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TOWARDS A MULTIDIMENSIONAL METACONCEPTION OF SPECIES

Catherine Kendig

Abstract
Species concepts aim to define the species category. Many of these rely on defining species in terms of natural lineages and groupings. A dominant gene-centred metaconception has shaped notions of what constitutes both a natural lineage and a natural grouping. I suggest that relying on this metaconception provides an incomplete understanding of what constitute natural lineages and groupings. If we take seriously the role of epigenetic, behavioural, cultural, and ecological inheritance systems, rather than exclusively genetic inheritance, a broader notion of what constitutes a natural grouping or lineage may be required. I conclude by outlining an alternative metaconception that is a de-centred metaschema for species.

1. Introduction

Although it may be relatively uncontroversial to suggest that species are the basic taxonomic units of classification (Dupré 1999, 18), to suggest that a species is a *natural* grouping or lineage is more problematic. In part this is because 'species' is ambiguous. 'Species' can refer to either the taxonomic rank of species or the category of species (Mayr 1992, 18–19). Most conceptions of species (often called 'species concepts') aim at the latter by providing characteristics, relationships, patterns of inheritance, or other conditions that must be met for something to be a species.

Perhaps the most well-known but also widely criticized of these is Ernst Mayr's Biological Species Concept (BSC). Still widely in use, the BSC has also spawned numerous amendments and alternative conceptions of species to it. At last count there were 27 different species concepts (see Wilkins 2011).

What constitutes a natural grouping or lineage is something Mayr (1992) considered self-evident. Species are populations of organisms that are genetically and reproductively isolated from members of other populations. Species are sharply separated from one another. They are 'protected gene pools' (Mayr 1992, 24). A natural grouping is an interbreeding population sharing a gene pool. An individual organism 'is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time' (Mayr 1992, 17). Mayr follows George Gaylord Simpson's (1961) definition of lineage as an ancestor-descendant series. His (Mayr 1992) conception of species is clearly shaped by a perspective that systematically privileges linear genetic causes: 'species have reality and an internal genetic cohesion owing to the historically evolved genetic program that is shared by all members of the species' (Mayr 1992, 17). What makes a species real is that the ancestor-descendant lineage is the direct linear-genetic inheritance from parent to offspring.

The target of my discussion is not Mayr's BSC. It is the gene-centred metaconception[1] (GCM) that underpins it – one that has also shaped more generally the notions of natural groupings and natural lineages.

2. GCM as a view about causes

The GCM is a view about causes – specifically, which type of cause is *the* privileged cause of evolutionarily significant variation among species. It both accepts that genes do not act alone and that genes interact with and utilise internal epigenetic factors and external factors in the environment in building an organism. But it treats the environment as a constant repeatable context which can easily be bracketed off. It constitutes the usual conditions of development which facilitate normal development, ceteris paribus.

The GCM is a perspective that takes organismal evolution and development to be principally gene-driven. For instance, Richard Dawkins (1989) understands genes to be both ontologically and explanatorily most important with respect to variation and evolutionary change. On his view, genes are 'selfish' in their pursuit to replicate themselves. They are 'immortal replicators' because they survive the demise of the individual organism, organisms are merely the transient vehicles the genes use for their own replication. Genes are the source of the continuity of form across gen-

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[1] In this paper, I use 'metaconception' to refer to a frame of investigation that prescribes the entities, events, mechanisms, processes, relationships, or kinds of things which are considered causally salient in answering a particular description or explanation-seeking question.

erations that we see in the biological world. Mayr uses the metaphor of a 'genetic program' that controls the development and organization of organisms: 'the activity of an orchestra . . . is just as much controlled by the score as the development of an organism is controlled by its genetic program' (Mayr 1968: 379).

Genes are privileged because it is thought that unlike epigenetic and ecological factors, only genes are directly transmitted from parent to offspring (Bateson 2001, 149 calls this a linear view). This direct transmission justifies the apportionment of causal priority to the genes over all other factors. By bracketing off all causes but genetic ones, it characterizes evolution as consisting of changes in gene frequencies over time (Futuyma 2005, 190).

What does the GCM do? The GCM provides a frame that guides the focus of investigation by delimiting the kinds of processes, products, events, and relationships taken to be causally significant in defining any group or lineage as a species. As such, it constrains membership within the category of species. Species are natural lineages of actual reproductive events of interbreeding organisms. Underlying the reliance on lineages has been a presumption that what makes lineages evolutionary units is that there is an exchange of genetic material between organisms. Descent with modification is defined in terms of change in gene frequencies and that in turn requires gene flow between conspecifics.

Empirical evidence of other hereditary patterns of descent and causally relevant evolutionary and developmental processes calls into question the GCM's privileging of this linear view. Niche constructionists (Odling-Smee, Laland, and Feldman 2003) have long argued that the causal priority of vertical genetic inheritance leads to a systematic overestimation of the causal contribution genes make. Recent research on epigenetic, behavioural, symbolic and cultural inheritance systems (Jablonka and Lamb 2005, Kendig 2011), and the inheritance of acquired characteristics and resources (see Gissis and Jablonka 2011) strongly suggest there are more resources than genes that are heritable and more inheritance systems besides the vertical genetic transmission from parent to offspring that affect natural selection. This research suggests that the GCM is not as ubiquitous and unchallenged as it once was. That said, assumptions of genetic priority continue to frame both ontological and epistemological questions concerning evolutionary change and development.

These assumptions and the use of the GCM are not held only by proponents of the BSC. Conceptions of species currently in use that aim to characterize species as natural lineages and/or natural groupings or include reference to these as criteria for species membership include not only the BSC (Mayr 1992), but also the genealogical species concept (Baum and Shaw 1995), the evolutionary species concept (Wiley 1981), the mate recognition species concept (Paterson 1985), and the genetic species concept (Wu 2001). Advocates of the BSC, isolation, reproductive, and mate recognition conceptions of species explicitly rely on the importance of potential or actual physical relationships of sexual reproduction and the exchange of genes between conspecifics it facilitates as justification for reliance on (what will later be shown to be problematic) notions of internal species genetic cohesion and genetic isolation from members of other species.

A group of organisms is an evolutionary unit that is 'held together by cohesive forces' and responds to natural selection as a unit (Williams 1970, 357). Mayr, following Williams, understands these cohesive forces in terms of gene flow, genetic homeostasis, and common selective pressure (cf. Williams 1985 and Ereshefsky 1992, 385–87). Reproductive relationships and genetic cohesion are also implicitly relied upon as necessary for the neatly bifurcating pattern of unbroken and unreticulated lineages central to both cladistic (Ridley 1989), and phylogenetic species concepts (PSC) (Panchen 1992, Staley 2006) as well. Genetic cohesion and genetic isolation are assumed by these species concepts in their definition of species as an unbroken lineage – a lineage maintained by a sequence of reproductive relationships restricted to conspecifics and ensured by exclusive vertical transmission of genetic material from one generation to the next. PSCs conceive of species in terms of the bifurcating branching tree pattern of evolution. In its weaker form, a PSC conceives of a species as 'a lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies' (Simpson 1961, 153). In its stronger form, it relies on identifying species in terms of a group of organisms which share a monophyletic lineage[2] (McKitrick and Zink 1988).

Reliance on the gene-centred view is unsurprising. It provides a means of cashing out what the unifying or cohesive forces that

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[2] A monophyletic lineage is an unbroken sequence of ancestor-descendents that includes all and only the descendents of one common ancestor. By ruling out polyphyletic lineages, the PSC denies specieshood to any groups of organisms that are the descendents of more than one common ancestor. By ruling out paraphyletic lineages, it denies specieshood to groups of organisms which includes some but not all of the descendants of a common ancestor.

make a species a unit of evolution – working as a causal whole. If not genes – then what, if anything, unifies? (see Hull 1976, 183, Williams 1985, 584, Dupré 1999, Richards 2010,177 for further discussion).

If cohesiveness can be ensured by means other than genetic, this suggests that lineages can be conceived of not only in terms of different levels of organization (identified in terms of the level of their cohesiveness, e.g., mode of extragenetic inheritance, mode of gene flow), but that their cohesiveness may be temporally defined. That is to say, their mechanisms of cohesion are temporally liminal. Put another way, what makes one species unified at one point in time may not be the same at another. That there is gene flow may not be a *persistent* causally significant factor or explanation of species cohesion.

But here's the rub. Treating species as cohesive units presupposes what the BSC and other conceptions of species try to explain – the nature of cohesion or unity. That they are cohesive then suggests that there is some mechanism of cohesion or some underlying relationship or substance responsible for its maintenance. Two problems seem to follow. The first has already been alluded to – the mechanisms of cohesion may not be the same over time. Second; the assumption of cohesion may artificially predispose a certain line of inquiry into the nature of species that is both ontologically and epistemologically question-begging. It is ontologically question-begging in its assumption that the category of species is that which is homogeneously realized in all those entities belonging to it, and epistemologically question-begging in its assumption that looking for unity is the best way to reveal their nature as species.

How the GCM's assumption of genetic priority shapes what is considered a *natural* grouping and a *natural* lineage will be discussed with reference to the alternative routes of inheritance (e.g. horizontal, vertical, and diagonal) and the inheritance of extragenetic (e.g. behavioural, ecological, epigenetic, and microbiotic) resources.

3. Inheritance: Multiple Routes, Multiple Resources

Extensive research on epigenetic inheritance shows many resources can be acquired vertically besides genes (Jablonka and Lamb 2005). For instance, a particular developmental or ecological stimulus that affects gene activity can be passed from parent cell to daughter cell. Genes may either be turned on or off by the cell in response to the stimulus. If these genes are turned on in the parent cell, the genes in the daughter cells and in subsequent descendants will continue to turn those genes on. The result is that there may be 'genetically identical cells [that] can be in two alternative states (*on* and *off*), and both states can be self-perpetuating' (Jablonka 2001, 104). These cell lineages can continue to produce offspring that are *on* even when the original stimulus is no longer present. This continues 'as long as the products of the self-sustaining cycle do not fall below a critical threshold' (Jablonka 2001, 104). In addition to the vertical inheritance of a cell's state, aspects of a cell's structure, pattern of growth (such as the pattern of cilia on cell membranes), fractal patterns of growth, or chromatin marks on protein or RNA complexes that affect methylation patterns can also be inherited epigenetically (cf. Jablonka 2001, 103–9). DNA methylation is inherited not only sub-organismally from one mother to daughter cells, altered DNA methylation patterns can also be inherited intergenerationally from parent organism to offspring organism (Gissis and Jablonka 2011, 414). DNA methylation contributes significantly to the development of the organism; it is in part responsible for the stabilization of centromeres and plays a role in the long-term silencing of the extra (inactive) X-chromosome (Gissis and Jablonka 2011, 414).

Organisms of a particular species may horizontally acquire various resources, such as microorganisms. Ruminant mammals such as cattle and sheep and other mammals inherit symbiotic microflorae that they utilize in digestion. These microflorae are inherited from multiple sources (both horizontally and vertically). These may include ingesting the milk from the mother; from other related and unrelated conspecific females of the same group (e.g. within prides and packs); in the regurgitant of carers, siblings or other conspecific peers (or other individuals besides parents); or the ingestion of faecal matter that is the product of different organisms (which may include both conspecifics and heterospecifics) (Peacock and Jenkins 1988).

In cattle, the symbiotic microflorae live within one of the stomachs, the rumen. The microflorae aid in the digestion of the copious amount of rough vegetation cattle consume. These symbionts partially decompose tough plant tissue allowing the cow to absorb energy and nutrients from cellulose that would otherwise be indigestible (Aber and Melillo 1991, 230–31). This increases the amount of energy the cow gains from the vegetation it consumes.

The acquisition of beneficial resources that may be used by organisms is of course not limited to mammals. The horizontal transfer of γ-proteobacterial endosymbionts occurs among many insects (especially microsporidia) that are present in a wide variety of arthropods and the parasitic fungi of several plants (Werren 2005, 291). The symbiotic microorganisms of termites quicken the rate of decay of high-lignin substances. Termites use this to their advantage. This quicker decay rate facilitated by their symbionts allows the hosts to consume large amounts of wood. Symbionts can be inherited from one organism to the next horizontally, but they can also be passed on through a mixture of partially vertical and partially horizontal inheritance. Symbionts such as the nitrogen-fixing bacteria *Rhizobium* of some legumes, algae-bearing symbionts of some corals, and the γ- and α-proteobacteria *Rickettsia* and *Wolbachia* of arthropods and nematodes are acquired through a mixture of heritable routes (Werren 2005, 290–298, Werren et al. 2008).

Some of the most well-known horizontally transferred symbionts are of those of the bacteria *Rhizobium*. These are acquired when the bacteria infect the roots of leguminous plants (e.g. peanuts and soybeans) causing the plant to grow root nodules. These root nodules serve to protect the acquired microbes from the acidic conditions of the surrounding soil (Aber and Melillo 1991, 149). In this protected environment, the microorganisms carry out the fixation of nitrogen gas from the atmosphere. By doing so, they provide the plant a greater amount of this valuable nutrient than is possible from the regular uptake of nitrogen by the plant from the soil in the absence of these microorganisms.

In addition to the horizontal inheritance of extragenetic resources, the horizontal inheritance of genes has also been observed. Although rare, horizontal gene transfer (HGT) has been found to occur between organisms belonging to different kingdoms such as between eukaryotic species and bacterial species. Eukaryotes may obtain genes horizontally from mobile genetic elements in the food they consume, retroviruses, and disease causing parasites such as trypanosomatids (cf. Doolittle et al. 1989, Doolittle 1998 and Hannaert et al. 2003). Although striking, it is a mistake to overemphasize the role of HGT. Not all genes can be horizontally transferred, in fact, only a small minority of genetic sequences are able to be horizontally transferred. However, HGT is notable because it provides organisms with another route by which genetic resources can be acquired. And it provides bacteria important access to useful genetic resources from a number of different organisms (either of a similar species or even of a different kingdom).

One of the most conspicuous and widely studied examples of HGT is the acquisition of virulence. Some plasmid and bacteriophage vectors carry the genetic materials necessary for virulence. These chunks of genetic resources are called 'islands of pathogenicity' (Hacker et al. 1997). They can be passed horizontally from a virulent bacterium of one species to a non-virulent bacterium of another species. The acquisition of these pathogenicity islands by the recipient bacterium provides it with the resources to become virulent. This dramatic change in the bacterium's phenotype (from non-virulent to virulent) means that it can now occupy an entirely new ecological niche.

Behavioural resources may also be inherited horizontally as well as vertically. In addition to the vertical acquisition of food preferences by oviposition, through the mother's placenta, or in her milk, these preferences may be acquired horizontally (perhaps 'diagonally' is better) from organisms that cross-feed (Jablonka 2004). Horizontal acquisition of behaviours from social learning within a niche such as the nut burying of squirrels and chipmunks, the waggledance of honeybees (used to communicate the location of food sources to other bees in the hive), the courtship behaviours and songs of grasshoppers and crickets, or the acquisition of a particular signed language from one's conspecifics, are widespread (Peacock and Jenkins 1988, Leadbeater and Chittka 2007). These behaviours are stabilized within the species if they increase the viability and fecundity of the organisms using them.

Learned behaviours may also include the avoidance of certain types of unpalatable prey or the avoidance of some highly dangerous predators on the basis of their observed phenotypic features. After learning from experience, from copying the behaviour of parents or peers, a bird may be able to recognize certain wing patterns and avoid eating bad-tasting prey, such as the many species of *Heliconius* butterflies where Müllerian mimicry is common (Joron et al. 2006). Or it may learn to avoid the red, yellow, and black striped markings characteristic of the many highly venomous coral snakes (e.g. the Texas coral snake

Micrurus fulvius and the Arizona coral snake *Micruroides euryxanthus*). Other species of non-venomous snakes may exploit the bird's learnt behaviours through Batesian mimicry of the phenotypes of the model species that are already recognized by birds as a dangerous predator. The result of this on the behaviour of the birds learning to avoid the phenotypic markings of the venomous snake is that both the models (e.g. the coral snakes *Micrurus fulvius* and *Micruroides euryxanthus*) and the mimic species (e.g. the Scarlet King snake, *Lampropeltis triangulum elapsoides,* and the Colorado Desert Shovel-nosed snake, *Chionactis occipitalis annulata*) are systematically avoided by birds that have acquired this learned recognition and avoidance behaviour (Stebbins 2003).

Changes in morphology, behaviour, the reordering of life stages and even the ability to change sex are common among echinoderms, crustaceans, molluscs, and fish. Reef fish of the family, *Pseudochromidae,* can change sex depending on the sex of other fish in its school. For instance, if a small all-female schools of reef fish (called a 'harem') loses its solitary male, the largest female changes sex to become male (Wittenrich and Munday 2005). This fish changes its female morphology and physiology to the coloration, behaviour (including those of defence and courtship), and physiology of a male. Although able to produce sperm after ten days, its full transformation from female to male takes a minimum of eighteen days. Male to female transformations take more time to complete – a minimum of 52 days (Wittenrich and Munday 2005). The changes in sex of reef fish are bi-directional as the same fish may change back and forth between female and male forms throughout its lifetime depending on the sex of other conspecifics whether living in schools or not (Wittenrich and Munday 2005). At different stages in the life cycle, various organisms may display different morphologies or behaviours associated with a particular stage or in a specific environment. This environmentally dependent development suggests that this co-operative development is, although perhaps less dramatic in other organisms' ontology, no less constant.

Environmental resources and constructed environments such as webs (spiders), dens (foxes), nests (wasps, robins), galls (mites), warrens (rabbits), dams (beavers), song dialects (whales), or libraries (humans) are also inherited vertically and horizontally. A classic example used throughout the niche construction literature is that of the beavers' dam. Dams change the beavers' environment by changing the depth and course of the river in which it is built. The dam may cause the water to pool into a small pond. This provides a new resource that the beavers which built the dam, as well as other organisms (e.g. plants, birds, fish, newts), may use in the construction of their environment. The dam and the pond may be inherited by later generations of beavers thus affecting the resources available to them, as well as being inherited as a resource by other organisms and used for the construction of themselves and their niche. And finally, constructed ecological resources may also be passed diagonally such as in those organisms that acquire resources from different species (e.g. hermit crabs' use of gastropod shells, rattlesnakes' use of tortoise burrows, bats' use of bears' caves, and the micro- and macrorganisms who rely on the burrowing of generations of earthworms to make the soil porous).

4. The Multidimensional Metaconception

The examples summarized in the previous section are a sample of the evolutionarily significant impact diverse routes of genetic and extragenetic inheritance (including the inheritance of acquired resources) may have on organisms and their environments. In *Evolution in Four Dimensions,* Eva Jablonka and Marion Lamb (2005) maintain that considering routes of inheritance besides just that of genes constitutes a dramatic shift from a gene-centred view of heredity and evolution to one that is multidimensional. The remainder of this paper considers some conceptual consequences of rethinking evolution as a multidimensional process. I discuss one upshot of the shift from the GCM to the multidimensional metaconception (MDM), namely, how this shift leads to a reconception of the products of natural selection – natural lineages and natural groupings. I begin by briefly considering how this shift leads to a reconception of natural selection.

Darwin's theory of evolution recognized that the individuals of a species may vary (Darwin 1859). If these variations benefited the organism – by improving its foraging abilities, skill in avoiding predators, ability to entice mates, and increased fecundity – these variations will be inherited by the next generation. If beneficial to this generation, they can in turn be similarly passed on to the next generation. And conversely, those that hinder are not. Changes in species over time are the result of descent with modification.

If evolution is multidimensional, natural selection may act on anything that makes a difference, including but not limited to alternative alleles, mutations in genes, chromosomal changes, drift, transposable elements, the acquisition of symbiotic micro-organisms, learnt behaviours, constructed elements and opportunities of niches, and ecological resources.

The shift from GCM to MDM amounts to a shift from a centred to a de-centred perspective. The de-centred MDM reframes our conception of natural selection, the source(s) of evolutionary relevant causes, natural lineage, and natural groupings. I discuss these in turn.

The MDM rejects the GCM's view of the environment as a stable set of background causes that either facilitate or frustrate the primary genetic cause and assumes that there is a single unidirectional flow of inheritance facilitated by the vertical transmission of genes from one generation to the next. Supporting a view similar to the MDM, Susan Oyama (2000) contends that the central claim of GCM – the causal priority of genes – is underpinned by a mistaken assumption that there is a unique replicator or discrete vehicle of species constancy: 'there is no vehicle of constancy (even though the coined term, "interactant" may have an unfortunate particulate connotation), unless the organism and its niche, as they move along time's arrow, are so conceived' (Oyama 2000, 27). Genes are not exceptional in being reliably inherited over generations.

Viewing natural selection and evolution from this multidimensional perspective means that evolutionarily significant resources may be inherited vertically or horizontally, they may be acquired at birth, learnt as a juvenile, or acquired from interacting with other conspecifics. Sources of resources may be distributed over space and time:

> genes are transmitted by ancestral organisms to their descendants, . . . but in addition, phenotypically selected habitats, phenotypically modified habitats, and artefacts, persist, [and] are actively "transmitted," by these same organisms to their descendants via their local environments" (Laland, Odling-Smee, and Feldman 2001, 120).

These resources are used in the construction and reconstruction of environmental niches by organisms of a particular species. The MDM conceives of the directionality of evolutionary causes differently from the GCM. The direction of organic cause is circular not linear: '[the] constructed components of the environment are both products of the prior evolution of organisms and, in the form of [ecological inheritance], causes of the subsequent evolution of organisms, both products and causes of evolution' (Laland, Odling-Smee, and Feldman 2001, 125). For instance, the construction of nests and galls is dependent on circular and distributed causes. These organic artefacts are the constructed product of contingent interconnected causal resources supplied by the tree, climate, the female insect, and her larvae. The female insect does not construct her gall on her own. The development of galls is contingent on such things as whether a plant has a particular susceptibility to galling from certain insects: 'specific properties of the plant genome or environment must play a role . . . not all [plants] are hospitable or responsive to galling insects' (West-Eberhard 2003, 109).

5. Natural Lineages, Natural Groupings, and Species

The GCM has shaped the conception of natural lineages, natural groupings, and species according to the implicit assumption of the causal priority of genes. What constitutes a natural lineage is a vertically inherited genetic lineage from parent to offspring, and what constitutes a natural grouping is an interbreeding population sharing a gene pool. In the final sections of this paper I suggest that a shift from the GCM to the MDM has consequences for how we conceive of lineages, groupings, and species.

The MDM discussed in preceding sections of this paper is the result of fully integrating the epi- and extra-genetic routes of inheritance characterized by Jablonka and Lamb and the niche constructionism and ecological inheritance of Kevin Laland, John Odling-Smee, and Marcus Feldman into an extended view of evolution and heredity akin to what Scott Gilbert and Jessica Bolker (2003) have called the resynthesis of ecological developmental biology. Instead of ignoring or downplaying the role of environment and development in favour of that of genes, this view takes the context-dependence of development, the ubiquity of phenotypic plasticity, and the variability of life history strategies as all having significant and wide ranging evolutionary consequences (Gilbert and Bolker 2003, West-Eberhard 2003).

Instead of restricting the conception of *natural grouping* to organisms that share a gene pool, and *natural lineage* to organisms connected by vertical genetic inheritance, if we take the MDM seriously, *natural lineage* must be conceived of as including lineages of genetic, epigenetic, behavioural, symbolic, cultural, and ecological routes of inheritance. And natural groupings must be conceived of as including populations sharing genetic as well as extragenetic resources. This has a knock-on effect to other conceptions based on or defined in terms of natural lineages and natural groupings, for instance, those of species.

A shift from the GCM to the MDM would constitute a new, wider *metaschema of species* – one that would be best described as providing a de-centred rather than gene-centred view of species. It would encompass not replace the dominant gene-centred view of species, lineages, and groupings. These would constitute a subset of lineages, groupings and species that would fall under the metaschema of species.

6. A De-centred Metaschema of Species

The MDM is a de-centred metaschema of species that re-conceives species as co-constructing and reconstructing themselves and their environments over generations from a combination of genetic and extragenetic resources. All of these resources can be conceived of as potential causes of evolutionary significant change and developmental organization depending on which ones are used, how they are used, when, in what order, and in what combinations they are used during the course of an organism's life cycle. Organisms of a species select by their acquisition and use which resources are utilized *as* causes of their own development.

A species is a lineage of reciprocally constructed generations of organisms from similar sets of resources. As such, a species is a process of constant reconstruction where organisms come into being with certain resources and capacities. Their constructive activities shape their environment, interactions with conspecifics, and the resources and capacities of future generations of conspecifics. Organismal form and organization is the result of common capacities and shared resources.

Rather than being understood primarily as groups of interbreeding organisms that share a gene pool and whose reproductive events form a lineage, this alternative species metaschema conceives of species as sequences of dynamic populations that share similar (genetic and extragenetic) resources in constructing and reconstructing themselves generation after generation. By doing so it integrates the individual organism's ecologically embedded ontogeny back into the conception of species. And it accommodates the possibility of organisms changing their own selective environments. If niche constructionists are right and organisms can construct their own selective environments, a meta-notion of species more inclusive than the dominant gene-centred one may be needed. I suggest that the MDM outlined here is one that can accommodate and make sense of the kind of circular selectivity, multivariant mechanisms of inheritance, and co-development and co-evolution discussed in the niche construction literature.

Unlike the many species concepts mentioned in earlier sections, the MDM sketched here does not provide any criteria that all species must have, such as morphological or genetic cohesion, monophyly, or reproductive isolation, in virtue of belonging to the category of species. It is not a specific species concept, so it is not at the same level as the BSC. It is a general, higher-level umbrella conception that states only the nature of specieshood.

This metaschema includes all lineage-based species concepts that conceive species as 'separately evolving metapopulation lineages' (see de Querioz 2005, 1263). Although Kevin de Querioz's *metapopulation lineage* concept is conceived of as a general species concept, it is narrower than my own. My MDM is a pluralist account. Natural lineages, populations and groups can be conceived from a multidimensional perspective. Natural lineage could be traced genetically, epigenetically, behaviourally, culturally, or ecologically. As for natural groupings, the MDM species metaschema would include gene-centred conceptions such as Mayr's interbreeding populations that share a gene pool, but it would also include those that conceived of species as populations sharing an inherited niche.

De Queiroz (2005) suggests that all specific species concepts have something in common – they all talk about species as segments of a lineage. His metapopulation lineage concept refers to a spatiotemporally extended sequence of ancestor-descendant populations. As such it takes a monistic view of species. The species metaschema suggested here could be considered to be a pluralist extension of de Querioz's metapopulation lineage concept – considered *in four dimensions,* (to borrow a phrase from

Jablonka and Lamb) – one that conceives *lineage* to include the inheritance of genetic, epigenetic, behavioural, cultural, and ecological inheritance systems. As such, the MDM can be thought of as a general lineage concept of species but one that conceives of lineage multi-dimensionally.

7. Pluralism as a frame of diverse scientific practices

Two questions remain unanswered: 1) Why is the shift from GCM to MDM significant? and, 2) Does the shift affect how species taxa are identified or individuated on the basis of a species concept? The second can be answered briefly. The MDM extends de Querioz's criteria for species membership by extending the notion of lineage to include not only the genetic but also epigenetic, behavioural, cultural, and ecological-based lineages and inheritance systems. That said, what does this do? This leads back to the first question which will require a more lengthy response.

The MDM provides a pluralist meta-schema that reflects the diversity of scientific practices. It presents alternatives to the lineage concepts that are currently in use in biology. By taking into account different mechanisms of inheritance that include epigenetic, ecological, and cultural inheritance, the MDM encompasses a diversity of lineage-generating events besides reproduction.

Biological practices across different sub-disciplines of biology suggest that all species do not evolve by the same processes or patterns. The above cases provide empirical evidence that suggests the GCM is an unnecessarily restrictive frame through which evolutionary significant causes can be identified as such. Other events at different levels of biological organization can be traced as lineages not primarily construed as genetically contiguous ancestor-descendent sequences.

Much of recent discussions of what makes the GCM most problematic concerns the species concepts developed to apply to microbial, fungal, and archaeal species in response to the unsuitability of those assuming sexual reproduction; for example, the BSC, mate recognition concept, and reproductive cohesion concept. These suggest that the organizational structure of the vast majority of the earth's species resist a univocal monistic account of species in terms of a lineage of reproductive events

(Dupré and O'Malley 2009). Thinking about different systems of evolutionary inheritance and the reticulated structure of microbiological evolution radically changes what we consider species to be. Microbiological species may not be the same kind as macrobiological species (Kendig 2012). This would suggest that members of the species category may be highly heterogeneous – that is, what constitutes specieshood may be wildly discordant across disciplines. Such thinking makes GCM seem less plausible as it cannot accommodate the diversity of species concepts in use within the various sub-disciplines.

The shift to the pluralist MDM amounts to a reframing of what are conceivable causal mechanisms, events, and lineages used in defining species across a wide variety of biological sub-disciplines that comes as a direct consequence of the diversity of disciplinary practices in conceiving of and identifying species.[3]

Missouri Western State University
Department of Philosophy and Religion
4525 Downs Drive
Saint Joseph, Missouri 64507, U.S.A.
ckendig@missouriwestern.edu

References

Aber, John and Melillo, Jerry. (1991). *Terrestrial Ecosystems*. Philadelphia: Saunders College Publishing.

Bateson, Patrick. (2001). 'Behavioral Development and Darwinian evolution.' In Susan Oyama, Paul Griffiths, and Russell Gray eds., *Cycles of Contingency*. Cambridge: MIT Press.

Baum, David and Shaw, Kerry. (1995). 'Genealogical Perspectives on the Species Problem.' In *Experimental and Molecular Approaches to Plant Biosystematics*, ed. P. Hoch and A. Stephenson. St. Louis: Missouri Botanical Garden.

Darwin, Charles. (1859/1872/1959). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. 6th edition. The Modern Library. New York: Random House.

Dawkins, Richard. (1989). *The Selfish Gene*. Oxford University Press. 2nd edition.

De Querioz, Kevin. (2005). 'Ernst Mayr and the Modern Concept of Species.' *Proceedings of the National Academy of Sciences* CII (1): 6600–6607.

Doolittle, W. Ford. (1998). 'You are what you Eat: Gene Transfer Ratchet could Account for Bacterial Genes in Eukaryotic Nuclear Genome.' *Trends in Genetics* 14 (8): 307–311.

Doolittle, R. F., Feng, D.-F. and Johnson, M. S. (1989). 'Origins and Evolutionary Relationships of Retroviruses.' *Quarterly Review of Biology* 64: 1–29.

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Dupré, John. (1999). 'On the Impossibility of a Monistic Account of Species.' In *Species: New Interdisciplinary Essays*, ed. Robert Wilson. Cambridge: MIT Press.

—— and O'Malley, Maureen. (2009). 'Varieties of Living Things: Life at the Intersection of Lineage and Metabolism.' *Philosophy & Theory in Biology* 1: e003.

Ereshefsky, Marc. (1992). 'Species, Higher Taxa, and the Units of Evolution.' In *The Units of Evolution*, ed. Marc Ereshefsky. Cambridge: MIT Press.

Futuyma, Douglas. (2005). *Evolution*. Sunderland: Sinauer.

Gilbert, Scott and Bolker, Jessica. (2003). 'Ecological Developmental Biology: Preface to the Symposium.' *Evolution & Development* 5 (1): 3–8.

Gissis, Snait and Eva Jablonka, eds. (2011). *Transformations of Lamarckism*. Cambridge: MIT Press.

Hannaert, Véronique, Saavedra, Emma, Duffieux, Francis, Szikora, Jean-Pierre, Rigden, Daniel, Michels, Paul and Opperdoes, Fred. (2003). 'Plant-like Traits Associated with Metabolism of *Trypanosoma* Parasites.' *Proceedings of the National Academy of Sciences* 4 100 (3): 106.

Hacker, J., Blum-Oehler, G., Muhldorfer, I. and Tschape, H. (1997). 'Pathogenicity Islands of Virulent Bacteria: Structure, Function and Impact of Microbial Evolution.' *Molecular Microbiology* 23: 1089–1097.

Hull, David. (1976). 'Are Species Really Individuals?' *Systematic Zoology* 25: 174–191.

Jablonka, Eva. (2001). 'The Systems of Inheritance.' In *Cycles of Contingency*, eds. Susan Oyama, Paul Griffiths, and Russell Gray. Cambridge: MIT Press.

—— (2004). 'Epigenetic epidemiology.' *International Journal of Epidemiology* 33 (5): 929–935.

—— and Lamb, Marion. (2005). *Evolution in Four Dimensions*. Cambridge: MIT Press.

Joron, M., Jiggins, C. D., Papanicolaou, A. and McMillan, W. O. (2006). '*Heliconius* Wing Patterns: an Evo-devo Model for Understanding Phenotypic Diversity.' *Heredity* 97: 157–167.

Kendig, Catherine. (2011). 'Race as a Physiosocial Phenomenon.' *History and Philosophy of the Life Sciences* 33 (2): 191–222.

—— (2012). 'Review of *The Species Problem* by Richard Richards.' *The Philosophical Quarterly* 62 (2): 405–408.

Laland, Kevin, Odling-Smee, John and Feldman, Marcus. (2001). 'Niche Construction, Ecological Inheritance, and Cycles of Contingency in Evolution.' In *Cycles of Contingency*, eds. Susan Oyama, Paul Griffiths and Russell Gray. Cambridge: MIT Press.

Leadbeater, Ellouise and Chittka, Lars. (2007). 'Social Learning in Insects – From Miniature Brains to Consensus Building.' *Current Biology* 17: R703–R713.

Mayr, Ernst. (1968). 'Comments on Theories and Hypotheses in Biology.' *Boston Studies in the Philosophy of Science* 5. Reprinted in Mayr, E. 1976. *Evolution and the Diversity of Life*. Cambridge: Belknap Press of Harvard.

—— (1992). 'Species Concepts and their Application.' In *The Units of Evolution*, ed. Marc Ereshefsky. Cambridge: MIT Press.

McKitrick, M. C. and Zink, R. M. (1988). 'Species Concepts in Ornithology.' *Condor* 90: 1–14.

Odling-Smee, John, Laland, Kevin and Feldman, Marcus. (2003). *Niche Construction: The Neglected Process in Evolution*. Monographs in Population Biology 37. Princeton: Princeton University Press.

Oyama, Susan. (2000). *The Ontogeny of Information*. 2nd edition. Durham: Duke University Press.

Panchen, Alec. (1992). *Classification, Evolution, and the Nature of Biology*. Cambridge: Cambridge University Press.

Paterson, Hugh. (1985). 'The Recognition Concept of Species.' In *Species and Speciation*, ed. Elizabeth Vrba. Pretoria: Transvaal Museum.

Peacock, Mary and Jenkins, Steven. (1988). 'Development of Food Preferences: Social Learning by Belding's Ground Squirrels *Spermophilus beldingi*.' *Behavioral Ecology and Sociobiology* 22: 393–399.

Richards, Richard. (2010). *The Species Problem.* Cambridge: Cambridge University Press.

Ridley, Mark. (1989). 'The Cladistic Solution to the Species Problem.' *Biology and Philosophy* 4: 1–16.

Simpson, George Gaylord. (1961). *Principles of Animal Taxonomy.* New York: Columbia University Press.

Staley, James. (2006). 'The Bacterial Species Dilemma and the Genomic-Phylogenetic Species Concept.' *Philosophical Transactions of the Royal Society London B* 361: 1899–1909.

Stebbins, Robert. (2003). *A Field Guide to Western Reptiles and Amphibians.* 3rd Edition. U.S.A.: Houghton Mifflin Company.

Werren, John. (2005). 'Heritable Microorganisms and Reproductive Parasitism.' In *Microbial Phylogeny and Evolution, ed.* Jan Sapp. Oxford: Oxford University Press.

Werren, John, Baldo, Lauren and Clark, Michael. (2008). 'Wolbachia: Master Manipulators of Invertebrate Biology.' *Nature Reviews Microbiology* 6 (10): 741–751.

West-Eberhard, Mary Jane. (2003). *Developmental Plasticity and Evolution.* Oxford: Oxford University Press.

Wilkins, John. (2011). 'Philosophically Speaking, how many Species Concepts are There?' *Zootaxa* 2765: 58–60.

Williams, Mary. (1970). 'Deducing the Consequences of Evolution.' *Journal of Theoretical Biology* 29: 343–385.

—— (1985). 'Species are Individuals.' *Philosophy of Science* 52: 578–590.

Wiley, Edward. (1981). *Phylogenetics: The Theory and Practice of Phylogenetic Systematics.* New York: John Wiley and Sons.

Wittenrich, Matthew and Munday, Philip. (2005). 'Bi-directional Sex Change in Coral Reef Fishes from the Family Pseudochromidae: an Experimental Evaluation.' *Zoological Science* 22 (7): 797–803.

Wu, Chung-I. (2001). 'The Genic View of the Process of Speciation.' *Journal of Evolutionary Biology* 14: 851–865.