

Species: demarcation and diversity

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Arguments about conservation are almost always arguments about species. Lists are compiled of endangered species, conservation schemes are prioritised on how many species are preserved, and legislation is phrased in terms of species. In the political economy of biodiversity, species are the currency. Despite this central role, the very term ‘species’ is deeply ambiguous. Practitioners clash not only over the boundaries of individual species, but also over what ‘species’ means. Where once ‘the species problem’ referred to the puzzle of how species arose, it now refers to how species can be defined (Mallet 2001).

This argument has deep implications for conservation biology. As species definitions (and thus boundaries) shift, species counts may rise and fall. Areas of endemism based on species counts could change, and the conservation worth of populations with an ambiguous status (such as hybrids and sub-species) will fluctuate based on their taxonomic rank (Collar 1997). Given such doubt, how precise are our current understandings of species numbers and identity? Are these estimates good enough for conservation practice?

A DIVERSITY OF CONCEPTS

The argument over how species should be defined is endless, with over 20 species concepts presently in circulation (Claridge *et al.* 1997; Mayden 1997; Howard & Berlocher 1998). The problematic issue (at least for biodiversity studies) has been the gap between theory and practice. Although many concepts have been based on seemingly sound ideals, these

tend to founder in the real world. Where concepts are based on practice and what can be achieved in the field, their theoretical foundations are uncertain.

Emblematic of these problems and pre-eminent among modern species definitions is the biological species concept (BSC). Formalised in the modern era by Mayr, it depicts species as:

groups of interbreeding natural populations that are reproductively isolated from other such groups. (Mayr 1982)

Its intellectual appeal is that such ‘biological species’ necessarily represent separate evolutionary lineages, a reflection of an objective reality that underlies species rather than a taxonomic rule-of-thumb. Furthermore, any proposed species boundary could be refuted by the natural (and substantial) production of fertile ‘hybrids’ across it. Thus, the BSC not only offers an explanation of what a species is, it also refers to how species identity is created and maintained and indicates how a proposed species can be falsified. The BSC was simple, obvious and arguably inadequate.

Outside the ideals of the BSC, reproductive barriers can be impossible to discern. Breeding patterns may be difficult to observe in the wild, and observation in the laboratory can be thwarted if the organisms are hard to raise in captivity (Taylor *et al.* 1999). Applying the BSC to allopatric populations is problematic. For extinct or asexual organisms, the concept is simply inapplicable (Claridge *et al.* 1997). The treatment of hybridising populations is ambiguous (Donoghue 1985); such ambiguity is clearly a problem in a world where around half of all flowering plants are hybrids (Levin 1979). It has been argued that – by the precepts of the BSC – asexual and hybrid populations are *ipso facto* not species (Ghiselin 1987). So what are they? Does this mean that species did not exist until sexual reproduction had evolved? In the end, the BSC can only be applied to a small fraction of the tree of life.

In practice, therefore, workers have often employed the proxy of a phenotypic definition, using overall physical similarity (‘morpho-species’) to infer an underlying biological species. Yet even this most basic of concepts has problems. The degree of difference in a character that equates to the species level (and even what constitutes a reasonable character) is necessarily subjective. In addition, analysis of morphology can be confounded by convergent evolution, cryptic or simple morphology (Klautau *et al.* 1999; Ameziane & Roux 1997), ring species (Mayr 1963), natural intraspecies variation and phenotypic plasticity (Mishler 1985).

Although many alternatives to biological and morpho-species have been suggested, until recently none has become prevalent in taxonomic practice. However, with the advance of molecular systematics, the phylogenetic species concept (PSC) is becoming increasingly popular. Although there is a frustratingly complex spectrum of definitions (see, for example, Hennig 1966; Cracraft 1983; Nixon & Wheeler 1990; Baum & Donoghue 1995), a common form of the PSC defines a species as:

an irreducible basal cluster of organisms, diagnosably distinct from all other clusters, and within which there is a parental pattern of ancestry and descent.
(Cracraft 1997)

Although not all versions of the PSC include the latter qualification of shared lineages, diagnosis by a unique combination of characters is a universal requirement. In this way, the PSC eschews the mechanisms of speciation, reproductive isolation and gene flow for the operational details of how a 'phylo-species'¹ may be defined.

For the biodiversity researcher, therefore, the PSC carries many benefits. It can be applied to asexual organisms and allopatric populations. When compared to the morpho-species, the PSC is more objective and may reveal morphologically unremarkable but important populations (Bruna *et al.* 1996). It has been argued that phylo-species are a better indicator of biodiversity and conservation worth of a population than are other species definitions (Cracraft 1997; Soltis & Gitzendanner 1999), being closer to the idea of an evolutionarily significant unit (ESU) (Ryder 1986). Some would also argue that, in an age of dwindling taxonomic expertise, it is useful that diagnosis under the PSC requires less training and experience than more traditional classification.

To what extent will different species concepts arrive at the same entities? There are several reasons why they should roughly concur. The PSC's diagnosis based on characters has some congruence with morpho-species. Its historical aspects (ancestry and descent) overlap with biological and evolutionary concepts. If speciation has been sympatric, different populations should differ in at least the character responsible for isolation, leading to congruence between phylo-species based on that character and biological species (Knowlton & Weigt 1997; Geiser *et al.* 1998; Avise & Walker 1999).

¹ Strictly speaking, one cannot talk of a 'phylogenetic' or 'phylogenetically defined' species as not all versions of the PSC consider evolutionary history or phylogeny. In this chapter, I use 'phylo-species' to refer to an entity defined under any of the many versions of the PSC.

Conversely, it has also been argued that the PSC is detecting a level of entity fundamentally different from that of other species concepts, populations that are more finely grained, or a stage along the speciation trajectory different from that seen by previous methods (Harrison 1998). There is no privileged phylogenetic level that corresponds to a species (McKittrick & Zink 1988; Horvath 1997), and thus taxonomic resolution is sensitive to sampling effort (Sites & Crandall 1997; Walsh 2000). Subspecies or – extremely – even individual organisms could be cast as species (Amadon & Short 1992). Where the PSC refers to lineages, species identities could be confused by the practice of inferring a species' phylogeny from a phylogeny of the population's genes. Where horizontal transfer, gene loss or duplication, or lineage sorting takes place, the evolutionary history of a given gene may not match that of its host (Slowinski & Page 1999; Mindell & Meyer 2001). Thus, it is widely thought that the PSC will often arrive at different and generally less inclusive groups than will other methods of defining species (Corbet 1997; Cracraft 1997; Knowlton and Weigt 1997).

CONTRASTING SPECIES

Surveying the literature, a large number (91) of studies were found in which sets of organisms were classified by using the PSC that had previously been classified by other means². These data were collated and examined for changes both in the number of species and in the identity of groups. Although the data covered a wide variety of taxa from many different environments, the sample is inevitably biased by the availability of suitable studies, taxonomic attention and whatever circumstances might have caused investigators to reanalyse groups. Thus, despite their prevalence and conservation importance, there is a relative paucity of suitable studies on fish and amphibians. It should also be noted that there are a variety of methods for applying the PSC (see below). Any study counting phylo-species will therefore show at least some variation.

In total, the studies covered between 1256 and 1294 non-PSC-based species, which on reanalysis gave rise to between 1924 and 2124 PSC-based species, an increase of 48.7%³. Across studies, the average size of group

² Given the length of the data, it has been merely summarised in Table 3.1. The full dataset can be found in Agapow *et al.* (2004).

³ In many cases a span of possible species numbers was reported. Where it was necessary to calculate a change in species numbers, these were interpreted as the least possible change within the range. For example, if 2–3 biological species expanded to 3 phylo-species, this would be recorded as no change.

Table 3.1. Contrasts of species identity: the number and identity of species found under differing species concepts

The number of non-nesting studies counts those studies in which at least one new species was formed across previous species boundaries. The number of non-phylo-species counts species defined under biological and morphological concepts. The percentage change records the difference in species numbers over the entire group when reclassified by using the PSC. The percentage change per study gives the mean change in species numbers across the group. Note that where a span of species numbers was reported, the change was interpreted as the most conservative within that range. The full set of data can be found in Agapow et al. (2004).

Group	No. of studies	No. of non-nesting studies	No. of non-phylo-species	No. of phylo-species	Percentage change	Percentage change per study
Plants	9	2	82–3	82–93	–6	158
Fungi	13	2	44–67	137–8	104	289
Lichens	5	4	24	91–2	279	259
Mammals	9	2	14	24	71	87
Reptiles	7	2	13	30	131	137
Birds	20	4	507–15	807–50	95	89
Arthropods	13	2	74–6	100–01	32	77
Echinoderms	3	1	17	19	12	8
Molluscs	3	0	6	3	–50	–50
Other	10	0	475–9	631–774	25	63
All taxa	91	19	1256–1294	1924–2124	49	121

studied increased by 121.0%. (The increase in group size was assessed with a sign test to be significant, with $p < 0.0001$.) Given that a number of studies overlap in the taxa studied (e.g. a vertebrate-wide survey (Avisé & Walker 1999) and several bird-of-paradise studies (Cracraft 1992; Collar 1997)), these numbers might be distorted by a small number of atypical taxa. However, if all such studies are excluded, the increase in species numbers is 60.3% and the average increase per study is 118.3%. (This increase was significant with $p < 0.0001$).

Given the caveats of the sample size and possible bias, any trends extracted from the data should be treated cautiously. With this in mind, the greatest increase in species count was seen in fungi (289%), with lichens and plants also showing huge increases (259% and 158%, respectively). This may in part reflect the confused taxonomy in these groups, where cryptic morphology and horizontal gene transfer can confuse attempts to distinguish morpho- or biological species (Hawksworth 1993). These cannot,

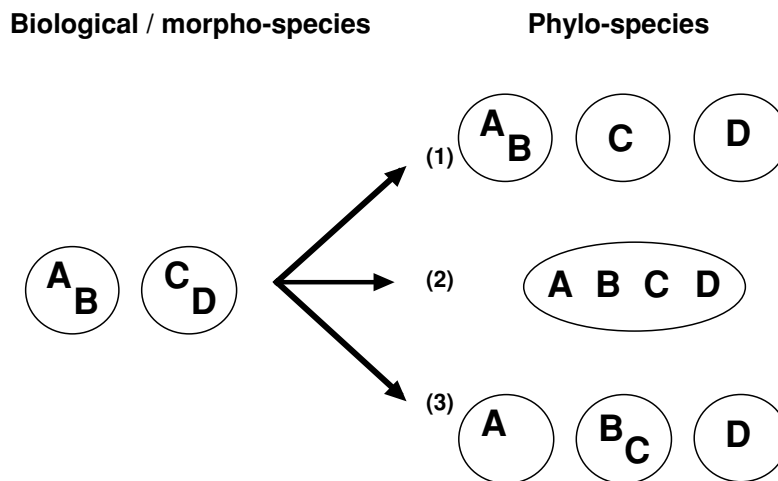


Figure 3.1. Shifts in species boundaries. Three types of change in taxonomic identities are possible: (1) nested redefinition or splitting, where a single species is split into two or more; (2) merged redefinition where species are 'lumped' into a new larger species; (3) non-nested redefinition, where a new species is formed that contains members of previously distinct species.

however, explain the increase in all groups. It is startling that taxonomically well-studied groups such as mammals, arthropods and birds showed large and roughly equivalent increases (87%, 77% and 89%, respectively). The relatively small increase in echinoderms (8%) is perhaps due to this group's being relatively species-poor and well characterised. The decrease in the number of mollusc species (50%) is markedly different from the change found in all other groups and can perhaps be explained by the large numbers of amateur taxonomists that have worked with this group in the past. Reassessment under the PSC may be merging many of the oversplit morpho-species they had identified. Although taxonomic reassessment will tend to occur in groups where there is dissatisfaction with the status quo, the widespread increase in numbers and its agreement with previous estimates (see, for example, Zink & McKittrick 1995) implies that the trend is real and approximately correct.

With conflicting species identifications, the newly defined species may rest wholly within the boundaries of previously recognised species ('nested redefinition') (Fig. 3.1, case 1), represent the fusion of several species ('merged redefinition') (case 2), or cross the boundaries of two or more of the former species ('non-nested redefinition') (case 3). Although it was only possible to establish boundary changes for 79 studies, 16 of those (17.8%) showed phylo-species that did not nest within the older species boundaries. However, this fact should be tempered with the knowledge that another eight studies (8.9%) showed merged redefinition, i.e. fusion of two or more

non-phylo-species into a single entity. Again, one should be cautious in drawing trends, but non-nested redefinitions may be more prevalent in the birds. This may again be due to increased taxonomic attention.

THREAT IMPLICATIONS

What are the consequences of this (apparent) increase in species number? If one accepts the phylo-species as real, then reclassification under the PSC will lead to a rise in the number of endangered species. This rise is due not only to an increase in the number of species – and thus a proportionate increase in the number of endangered species – but also to a general increase in the threat status across all species. New species are carved out of pre-existing ones, and so the abundance of and area occupied by each can at best be a sub-set of the previous values (Collar 1996). Both measures can therefore be expected to decline on average. Species will have fewer individuals and occupy a smaller area, and this necessarily makes them more vulnerable to extinction.

It is difficult to formally quantify the extent of this effect, but approximations can be made. For example, the IUCN category ‘Vulnerable’ identifies species that are at a high risk of extinction, given that (among other criteria) the candidate species has fewer than 1000 mature individuals (Baillie & Groombridge 1996). The next threat category, ‘Endangered’, encompasses those species at a very high risk of extinction by having fewer than 250 mature individuals. The 48.7% increase in species number (the smallest noted above), infers an average decrease in mature individuals per species of 32.8%. If we assume that the number of mature individuals in ‘Vulnerable’ species are distributed evenly across the band of possible values (250 to 1000), a 32.8% drop will cause 10.9% of these species to have fewer than 250 mature individuals and so be reclassified as ‘Endangered’. This is a conservative estimate as it assumes that the new species are of equal size, whereas unequal splitting will produce more small groups in the ‘Vulnerable’ category. It should also be repeated that this increase in threatened species is separate from the general increase in species numbers.

The impact on species range is more difficult to estimate. For example, a 50% drop in the number of adult individuals does not necessarily imply a 50% drop in range. None the less, as use of the PSC splits and therefore shrinks species, the new entities will tend to have reduced ranges. By virtue of this, the proportion of species formally classified as endangered will also increase.

ECONOMIC AND POLITICAL IMPLICATIONS

An increase in the number of endangered species requires a corresponding increase in resources devoted towards conserving those species. Again, gauging the impact is an exercise in educated guesswork, if only for the reason that 'saving' a species is a task with ill-defined goals. None the less, the US Fish and Wildlife Service (USFWS) has estimated that 'complete recovery' of any of the species listed by the US Endangered Species Act will require about US\$2.76 million (USFWS 1994). Thus, recovering all currently listed species would cost around US\$4.6 billion. An apparent increase in species numbers under the PSC would increase this already formidable amount to US\$7.6 billion: the entire annual budget for USFWS for more than a century. As the cost of rescue rises with the degree of threat and reclassification will cause average species size and range to fall, total costs could actually be far higher.

Even more modest taxonomic and conservation activities could expend huge amounts of money. A survey of the threat status of potentially endangered tropical taxa has been proposed. This would entail a mere US\$12.1 million for the 120 000 species (Pitman & Jorgenson 2002)⁴. If, by virtue of analysis under the PSC, this resurvey were to reveal 10% of these taxa as endangered, the rescue bill could amount to US\$33.1 trillion. Even just formally listing these taxa as endangered would, by USFWS figures, require US\$816 million. If the economic cost of current conservation practice is already unacceptable (Mann & Plummer 1995), the PSC serves only to reinforce this point and draws a line under the futility of the 'Noah's Ark' principle of trying to save every species (Moulton & Sanderson 1999).

If more resources are needed, then there is also a need for more education and mobilisation of opinion. Unfortunately, use of the PSC may make this much harder. Although it is a virtue that the PSC may recognise more obscure and less identifiable populations, it is far easier to find money for the preservation of charismatic and easily recognised organisms, regardless of their evolutionary or ecological significance or conservation status (Ando 1999; Gittleman *et al.* 2001). This and an apparent inflation in species number may induce a form of 'conservation fatigue', in which a flood of threatened species overwhelms both experts and the public. Taxonomy may become seen as the enemy of conservation owing to its unpalatable implications (Collar 1997). Complex ideas of phylo-species identity may also thwart

⁴ Other estimates of taxonomic costs could elevate these costs by a magnitude (Platnick 1999).

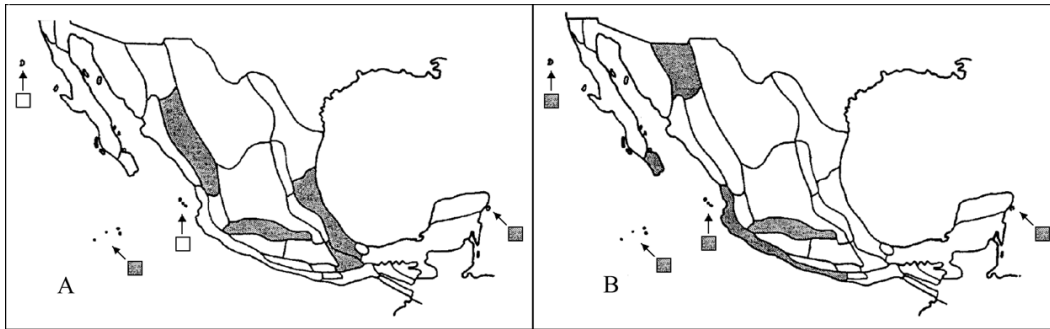


Figure 3.2. Endemism and species concepts. The shaded areas represent the top 20% for richness of endemic avian species in Mexico under (A) non-phylogenetic and (B) phylogenetic species classification. Adapted from Peterson & Navarro-Sigüenza (1999).

the use of amateurs and parataxonomists, trained locals who have proven useful in surveying remote biodiverse regions.

CONSERVATION IMPLICATIONS

Where taxonomic ambiguity exists, conservation efforts may be directed towards saving the wrong entity. As species identities and numbers change, so do recognised areas of endemism. For example, under the BSC the endemic birds of Mexico assemble into 101 species, concentrated in the mountains of southern and western Mexico (Peterson & Navarro-Sigüenza 1999). Under the PSC, however, the number of species increases to 249, with a general concentration in the west of Mexico (Fig. 3.2). Any effort directed at widespread preservation of Mexico's avian biodiversity based on one classification would – from the point of view of the other – be preserving many of the 'wrong' regions.

Where redefinition merges species together, we might optimistically expect few problems. Schemes directed at saving the old species should be apt and perhaps even excessive for saving the new species. In addition, the number of individuals and range of the species have increased. Where species are rearranged on other lines (splitting and across boundaries) we are on less certain grounds. Conservation measures for 'old' species may not be apt for 'new' species, which are likely to be more threatened. Furthermore, as these 'new' phylo-species may be capable (at least in theory) of interbreeding, their continued existence is in even more doubt. Given the relatively small number of groups that demonstrate non-nested rearrangements, it is not clear how severe this problem will be. None the less, confusion and wasted effort could arise from attempts to preserve entities that are reified under one species concept and not another.

SPECIES IDENTITY

It is not surprising that different methodologies of diagnosing species, methods that examine different characteristics of populations, arrive at different answers. Unless those characters are signifiers of the process that creates and differentiates species – a process the PSC largely ignores, and the BSC defines rigidly – the diagnosed species boundaries need not concur. The most obvious instance of discrepancy would be where a single morpho-species contains multiple biological or phylo-species (case 1 in Fig. 3.1), owing to cryptic morphology or where a limited number of characters are studied. Examples of such discrepancies can be found in the fungi (Kasuga *et al.* 1999; Taylor *et al.* 2000). In the opposite direction, a single species (*sensu* BSC or PSC) could be split into multiple morpho-species (case 2 in Fig. 3.1) if there is a great deal of morphological variation within a species, such as sexual dimorphism. Although this would be most common in fossil taxa, it is not unknown in extant taxa such as snails (Thacker & Hadfield 2000). More subtly, it could be argued that the diagnostic form of the BSC conflates potential gene flow with actual gene flow. Species that are recognised as separate by the PSC may be lumped into a single species by the BSC (case 1 again), even if they are genetically and geographically separated and their reticulation is implausible. Many taxa with limited dispersal, such as echinoderms (Lessios *et al.* 2001) could fall into this category. Conversely, where genetic isolation precedes the loss of shared polymorphisms, shortly after the separation of two biological species, the PSC may only recognise a single species (case 2 again) (Doyle 1997). Examples of this include sibling species in fish (Taylor 1999). Cases in which different species do not neatly nest within each other (merged redefinition, case 3) are most easily explained by misdiagnosis of species. For example, a morpho-species based on a highly variant primitive character may partly intersect two or more phylo-species. Explaining merged redefinition without invoking researcher error is more complex. One possible cause is the diagnosis of phylo-species in populations of hybrids, such as can be often found in plants. (This obviously applies only for versions of the PSC that do not require monophyly.) Another possible scenario would be one in which recently split biological species have partly lost shared polymorphisms. Depending on the characters sampled, a phylo-species may be detected that crosses the biological species boundary. Thus, we cannot even state that differently defined species will nest in a consistent order.

This lack of certainty, coupled with the ballooning of species numbers and conservation costs, underlines the tyranny of taxonomy in conservation

biology (May 1990) and the pitfalls of a species-centred point of view. For what, indeed, is a species? The vast majority of biologists would not hesitate to say that species are 'real'. But are species 'real' like atoms, automobiles and Austria, or 'real' like love, liberty and the Libyan desert? We may wish it were the former, but it is probably the latter.

In practice, species mean many things to many people. Species are used as both historical and contemporaneous entities, as descriptions of process and state, and as descriptions of isolation in evolutionary and current landscapes. Species are used as theoretical entities (for example, in modelling and simulation) and as operational entities (for example, in descriptions of the real world, and in taxonomy) (Hey 2001). Even when practitioners have a common purpose, species resist simple definition. Speciation is not an atomic event; new species do not appear suddenly but clarify over time. Furthermore, even long-standing historical species boundaries can be transgressed by rampant gene transfer (Syvanen 1999) and need not disrupt the evolutionary or ecological identity of a population. Species are not hard-edged entities but exist on a spectrum, with some species distinct and others blurred by recent isolation, horizontal gene transfer and hybridization (Turner 1999; Hey 2001; Mallet 2001). Looked at in this way, we can see how different species concepts can arrive at different boundaries for the same population. There are many different ways of being a species and many different ways of maintaining species identity (Wilkins 2005). Every species concept is correct, for a given local value of correctness.

Even where investigators use the same criteria for identifying species, it is still possible to arrive at different species boundaries (Mayr 1992; Gornall 1997). Phylo-species have been diagnosed under a wide variety of methodology and it has been shown that these methods need not agree (Wiens & Penkrot 2002). Where biological species must be inferred, boundaries are necessarily subjective. Given the continuing decline in taxonomic expertise (Godfray 2002), this problem will only get worse. Basing conservation decisions on an ideal of species, waiting for a perfect understanding of species boundaries, is folly because it is not going to happen.

Indeed, even if species could be unambiguously identified, what would that tell us about their conservation worth? There is a general correlation between species numbers and ecosystem stability (Loreau *et al.* 2002), but this does not mean that every species contributes equally to that stability. Establishing that a species is identifiable does not say anything about its evolutionary distinctiveness or ecological importance. Certainly, current conservation measures are often biased towards charismatic taxa, but diagnosing biodiversity by counting species errs in the other direction by

insisting that all species are equally and independently important⁵. Many hybrid populations and sub-species are held to be worth saving (see, for example, Balharry *et al.* 1994; Rieseberg & Gerber 1995; Garcia-Moreno *et al.* 1996), yet are unvalued by methods that only recognise species. (A possible advantage of the PSC is that it can give some of these populations a proper status by elevating them to ‘full’ species.) Conservation based on species attempts to place a value on a population removed from any ecological context, and is open to overinterpretation and misuse (Possingham *et al.* 2002). Finally, phylo-species may be like ESUs but this advantage is lost in the apparent lack of applicability of ESUs to the real world (Crandall *et al.* 2000).

One could argue that, in the absence of any other entity, species can at least be counted and in some way compared. This is simple expedience, akin to the man who having lost his keys looks for them under the streetlight instead of where he actually lost them, ‘because the light is better there’. Encyclopaedic efforts to catalogue species are laudable (Wilson 2003) but fall short of the point⁶. Species counts – regardless of how they are defined – are only the first step in diagnosing conservation worth.

LIVING WITHOUT SPECIES

Should we then look for methodologies that are species-free, or at least species-light? One possibility is to assess the conservation worth of populations in an alternative currency such as economic value, rapid speciation rate (and hence ability to repopulate niches), or unique genetic and evolutionary information. Much work has been done on this last possibility; metrics include phylogenetic diversity (Faith 1994), genetic diversity (Crozier 1997), phenotypic diversity (Owens & Bennett 2000) or taxonomic units based solely on evolutionary time (Avisé & Johns 1999). In this way,

⁵ One could argue that species-centred approaches are still biased towards charismatic taxa, as they tend to be the organisms in which it is easiest to diagnose species. For example, contrast the number of hybrid populations in mammals as opposed to plants.

⁶ There are other problems with these approaches. The All Species Foundation (now sadly defunct) aimed to catalogue every living species within 25 years. Although this was an exciting goal, it is worth pointing out that the reason only 10% (at most) of species have been described is not solely because of lack of taxonomic activity. It is because those species were the most prominent and easy to identify 10%. The remainder will be much harder, perhaps intractably so.

biodiversity value can be measured in information: diversity measured as millions of years, allelic distance or character richness. Conservation schemes can be designed so as to maximise the amount of information preserved, the so-called '*Saving Private Ryan*' strategy (Chapter 17). Alternatively, one could value populations with high speciation rates, hoping they might eventually repopulate niches left vacant by extinction: the 'Adam and Eve' strategy (Chapter 17).

These methods are not without their problems. The need to consider populations and putative species boundaries is not entirely obviated. For example, phylogenetic information will increase monotonically as sampling of a population is increased. However, where populations are distinct, for example geographically, a phylogeny can be constructed between them, allowing prioritisation to take place. A more troubling problem is that saving all the rapid speciators or all the evolutionarily unique populations could be achieved without regard to the stability of the underlying ecosystems, leaving us with a disrupted (and expensive to maintain) ecology. The first strategy leaves us with a planet of weeds; the second with a planet of Pokemon. It would be useful to moderate any valuations with ecological significance, but there are unfortunately no obvious ways to make such objective judgments.

At the opposite end of the scale, the species problem could be avoided by working to conserve higher, supraspecific groups. The membership of these can at least usually be identified without controversy and the broad outline of biodiversity preserved, at the possible expense of the fine detail of diversity and ecosystem stability (Williams & Gaston 1994). Given that many species identities may remain ambiguous – or even undiscovered – for a long time yet, perhaps planning should concentrate on preserving areas where new species are likely to be uncovered. For example, one scheme (ICBP 1992; Jepson & Whittaker 2002) proposes preserving 'Endemic Bird Areas', based on the observation that areas known to contain some endemic avian species are likely to contain unknown endemic avian species as well (Balmford & Long 1995). This would also circumvent the problems of conservation fatigue and a flood of 'new' species, by focusing on saving areas with many species rather than on saving species individually. Conversely, there is a poor correlation of biodiversity between higher groups, i.e. the local biodiversity of birds does not imply anything about the local biodiversity of mammals or plants. Still, the preservation of areas is a more palatable solution than waiting for a perfect understanding of species boundaries that may never arrive.

LIVING WITH SPECIES

However, such measures do not entirely obviate the need for identifying species. Even superspecific schemes of conservation require some consideration of the numbers of types of individual and the diversity between populations. In addition, political and legislative ends demand identifiable organisms.

It may be futile to hope for uniformity across studies in defining species, but some consistency would still be useful. Where species lists are being used in conservation, it would be helpful to know how the species were diagnosed. In this way, one can allow later researchers to reinterpret the data or at least be clear about how the conclusions might be flawed. Where the PSC is used, sufficient individuals, locations and characters should be sampled to ensure an adequate and even resolution of the species status across clades.

We need not entirely abandon the idea of species. It makes a useful conversational shorthand (representing a complex reality); stating that species are undefinable does not mean they are not real. The problems arise when we treat species as quantifiable, discrete entities. Perhaps we should move towards a more relaxed idea of species, to be used solely where they are meaningful, a 'good enough' species concept. Different species concepts and methods could possibly be used to reinforce each other, so as to reach consistent if conservative conclusions on species boundaries. In conservation matters, putative species could be given the benefit of the doubt. This is the effect of the US Endangered Species legislation, in which a species is legally defined as a species, sub-species or population. Finally, much of the doubt surrounding species occurs when they are viewed over extended spatial and temporal ranges, bringing in complications such as allopatric species, hybrids and ring species. It is arguable that the conservation worth of a given population should not be determined by its resemblance to another population elsewhere in the world. In a conservation context, perhaps species should only be defined in a restricted, local scope.

In short, we should stop wasting time trying to solve the 'species problem'. Political, legislative and economic ends may demand quantifiable means but attempting to shoehorn species into that role is a doomed effort. 'One size fits all' solutions based on identifying the 'right' species may have to be abandoned for a flexible spectrum of methodologies that either employ a range of species concepts or dispense with species altogether. Most difficult of all may be the task of translating ambiguous species

boundaries into workable guidelines for legislators, decision-makers and the layperson.

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