

The Biological Species as a Gene-Flow Community. Species Essentialism Does Not Imply Species Universalism

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Abstract:

We defend a realistic attitude towards biological species. We argue that two species are not different species because they differ in intrinsic features, be they phenotypic or genomic, but because they are separated with regard to gene flow. There are no intrinsic species essences. However, there are relational ones. We argue that bearing a gene flow relation to conspecifics may serve as the essence of a species. Our view of the species as a Gene-Flow Community differs from Mayr's definition of the species as a reproductive community. In a reproductive community, each organism is able to successfully reproduce with each other. However, there are species in which geographically distant organisms lost their ability to successfully reproduce, due to strong genetic adaptations to the respective local environmental conditions. Despite this loss of the ability to mutually reproduce, they are still bound by gene flow via continuous intermediate populations. This replacement of Mayr's notion of an interbreeding potential as a criterion for species membership has important implications for the treatment of populations in allopatry and sympatry.

Keywords: species in biology, species essence, relational essence, Mayr's species concept

1. Species Essentialism

What is it that makes an organism a member of a biological species? That very feature of the organism is what we will call a species essence. Assume of a particular organism that it be a Chaffinch (*Fringilla coelebs*). If species essences exist, the following two statements hold true of that organism: (i) If that particular organism did not have the species essence of chaffinches, it would not be a chaffinch. And (ii) whatever organism were to have the species essence of chaffinches would belong to the same species as that particular organism. The species essence, hence, is a feature that supports counterfactual conditionals and is thus not merely contingent, but has modal force. The species essence furthermore is both necessary and sufficient for an organism to belong to a species. Species essentialism is the claim that there are species essences.

In a continuous line from Aristotle to Putnam (1975) and Kripke (1980), species essentialism had been intimately linked to the claims (i) that species essences are intrinsic properties of the species members, (ii) that species are universals instantiated by the species members, and (iii) that species are natural kinds. In the light of modern post-Darwinian biology, however, neither morphological, physiological, ethological, chromosomal, genomic or DNA sequence characters nor any other intrinsic properties can any longer be regarded as essential to a species. Supported by the anti-typologist attitude of the evolutionist Ernst Mayr (2000), some philosophers of science conclude that species essentialism is “untenable” (Dupré 1999). Only recently Okasha (2002) has defended species essentialism by loosening the link between being an essential and being an intrinsic property. Instead, he claims that species essences are relational properties.

In this paper we reject (i)-(iii), but still hold on to species essentialism. We argue that species essences are relational properties: What makes an organism a member of a biological species is its bearing a biparental gene flow relation to its conspecifics. We will argue that the essential character of the gene flow relation excludes the view that species are universals and *a fortiori* that they are natural kinds. Instead, biological species have to be taken as individuals (Ghiselin 1997).

2. Are Species Universals or Individuals?

Species universalism, our primary target in this paper, is the claim that species are universals. Something is a universal if and only if it can possibly occur more than once. Here “more than once” means that (i) the occurrences of the universal may be in distinct regions of space at the same interval of time, (ii) in each occurrence the universal occurs wholly and (iii) the various occurrences of the universal are ontologically independent of one another. The notion of a universal contrasts with the notion of an individual. Something is an individual if it can occur only once. More explicitly, if *x* is an individual, then (a) and (b) are the case.

The first option deals with the possibility of temporal succession:

- a) If *x* occurs wholly in the spatial region A and wholly in the therefrom distinct spatial region B, then the temporal interval *x* occurs in A is distinct from the temporal interval *x* occurs in B.

The second option focuses on individuals with parts:

- b) If x occurs in the distinct non-overlapping spatial regions A and B at the same temporal interval, then it occurs in A and B not as a whole, but only with some proper parts of it.

It is sometimes held that the distinction between universals and individuals is rather arbitrary and not grounded in matters of facts (LaPorte 2004). One might argue, e.g., that for every universal there is an individual that has just all the instances of the universal as parts. And in fact, the conditions (a) and (b) will easily be fulfilled then. This is why condition (iii) in the definition of a universal is so important: It claims that the instances of a universal should be ontologically independent of each other. A piece of gold on Earth and a piece of gold on Mars are independent occurrences. It is not true that the piece of gold on Mars would not have existed, if the piece of gold on Earth had not existed. This is because gold is a universal. In contrast to the many instances of a universal, the parts of an individual are tied together in a way that is essential for them as being parts of the very individual. This “ontological glue” is what constitutes the ontological dependency among the parts of an individual.

The notion of a universal is closely related to the notion of a class and to that of a natural kind. Nominalistically understood classes are linguistically or mentally constructed aggregations of objects that need not have a property in common other than falling under a certain predicate or concept. In contrast, realistically understood classes are constituted by the fact that its members have language- and mind-independent properties in common. Under the presumption of scientific realism the properties in question should make the members of a class subject to nomological generalizations of our best scientific theories. Those classes then are natural kinds and thus are the only classes, the only universals that deserve to be understood in a realistic way (Armstrong 1978).

In biological taxonomy, organisms frequently are grouped into classes along feature similarity. These classes, however, are not natural kinds because each particular intrinsic feature that is diagnostic for a species may be absent from a few members of that species, although those organisms still belong to that species. No intrinsic feature exists that unexceptionally belongs to each member of a species. Hence, species can't be natural kinds. Remarkably, taxonomists do not have any problems to treat organisms with exceptional properties as conspecific to other (regular) organisms. This reveals that something more

fundamental than phenotypic or gene sequence characters guides us in taxonomy (Davies 2005).

If one identifies the species essence with the gene flow relation, it is an immediate consequence that species are individuals rather than universals (Ghiselin 1997). Given that bearing a gene flow relation to its conspecifics is what makes an organism a member of its species, the organism's being a species member is ontologically dependent on the existence of other members of the species. It is thus impossible to regard a species member as occurring independently from other species members as should be the case if species were universals. The ontological dependency of a species member on the existence of conspecifics has a number of further consequences for the metaphysics of species: Firstly, since a species occurs in distinct spatial regions at the same time, it does not occur wholly in each of those regions, but only with some of its proper parts. Organisms and populations thus aren't instances of the species, but parts. Secondly, species are spatio-temporally continuous entities. Gene flow is a real causal bond between the various species members. Thirdly, species are individuals also in the sense that they are spatio-temporally restricted entities. Everything that does not stand in a gene flow relation to species members and does thus not partake in the thereby constituted spatio-temporal continuity is not a species member.

Those considerations allow us to conclude that a species is an individual occurring wholly and independently only once. Note, however, that species are individuals in spite of the fact that there are species essences. Species essentialism thus does not entail species universalism, but is fully compatible with the view that species are individuals. This is a metaphysical message that reaches far beyond the philosophy of biology. The widespread tenet that essentialism implies universalism, as among others advocated by Ghiselin 1997, seems to rest on the presumption that essences have to be intrinsic properties.

3. Intraspecific Polytypes

The claim that no systematic grouping of organisms into classes along intrinsic features would constitute the class as a natural kind is a crucial premise of our argument. It is also supported by considerations about allelic polymorphisms and geographic races.

The Case of Polymorphs:

Allelic variants that arise by mutations are not stably maintained for long evolutionary times under normal conditions, because they disappear by selection or genetic drift, particularly when the population is small. However, in some particular exceptions, selection rewards the synchronous existence of several allelic variants within one and the same population. Well-known examples are blood group alleles or the alleles of the major histocompatibility complex (MHC). Such stable allelic polymorphisms are striking examples for the impossibility of the attempt to group organisms into classes along primarily intrinsic features. Certain alleles of the human MHC locus are more similar to certain respective chimpanzee alleles than they are to the other human alleles of that locus (Figuroa et al. 1988).

At the more complex organismic level, polymorphs are striking examples for intraspecific polytypy. Sexual dimorphism and other kinds of polymorphisms, like mimicry polymorphism, seasonal and ecological polymorphism are well-known examples for intraspecific varieties. Such different types within one and the same species are called morphs. Morphs maintain their different distinct shapes within the population of reproductively linked organisms, without being immingled by crossmating of the organisms.

The most widespread example of morphs is sexual dimorphism. The difference in morphology, behaviour, physiology, and also in the patterns of transcribed genes (transcriptomes) or coded proteins (proteomes) between conspecific males and females may exceed the difference in features between two organisms of different species (Billeter et al. 2006). Understandably, historical examples are frequent where males and females were described as belonging to very different species. In most cases, this has later been corrected by the field observation of copulation, basing con-specificity not on character differences, but on reproductive linkage.

The Case of Geographic Races:

In cases where organisms are distributed over a wide geographic area, the probability continuously decreases that certain alleles from organisms of distant populations ever reach each other. The homogenizing effects of gene flow among distant organisms become more and more ineffective in overriding local adaptations that are caused by environmental factors (Blondel et al. 1999). Consequently, distant organisms tend to acquire different traits and become typologically distinct from the populations of the rest of the species, although they

still may belong to a continuous uninterrupted Gene-Flow Community. Such distant populations that are diagnostically distinct are called subspecies or races.

Speciation can be an evolutionarily very slow process allowing the accumulation of considerable within-species divergence, without the different races finally becoming split into separated species (Magurran 1999). *Vice versa*, the speciation process can be fast, giving rise to separate species without notable genetic differences among them (Sturmbauer and Meyer 1992; Schliewen et al. 2001). In evolution, sexual incompatibility may occur much faster than genetic divergence and, hence, the decision whether two related populations have attained the species rank cannot be inferred from the extent of DNA sequence divergence (Coyne & Orr 1999). Substantial genetic differentiation can accumulate over long time periods without any speciation event. Genetic processes involved in speciation should be clearly distinguished from the genetic characteristics that differ between two extant species. Within-species divergences may exceed many between-species divergences (Ferguson 2002).

We have shown in all these examples that any kind of grouping of organisms by intrinsic features, including DNA sequence differences that indicate genetic distance, has to be set apart from relational grouping by the gene flow cohesion criterion. Two realistically understood biological species are not different species, because they differ in characters or even genetic distance, but they are different species, because they are separated by the exclusion from gene flow. This view of the biological species rejects typological classification.

4. The Gene-Flow Community vs. the Reproductive Community

In a Gene-Flow Community all species members are connected to each other, because the genes “flow” between them. This phenomenon creates the cohesion of the Gene-Flow Community. Yet this shouldn’t be understood in a way that the genes are exchanged (or even just could be exchanged) between all currently existing organisms. Instead, in many cases, this is not the case. If the organisms of two neighboring populations A and B, as well as B and C are connected by mutual successful reproductive capability, then the organisms of population C must not necessarily be connected to A in all cases. From the connection of A and B, as well as simultaneously B and C, the same connection between A and C cannot be inferred.

Yet not even a potential mutual reproduction is given in many cases. With a potential reproductive community are meant the members of a community that, while they don't actually reproduce with each other, they could do so successfully, if they encountered each other (Mayr 2000). But this doesn't seem to be given in several cases, although there are only a few investigations on this. Those organisms that live geographically far distant from each other often have developed strongly diverging genetic characters that have prevailed as local adaptations to the respective regional requirements. In recent biology, examples are accumulating, which show that these local adaptations are in many cases no longer genetically compatible to each other (Pulido 2001). Crossbreeding between such distant organisms should in many cases not lead to long-term competitive offspring, since a large number of different adaptive characters are torn apart by genetic recombination and intermediate combinations of the respective genes are to be expected in the hybrid.

The distant organisms in a Gene-Flow Community are only incrementally connected to each other. The gene flow connection must not be understood in a way that the path of one particular allele from one organism to the others is tracked. One particular allele of a Great Tit (*Parus major*), for example, living in the far west of Europe can only enter an Eastern European Great Tit through subsequent generations, and this can take a long time. But this doesn't matter here. What matters here, is which type of connection combines the organisms of a Gene-Flow Community simultaneously. It can also take an individual water molecule in a river a long time to travel from the spring to the mouth. Nevertheless, the entire river forms a simultaneously coherent unit, because all its water molecules are connected to each other via intermediate steps.

An example for reproductive incompatibility of distant populations is the Black-Capped Warbler (*Sylvia atricapilla*). This bird is migratory in Central and Northern Europe. Its migration direction is genetically fixed and inherited in a Mendelian fashion (Berthold and Querner 1981). Western European and Eastern European Black-Capped Warblers migrate in autumn into different directions. The Western Birds migrate to the South-West; those breeding in Eastern Europe migrate to the South-East. Experimentally produced hybrids between Western European and Eastern European Warblers are phenotypically intermediate and would migrate along the bisecting line of the angle to the South, and thus they would not find their correct wintering area. If all European Black-Capped Warblers were to be understood as a reproductive community in a way that each single selected organism must

possess the ability to reproduce successfully with any other, Western European and Eastern European Black-Capped Warblers would have to be different species, because they cannot be crossed successfully. However, all Black-Capped Warblers are presumably linked by gene flow via intermediate populations. Hence, if all European Black-Capped Warblers were to be understood as a Gene-Flow Community, all organisms would belong to a single species, because mutual gene flow links them all incrementally.

The case of the Black-Capped Warblers is in principle the same as the case of the classical ring species (Irwin et al. 2005). In a ring species, several populations of a species are connected with each other by overlapping populations where the organisms interbreed. If such a connected chain in the course of an expansion circles an uninhabitable geographic region, like a desert or a mountain massif, the distantly residing organisms can meet with each other secondarily after expansion. In a number of examples, it could be shown that these secondarily joining populations have lost their ability to successfully interbreed with each other. Crossbreeding is possible among the adjoining populations, but not between the terminal populations of the ring.

To sum up, we recommend to replace the term “reproductive community” (Mayr 1942) by the term “Gene-Flow Community”, because it is more precise and more unambiguous than the term “reproductive community”. The relation “X interbreeds with Y” is not an equivalence relation, because it is not transitive. Transitivity would mean here that A’s potential to interbreed with B and B’s potential to interbreed with C implies that A has a potential to interbreed with C. But this need not be the case among the members of a species. The relation of interbreeding is more analogous to the relation of adhesive connectedness. The nose is adhesively connected to the frontal bones of the skull, those in turn are connected to the spine, etc. up to the toes. By this stepwise connectedness of the parts, an individual, the body, is constituted. The parts are ontologically glued together and thus ontologically dependent on each other as parts of one and the same individual.

5. The species status of populations that live in allopatry

Understanding reproductive linkage not as a community of organisms that all have the property to breed with each other, but as a community of organisms that are connected by gene flow, has a remarkable impact on the classification of those populations that are separated by allopatry. Two populations live in allopatry if their members, due to external

conditions, have no chance to meet each other. External barriers that prevent mutual contact are in most cases geographic barriers: oceans, mountains, rivers. Allopatric separation contrasts with sympatric separation. In the latter case the organisms do not reproduce due to internal conditions of separation, for example, incompatible mate recognition signals or different courtship behaviours.

Allopatry interrupts gene flow and therefore irrefutably delimits species. If species essence rests on gene flow rather than interbreeding potential, allopatrically separated populations constitute distinct species. This viewpoint has considerable consequences for taxonomical practice: If, e.g., land snails or lizards on marine islands have no chance to meet each other due to the external salt water barrier between them, they are distinct species. Our gene flow notion of the species contrasts with Mayr's notion of a species as a reproductive community. Mayr's definition is: "Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1942). Populations that do not live sympatrically, but are allopatrically isolated, are classified as conspecific by Mayr, provided they would be able to successfully interbreed, if they were brought into contact. The Gene-Flow Community differs from Mayr's reproductive community in two ways:

Firstly, organisms in a contiguous, but large distribution range may lose their mutual cross-fertility if they live far from each other, but are still connected by gene flow. They are still conspecific in our view, but are regarded as different species by Mayr due to their inability to interbreed.

Secondly, organisms that are genetically separated by external barriers are regarded as different species in our view, but they are considered as conspecific by Mayr as long as they have the potential to interbreed with each other.

6. Concluding Remark

Given that intrinsic features of organisms cannot be regarded as essential for species without compromising a realist attitude toward species, the only way to hold on to species essentialism, as it seems, is to look for non-intrinsic, i.e., relational species essences. We argue that (i) the only viable way to understand species realistically is to identify the species essence of an organism with the gene flow relation it bears to its conspecifics, that (ii) since

this gene flow relation is essential for an organism as belonging to a species, each species member is ontologically dependent on other species members and that (iii) a species must consequently not be understood as a universal, but as an individual.

Grouping taxa along intrinsic features or along gene flow relations leads to two different taxonomic systems, whose species units do not match with each other. What has to be strictly avoided is a mixed taxonomy, where intrinsic grouping principles are combined with relational ones. The usage of two different speciation criteria at the same time, as proposed by some evolutionary systematists, results in an uninformative, incoherent system because typological and relational systems delimit species differently (Meier and Willmann 2000). The usage of two different boundary criteria of species also does not allow an objective counting of species or comparing biodiversity in different taxa.

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