

Species and organisms: what are the problems?

Why do we sometimes have trouble deciding if some thing is an organism or not? Or how many species of, say, bird, there are in a particular genus?

A non-biologist's first response to these questions might reasonably be to deny that we do have such troubles. Intuition will be on her side, because both concepts – that of an organism and of a species – are amongst the most well-entrenched in our folk-scientific repertoire. We do not tend to have much trouble, on a day-to-day basis, differentiating between organisms and non-organisms. We know that dogs are organisms, whilst their tails are not. Children grasp the organism concept readily when confronted with books full of little blobs and asked 'how many sheep are there?' Likewise, many bird enthusiasts will feel very confident telling us just which species of bird they have spotted recently. Surely then any attempt to claim that species and organisms are problematic notions, calling out for the attention of philosophers, is just an example of professionals making work for themselves?

But the truth, as we will see, is that scientists really do encounter these problems, and the apparent obviousness of the intuitive concepts just makes our opening questions all the more pressing. The notion of a species and the notion of an individual organism¹ are fundamental to modern evolutionary biology. Yet both are the object of ongoing conceptual and philosophical disagreement. The species problem is well-known, whilst the problem regarding biological individuality, or 'organismality' is less notorious. Yet the latter problem has generated similar levels of dead-lock, and has recently seen its star rise after work on areas such as levels of selection, evolutionary transitions and 'superorganisms' has made its centrality freshly apparent. It is relatively unusual in a mature, successful science – as evolutionary biology certainly is - to have such a lack of clarity about the fundamental concepts of that science. We do not find chemists unable to agree on what a molecule is, or cosmologists unable to agree on what a black hole is, or economists unable to agree on what a market is. Why, then, in evolutionary biology do we find such disagreements

¹ We use the terms biological individual and organism interchangeably. This is a different use of the word 'individual' to that of Hull, who famously argued that 'species are individuals'. Hull was using 'individual' to mean particular (as opposed to kind or class); his suggestion was that species are particulars, not that they are akin to organisms (Hull 1978).

concerning the notions of species, and of individual? What makes these notions so problematic?

Our aim in this paper is to investigate the source of both the 'species problem' and the 'individual organism' problem, and to examine some parallels between the two. It is striking that despite the extensive literature on both problems, there remains unclarity, in both cases, about what exactly the problem is and where it stems from. We argue that in both the species case and the individual organism case, the literature contains two rather different characterizations of what the problem is meant to be, that are often not clearly distinguished from each other. On the first characterization, the problem is at root one of *vagueness* – both 'species' and 'organism' are vague concepts, so admit borderline cases that we do not know how to handle. On the second characterization, the problem is one of *multiple criteria* – biologists have proposed several defining criteria of both a species and an individual organism, which usually but not always co-incide in extension. In what follows we illustrate how this dual characterization is at work in the literatures on both problems, examine the relation between the rival characterizations, and propose a reconciliation.

The Species problem

Aristotle took species to be exemplars of natural kinds² (and many analytic philosophers still do (Putnam 1973; Kripke 1981; Wiggins 2001; Devitt 2008)) whilst Darwin was ambivalent about the reality of species (C. Darwin 1859) and the debate has showed no signs of going away right up to the present day (Dobzhansky 1935; Mayr 1942; Simpson 1951; Maynard Smith 1966a; Van Valen 1976; Cracraft 1987; Ruse 1987; Templeton 1992; Ereshefsky 1998; Mayden 2002; Okasha 2002; LaPorte 2005; Reydon 2005; Hey 2006; Velasco 2008; Barker & Wilson 2010; Hausdorf 2011). Everyone is familiar with the idea that organisms come in different kinds. There are tigers and lions and dogs, as well as oaks and fruitflies. The intuitive idea is that these kinds partition the set of all living things into non-overlapping groups in an objective way, where the members of each group share some set of properties in common. These properties allow us to tell the members of different species apart. For example, tigers are not the same as lions, despite both being large cats, because tigers are

² Several authors assert this, e.g. (Ereshefsky 2010b) although Wilkins claims that it was Mayr, and not Aristotle, who forged the link between species and essences (Wilkins 2007).

stripey and live in Asia whereas lions have plain yellow fur and live in Africa. The properties of tigers, like many species taxa, are by and large projectible; we are confident in making many inductive inferences about the properties of unobserved tigers. We count species in order to measure biodiversity within conservation science. Veterinarians learn species-specific animal medicine. Museums and zoos keep specimens which are taken to be exemplars of their type. The species concept even has legal implications as a consequence of laws concerning endangered species.

In order for all this to work, we need to be able to delineate species in an objective way. That is, we need to be able to say, of any organism, which species it belongs to. But as is well-known, in some cases we cannot do this. No ornithologist can tell us definitively whether a finch he spots on the Hawaiian Island of Nihoa is a *Telespyza cantans* or a *Telespyza ultima*. This ambiguity is independent of how experienced the bird spotter is, or how much genetic information he has access to, so it does not reflect a mere epistemic limitation (O'Hara 1994). Similarly, there is no consensus amongst scientists as to just how many species of black-backed gull circle the arctic (Mayr 1942), nor how to assign many bacteria to species.

There are various different respects in which the task of assigning organisms to species is difficult, which is why it is perhaps more accurate to think of the species problem as a problematic, a cluster of closely related issues, rather than a single one. Much of the modern species debate is about whether the species category itself is a natural kind³, and if so what is the essential nature that all species taxa have in common. It seems natural to think that it is a natural kind; however one reason to doubt this is that biologists use a multiplicity of distinct definitions of a species, as we will see. These definitions, or 'species concepts', number as many as twenty-six (Wilkins 2010) and invoke numerous criteria including actual or potential reproductive isolation or gene flow, phenotypic similarity, mate recognition, geographic isolation, shared ecological niche, synapomorphies, theoretical significance, shared ancestry and more. In addition to the lack of consensus about how to define the species category, there is disagreement about whether the species category

³ This is different from the question of whether particular species taxa, such as *Homo sapiens* or *Canis familiaris* are natural kinds, a question discussed primarily by philosophers. For the distinction, see (Hull 1980).

should be viewed as just another taxonomic rank alongside genus, family, order etc, or whether it has some privileged status in the hierarchy (Okasha 2011).

Finally, note that the species problematic has both a synchronic and a diachronic dimension. For practical purposes, the most pressing issue is how to assign *extant* organisms to species; this is the issue on which most of the biological literature focuses. But in principle, an ideal taxonomic system should be able to assign all organisms, extant and extinct, to species groups (Maynard Smith 1968). This introduces additional difficulties not present if we focus only on extant organisms – such as deciding whether speciation necessarily involves lineage-splitting or whether so-called ‘chrono-species’ should be admitted, for example. We revisit the distinction between synchronic and diachronic formulations of the species problem below.

The Organism problem

The problem of what an organism, or biological individual, is, is perhaps less well known at the present time, although it too has a remarkably ancient pedigree. More than two hundred years ago, Darwin’s grandfather Erasmus was writing at length about the perplexing nature of individuality in plants (E. Darwin 1800), but in the last decade or so there has been an explosion of interest in the topic from both biologists and philosophers (J. Wilson 1999; Santelices 1999; Ruiz-Mirazo et al. 2000; R. Wilson 2007; Pepper & Herron 2008; Queller & Strassmann 2009; West & Kiers 2009; Gardner & Grafen 2009; Godfrey-Smith 2009; Dupré 2010; Folse 3rd & Roughgarden 2010; Pradeu 2010; Clarke 2011a; 2011b). Yet again the stubbornness of the problem is all the more surprising given the concept’s foundational role in our everyday ontology. Biological individuals are indispensable items in our everyday ontology, as well as in our biological theories. We encounter living matter not as a homogeneous soup, but as a collection of discrete objects. The concept of the organism plays a pivotal role in evolutionary biology as the bearer of fitness and as the demographic unit. We need organisms in order to make predictions about the outcomes of selective processes. Our capacity to understand evolution depends on interpreting them as causal loci of selection, as interfaces between genes and the environment, whose births and deaths are significant events in the story of life. Biological

individuals play equally pivotal, though slightly less obvious, roles as the unit of physiological study, of ecological interaction and of immunological response.

Despite all this there are portions of living matter which we just don't know how to parcel up into organisms. Consider the cellular slime-mould *Dictyostelium discoideum*. Most of the time *Dictyostelium* exists in the form of single celled amoebae, invisible to the naked eye, crawling around in dirt looking for bacteria to eat, and reproducing clonally. In times of famine, they send out chemical signals which attract other amoebae, and coalesce. They aggregate into 'slugs' which are composed of thousands of cells. The slug responds to light and climbs to the surface of leaf litter, where it starts to differentiate – the cells assume different morphologies. Some of them form a stalk, which others climb up to form a spore at the top. The spores then catch a breeze and sail off to better food sources before hatching into baby amoebae. This aggregating behaviour is suicidal for all of the cells in the stalk, who die without reproducing (Bonner & Savage 1947). Are the cells organisms? We could view slug formation as a social strategy undertaken by individuals in extreme circumstances. Conversely we could treat the slug as an organism, whose parts undergo a clonal proliferation phase analogous to the growth of a multicellular organism, only without spatial contiguity. There is no obvious choice between these alternative views.

As with the species case, there is a cluster of associated problems here. In order to play the theoretical role we demand of it in biology, the concept of the organism must be such that we can count organisms. We need a way to distinguish organisms from mere parts, and also from groups or colonies, as well as to distinguish reproduction from growth. Some authors insist that in addition to the individual as a counting unit in evolutionary biology, we need a separate concept to capture a more intuitive, non-evolutionary organism that can include physiological units such as certain symbioses (Pradeu 2010; Austin Booth, pers. comm.). At least thirteen different definitions of the individual or organism are in active use in the biological literature, and each one divides the fauna and flora into a subtly different parade of individuals (Clarke 2011b).

The problem of biological individuality has taken on fresh significance and urgency with the recent maturation of work on evolutionary transitions and levels of selection (Buss 1987; Calcott & Sterelny 2011; Okasha 2006; Godfrey-Smith 2009; Maynard Smith & Szathmáry

1995; Michod 1999; Michod 2007; Queller 2000). These are events during which formerly free-living entities aggregate to form new higher-level individuals. They have occurred many times in the history of life – examples include the origin of eukaryotic cells, the formation of multicellular organisms, and the appearance of social insect societies. Recognising paradigm organisms as being fundamentally derived from complexes of smaller individuals forces us to reassess what it is to be an individual, and how individuality can come into existence at new hierarchical levels, prompting a rehabilitation of the controversial superorganism concept (Allee 1951; Emerson 1939; Gardner & Grafen 2009; Hölldobler & E. O. Wilson 2009; Marais 2009; Wheeler 1911; D. S. Wilson & Sober 1989). This new dimension adds a diachronic challenge to this problematic – the concept should allow us to judge which collectives have completed an evolutionary transition, and so deserve to be called organisms in their own right rather than a group of smaller organisms.

To summarise, there is confusion about whether or not some entities are species/organisms. Given the ubiquitous and familiar natures of those concepts, and their deep roles in important scientific theories, this is surprising. So we want to ask where that confusion comes from. *Why* do we have trouble deciding whether things are species/organisms? What is the underlying source of the problem? Perhaps surprisingly, the literature does not contain an unequivocal answer to this question. We propose that in both cases, two alternative characterisations of the underlying problem can be found in the literature, at times not sharply distinguished from one another.

Characterization One: it's a problem of vagueness

In each case there is a long tradition of seeing the problem as one of vague boundaries. This account holds that there are particular cases which resist determinate classification as falling either inside or outside of the category in question. These borderline cases reveal that the biological predicates – species and biological individual – are vague. For this reason, we cannot achieve consensus about the boundaries of the categories; they will always resist precise definition. For example, there is no fact of the matter as to whether a particular finch is a *Telespyza cantans* rather than a *Telespyza ultima* because there is no determinate

boundary between these groups⁴. Species shade into each other just as cloud shades into non-cloud.

A number of authors appear to think that this is what the species problem amounts to, or at least that it is an important part of it (Hull 1980; Sterelny & Griffiths 1999). Darwin sometimes wrote as if he thought that the variety/species distinction is just arbitrary; he said “we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience.” (C. Darwin 1859). Darwin’s suggestion fits naturally with the idea that the species category admits borderline cases, i.e. that the predicate ‘is a species’ is vague. The vagueness account also fits with Maynard Smith’s characterisation of the species problem. He says “there is no reason to suppose that either the processes of modification in time, or the processes of division of a single species into two, have always, or even usually, occurred in a series of sharp discontinuous steps. Therefore any attempt to group all living things, past and present, into sharply defined groups, between which no intermediates exist, is foredoomed to failure.” (Maynard Smith 1966b, pp.216-7)

In principle, two versions of the idea that the species problem arises from vagueness can be distinguished. The first is that the predicate ‘is a species’ is vague, i.e. there are some populations of which it is indeterminate whether they constitute species or not. The second is that predicates such as ‘is a member of *Canis familiaris*’, for example, are vague, i.e. there are some organisms of which it is indeterminate whether they belong to a particular species or not. Though these two theses are distinct as a matter of logic, there is arguably a close relation between them. If it is indeterminate whether some organism belongs to *Canis familiaris*, for example, then there must be some populations of organisms such that it is indeterminate whether they constitute species. Conversely, if every organism can be determinately assigned to a species, it is hard to see how there can be any populations whose status as species is vague. Given this close relation, we can talk of the ‘vagueness characterization of the species problem’ without specifying which version we mean.

⁴ Here we assume that ‘vague boundary’ implies ‘no fact of the matter in borderline cases’, i.e. that the ‘epistemic theory of vagueness’ of (Williamson 1994) is incorrect.

Turning to the organism problem, vagueness also provides a plausible characterization of the root of the problem. This is particularly clear in relation to major evolutionary transitions, during which organisms change from being bona fide individuals to being mere parts in new higher-level wholes. Transitions are driven by selection and so they take time; they cannot happen overnight. This means that intermediate cases are always going to occur along the way. A lineage of unicellulars becomes a lineage of multicellulars *gradually*, without crossing any sharp threshold. At intermediate stages of any transition, there is a group that has some properties of an individual and some of a colony. The view that falls naturally out of this perspective is that whether or not something is an organism is vague – there are degrees of individuality, corresponding to a group’s progress along a transition continuum. *Dictyostelium*, for example, may have taken some but not all of the steps on the way to higher-level individuality, which leaves us uneasy about whether to call the cells organisms or not.

The vagueness account fits with J Wilson’s characterisation of the organism problem. He claims “The main problem with the concept of a functional individual or organism is that the properties that determine whether or not something is a functional individual can be, and often are, held to varying degrees.” (J Wilson 2000, 302) Similarly, Sterelny and Griffiths argue that ‘individual organism’ is a vague concept, because there are some concrete cases about which our intuitions could go either way. In these cases they say there just is no fact of the matter about whether the object in question is an individual or not (Sterelny & Griffiths 1999).

In both the species case and the organism case, one might think that vagueness can only be a partial account of the source of these problems, because vagueness is not a distinctively biological problem. Almost all predicates are vague, after all, so biological predicates shouldn’t be an exception. But we can supplement this characterisation with the observation that the borderline cases exist because of the gradualness of the Darwinian process (Okasha 2006). Evolution causes species to change gradually into new species and this causes problems for our categories because we see examples that are halfway through such a change and don’t know how to classify them. Similarly, the gradualness of the major evolutionary transitions means that at a particular point in time, entities may exist of which

it is indeterminate whether they are individual organisms or mere parts in a larger organism.

On this characterisation borderline cases are to be expected, and are theoretically interesting, in that they teach us about the underlying dynamical process. This facet – the borderline cases being temporal stages between bona fide cases – doesn't apply to all cases of vagueness. Nor does the further facet – that the underlying dynamical process is such as to lead to borderline cases. So the supplementation makes this a more interesting point, not just an example of the general phenomenon of vagueness.

Another facet of the debate that this characterization fits is the discussion in the 1980s over punctuated equilibrium and its relation to the species problem (Eldredge & Gould 1972; Rhodes 1983). Punctuated equilibrium theorists (or 'punctuationists') argued against the gradualness of evolution, claiming that most species existed in a state of 'stasis' for most of their duration, that intermediate forms are not found in the fossil record because they never existed, and that major phenotypic change happens rapidly and only when lineages split, i.e. at speciation. Significantly, the advocates of punctuated equilibrium tended to believe strongly in the 'reality' of species, more strongly than their 'gradualist' opponents. This correlation – between accepting punctuated equilibrium and regarding species as real not conventional entities – fits naturally with a characterization of the species problem as resulting from the existence of borderline cases, which themselves result from gradual evolution. For punctuated equilibrium theorists held precisely that evolution was not gradual, and that borderline / transitional cases were rare.

So the idea that the species problem and the organism problem both stem from vagueness/borderline cases, which themselves arise because of the gradualness of evolution, has considerable explanatory power and makes sense of a considerable portion of the literature.

Characterisation Two: the criteria are to blame

An alternative is to view the species and organism problems as being about the choice of criteria by which to define the categories. The second characterisation identifies the problems as arising from the fact that biologists use multiple criteria for defining the

categories in question, and that these criteria don't have universal application. They coincide in some, 'paradigm' cases, but not others. This results in confusion as to which if any of the criteria are the essential ones. Some authors favour a single criterion, or set of criteria, and regard the others as mere empirical correlates (or not) of it. Others argue that we need to be pluralists about the category in question, and accept different criteria as singling out distinct kinds. Others argue that the choice of definition is subjective, or that we should throw out the category altogether. Each of these responses finds proponents in both the species and organism cases.

For example, Tasmanian devils, or *Sarcophilus harrisii* make up a group that most would be content to call a discrete species, and which qualifies on multiple definitions. They qualify on the biospecies definition (Mayr 1942), because their long term isolation on the island of Tasmania has guaranteed their reproductive isolation. Their closest living ancestors, the quolls from the genus *Dasyurus*, are separated from them by thousands of miles of ocean. Tasmanian devils are rather versatile, and thrive in various different habitats in Tasmania, from the edges of urban areas to dry forests and coastal heaths. There is no evidence of niche specialisation within Tasmania, rather they all seem to compete for the same resources. *Sarcophilus harrisii* thus qualifies as a species on the ecospecies concept (Van Valen 1976). Genetic analysis reveals *Sarcophilus harrisii* to be a phylogenetic species also (Cracraft 1987). Although there is a subpopulation in the north-west of the state that differs genetically from other devils there is also evidence of significant gene flow across the two groups (Jones et al. 2004). All of these verdicts line up nicely with the phenetic species concept (Sokal & Crovello 1970) and with the common sense observation that all Devils share certain phenotypic and morphological properties such as black fur, ferocity, and a loud screeching call. They even share a famous and unfortunate parasite – the Devil Facial Tumour Disease (DFTD). It is plausible, therefore, that if this was the only species you ever examined it might seem unimportant which species concept we give priority to, because they coincide anyway.

Yet in many, or even most, cases, the criteria come apart, i.e. they pick out non-overlapping groups of organisms. The literature abounds with examples of groups identified as species

by the biospecies concept, which get split up into further species by the phylopecies concept. For example, the biospecies concept counts around 10,000 bird species, while the phylospecies concept doubles that number (LaPorte 2005, 360). Few people are likely to realise that the cherished mascot, the Giant Panda or *Ailuropoda melanoleuca* comprises two morphologically different subspecies, which are further separated into distinct subpopulations that occupy different mountain range habitats (Wan et al 2003). If you think that *actual* interbreeding between two populations is necessary for them to form parts of single species then *Ailuropoda melanoleuca* should be split into separate species, because habitat destruction means that individuals from these groups can never meet in the wild. On the other hand, those individuals can mate in captive breeding programs to produce fertile offspring. The Qinling population are officially termed a subspecies *Ailuropoda melanoleuca qinlingensis*. However, the fact that the Qinling individuals are morphologically distinct (they sport a dark brown and light brown colouring instead of the more familiar black and white, as well as a smaller skull) and live at a much higher elevation from other pandas might lead proponents of ecospecies or phenospecies definitions to give them the status of a distinct species. These details have practical consequences for the planning of conservation strategies, because it is not clear whether idiosyncratic strategies should be formulated for each population, or whether efforts should be concentrated on increasing gene flow between the groups by opening up habitat corridors between them, in order to maximise genetic variation in the larger group (Loucks et al. 2003; Lu et al. 2001).

So before we can say of any individual panda what species it belongs to, we are obliged to decide *which* definition of a species we think is correct. This gives weight to the second characterisation of the species problem, according to which the problem consists in the fact that different criteria pick out non-overlapping groups of organisms. This fact stands in the way of any desire to find shared criteria that all and only species meet. This characterisation yields the diagnosis that the confusion stems from the traditional assumption that species meet a shared set of criteria – reproductive isolation, phenotypic similarity, common ancestry and so on. This assumption holds in some cases such as Tasmanian devils, humans and certain birds, but as soon as you turn your attention to other examples the criteria fail to coincide. We are then left wondering whether to privilege one criterion over the rest

(Mayr 1942; Ruse 1987; Sober 1987) or to admit a plethora of species concepts, as recommended by certain 'pluralists about species'. Constructivist pluralists want us to recognise as many distinct kinds as seem useful. For example, botanists may want to call *Rubus* a single morphologically diverse species, while greengrocers feel it useful to distinguish raspberries from loganberries (Dupré 2001). Other authors reject the species category altogether in the face of this plurality (Ereshefsky 1998) or try to find a new multi-criterial notion which can combine inconsistent criteria (Boyd 1999).

Likewise, different definitions of the individual organism tend to overlap in higher vertebrates, but once you move away from that group the criteria dramatically diverge. A pig meets many of the different criteria that have been touted as definitional of a biological individual – unique/homogeneous genotype (Janzen 1977), germ soma separation (Buss 1987), bottleneck life cycle (Maynard Smith & Szathmáry 1995), functional integration (Sober & Wilson 1999), immune response (Pradeu 2010), policing mechanisms (Wolpert & Szathmáry 2002), spatial cohesion (Hull 1980) and so on. But now consider *Dictyostelium*. If we hold that germ soma separation and functional integration are essential properties of organisms then we might say that the slug is the organism. On the other hand, if spatial cohesion and development from a bottleneck are more important, then we will be moved to view the *cells* as individual organisms.

Characterised this way, the range of responses to the organism problem closely mirrors that to the species problem. Some authors prioritise a single criterion or set of criteria (TH Huxley 1852; Janzen 1977; Buss 1987; Maynard Smith & Szathmary 1995; Pradeu 2010), while pluralists split the organism category into numerous kinds. Disjunctivist pluralists argue that the organism concept conflates several distinct natural kinds. For example, J Wilson says that the functional individual sometimes overlaps with the genetic individual, although in cases of organ transplantation or tissue culture they come apart (J Wilson 1999). Eliminativists argue against the necessity of any organism concept (J Wilson 2000) while others search for ways to reconcile the multiplicity of criteria with a single underlying category. (R. Wilson 2007) does this by making use of Boyd's HPC kind concept, while (Clarke Forthcoming) tries to reconcile monism and pluralism by arguing that different criteria constitute lineage-specific ways of achieving or maintaining individuality.

Note that similar problems dog each of these solutions in the organism and in the species cases. Monists argue about what to do with the organisms that don't fit their model. Certain organisms, especially higher metazoans and vertebrates, are taken to be exemplary, without much justification. Constructivists fail to explain how the concept of the individual organism manages to be so useful and predictively powerful, or why birds and parasites should be sensitive to some of the same taxa distinctions as humans (Wilkins 2003). Disjunctivists have nothing to say about the ways in which different concepts overlap or coincide. Eliminativists struggle to account for the enduring robustness of the concepts in biology and evolutionary theory.

So the diagnosis on this account is that specieshood/organismality has been defined by many separate properties, and the problem arises because sometimes they come apart. Scientists are talking past each other because they are using non-equivalent definitions, and therefore including non-overlapping groups of living objects within the extension of the terms.

This characterisation of the problem makes sense of many facets of the debate, especially the opposition between 'monism' and 'pluralism' in the philosophical literature. It also explains why taxonomists who focus on birds, for example, often believe in the reality of species, while those who focus on bacteria typically think the category is a bit of a mess and not useful anyway. Similarly, people who work on plants have used many different words to distinguish kinds of individual organism, such as individuoid, colonoid, morphont, phytomer, metamer, ramet, genet, module and meristem (White 1979; Pepper & Herron 2008) whereas zoologists generally treat the term as unproblematic. A common complaint from researchers who take this perspective is that key concepts in the theory of natural selection have been formulated with 'charismatic eukaryotes' (higher metazoans, often vertebrates) in mind. Once you move away from that group, totally different phenomena become important. Ereshefsky, for example, says "General discussions of the species problem tend to focus on species concepts that were designed with eukaryotes in mind. (Ereshefsky 2010a, p.553). He argues that microbiology requires its own unique 'recombination' species concept, in order to handle the fact that prokaryotes exchange genes preferentially within groups, but without ever totally blocking gene flow with outsiders. Similarly, Niklas claims

that “Most attempts to define what is meant by species are based on animal biology, and many have neglected the conspicuous differences between plants and animals.” (Niklas 1997, p.73). The vertebrate bias has also infected many discussions of how to define organisms, so that certain properties are often thought of as being necessary to individuality despite being entirely absent from the majority of living phyla. Germ soma separation, for example, often pops up in definitions of the individual (Buss 1987; Godfrey-Smith 2009) but is present only in multicellular animal lineages – leaving plants, prokaryotes and many fungi out of the class of organisms altogether (Clarke 2011a). These insights are startling because they concern absolutely central terms in our theory of natural selection, radically undermining that theory’s generality.

This second characterization of the species / organism problem is quite different from the first one, at least at first blush. The first characterization regards borderline cases, which resist easy classification, as giving rise to the problems; this is quite different from the idea that multiple non-equivalent criteria are the root cause. For the ‘multiple criteria’ problem would exist even if each of the criteria for being a species, or an organism, was not vague, so did not admit borderline cases. Conversely, even if all biologists could agree on a single defining criterion, for species or organisms, we could still end up with borderline cases so there would still be a problem. So it seems that the our two characterizations, one in terms of vagueness/lack of sharp boundaries, the other in terms of multiple criteria, speak to two logically distinct aspects of the species problem and the individual organism problem respectively.

Clearly, both characterizations have something going for them, in that they both make sense of certain aspects of the literature. But what is the relationship between them? Should we think of them as offering competing diagnoses of where biologists’ difficulties with delimiting species, and organisms, come from? Or should we view them as compatible, i.e. as addressing different facets of the overall problematic? On this latter view, we would not need to decide between the two characterizations, for both could be correct. We incline towards the latter view. But nonetheless, and despite the logical independence of the ‘borderline cases’ and ‘multiple criteria’ issues, it does not follow that nothing useful can be said about the relation between the two. Indeed, we think that it can.

We will argue that depending on the context of enquiry, i.e. on the particular question being asked, one characterisation rather than the other may yield a superior analysis of the problem. That is to say, in some contexts the existence of borderline cases is the source of difficulty, while in other contexts the existence of multiple criteria is the source.

Different temporal contexts

One suggestion worth exploring is that the 'borderline cases' characterization fits best with the 'diachronic' dimension of the species / organism problems, while the 'multiple criteria' characterization fits with the 'synchronic' dimension. To recall, the diachronic issue is about separating lineages into discrete species, or organisms, over time; while the synchronic issue is about how to produce an objective count of species, or organisms, at any one time. Plausibly, those who emphasize borderline cases and evolutionary gradualism are thinking of the species / organism problem in diachronic terms. Those who emphasize multiple criteria, on the other hand, are probably thinking of the problem synchronically – as the point they make is that the criteria fail to co-incide in extant organisms / species. So one possible thesis is that the choice of a diachronic versus synchronic perspective might fix our choice of characterisation of the species/organism problem.

Several authors have been explicit that the biospecies concept just isn't meant to apply over time, but should only be used to divide extant organisms into species. For example, "the Biological Species Concept is principally meant to be applied at a given point in time" (Lee & Wolsan 2002, citing Mayr 2000) This implies that in diachronic settings there can be a problem of vagueness, even in the absence of dispute over the correct definition to use (i.e. even if we agree that the biospecies concept is the right concept). All living humans are unambiguous members of *Homo sapiens* according to the biospecies concept, because they all belong to populations which are able to interbreed with one another. However, if we want to answer a question about when in time *Homo sapiens* came into existence all clarity evaporates. It seems reasonable to suppose that no non-vague answer can be given because the process by which *Homo sapiens* formed an isolated breeding population separate from other *Homo* groups will have occurred gradually, over a long period of time. The extent to which one population is able to interbreed with another is likely to gradually

deteriorate as drift brings about an accumulation of differences that make interbreeding first difficult and then impossible.

This example seems to make it plausible that diachronic species questions are always going to encounter indeterminacy. But for at least some species concepts synchronic questions can be given determinate answers. If there is any species problem at all in synchronic contexts, the issue is more likely to be over whether the chosen concept is the right concept to use, than to do with vagueness.

Likewise, if you are looking at the diachronic problem of individuality then you might be interested to find out when the first true multicellular organisms appeared, but you will not expect there to be a precise answer. The diachronic perspective seems especially compelling if you are thinking about a case like the volvocine algae. This clade of water living creatures comes in a variety of separate species, which show an almost perfect continuum from unicellular, solitary forms up to tightly integrated groups with germ-soma separation. The various species in the volvocale lineage are often interpreted as representing different temporal stages in an individuation trajectory, even though they are really separate lineages. It seems to come naturally to people, when thinking about which of the clade are higher-level multi-celled organisms, and which are mere colonies, to treat some of the species as being halfway along this trajectory. *Gonium pectoral* shares *some* features with its unicellular cousin, *Chlamydomonas reinhardtii*, but others with its multicellular cousin *Volvox carteri*. It shows some clustering of cells, and a small amount of differentiation, but each cell retains reproductive and metabolic independence, and the group fractures on reproducing to produce separate cells, not balls. Many people therefore characterise *Gonium pectoral* as being an intermediate stage between uni and multi-cellularity (Kirk 2003; Michod 1999). This shows that organismality appears to be very much a vague phenomenon, in so far as we are focused on the process by which individuals at one level of hierarchy emerge over time from ancestors at a lower level of hierarchy.

However this neat alignment of 'vagueness' with diachronic questions and 'multiple criteria' with synchronic questions is too fast, because there are obvious counterexamples. Recall the Hawaiian finches. There is indeterminacy over the status of *Telespyza cantans* and *Telespyza ultima* even when we consider only current, living finches. In other words, even if

we take a synchronic perspective, and agree to apply the biospecies concept⁵, it's still not clear whether these are two species or one. The reason is that the population-level property of being able to interbreed with another population comes in degrees – it is not a 'yes/no' matter. Some populations might interbreed more easily, or more frequently, than others. Certainly we can often find examples where interbreeding applies to a very high degree, even perfectly. But we can equally easily find examples where there is only an intermediate degree of interbreeding between two populations.

Similarly, *Gonium pectorale* is an extant, living species and thus falls within the domain of 'synchronic' organism problems. If vagueness were strictly limited to diachronic contexts – to historic organisms – then there should not be any indeterminacy over whether *Gonium* is an organism or not. Yet *Gonium* seems to fall precisely into the grey area of our organism concept.

The reason is, again, that the Darwinian process is gradual. Even supposing the punctuationalists are right, speciation does not happen overnight, and so intermediate forms must occur. The criteria by which species are defined are continuous; they can be met to a greater or a lesser extent. The same points apply to the criteria by which organisms have been defined. Integration, autonomy and so on are obviously not discrete properties. Germ-soma separation can come in a range of different numbers of cell types, or ratios of germ to soma. Even the predicate 'possesses a bottleneck in its life cycle' admits of degrees, because we can have a range of values for the size of the adult phenotype relative to that of the propagule. This all shows that even if we only consider living things at an instant, we are still likely to encounter cases where the relevant properties obtain to an intermediate degree, and where, therefore, the status of the living thing as a member of some species, or as an organism, is ambiguous.

There is another way to classify the characterisations according to temporal contexts however. Vagueness is a problem for diachronic perspectives, but also for all those

⁵ In fact all of the other concepts define a species according to continuous properties too. For example Van Valen says his ecospecies account, on which a species "occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range" (Van Valen 1976, p.70) will be vague "as is the case in the real world."

synchronic perspectives which look at a species during that period of its history when it is speciating. We can eliminate vagueness by choosing to treat each species only during one of the time slices at which, like *Homo sapiens* today, there is no speciation in progress. During such time slices, any remaining controversy can be safely assumed to concern the choice of criteria. Similarly, we can choose to ask questions about the organismality of an entity only during those instants in the history of its lineage when the entity is not in the process of any transition between levels. This may seem an ad hoc approach, but it should seem more reasonable when we consider that for punctuationists such periods are going to comprise the vast majority of any lineage's history. The messy, vague moments are going to be short, sharp intervals between long periods of stasis during which the species/organism defining properties are practically discrete. The suggestion would be that while *Gonium* and *Telespyza* are indeterminate members of the organism/species classes right now, this is merely a temporary aberration, one that natural selection is sure to fix in (a short amount of) time.

This approach has the advantage of saving the intuition reflected in Lee & Wolsan's quote, that temporality is somehow to blame for the species problem. On the other hand, the approach is only feasible to the extent that punctuationists are right. If there are lineages which spend a majority of their time in messy, indeterminate phases of specieshood or of organismality, then this analysis will not help. To put it another way, this approach only has traction to the extent that all of the vague cases are in fact transitional. If, on the other hand we find lots of examples of living things that defy precise species/organism classification, and in whom this state seems to be a long-lived, stable mode of being, then the plea that vagueness only applies to transient, minority segments of lineages as they switch from one species/level to another is less convincing.

Different questions

Another way in which the context of enquiry might influence which of vagueness and/or multiple criteria we take to be diagnostic of the species/organism problems concerns the particular kind of question we want to answer. There are two distinct kinds of enquiry we might choose to make;

1) Is x a species? Is x an organism?

2) Is y a member of species x? Is y a part of organism x?

We might call the first questions category questions, while the second ones are taxa questions.

If we are concerned with category questions we are concerned with whether there is any generality to the species/organism category, i.e. whether what it means to be a species/organism is the same across all lineages. This kind of question naturally invites concern over the multiplicity of criteria that we use for defining the category in question. If, on the other hand, we are dealing with taxa questions then the challenge is to carve up the tree of life into particular discontinuous groups, and identify the boundaries of such groups in space and time. Here we are far more likely to think that our difficulties are caused by the gradualness of the Darwinian process giving rise to vagueness.

In both the species and the organism case we are thinking about a smoothly changing lineage, where early parts of the lineage are very different from later parts. In the organism case those later parts are multicellular, for example, where the early parts are unicellular. In both cases we think it is useful to divide these lineages into discrete stages, to describe the characteristics that the organisms within it have – multicellular, for example, or *Homo sapiens*. Taxa problems confront the fact that the lineage we are trying to draw stages onto changes smoothly from one stage to another, so drawing actual boundary lines is an impossible task.

Category problems, on the other hand, confront the fact that it is not at all clear that the way in which one lineage changes over time is in fact similar to, let alone identical to, the way in which other lineages change over time. For example, the manner in which *Homo habilis* was transformed into *Homo sapiens* might be so different from the way in which *E. coli* was differentiated from its own ancestor that there is no general phenomenon for us to point at and say 'this is speciation.' Instead it might just be that we have to use different criteria, in each case, to characterize the change. Similarly, the move to multicellularity in plants might involve a whole different set of phenomena from the move to multicellularity in animals, just as eukaryocity was achieved in different ways in those two kingdoms.

So it might be that the vagueness/multiple criteria views are concerned with subtly different problems. Vagueness becomes salient when we ask taxa questions, such as ‘Is humanoid x a member of *Homo sapiens*⁶?’ (in the case of species problems), and ‘Is tree x a mere part of a *Populus tremuloides* individual⁷?’ (in the case of organism questions), because here we are trying to impose sharp boundaries onto smoothly changing lineages. We quickly run into questions about how and when the lineage in question changes from one stage to another. Multiple criteria become salient instead when we ask category questions, such as ‘Is this bacterial group a species?’ and ‘Is this *Dictyostelium* cell an organism?’, because here we are prompted to think in a more general way, about what it is to be a species or an organism. We are thinking about whether or not the entities in question constitute members of a general class.

It is well known in philosophy that the context of enquiry can determine the appropriateness of the response. For example, suppose we were to ask a famous bank robber ‘Why do you rob banks?’ The answer ‘Because that’s where the money is’ makes good sense *if* we suppose that the implicit question was ‘Why do you rob banks rather than robbing other places?’ There is no sense in which this response is inconsistent with an answer about why he robs banks rather than stealing nothing at all. He is simply answering a different question. Similarly, on this view there is no tension between responding to the problem of species/organisms by appealing to vagueness, and responding instead by appealing to multiple criteria. The two positions are simply responses to subtly different problems. While vagueness gives a perfectly reasonable response to a question about why we have problems placing objects into organism/species taxa, multiple criteria give an equally reasonable response to a different question, about why we have problems elucidating general species/organism categories.

We might have a remaining worry that these two contexts of enquiry collapse into one another. As we saw earlier, if species taxa are vague, then this implies that the species category will be vague also. So we might think that these kinds of question aren’t distinct at all. However, we can see that they are in fact logically distinct when we consider that

⁶ rather than a member of *Homo habilis*.

⁷ rather than an individual organism in its own right.

species category problems might exist even if species taxa are not vague. For example, it could be the case that species taxon x is found to be perfectly determinate in space and time according to species definition A, while species taxon y is found to be perfectly determinate according to species definition B, but species definition A bears little or nothing in common with species definition B. Furthermore, it might be that everyone who investigates species taxon x agrees and has good reason for thinking that species definition A is clearly the right species definition to use with respect to that taxon (and likewise for taxon y with respect to definition B). Then there is no problem of vagueness in answering species taxa questions, and there is no problem of multiple criteria with respect to each species taxon but there is a problem of multiple criteria when answering species category questions. This shows that the two kinds of question are logically distinct.

Are the problems perfectly symmetrical?

A final question we will consider is whether the two characterisations, in terms of vagueness and in terms of multiple criteria, imply that the problems of species-hood and of organismality are equally serious?

On the face of it, it might seem as if indeterminacy is more of a problem in the organism than in the species case, because the central purpose of the organism concept – at least as far as evolutionary biology is concerned - is to allow us to count organisms in such a way that we can generate clear demographics for fitness surveys. This is much more pressing than in the species case, because although we do sometimes want to count the number of species in a region (e.g. for conservation purposes) this does not exhaust our use of the species concept in the same way. The species problem is equally concerned with identifying the *nature* of species, perhaps because they are somewhat less obvious items of ontology than are organisms. So it might seem as if vagueness is more problematic in the organism than the species case, because of the greater significance of being able to count organisms than species.

However, deeper reflection on the role that we expect each concept to play does not support this verdict. The need for a discrete judgment about the individuality of an organism disappears once a multilevel analysis is available. That is, we can successfully

describe and predict the change in frequency over time of a particular trait even if we think that those entities carrying the trait have an intermediate degree of individuality, simply by carrying out our analysis of trait-fitness covariance at more than one hierarchical level (Okasha 2006; Price 1970; Clarke Forthcoming). Godfrey-Smith, like many other authors, is perfectly comfortable with describing organismality as including a “blending-off into marginal cases, precursors and not-quites” (Godfrey-Smith 2009, 108). We are even making progress in elaborating the numerous small steps on the path of some transitions, such as to multicellularity, which certainly takes away some of the mystery of how intermediate degrees of organismality can obtain. For example, Kirk and others discuss in great detail the evolution of intermediate forms of higher level individuation in the volvocine clade (Kirk 2005). Similar research is underway to discover the key changes that took place on the way to eusociality in insect groups (e.g. Khila & Abouheif 2008).

No analogous multilevel analysis is available for describing a population as having an intermediate degree of ‘species-hood’. Furthermore it does a considerable amount of violence to our folk concept of species to even consider ‘species-hood’ as something that is not a yes/no matter. There is a sense in which answering questions about the origin of species is about explaining the discontinuities that we observe around us. The notion of a smoothly continuous property for defining species is at odds with the idea of a branching tree of life.

So whilst vagueness is likely to affect each of the organism and species cases equally, and whilst both of the problems – indeterminacy and multiple criteria – will frequently coexist, nonetheless there are good reasons why vagueness might be more acceptable when associated with the organism concept than with the species concept.

Conclusions

We need the concept of a species and the concept of an individual organism in order to describe and investigate the living world. Yet both concepts are notoriously problematic. A first step on the way to resolving the problems is to formulate a clear account of just where the problems come from, and what are the questions that need to be answered. We showed that there are two logically distinct sources of difficulty that are often conflated. We

can make progress in clarifying our organism and species concepts by tackling the problem of vagueness separately from the problem of multiple criteria. First of all, we should decide what kind of question we want to answer. If we are concerned about delimiting particular organisms, or particular species taxa, then we need to accommodate the indeterminacy that is a logical consequence of the gradualness of the evolutionary process. This indeterminacy may be limited to particular cases that are transitional or in-between levels/species, but it is an open question just how much this reduces the scale of the problem. If, on the other hand, we want to clarify our concept of the organism category, or of the species category, then we will need to decide what to do about the multiplicity of definitional criteria that are on the table. Finally, it might be that while vagueness can easily be accommodated in our organism concept, our species concept is more difficult to parse in continuous terms.

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