometimes in an attempt to promote greater conservation of biodiversity, can actually prevent conservation actions necessary to preserve taxa with a small population size, and thereby result in greater loss of existing biodiversity. In case 3, use of reproductive isolation (defined as any adverse effect on pre-zygotic or post-zygotic fitness and equivalent to outbreeding depression) to delineate species a versus species b both minimizes the risk of outbreeding depression, and allows genetic rescue of small populations within species. Thus, to minimize harm and maximize benefits, species definitions and delineations need to define and identify populations that have or have not yet become reproductively isolated to a substantial degree. A possible approach to defining "substantial degree" is to compare the degree of reproductive isolation with that for well researched and widely accepted BSC species. Reluctance to test reproductive isolation may exacerbate the difficult process of implementing managed gene flow.

We did not attempt to address definitions of units within species (e.g. sub-species and evolutionarily significant units) due to space constraints.

3. How do excessively broad species delineations occur?

Excessively broad species delineations arise primarily from the use of characters (mainly morphological) with insufficient resolving power to delimit cryptic species. For example, the endangered grassland daisy *Rutidosis leptorrhynchoides* has been found to con-

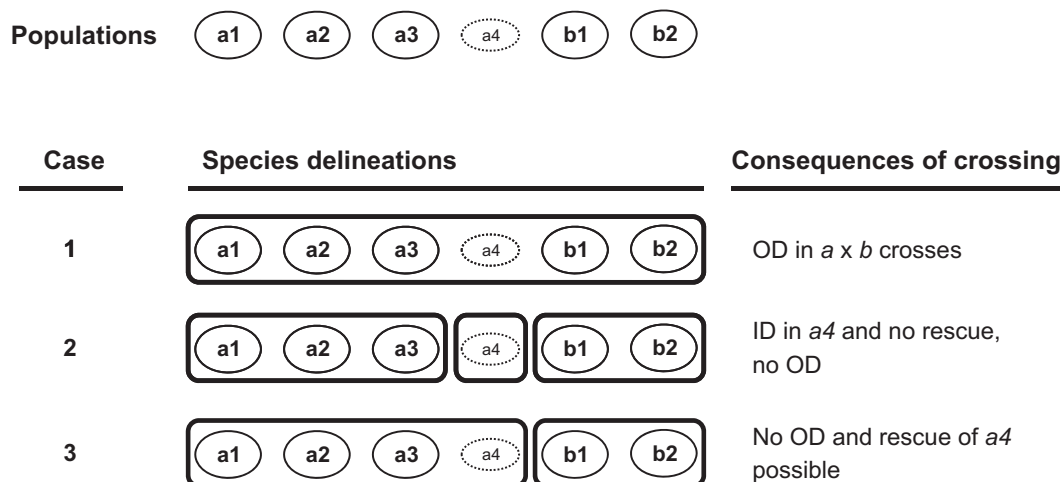**Fig. 1.** Consequences of crossing populations following different species delineations in relation to outbreeding depression (OD), inbreeding depression (ID) and genetic rescue. Populations a and b are reproductively isolated (show OD on crossing), but populations within them do not show reproductive isolation. The $a4$ population has a small effective population size, is inbred and has low genetic diversity.

sist of diploid, tetraploid and hexaploid forms that are highly sterile upon crossing (Murray and Young, 2001). Further, well studied African elephants have recently been separated into savannah and forest species despite regions of contact, based upon genome wide deep sequence divergence between the two forms (Rohland et al., 2010).

A second cause of excessive lumping occurs when speciation occurs in the face of gene flow, as may occur when strong adaptive differences drive reproductive isolation in sympatry. For example, Papadopulos et al. (2011) described 13 potential instances of speciation with gene flow for plants on Lord Howe Island, Australia. Use of neutral genetic markers (or organelle DNA) may result in such populations lacking fixed differences or reciprocal monophyly being classified as a single species under PSC, ESC or the BSC.

Third, populations that diverged in allopatry may later come into contact and form hybrid zones with some introgression of alleles in each direction. If such populations do not show reciprocal monophyly or fixed differences they may be classified as a single species (Eldridge and Close, 1992). For example, several rock wallaby species in Australia that exhibit hybrid zones and lack reciprocal monophyly for mtDNA and allozymes were the subject of conflicting taxonomic delineations. Combined evidence from mtDNA, allozymes and chromosomes eventually led to resolution of their taxonomy, largely following chromosomal discontinuities (Eldridge and Close, 1992).

4. How does excessive splitting of small populations occur?

Small isolated populations of conservation concern are subject to large genetic drift effects that can quickly result in genetic differentiation, without adaptation to different environments or the evolution of reproductive isolation. Further, fragmented populations that are now geographically isolated (allopatric), but not reproductively isolated may later come into contact and merge, as has happened many times in nature through environmental change (especially expansion and retreat of glaciers). For example, many mammal, bird, fish, lizard and plant species in Australia, Europe and the Americas show evidence of the merging of previously isolated and differentiated populations following climatic cycles (see Frankham et al., 2011 Supporting information).

From a conservation perspective, such small populations are susceptible to being classified as different species according to the diagnostic version of PSC, especially when maternally inherited markers (mtDNA and cpDNA) and/or highly mutable genetic markers (microsatellites and animal mtDNA) are used in delineations. Relying on neutral markers is also problematic since they have been shown to be poor predictors of reproductive isolation, compared to adaptive differentiation in a diverse array of taxa (Nosil et al., 2002; Zigler et al., 2005; Stelkens and Seehausen, 2009; Thorpe et al., 2010; Wang and Summers, 2010).

Below we discuss theory and empirical observations bearing on the problem of excessive splitting of small threatened populations.

4.1. Theory predicting generations to attain reciprocal monophyly or no shared alleles

The issue of diagnosability under PSC has as its purpose to delineate populations where gene flow has ceased through either intrinsic (e.g. failure to mate, or F1 sterility) or extrinsic factors (e.g. geographic isolation, rivers, and mountains). Fixed gene differences (populations homozygous for different alleles) and reciprocal monophyly are required under different implementations of the diagnostic PSC (Cracraft, 1997; Groves, 2004; see Supplementary material). Lack of shared alleles between populations at one or more loci is sufficient to diagnose clusters that have experienced

a long history without gene flow (see Supplementary material). Fixed gene differences are one form of unshared alleles, but more stringent than necessary to delineate lack of gene flow with multiple alleles. Confusingly, different authors use diverse definitions for fixed gene differences (see Supplementary material).

The relevant theory on generations required for populations to be diagnosably different is couched in terms of reciprocal monophyly, no shared alleles or fixed gene differences. We present the first two estimates in the main text and the third in the Supplementary material, as the theoretical studies consider different scenarios, often with different assumptions. For reciprocal monophyly, it takes about $4N_e$ generations from the time that two populations separate for there to be a high probability of their having reciprocally monophyletic alleles for mtDNA (Niegel and Avise, 1986; Moritz, 1994; Hudson and Coyne, 2002), where N_e is the effective population size (defined in the Supplementary material; Frankham et al., 2010). Since the N_e for autosomal nuclear loci is four times that for mtDNA loci under the conditions of the models, it takes approximately $16N_e$ generations to attain reciprocal monophyly for nuclear autosomal loci (Hudson and Coyne, 2002).

The probability of shared alleles/haplotypes for DNA sequences at a neutral nuclear autosomal locus approaches zero for divergence times greater than $10N_e$ generations (Hey, 1991; Supplementary material), and by extension $2.5N_e$ generations for mtDNA. The number of generations is also partially dependent upon allele frequencies in the common ancestral population (Kimura and Ohta, 1971).

The number of generations to diagnosability will be less if multiple independent (unlinked) nuclear autosomal loci are genotyped (Hudson and Coyne, 2002). For example, if the probabilities that two populations are diagnosably different at each locus are all 0.5 (at the tth generation), then with 1, 2, 3 and 10 loci the probabilities of diagnosing populations as different are 0.5, 0.75, 0.875 and 0.999, respectively.

Since we have a conservation focus, we ask how long it takes for reciprocal monophyly or no shared alleles to be detectable for threatened species (Table 2). For species with stable population sizes, the critically endangered (CE) IUCN (World Conservation Union, 2011) Red List category criterion D is defined by an adult census population size for the entire species (N) <50, the endangered category (E) by $N < 250$ and the vulnerable category (V) by $N < 1000$ (Table 2). If each of these categories has two equally sized isolated populations, then they will be half the above numbers. We translated these census numbers into genetically effective sizes (N_e) using empirical estimates of the N_e/N ratio. Frankham (1995) and Palstra and Ruzzante (2008) reported average ratios of 0.11 and 0.15 for nuclear loci, respectively. Using the mid-point of this range (0.13), reciprocal monophyly for autosomal loci is achieved in <52 (=16 × 25 × 0.13) generations for populations of CE species, <260 generations for populations of E species and <1040 generations for populations of V species (Table 2). Somewhat fewer generations are required for almost all population pairs to be diagnosable using no shared alleles at a single locus. Given the stochastic nature of differentiation, there will be many diagnosable population pairs in even fewer generations. If the extent of fragmentation is greater, the numbers of generations will be correspondingly reduced.

If such isolated populations inhabit similar environments, they will be diagnosably different long before they show outbreeding depression (especially for CE and E species) because OD has not evolved in populations isolated for up to 6000 generations under these conditions (Frankham et al., 2011). Full reproductive isolation typically takes on the order of millions of years to evolve (Coyne and Orr, 2004). In contrast, populations in different environments show the first signs of outbreeding depression within a few dozens of generations (Hendry et al., 2007).

Random mating populations of threatened species, maintained at the above effective population sizes for the number of genera-

Table 2
Census (N) and effective population sizes (N_e), and predicted generations to reciprocal monophyly, and no shared alleles/haplotypes for autosomal and mtDNA genetic markers for critically endangered, endangered and vulnerable species with stable population sizes.

Item	IUCN red list category		
	Critically endangered	Endangered	Vulnerable
N (IUCN criterion D)	<50	<250	<1000
N when split into 2 equally sized fragments	<25	<125	<500
Autosomal loci			
$N_{e\ autosomes}$	<3.25	<16.25	<65
Generations to reciprocal monophyly	<52	<260	<1040
Generations to no shared alleles	<32.5	<162.5	<650
mtDNA			
$N_{e\ mtDNA}$	<0.73	<3.65	<14.6
Generations to reciprocal monophyly	<2.9	<14.6	<58.3
Generations to no shared haplotypes	<1.8	<9.1	<36.5

tions required to achieve reciprocal monophyly will be highly inbred, will suffer substantial inbreeding depression, and exhibit large genetic rescue effects upon crossing (Frankham et al., 2010). The expected inbreeding coefficient (F) for a closed diploid random mating population of size N_e over t generations is (Frankham et al., 2010):

$$F = 1 - [1 - 1/(2N_e)]^t \tag{1}$$

For example, a CE population with an N_e of 3.25 maintained with random mating for 52 generations has an expected inbreeding coefficient of >0.99, and similar calculations for N_e and generations to achieve reciprocal monophyly in E and V populations also yield inbreeding coefficients of >0.99. At these inbreeding levels, populations of naturally outbreeding species have high probabilities of extinction from their inbreeding (Frankham et al., 2010).

Mitochondrial DNA is extensively used to delineate species (see Karl and Bowen, 1999; Hebert et al., 2003; Craig et al., 2009). For example, DNA barcoding, based on sequencing a ~650 base pair section of the mtDNA cytochrome oxidase I locus (CO1), is being used to discover new species and to estimate the approximate number of animal species on Earth (see Hebert et al., 2003; Rubinoff et al., 2006). mtDNA is maternally inherited in most animal species and its effective population size ($N_{e\ mtDNA}$) is less than ~3% of potentially breeding adults, due to the combined effects of mode of inheritance, deviations from the idealized population structure and selection (see Supplementary material). With such low ratios of $N_{e\ mtDNA}/N$, even populations with reasonable sizes rapidly exhibit reciprocal monophyly. For example, isolated populations of CE, E and V species are expected to show reciprocal monophyly in mtDNA within less than ~3, ~15 and ~58 generations, and require even fewer generations to achieve no shared haplotypes (Table 2). Further, mtDNA has a nucleotide mutation rate about 10 times higher than for nuclear loci in animals (see Ballard and Whitlock, 2004; Frankham, 2012). Consequently, mtDNA shows large divergence due to mutation and drift effects in animals, and excessive splitting of populations into species based on mtDNA is a serious conservation problem (Rubinoff et al., 2006; Frankham, 2012). Chloroplast DNA is widely used in plant taxonomy, and is also expected to suffer low N_e/N ratios, but there is very limited information on which to estimate ratios (Frankham, 2012).

Microsatellites have higher mutation rates than for other DNA sequences or allozymes (Frankham et al., 2010), and their use will be more likely to result in excessive splitting of populations (other things being equal).

4.2. Empirical data on rapid attainment of diagnosable differences between populations

Empirical data support the above theory indicating that isolated populations of threatened species will be diagnosably different within a small number of generations (well before they are likely to evolve reproductive isolation). First, eight replicate populations of *Drosophila melanogaster* derived from the same wild source populations and maintained in isolation for 48–49 generations at effective population sizes of 25 in the same environment were diagnosably different in 27 of 28 comparisons (did not share alleles at one or more of the eight loci; see data in the Supplementary material). Note that these were diagnosably different in ~$2N_e$ generations, many fewer than estimated in Table 2, as a result of using multiple loci, rather than a single locus. These populations suffered 30% and 88% inbreeding depression in reproductive fitness in benign and stressful conditions and showed 59% and nearly sixfold genetic rescue effect in the two environments, respectively (Woodworth et al., 2002). These diagnosably different populations would be classified as distinct species according to the PSC if only two populations survived, or if a taxonomist only sampled two populations and typed them as done in this study. It would be inadvisable to classify interfertile threatened populations with such poor fitness as distinct species after such a short period without gene flow.

Second, six island populations of black-footed rock-wallabies (*Petrogale lateralis*) in Australia are all diagnosably different from each other (fixed gene differences) based on genotypes for eight autosomal microsatellite loci (Eldridge et al., 1999), and all Island populations have distinct mtDNA haplotypes (Eldridge et al., 2001; Eldridge, unpublished data). However, the island populations were isolated by sea level rises only 1600–3000 generations ago and the threatened mainland population contains almost all of the alleles present in the combination of the island populations. Some island populations have been crossed to the mainland population and there are no indications of reproductive isolation (Close and Bell, 1997). In the absence of the threatened mainland population, the six island populations would be classifiable as six PSC species. The Barrow Island population (the only population investigated) is suffering inbreeding depression (Eldridge et al., 1999). Each of these island populations would probably benefit from augmented gene flow, so it would be counter-productive to designate them as separate species that cannot be crossed.

Third, inbred strains of laboratory animals, such as mice (*Mus musculus*) (typically maintained using one pair of parents per generation) show fixed differences at many molecular loci and are diagnosable different within ~20 generations (Falconer and Mackay, 1996), but strains within species cross readily with beneficial effects on fitness (Atchley and Fitch, 1991). These inbred mice populations would be delineated as separate species if we applied diagnostic PSC to pairs of populations in the absence of their ancestral wild species. While the population sizes used in these populations are continuously smaller than in most threatened species, the same processes occur in threatened populations at a slower rate. In fact, several wild species, including Mauritius kestrels (*Falco punctatus*) and Chatham Island black robins (*Petroica traversi*) have expe-

rienced single pair bottlenecks (Ardern and Lambert, 1997; Groom-bridge et al., 2000).

5. Discussion

The arguments above lead us to recommend that substantial reproductive isolation (pre- and/or post-zygotic) be used to define species of outbreeding sexual organisms for conservation purposes. In this way genetic rescue efforts will be possible and the risk of outbreeding depression minimized. DFSC satisfies these criteria, whilst BSC captures large components of it, especially if it is used in a 'relaxed' form that accepts limited gene flow. Consideration of these issues for taxa (mainly plants) that are not outbreeding diploids is given in the Supplementary material.

We are strongly opposed to the use of a non-defined approach to species delineations, as used in the taxonomic species concept. The current situation in taxonomy is clearly unsatisfactory with use of different (and often contradictory) species concepts, traits, sampling regimes, methods of analysis, etc. that results in many controversies about the taxonomic status of populations (Mace, 2004). Current practices often fail the usual scientific requirements of robust sampling, repeatability and adequate statistical support.

How then should we distinguish species for sympatric, parapatric and allopatric populations? Lack of shared alleles at one or more autosomal loci (given sufficient sampling) is sufficient to establish lack of gene flow and reproductive isolation between two sympatric or parapatric populations and for them to be to be classified as separate species (even evidence of very limited gene flow should be acceptable). For example, samples of Onychophora from the same log in the Blue Mountains west of Sydney, Australia showed fixed gene difference at 70% of loci and were reclassified from belonging to the same morphologically defined species into two species (Briscoe, DA pers. comm.; Briscoe and Tait, 1995). When there is lack of gene flow between sympatric or parapatric populations, classifications with BSC, PSC, ESC and DFSC should be concordant (Knowlton and Weigt, 1997).

Allopatric populations will be classified appropriately using the DFSC, as such species are delineated using pre- and/or post-zygotic isolation, while BSC uses mating isolation and sterility to delineate species. However, allopatric diagnostic PSC species may not be reproductively isolated. In such cases, genetic rescue of small populations may only be possible by carrying out crosses between distinct PSC species. If this is to be done to save biodiversity, regulatory and legal hurdles will need to be removed (O'Brien and Mayr, 1991; Haig and Allendorf, 2006; Ellstrand et al., 2010). Given the difficulties involved, we recommend that allopatric PSC species that require conservation management have their taxonomy reassessed on the basis of outbreeding depression following DFSC or BSC.

It has been argued that it is difficult or impractical to determine whether populations are reproductive isolated, as experimental crossing through multiple generations is frequently impractical. However, fixed chromosomal differences and/or adaptation to different environments are good predictors of outbreeding depression if populations are crossed (see Frankham et al., 2011; Sexton et al., 2011). Further, Coleman (2009) reported that DNA sequence similarity in the 5′ region of helix III of ITS2 of nuclear rRNA predicts ability to successfully cross populations within a broad range of major taxa (algae/protozoa, fungi, plants and animals), while differences predict outbreeding depression.

Given the important implications of using different species concepts in delineating species, it is critical that the species concept used in delineations be routinely provided in the conservation literature. Worryingly, this is rarely the case. We recommend that journals require that the species concept used be identified in pa-pers where new threatened species are described, where taxonomic disputes are resolved, or where boundaries for threatened species are described.

6. Conclusions

- Conservation biology is bedevilled by the existence and use of at least 26 definitions of species. Consequently, it is important to determine which definition(s) best accord with the purposes and methods of biological conservation.
- Definitions that are too broad will often lead to outbreeding depression when populations are crossed, while those that split excessively may preclude genetic rescue of small inbred populations with low genetic diversity.
- Minimum harm is done and maximum potential benefits in terms of fitness and adaptive evolutionary potential accrue when reproductive isolation (pre- and/or post-zygotic) is used as the criterion to define distinct species.
- Many 'good' species exhibit low levels of gene flow from other taxa.
- Use of the differential fitness or biological species concepts will typically yield a classification appropriate to conservation concerns.
- Conversely, use of the diagnostic phylogenetic or the taxonomic species concepts will often lead to inappropriate classifications.
- For sympatric or parapatric populations, distinct species are diagnosed by any genetically based distinctiveness that indicates lack of (or very limited) gene flow, and different species concepts typically yield concordant delineations.
- For allopatric populations the appearance of detectable divergence due to lack of recent gene flow alone is not necessarily diagnostic of intrinsic reproductive isolation. In addition, such diagnoses require evidence of reduced reproductive fitness in population crosses, or inferences from fixed chromosomal differences, or adaptive differentiation among populations that predict reproductive isolation.
- It is critical that the species definition being used be stated explicitly when new species are designated, and conservation decisions prescribed or proscribed by taxonomy need to identify the species concept that was used in the delineation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.04.034.

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