

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

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. Within the continuity of this ontological view, species essences were identified with varying biological properties that range from phenotypical ones to DNA sequence features. In the light of modern post-Darwinian biology, however, neither morphological, ethological, physiological, chromosomal, genomic or DNA sequence features nor any other intrinsic properties can any longer be regarded as essential to a species. But what does this mean for the tenability of species essentialism? Supported by the anti-typologist attitude of the evolutionist Ernst Mayr [2000], some philosophers of science conclude that species-essentialism is “untenable” (Dupré [1999]). Ghiselin [1997] goes even

further and takes anti-essentialism as an argument to the effect that species aren't universals, but individuals. Only recently Okasha [2002], who remains neutral with regard to the individual/universal controversy, 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.

Individuals and Universals

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. 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]).

Are Species Natural Kinds?

In biological taxonomy, organisms frequently are grouped into classes along feature similarity. These classes, however, are not natural kinds because mutant organisms may occur that do not share a feature that characterizes the bulk of the other members of the class. Particular organisms that are affected by those mutations do not lose their species membership. No intrinsic feature exists that unexceptionally belongs to each member of a species. A 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.

Vice versa, a particular feature that is diagnostic for a certain species, may occur in some exceptional members of a different species. Even DNA sequence features, which are considered to be “more fundamental” by Putnam [1975] and Kripke [1980], are not essential for species membership. A particular organism that is affected by gene or chromosomal mutations that, for example, may change or delete entire genes or even clusters of genes in its genome, would not necessarily lose its species membership. As a consequence of evolution, features alter in time. Mutation and selection create new features that may spread over the organisms of a population (or may not), and ancient features may gradually disappear. This variation and flux make it hopeless to find any morphological, physiological, behavioural or gene sequence feature that are essential for a given organism as belonging to a given species. 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 features guides us in taxonomy.

Some people may object that our notion of a natural kind is too restrictive. LaPorte ([2004], p. 19), e.g., proposes that a natural kind be a kind with explanatory value. He says, e.g., that “a lot is explained by an object’s being a polar bear. That it is a polar bear explains why it raises cubs as it does, or why it has extremely dense fur. Similarly there are theoretically satisfying answers”, he continues, “as to why polar bears on the whole raise cubs as they do, or have dense fur, or swim miles through icy water. The polar bear kind”, he concludes, “is a useful one for providing significant explanations. It is a natural kind.” Having explanatory value, we reply, is too weak a criterion for natural kinds. Many kind terms have instrumental explanatory value, but no ontological significance. That something is toothpaste, e.g., explains several things: why people take it with them when they travel, why one can buy it in drug stores etc. However, toothpaste certainly is not a natural kind. It is not because it has no essential features that support laws of nature. There are a number of features of a specific tube of toothpaste that might support laws of nature: its mass, its viscosity etc. However, being toothpaste is clearly not among them. The problem with the polar bear is that there is no other essential feature than its bearing a gene flow relation to its conspecifics that makes it a polar bear. However, if there are no intrinsic features essential to polar bears, but only the mentioned relational feature, the polar bear can’t be a universal, and *a fortiori* not a natural kind.

LaPorte ([2004], p. 15), when he defends his view that species are natural kinds, argues against Ghiselin’s species individualism that any talk about a species regarded as an individual could also be satisfactorily interpreted as talk about a species regarded as a kind: “Although the species-individual is not a kind, but rather an individual, there is a property, for any such individual, of being part of that individual. For that property, just as for any other property, there is a corresponding kind, such that possession of the property is the essential

mark of the kind.” The problem with this view is that, even though for any species-individual there, indeed, is a corresponding species-kind, the explanatory potential of the individual may fundamentally differ from the explanatory potential of the kind. Take for example the individual Eiffel tower. There is a corresponding kind: the class of all the rods making up the tower. In purely referential contexts, the talk of the Eiffel tower may indeed be re-interpreted as a talk of the class of Eiffel tower rods. For, the Eiffel tower is identical to some mereological sum of the elements of the class. In explanatory contexts, however, the situation is different. When it, e.g., comes to the statics of the tower, we have to take into regard the relation of the different rods to each other. Any reference to the mere class of rods won’t do. Other issues of interest like the shape, the construction history, the aesthetic quality can only be explained if we talk about the individual Eiffel tower, rather than the class of rods.

The case of species is just alike. The explanatory interests here are defined primarily by evolution theory: And what matters here is gene flow. The explanations of evolution theory recur to the rate of genetic exchange, the size of the gene flow community, the way physiological, ethological, ecological and other factors influence gene flow, etc. If we were to talk just about the organisms as elements of the species-kind, virtually the entire explanatory potential of the species regarded as an individual would be lost, given that the species essence is the gene flow relation.

The Case of Polymorphs

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 balanced allelic polymorphisms. Allelic variants that arise by mutations are not stably maintained 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 balanced 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. (Figueroa et al. (1988)).

At the more complex organismic level, balanced polymorphs are striking examples for intraspecific polytypy. Sexual dimorphism, seasonal polymorphism, mimicry and ecological polymorphism are well known examples. Morphs co-exist without sexual barriers within one and the same population of reproductively linked organisms.

The most widespread example of morphs is sexual dimorphism. The difference in morphology, behaviour, physiology, and also in the patterns of transcribed genes (transcriptome) or coded proteins (proteome) between conspecific males and females may exceed the difference in features between two organisms of different species (Billeter, Rideout, Dornan, and Goodwin [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 feature differences, but on reproductive linkage.

Other examples of morphs are seasonal and mimicry polymorphs. For example, in the Eurasian Map Butterfly (*Araschnia levana*) the first imaginal generation, which hatches in spring, is very different in colour and wing pattern from the second imaginal generation

hatching in summer. Females of the East African Mocker Swallowtail (*Papilio dardanus*, family *Papilionidae*) occur in very different morphs in one and the same population. The mimetical morphs do not resemble each other, but are almost indistinguishable from some very distantly related butterfly species of the *Danaidae* family with respect to visual cues and behaviour. The latter are unpalatable to birds and are thus avoided as a prey.

The Case of Geographic Races

In cases where organisms are distributed over a wide geographic area, gene flow continuously decreases between organisms of populations that inhabit distant areas. 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 [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. Usually, such distant populations that are diagnostically distinct are called subspecies or races.

Speciation can be an evolutionary very slow process allowing the accumulation of considerable within-species divergence, before the daughter species finally become splitted. *Vice versa*, the speciation process can be fast, giving rise to separated species without notable genetic differences among them. For example, the speciation process of cichlid fish in lake Victoria has probably occurred within only a few ten thousands years (Sturmbauer & Meyer [1992]). Sexual incompatibility and interruption of gene flow was completed several times within this time interval, but differences in DNA sequences among the species still remained very low. In some adjacent East African Lakes, Malawi and Tanganyika, a quite similar speciation process of several hundred cichlid species took place, but it had occurred more than

a million years earlier. Here, different species differ in one order of magnitude as much in DNA sequences as the Lake Victoria species flock. We are faced with the situation that sexual incompatibility occurred much faster than genetic divergence. Sexual incompatibility 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 along intrinsic features, including DNA sequence differences that indicate genetic distance, has to be set apart from relational grouping along the gene flow cohesion criterion. Two realistically understood biological species are not different species, because they differ in features 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.

Species Essence and the Gene Flow Relation

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.

Ring Species

The biological species as a gene flow community unites all organisms that are causally linked by introgression of genes from one genome into that of another organism of the species. The notion of the species as a gene flow community can easily be misunderstood in a sense that each randomly selected organism of the community is actually or potentially reproductively connected with any other. In fact, several are not. Males cannot reproduce with males; sterile mutants cannot successfully reproduce; and moreover, a variety of other incompatibilities may exist that prevent mutual cross-fertilization of many organisms belonging to a single gene flow community. This is illustrated by the following example:

Several bird species that breed in Western Europe migrate in autumn to the South-West, those breeding in Eastern Europe migrate to the South-East. In cases where this behaviour is genetically anchored, birds migrating to South-West and those migrating to South-East are clearly reproductively isolated and cannot be crossed. An example is the Black-Capped Warbler (*Sylvia atricapilla*). Its migration direction is genetically fixed and inherited in a Mendelian fashion (Berthold [1981]). 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. In the wild, these hybrids cannot survive, because they will not find their correct wintering area. This is an example for a postzygotic reproduction barrier (inability of the offspring of a hybrid pair to grow or survive) between Western European and Eastern European Black-capped Warblers, although they are presumably linked by gene flow through intermediate populations.

If the notion of the species as a gene flow community were to be misunderstood 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. Since the Black-Capped Warbler is distributed from Inner Asia as far as to the Cape Verde Islands of Africa, where it is not migratory, an estimation of more than ten species of Black-Capped Warblers would not be unrealistic. However, despite these postzygotic barriers, all Black-Capped Warblers are presumably linked by gene flow *via* intermediate populations, and therefore all Black-Capped Warblers belong to a connex whole of related parts whose existence is not independent from each other, because mutual introgression of genes presumably links them all.

The case of the Black-Capped Warblers is in principle the same as the case of the classical ring species. A ring species is a geographically widely distributed group of populations that are connected with each other by overlapping populations where the organisms interbreed. Distantly residing organisms gradually lose their ability to successfully interbreed with each other. Historically, this situation has been discovered in species that breed in the Northern hemisphere circumpolarly. This gave them the name “ring species”. If a species spread out from West to East through Northern Eurasian to North America around the North pole, and secondarily came into contact across the Northern Atlantic with Europe, it was found that the organisms in this contact zone were mutually infertile, although all were fertilely interconnected in the opposite direction.

It is important to notice in this context that the relation “X actually or potentially interbreeds with Y” is not an equivalence relation, because it is not transitive. Transitivity means 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 within the members of a species.

Equivalence relations are well known candidates for class building relations. However, the relation of actual or potential interbreeding is not an equivalence relation and thus not as such class building. 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 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.

Allopecies

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 extrinsic conditions, have no chance to meet each other. Extrinsic barriers that prevent mutual contact are in most cases geographic barriers: oceans, mountains, rivers. However, extrinsic barriers between populations may also exist at the same geographic location, e.g., when organisms are permanently enclosed in a host where they reproduce and cannot leave their hosts, as in the case of some parasites or plant-feeding animals (for example nematodes). Allopatric separation contrasts with sympatric separation. In the latter case the organisms do not reproduce due to intrinsic 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 extrinsic salt water barrier between them, they are distinct species. Whereas the gene flow notion of a species treats allopatry and sympatry alike – what counts is the interruption of gene flow and not if it had intrinsic or extrinsic causes – the advocates of the interbreeding potential see an asymmetry. Mayr's definition is: "Species are groups of individuals that can breed with each other unrestrictedly, but which are genetically isolated from other such groups *at the same location*" (Mayr [2000]). Populations that do not live sympatrically, i.e., *at the same location*, but are allopatrically isolated, are classified as conspecific by Mayr, provided they *would be* able to successfully interbreed, if they were brought into contact. Such populations are called "allospecies". Our gene flow notion of the species contrasts with Mayr's notion of a species in two ways: First, organisms in a contiguous, but large distribution range frequently lose their mutual cross-fertility if they live far from each other, but are still connected by gene flow (see above). They are still conspecific on our view, but are regarded as different species by Mayr due to their inability to interbreed. Second, organisms that are genetically separated by extrinsic barriers are regarded as different species on our view, but they are considered as conspecific by Mayr as long as they have the potential to interbreed with each other.

Two Taxonomic Systems

One major source of conflict in biological taxonomy rises from the fact that evolution affects populations of organism in two fundamentally different ways: (i) their intrinsic nature regarding the change of genes within populations and (ii) their extrinsic nature regarding the flow of genes between populations. Due to mutation and selection, organisms can change their features. How shall taxonomists treat a group of organisms that has acquired new phenotypic or DNA sequence properties in the course of evolution without splitting off from

the stem species? Assume that all organisms of a gene flow community change their features within a certain time interval. We now face a group of organisms characterized by new intrinsic features. This evolutionary process is called *anagenesis*. A classification system that is based on likeliness of features, be they phenotypic or genomic, must accept such anagenetic changes to be taxonomically relevant and acknowledge that this group of organisms has transformed into a new species. The old species has to be regarded as extinct, being replaced by a new species.

Anagenesis cannot be accepted if taxonomy is based on relational species essences such as gene flow. For the gene flow boundaries among organisms need not change in the course of intrinsic alterations. No split into genetically separate populations occurs. The relational view of the species as a group of cohesively linked organisms is completely dependent on the existence of bonds between the organisms. If these bonds do not break, there is no speciation. This kind of ontological “glue” implies that only biparental organisms, that are connected by gene flow, make up a species. The term “species” does not make sense for uniparental or clonally propagating organisms (Mayr [2000]).

If species essence rests on gene flow the only way of speciation is *cladogenesis*, i.e., the origin of two daughter species from a stem species constituted by an interruption of gene flow. This process has primarily nothing to do with any changes in characters. A new species can be brought into being without any alteration in its intrinsic features. The choice between an anagenetic or cladogenetic taxonomy may depend on one’s preferences for epistemological or ontological concerns. However, 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,

anagenesis and cladogenesis, 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 & Willmann [2000]). The usage of two different boundary criteria of species does not allow an objective counting of species or comparing biodiversity in different taxa.

Species as Individuals

If one identifies the species essence with the gene flow relation, it is an immediate consequence that species are individuals rather than universals: 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 (see §1). 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 as a universal would, 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 wide-spread tenet that essentialism implies universalism, as among others advocated by Ghiselin [1997], seems to rest on the erring presumption that essences have to be intrinsic properties.

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