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Species individualism

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There has been a long-standing debate regarding the theory of "Species as Individuals (SAI)" within biological philosophy. Scholars such as Ghiselin, Hull, Mishler, and Brandon have played pivotal roles in defending this theory, demonstrating species as logical, historical, and causal entities in detail. However, the term "individual", which has become exclusive to species, is actually used in a metaphorical sense. When combined with the aggregation phenomenon and integrative nature of species, the hypothesis of SAI can be inferred. Nevertheless, the theory of "Species as Classes (SAC)" also has a strong foundation. Scholars have proposed several reconciliation frameworks to address the issue of whether species are classes or individuals, arguing that species can be both classes and individuals. In fact, SAI can account for the integration and diachrony of species, which are products of processes and processes themselves, with similarity arising from genetic processes. Consequently, SAI exhibits stronger explanatory power, encompassing the content of SAC while achieving its transcendence. This thus forms a new theoretical framework: SAI = SAC + Process/Lineage Relationship + Systematicness/Causal Integration.

KEYWORDS

species, individual, biological individual, individuality, natural kind

1 Introduction

Biological individuals typically include organisms, "gene individuals", and "species individuals", collectively referred to as "Darwinian individuals" by Gould and Lloyd (1999). The definition of an individual often hinges on the theoretical perspective adopted; for instance, replicator theory identifies genes as individuals, whereas evolutionary theory regards species or populations as units of evolution. In the latter case, discussions about species as units and species selection theory (Stanley, 1975) essentially involve treating species as individuals, which represent advanced stages of biological evolution. This article aims to address the question: How can species be considered individuals? This issue pertains to conceptual clarification in the philosophy of biology and involves understanding the ontology of species. It has sparked extensive debate, with support from Haeckel (1866), Ghiselin (1981), Hull (1978), among others. However, Ruse (1987) argues that species cannot be individuals but are instead classes. Chinese scholars such as

Zhao (1993)¹, Dong (1994)², Yang and Li (2018)³, and Chen (2016)⁴ have also made significant contributions to this discussion. Currently, most biologists and philosophers agree that species are individuals composed of organisms rather than classes whose members are organisms. Academically, it is widely acknowledged that discussing species is a challenging endeavor due to natural exceptions in biology and debates over commonalities and differences within the species concept, making consensus elusive. This article reviews and defends the prevalent notion of "species as individuals (SAI)". The argument is termed "species individualism", where the term "individual" is used metaphorically to describe how different organisms under a species integrate into a unified entity. Importantly, biological species are situated within phylogenetic trees and geological strata, representing spatiotemporally bounded entities. Any species is a branch of the tree of life and a unit within the biological lineage. Beyond their overall similarity, we must explain species based on their causal processes and relational spectra. However, the concept of "species as classes (SAC)" remains intuitively compelling. Consequently, grounded in the harmonious framework of "species being both individuals and classes", this article proposes a novel combinatory scheme, arguing that SAI encompasses SAC and provides a more explanatory and coherent argument.

2 The formation of the SAI viewpoint

2.1 Expansion of the meaning of "individual" in biology

Traditionally, the term "species" has been widely regarded as a natural class or collective noun. Therefore, when we attempt to defend the claim of SAI, which deviates from common daily understanding, it may appear confusing and invite criticism. The primary task here is to clarify the concept of "individual". Many people equate biological individual with living organisms, but M. Smith and Szathmáry (Cf [1]) have pointed out that this view is incorrect. In reality, the components of many complex biological individual are themselves living organisms. Darwin employed the concept of "individual" as a key term in constructing the theory of natural selection in *On the Origin of Species*. However, his use of this concept was limited to sexually reproducing animal and plant organisms, without extending its semantic scope or conducting a detailed analysis. We observe that the widespread application of the

1 Zhao believes that species is a set concept rather than a class concept.

concept of "biological individual" is metaphorical rather than literal, and its connotation and extension have expanded significantly within a biological context.

Individuals capable of survival and reproduction can be categorized into paradigmatic individuals and non-paradigmatic individuals. As a set concept (plural representation), "paradigmatic individual" refers to organisms with prototypical properties, a term first introduced by Ghiselin (1981) and primarily referring to certain higher animals and plants. Subsequently, J. Wilson elaborated on this concept⁵. These prototypical attributes are possessed only by a subset of Earth's organisms. When an organism exhibits only some of these prototypical attributes, it is classified as a "non-paradigmatic individual". Non-paradigmatic individuals occupy a broader range within Earth's ecosystem, such as microbial organisms, which are often referred to as the "ecological overlords" of the planet. Examples include blackberries, ferns, poplars, bamboos, and certain fungi, which can reproduce either sexually or vegetatively. These organisms are interconnected via underground rhizomes, making their spatial boundaries difficult to define. They are thus considered nonparadigmatic individuals. If we restrict biological individual to clear spatial boundaries, we would be unable to delineate or count such entities. For instance, uprooting a blackberry or bamboo reveals roots and stems connected to countless other plants, some of which are intermittently linked. Numerous similar clusters exist, suggesting that treating them as a unified whole—a single organism-regardless of the number of smaller constituents, is more appropriate. Here, the concept of biological individual has been expanded to include at least some clustered organisms as individuals. In terms of biodiversity, as Yang and Li (2018) have noted, three scenarios emerge: spatially, the living world forms a multi-level nested hierarchy; temporally, the vast "Tree of Life" has grown and branched over evolutionary history, creating a highly diverse biosphere; environmentally, even the same organism may switch between different organizational patterns in response to environmental changes, thereby exhibiting varying individualities across its life history (Godfrey-Smith 2009, pp.109-115). The complexity of the living world underpins the extension of the meaning of individuality in organisms.

Furthermore, the concept of biological individuals can also be extended to groups and populations. Particularly in microbial communities, the entire population of a specific microbial species is often regarded as an individual. For instance, slime molds exhibit dynamic behavior by gathering and dispersing at different times. When food is abundant, they exist as single cells; however, when food becomes scarce, they aggregate to form a multicellular structure known as "slime molds". In this context, only the population of slime molds can be considered an individual.

² Dong posits that species represent the integration of structural and functional units. Moreover, species as individuals provide a new interpretive framework for evolutionary studies. The SAI proposition encompasses all these crucial conclusions.

³ Yang and Li analyze the boundary problem of "biological individual" and its ontology.

⁴ Chen suggested that we adopt a dynamic system theory to explain species and natural classes, so that the traditional status of species as natural classes can be preserved.

⁵ Wilson, 1999 (p.9) outlined a total of seven attributes: (i) spatial and temporal continuity; (ii) spatial and temporal boundedness; (iii) composed of heterogeneous causally related parts; (iv) development from a single cell to a multicellular body; (v) subject to impaired function if some of its parts are removed or damaged; (vi) ability to reproduce sexually, and (vii) genetic homogeneity.

Consequently, at least some species' groups and populations qualify as individuals.

Can this concept be extended to the species level? Our answer is affirmative. If the existence of a species is confined to such groups, then group individuals and population individuals are equivalent to species individuals, thereby substantiating the feasibility of the SAI thesis. However, the SAI thesis employs the term "individual" in a metaphorical sense, expanding the understanding of individuals from tangible and visible entities to intangible and abstract ones, thus transcending the intuitive nature of everyday cognition. Biological individual demonstrate spatial dispersion, internal functional integration, and external interaction. The definition of species based on individual characteristics, such as cohesion, will be explored in the second part of this article.

In addition, the investigation of biological individual should not be confined solely to their closed or discrete spatial properties but should also encompass their temporal characteristics. Biological individual are four-dimensional entities (Brogaard, 2004). Each biological individual undergoes a continuous process from inception to termination, which is interconnected with other biological entities both preceding and succeeding this process. Consequently, we can extract a finite segment of events from longer, continuous evolutionary processes as individual events when necessary, categorizing them as biological individuals within a temporal sequence. The evolutionary unit of species, serving as the terminal end of a branch and a transient carrier in the flow of life, exhibits a high degree of dependence on the temporal dimension.

In general, to employ the concept of biological individual in a metaphorical sense, it is essential to expand its meaning across three dimensions (Wan et al., 2024):

- Expanding from paradigmatic individuals to nonparadigmatic individuals;
- II. Extending from individual organism to genes, cells, groups, populations, and species;
- III. Broadening from spatiality to temporality.

2.2 Aggregation phenomenon among organisms within a species

T. H. Huxley observed that coelaconic animals can form larger functional units through partial division, wherein each animal assumes distinct functions such as reproductive, nutritional, and motor roles, thereby creating a coordinated whole (Ghiselin, 1981). Each animal appears to function as an organ within this collective system. Should we consider an individual member or the entire group as an individual? Huxley's resolution is as follows: Given that in the life history of many coelaconic animals, the sexual reproduction phase is succeeded by the asexual reproduction phase, and all animals from one sexual event to the next constitute a single unit, each life cycle can be regarded as an individual (Ghiselin, 1981). This approach treats the biological events occurring during this process as individuals, defining a

group of functionally integrated and aggregated organisms as a single individual.

In addition to typical coelaconic animals, numerous analogous biological aggregation phenomena exist in nature. Locke once argued that bird flocks can be regarded as individuals (Ghiselin, 1981). In the ant kingdom, the queen ant reproduces, worker ants perform labor, and male ants perish shortly after mating. These distinct social classes aggregate into a single functional unit. For instance, corals, hydroids, sponges, mollusks, mosses, hemichordates, and even certain worms are all composed of a multitude of multicellular units. Each species is socially integrated and exhibits a high degree of interdependence, often referred to as "superorganisms". Superorganisms typically denote larger entities formed by organisms of the same species, whereas "holobionts" generally refer to biological entities resulting from interactions between different species. Based on this, J. S. Huxley (1926) proposed the "unit aggregation principle", which describes the combination of many originally similar units (each unit being a small or sub-individual) to form a collective. When such a collective forms, it tends toward becoming a unified unit, thereby creating a cohesive entity. When this unity reaches a level where it can be considered a single individual, it must (Huxley, 1926):

- Maintain the foundation of communication among its members and provide increasingly effective means of communication between them;
- II. Establish a division-of-labor mechanism among members at different hierarchical levels;
- III. Construct a hierarchical system of dominance and control, through which one region or category composed of its members is controlled by another region or category, and so on, until a final region or category that dominates all other regions or categories is identified.

Only in this way can the set originally composed of independent units evolve into a new whole with biological unity and singularity.

2.3 Integration properties between organisms within a species

In the context of organisms, integration refers to the evolutionary development of various parts within an organism toward a state of coordination and cooperation to fulfill the organism's survival and reproductive goals. For example, the coordinated functioning of the organs in humans constitutes a highly integrated life system. At the species level, integration denotes the high degree of interdependence among various components (i.e., organisms) within a species, such as malefemale relationships, functional combinations, altruistic behaviors, and self-sacrifice—all of which are manifestations of integration. Dobzhansky (1951, p.6) stated that in organisms engaging in sexual reproduction and cross-fertilization, if we observe mating and reproduction, we will quickly discover that they typically form

highly discrete reproductive communities. These communities consist of individuals interconnected through sexual reproduction, shared lineage, and common parental relationships. Therefore, a species is not merely a group or a taxonomic category but also a super-individual biological entity. In principle, this holds true regardless of whether the species exhibits common morphological characteristics. By analogy, entities such as ethnic groups, religious organizations, or large-scale social events—based on causal forces and their comprehensive nature—are qualitatively referred to as "social individuals" or "superorganisms" rather than merely a collection of individuals or events. Another example is the Mendelian population, where different organisms within the population form an integrated unit by sharing a common gene pool through reproduction and inheritance. Spencer's term "superorganism" was initially used metaphorically to describe social organization but later came to refer to large, integrated populations in nature (Ghiselin, 1981). Symbiotic superorganisms emphasize that individuals of different species form a higher-level, functionally unified "organism" through close collaboration, maintaining reciprocal and equal relationships rather than master-servant dynamics. Take lichens as an example: while appearing as a single plant, they are actually symbiotic communities composed of fungi and algae (or cyanobacteria). Earth's biosphere highlights that all life and non-living environments on the planet form an interconnected, selfregulating macro-system. This complex phenomenon allows us to view multi-species systems as vast biological entities. The collaboration, integration, and wholeness among species unite numerous small components into a unified organism in biological terms rather than physical ones.

2.4 Proposing the SAI viewpoint

Given these biological examples and the principles they embody, species can easily be regarded as independent units or special entities, meaning that they are individualized species. When the expanded concept of individuals encompasses all species, the SAI thesis evolves into the SAI viewpoint.

Haeckel first proposed in 1866 that species could be viewed as individuals, a perspective later echoed by T.H. Huxley. Phylogenetic biologist Hennig leaned toward the SAI view, arguing that species individualization is achieved not through intrinsic attributes but through relationship (Rieppel, 2007). Ghiselin (1974) was the first to explicitly propose the viewpoint that "species are not classes but individuals", providing logical reasoning for this claim. However, this seemingly "erroneous" viewpoint initially garnered little attention until Hull joined the discussion and defended it, sparking widespread debate. At the same time, Löther also contributed arguments on this topic (Rieppel, 2011). Ghiselin and Hull's proposition can be summarized as follows: species are real, spatiotemporally bounded individuals (entities, particulars, things, bodies, objects) rather than infinite universals in space-time (sets, classes, concepts, natural kinds). Evolutionary cladist Wiley and evolutionary systems scholar Mayr both agree with the view that "a particular species is an individual (Zhao, 1993)." Dong (1994) pointed out that the SAI viewpoint has two meanings: on the one hand, it emphasizes that species are not collectives or natural classes, meaning species are not defined by principles or fundamental properties of laws, and there is no necessary law governing the classification of some objects into a certain species; on the other hand, it emphasizes that species are natural individuals, meaning systematic evolutionary relationships provide a spatiotemporal framework that establishes causal connections between one species and another.

For metaphysical philosophers, this represents a bold departure from tradition; for biologists, it constitutes a highly counterintuitive statement. However, as the discussion deepened, many scholars in the evolutionary biology community—particularly those who embraced Hennig's phylogenetic approach—began to acknowledge this viewpoint. Biologists such as Mayr (1976), Wiley (1981, pp.74-76), Lidén and Oxelman (1989), Mishler and Brandon (1987) gradually recognized the growing applicability of species individualism, which holds unique value and significance in addressing certain theoretical questions in biology. In explaining biological altruistic behavior, species individualism (which acknowledges selection at the species level) demonstrates significantly greater explanatory power compared to "individual choice theory". Species individualism regards different organisms within the same species as internal parts or components of the species itself, attributing partial self-sacrifice to the inherent integrative behavior of the species. This approach offers stronger explanatory power, akin to proving in complex numbers that the product of any two sums of squares must be the sum of squares of two integers (a proposition difficult to prove within the realm of real numbers). In contrast, individual choice theory treats organisms as discrete individuals, dividing them into self and others. While it can explain conflicts and cooperation between individuals, it struggles to adequately account for self-sacrifice among individuals—a phenomenon commonly observed in nature. Under species individualism, organisms exhibit synergistic effects involving functional efficiency, novel traits, functional complementarity, aggregation or threshold effects, and other combination effects (Ghiselin, 1974).

3 Defense of SAI theory

The SAI viewpoint is both novel and counterintuitive, diverging significantly from the traditional SAC theory, with its greatest obstacle being this very deviation. Consequently, deconstructing SAC theory constitutes a critical aspect of defending SAI. Through multiple effective defenses, the SAI viewpoint has been elevated to SAI theory. Here, we first elucidate the essence of SAC theory before proceeding to defend SAI theory.

3.1 The essence of SAC theory

In daily intuition, we classify a swan as a swan because it exhibits a series of swan-specific traits. Consequently, when we

encounter a bird with these traits, we can swiftly make an accurate judgment. Why do we not mistakenly classify toads as swans? The shared traits derived from swans exist as abstract entities in our impressions and memories, serving as the basis for our judgments. Moreover, we understand species through samples or type specimens. Samples represent statistical instances, and describing them provides a rough approximation of a species. This approach aligns with the methods of natural history based on daily intuition.

In academic theory, the core of SAC theory lies in the concept of "shared attribute". What exactly is a shared attribute? In logic, propositions consist of a subject and predicates, with predicates introducing attributes into discourse. Attributes are non-material entities that can be simultaneously shared by many different things. Since attributes are universal entities rather than being possessed by specific or individual objects, multiple individual organisms can share a single attribute at the same time. This concise "one-tomany" pattern allows the same attribute to encompass all classes or sets of objects that share that attribute. Classes are defined by attributes, and different organisms only become members of a class when they possess shared attributes. Classes use shared attributes as the basis for induction, and inductive reasoning establishes the concept of species. Darwin believed that a species is a group of individuals that are highly similar to one another (Ruse, 1987); Linnaeus also held that organisms are grouped into taxonomic units based on their shared characteristics (Chen, 2016). Mayr (1963, pp.521-522) emphasized the role of gene flow in the formation and maintenance of species, which consist of local populations that either share genetic resources or have the potential to do so. This sharing promotes the stability and coadaptation of genes within species boundaries, resulting in significant similarity in genotype and phenotype among members of the same species. In the "Homeostatic Property Cluster (HPC)" theory proposed by new essentialists such as Boyd (1999, p.142), Barker and Wilson (2010), HPC classes exhibit two key characteristics: (i) members of the class share a cluster of co-occurring similarities, but no single similarity is necessary for membership in the class. While differences between members may exist, these attributes must be stable enough to allow successful induction. (ii) the co-occurrence of similarities among members of the class is caused by the self-balancing mechanisms of the class itself, such as hybrid reproduction, shared ancestry, and common developmental mechanisms. Species are considered typical examples of HPC (Chen, 2016). This bottom-up approach identifies what Mayr referred to as the "species taxon" and addresses the relationship between structure and function (Dong, 1994).

From top to bottom is the classification of organisms. The classification of organisms constitutes a fundamental task in biological science research. By classifying organisms based on their morphology, patterns, or genes, we can identify different species and categorize them into distinct biological lineages. Aristotle attempted to define a species by its genus and unique characteristics—that is, by specifying the characteristics shared by

all members of the species-thereby disregarding individual characteristics (i.e., the differing traits among organisms within a species) (Rejane, 1984). Aristotle's method follows the principle of "genus plus specific difference", and the species classified under this approach belong to what are termed "Aristotelian natural types" (Coleman and Wiley, 2001). Linnaeus first formulated the principle of defining biological genera and species, continuously providing definitions for each species through his universal classification system, as he believed these definitions captured the essence of various organisms (Dong, 1994). With technological advancements opening the door to the microscopic world, people began classifying microorganisms and determining their phylogeny based on gene types. The top-down approach identifies what Mayr referred to as the "species category", addressing the relationship between individuals and collectives (Dong, 1994). According to classical taxonomy, an organism is a member of a species, and each species is a member of the category of species (Rejane, 1984).

Obviously, the concept of species originated from induction and classification. Scholars have identified or agreed upon a species based on overall similarity, structural similarity, and other factors. Species are structurally similar clusters of organisms, and their similarity is objective and real. Even if we cannot reach a consensus on the criteria for judging similar attributes, we must acknowledge that certain shared attributes form the basis for the existence of the concept of species. Therefore, the determination of species has traditionally been grounded in essentialism. The essentialist concept includes but is not equivalent to the eternal and unchanging logos, which can express a steady state and an invariance amidst change. Essentialism is not static and should not be equated with the theory of species invariance. In the updated version of SAC's HPC theory, each species member possesses some of the attributes, and none of these attributes must necessarily be shared by all members of the species. HPC theory addresses the limitations of traditional essentialism to some extent (Casetta and Vecchi, 2019). Species, as clusters of integration processes, exhibit varying degrees of stability over different time periods. Paleontologists have observed that "the formation and extinction of many species occur suddenly (Keller et al., 2003); from formation to extinction, the morphology of species changes very little", especially in the case of inert species (Dong, 1994).

Under generalized and abstract shared attributes or common features, different organisms serve as instances. In this context, the debate between SAI theory and SAC theory ultimately revolves around the issue of commonalities and differences, and the defense of SAI must begin with logic.

3.2 Defense I: species as logical entities

Ghiselin (1966) directly refutes the notion that "only individuals are real, as universals are purely mental constructs", and explicitly proposes the proposition that "biological species are, in the logical

sense, individuals". The term "individual" carries not only biological significance but also logical significance. In a logical sense, species are individuals rather than classes because "a species name is a proper noun (Ghiselin, 1966)". (i) In addressing the question of "what constitutes an individual", Ghiselin specifically introduced the concept of "individual populations". (ii) Ghiselin (1974) pointed out that the concept of species in morphology, genetics, and physiology shares a common flaw: the composite whole is treated as a class defined by the intrinsic attributes of its members.⁷ (iii) Ghiselin (1974) explicitly rejects the "nominalistic species concept": classes are not real entities, species are treated as classes, and thus species are deemed unreal. However, in Ghiselin's view, species are not merely classes—they are real because they represent specific entities of existence, namely, a particular species. While Ghiselin's research on "species individualism" is groundbreaking, it is not fully comprehensive, and some expressions lack clarity, thereby facing a series of logical challenges.

In addition to Ghiselin, Hull's logical analysis of SAI theory posits that classes possess uniform properties and adhere to specific natural laws, whereas species are individuals with varying reproductive characteristics, making it challenging to establish strict natural laws. "One advantage to biologists of the historical entity interpretation of species is that it frees them of any necessity of looking for any lawlike regularities at the level of particular species (Hull, 1978)" Specific organisms belong to specific species because they are all part of a biological lineage, rather than based on some essential or common characteristics.

The fallacy of treating "species as a collection" is the easiest to deconstruct. Rieppel (2009) pointed out that regarding species as sets is incorrect because, in strict mathematical definitions, there can be no inherent similarities between elements within a set. Furthermore, species evolve, whereas sets cannot evolve, and any determined element within a set remains constant. Therefore, even if a species could be considered a class, it cannot be regarded as a set.

The logical defense of SAI is grounded in "the class-individual dichotomy" (Kluge, 1990), and the clarification of the concepts of class and individual often becomes entangled in intricate debates reminiscent of scholastic philosophy. Organisms within a species must exhibit some form of relationship, such as kinship or gene flow dynamics. They cannot be entirely independent of one another, nor can they be fully abstracted or reduced to mere logical representations.

3.3 Defense II: species as historical entities

Ghiselin's earlier analysis of species individual was confined to logical levels and did not address the spatiotemporal continuity of individuals. Hull redefined the notion of individuals and analyzed the concept of species from a historical standpoint, thereby granting species an ontological position within the evolutionary process.

Hull (1978) discussed individuals within the framework of evolutionary biology, defining them as "spatiotemporally localized cohesive and continuous entities". Hull (1978) argued that "species" can be viewed as "supraorganismic entities" in evolution—"historical entities" rather than "spatiotemporally unrestricted classes". The various parts of a species form a spatiotemporal sequence, wherein spatially adjacent parts and temporally continuous parts are causally interconnected. This perspective implies that a single species incorporates a temporal dimension or is composed of temporal slices (Hull, 1988, p.500). Hull's (1978) argument can be summarized into four points: (i) In sexually reproducing species, organisms must aggregate their genes for reproduction, resulting in offspring that contain a combination of parental genes; from the perspective of the gene pool, integrated species resemble individuals more than classes. (ii) To some extent, the genes of sexually reproducing species are recombined in each generation. (iii) Even if the entire species is not fully integrated as a selection unit, it remains an evolving entity; at lower levels, as a result of selection, the outcome inevitably forms a biological lineage rather than merely a group of similar organisms. (iv) For differences in gene frequency to accumulate within a population, species must maintain temporal continuity.

Hull's historical entity perspective emphasizes the evolutionary nature of species, situating them within a vertical evolutionary process and enabling a multidimensional analysis of their characteristics.

3.4 Defense III: species as causal entities

After conducting logical and historical analyses of species, philosophers of biology have introduced a new attribute—causal interaction. Causal effects encompass not only diachronic and evolutionary factors but also extend to other dimensions, elevating species from mere historical entities to "causal entities" and advancing species individualism to a new stage.

Mishler and Brandon (1987) contend that we should move beyond simplistic "class-individual" distinctions and differentiate causal effects in biological processes into two types—causal integration and causal cohesion—and then examine species based on their integration and cohesion characteristics.

Given that the concept of individuality is applied in species interpretation, Mishler and Brandon (1987) first refine individuality into four subparts:

I. Spatial boundaries——all known evolutionary processes certainly produce entities at all taxonomic levels that are spatially restricted. Thus it would seem that species taxa, properly named, would always meet this criterion.

⁶ Individual populations serve as "breeding communities" and "composite wholes". Consequently, based on characteristics such as "breeding", "composition", and "reproductive isolation", species as individual populations are no longer collective nouns but rather proper nouns (Ghiselin 1974).

⁷ It is a well-established principle in philosophy that parts cannot fully define the whole, and certain attributes of the whole are not merely the sum of its parts. Consequently, individual organism attributes cannot adequately define species, even though species are composed of living organisms.

II. Temporal boundaries——a taxon must have a single beginning and potentially have a single end in order to count as an individual under this criterion. Depending on one's definition of species, taxa could easily be recognized that are spatially, but not temporally, restricted.

- III. Integration—we have designated "integration" to refer to active interaction among parts of an entity. Examples of this type of causal interaction include the effect of the heartbeat on the circulatory system of an animal, mating relationships and gene flow within populations and species, and processes of frequency-dependent and density-dependent natural selection.
- IV. Cohesion—we have designated "cohesion" to refer to situations where an entity behaves as a whole with respect to some process. In such a situation, the presence or activity of one part of an entity need not directly affect another, yet all parts of the entity respond uniformly to some specific process (although details of the actual response in different parts of the entity may be different because of the operation of other processes). Examples of this type of causal interaction include the failure of developmental canalization in biological systems, and processes of density-independent natural selection.

Mishler and Donoghue (1982) introduced the concept of "phylogenetic species" within the framework of systems biology. The phylogenetic species concept can capture potential unity that the biological species concept cannot, such as certain lost common derived traits, and it also incorporates knowledge about genetic information from modern molecular biology (Mishler, 1985). Grouping (estimated through monophyletic taxa) is determined solely by studying synapomorphies, which refer to derived trait states shared by two or more terminal taxa in evolutionary biology and inherited from their most recent common ancestor. In cladistics, synapomorphies are used to infer phylogenetic relationships. This approach relies on shared and derived characteristics between different organisms, and the ranking concept employed typically involves varying degrees of inclusiveness (i.e., the number of shared derived features between any specific internode in the branching diagram), aligning with current taxonomic practices. The meaning of species under this system can be summarized as follows (Mishler and Donoghue, 1982): "A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly (usually, but not restricted to, the presence of synapomorphies), that is ranked as a species because it is the smallest 'important' lineage deemed worthy of formal recognition, where 'important' refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case."

In short, the theory of species as causal entities explains the individualization of species from the perspective of biological lineages. The defense along these three directions constitutes a key argument for the SAI theory, which elucidates and examines the intrinsic relationships among species far beyond the simplified explanation of species as classes. Even if it does not fully replace the "class explanation", it can constrain the level of explanation or

its scope of application. In this sense, SAI theory surpasses SAC theory.

4 Reconciliation between SAI and SAC

The aforementioned defense can be divided into two aspects: argumentation and refutation. In elucidating the cohesion, integration, diachronicity, causal interaction, and other aspects of species, as well as in analyzing species through monophyletic analysis, SAI theory deepens our understanding of species. However, in terms of refutation, the strong rejection of SAC theory may not necessarily succeed. This is because, although species lack the strict regulations characteristic of classes, using classes as a metaphor for species is based on the metaphorical meaning of classes—a point that scholars have often overlooked. Class is a complex and broad concept, not limited to natural laws or similar regulations. Some class-based regulations may not apply to species, such as the ability of a class to exist independently (which species cannot do, as they are relational groups), or the fact that natural classes within a class follow natural laws (while species are not subject to such laws). However, other regulations, such as identity, similarity, and related inductive principles, do apply to species. SAC theory, grounded in the cornerstone of "shared attributes", maintains objectivity, rendering any semantic sophistry ineffective. Moreover, SAI theory itself incorporates the concept of commonality in its defense, such as shared derivations and genetic similarity. Given this, some philosophers staunchly reject SAI theory. For instance, Ruse (1987) argues that SAI theory contradicts many established biological perspectives and defies logic. Species should be regarded as classes rather than individuals -- "any species effects are just epiphenomena on individual effects, or at most, on population effect" (Ruse, 1987). Nevertheless, this does not imply that SAC theory is without flaws, as it remains embroiled in debates over practical classification standards.8

So, how should we address the opposition between these two perspectives? Many philosophers have proposed harmonic solutions, but here we will only briefly summarize them.

The first harmonic solution is semantic blending—combining the concepts of "class" and "individual". The earliest proposal came from Van Valen (1976), who referred to species as "individualistic classes", where the conflicting concepts of "class" and "individual"

⁸ There are multiple theoretical approaches to the scientific classification of species, including biological species, ecological species, structural species, evolutionary species, and morphological species. To date, more than 20 such approaches have been proposed, yet no single standard is applicable to all cases of all species. Kunz categorizes these species concepts into three main types: First, the phenetic species concept, which defines species as groups of organisms sharing similar characteristics; Second, the cladistic species concept, which considers a species to be a group of organisms descended from a common ancestor; Third, the gene-flow community concept, which posits that species are groups of organisms interconnected through gene flow. (Cf. Chen 2016)

were forcibly merged. However, this approach does not advance the resolution of the problem but instead creates confusion. Consequently, Ghiselin (1981) pointed out that this statement represents a semantic deviation⁹, which could also be used to fabricate the concept of "classlike individuals". It appears that possessing class attributes does not necessarily make an individual a class. Wiley (1981, pp.74-76) emphasized the analogy between organisms and preferred to define species using the concept of "historical entities" that resemble individuals. Although Wiley supports the SAI theory, his approach exhibits a certain harmonic quality, contrasting sharply with Valen's in the central terms of the concepts he constructs.

The second harmonic solution is semantic clarification recognizing that entities possess both individual and class meanings. The analysis of many concepts involved in SAI theory is not without flaws. Dong (1994) once pointed out that individuality (differences among components) and collectivity (identity among components) represent the two poles of the genus relationship, which are essential attributes of any entity. In other words, individuality and collectivity can be unified within a single entity. However, Hull's argument for the SAI viewpoint focuses exclusively on individuality, leading to an extreme position. Zhao's explanation is more lucid. Although the distinction between class and individual is clear, there exist entities that embody both class and individual characteristics. For example, A is an individual, while his family represents a larger individual. A is both a part of his family and a member of it. Such "larger individuals" differ from narrow individuals. In biology, a specific species qualifies as a "larger individual". The term "larger individual" here actually refers to the extended meaning of individuality, namely, the generalized individual (Zhao, 1993)

The third harmonization scheme is language translation—the same part can be described using different languages. Okasha (2002) claims that whether a species is conceptualized as an individual, class, or historical entity is largely a matter of agreement, which aligns with Dupré's (1995, p.43) viewpoint and is known as the "interpretability viewpoint": in SAI, an organism is "a part of the species individual", while in the HPC viewpoint, the organism must be conceptualized as "a member of the natural class of species", and discussions about the organism can be translated accordingly (SAI is no exception) (Brigandt, 2009). The argument for interpretability suggests that two languages-mereology and set theory-possess equivalent expressive power. Additionally, set theory posits that they possess equal expressive power; conversely, the same part of reality can be equally well described through two different languages. In this way, SAI and HPC may be closer than we think. Rieppel (2007) also share a similar view: species are both classes and individuals, and "where there are properties, there also are kinds. As long as it is admitted that species have causally grounded properties, it has also to be admitted that talk about species as individuals can be translated into talk about species as natural kinds". The interpretability perspective avoids taking a stance on species from metaphysical and biological perspectives, focusing instead on their conceptual or linguistic issues: a certain aspect of the biological domain can be conceptualized and described using two terms.

The fourth harmonic scheme is context differentiation treating SAI and SAC as outcomes in different contexts. In Falk's framework, a species within the context of natural selection evolution is an individual, much like Mendelian populations. It is the diversity of hybrid organisms that renders species a coordinated and unique entity in the context of genetics and ecology; in other cases, species should be regarded as a category composed of natural classes. Not only do we classify organisms within a species into a natural class based on similarity criteria in daily discourse, but also in research on anatomy, physiology, behavior, development, and other biological aspects (Falk, 1988). Reydon (2003) further points out that the term "species" represents different concepts in different contexts of biological research, meaning that in some contexts, species may be best understood as individuals, while in others, their correct ontology is a class or even a natural class. Many discussions about species ontology focus on only one background, leading to differing conclusions: Ruse (1987) analyzed evolutionary biology and concluded that species are classes, whereas Lidén and Oxelman (1989) considered phylogenetic systematics and believed that species are individuals. These two conclusions may hold validity within their respective contexts, but their validity does not automatically extend beyond the boundaries of these contexts. Thus, Reydon (2003) summarized that biological science comprises several distinct (and sometimes partially overlapping) research backgrounds, each employing different species concepts to address its own specific problems. Therefore, the term "species" is best understood as the "common denominator" of many different scientific concepts. The "common denominator" does not imply that species have a universal meaning but rather that the word itself is universally used. Kitcher, Kornet, Shaw, and other scholars also share a similar view, arguing that different research backgrounds often impose incompatible demands on the concept of species, and no single concept can adequately satisfy all biological research contexts. The disciplinary backgrounds of SAI theory and SAC theory can be roughly summarized as follows:

- I. Academic background supporting SAC theory: evolutionary biology, functional morphology, anatomy, physiology, natural history, etc.;
- II. Academic background supporting SAI theory: evolutionary biology, systematics, genetics, ecology, etc.

Evolutionary biology is a rich and multifaceted discipline, with different subfields providing support for distinct theories.

Obviously, the approach of opposing SAI and SAC is no longer reasonable. The compromise plan represents a strategy to promote the coexistence of the two perspectives, and the fourth scheme already embodies a form of pluralism. Under the principle of open pluralism, the concept of species serves as both the "common denominator" and the "kaleidoscope", allowing for the

⁹ This means referring to deviating from the original semantics of individuals and classes.

coexistence of synchronic and diachronic perspectives. The representativeness of biological specimens presupposes classes, while the process of species formation presupposes individuals. However, the reconciliation plan does not imply any inherent connection between the two. How should we further understand the relationship between them? This involves integrating the two perspectives, in other words, seeking an effective integrative solution that can internally explain why SAI and SAC can coexist.

5 Conclusion: SAI's equation

Wilson (1996) once argued that it is absurd for something to be both a natural class and an individual, because "individuals and classes belong to fundamentally different ontological categories". However, Wilson's claim of "ontological incompatibility" has not been widely accepted. de Queiroz (1999, p.67) pointed out that the general concept of species is compatible with conceptualizing species as either individuals or classes. From a metaphysical (and biological) perspective, species can be viewed as both individuals and classes. The compatibility at the ontological level serves as both the premise and content for elucidating the relationship between SAI and SAC. Due to the complexity of the subject matter, this will be briefly outlined in separate sections below.

5.1 Species are essentially process-oriented wholes

5.1.1 Process oriented

The persistence theory of species permits the application of the "time-intrinsic theory" to explain time-indexed properties (Rieppel, 2009). Time has a direction (an arrow), and the continuous process of species does not involve repetition or reciprocity but rather involves creative advancement. The disintegration of ancestral systems corresponds to the reintegration of descendant systems. Ancestral and descendant species succeed one another due to a series of reproductive events, forming a process entity and part of the network lineage relationship. Simultaneously, this process also gives rise to the internal components and lineage relationships within species (as discussed later). For instance, the evolutionary chain of whale species is "Bucky whale \rightarrow Wandering whale \rightarrow Rodehou whale \rightarrow Thick whale \rightarrow Humpback whale", whose fossil evidence clearly shows the progressive changes in its skull, ear bones, limbs and pelvis.

5.1.2 Identity

Colless (2006) contends that species identity is determined by their integration principles. Species are path-dependent historical entities. The history of a species can only be established based on its unique evolutionary origins and phylogenetic relationships, such as the spatiotemporal aspects of lineage relationships (i.e., kinship relationships). Casetta and Vecchi (2019) further propose that the biological nature of the origin process is a key factor in species

identity, with the historical processes experienced by species being contingent (e.g., geographic segregation, mutation history, population dynamics). It is clear that each species has a unique history, forming and maintaining its distinctive gene pool in its own unique manner (i.e., through a specialized process of mixed evolutionary causality). For instance, there are over 7 billion people living on Earth. On average, 99.9% of the DNA series of any two random individuals are the same, which is used to build various organs (such as the FOXP2 gene that controls language ability), and the remaining 0.1% of the genome determines differences in race, appearance, etc.

5.1.3 Part-whole relationship

(i) Reproducing organisms are integrated and inevitably undergo stages of "material overlap" and "physical replication". During the replication stage of entities, life information polarizes into zygotes, and there is no strict similarity between offspring and parents. The relationship between mother and fetus can only be described as a "part-whole" relationship. For instance, in the immunological approach, the "mother-fetus" pair is considered to constitute an immune subject. Asexual reproduction also involves the direct development of new sub-individuals from the mother's body, which remain physically connected. (ii) Even after completing reproductive events and leaving the mother's body, organisms remain in a kinship relationship through genetic association. This relationship connects them not only to their immediate kinship group but also to broader kinship networks. Offspring of small individuals are linked together through both direct and indirect relationships. Through genetic tracing, every current organism has numerous biological ancestors and represents one terminal point of the entire species, becoming part of the gene pool and realizing certain possible combinations of genes. For example, grapefruit is the natural hybrid of sweet oranges (a cross between pomelos and oranges) and pomelos. Every cell in our body carries at least two ancient ancestors: one is the host cell, which can be considered an archaeon, and the other is a bacterium that was engulfed. All eukaryotes share these two ancient ancestors.

5.2 Species constitute a causally integrated relationship system

5.2.1 Systematicness

Any species is always a terminal in the phylogenetic system and must be considered as an open process system (Ghiselin, 1981). The systematic nature of a species is not only reflected in its internal connections, such as part-whole relationships, but also in its external connections, meaning that species do not maintain absolute genetic purity. Lateral gene transfer is widely present among bacterial species, leading to these open systems (Rieppel, 2009). If we further consider common phenomena such as gene drift and microbial gene embedding (especially microbial gene embedding into macro-biological genes), life is not merely a tree but more akin to a web. It would thus be more appropriate to replace the "tree of life" with the "web of life".

5.2.2 Integration

Species do possess collective attributes that transcend and are independent of their constituent organisms, and the integrative nature of species exemplifies the principle of synergy (Ghiselin, 1981). For instance, in the collective behavior of marine organisms, where lots of small individuals move in unison, the "music conductor" represents their collective attribute or integrative nature. As a system, a species has relatively vague boundaries (unlike individuals with clear boundaries in everyday contexts), or more appropriately, it should be likened to super-individuals, such as a coral community (Rieppel, 2009). Species are spatiotemporal, dynamic, and integrated systems, and in this sense, they are complex wholes-individuals. A causal integration network characterized by dependency relationships is a hallmark of an organism or individual organism. However, species also exhibit variability, bounded by temporal attributes (morphology, physiology, genetics, etc.), causal behaviors (sociality, migration, predation, etc.), and causal forces (reproduction, competition, etc.) (Rieppel, 2007). Species integration mitigates internal competition and fosters internal cooperation, and Darwin's concept of the struggle for survival inherently encompasses the meaning of cooperation between organisms.

5.2.3 Cohesion

Species cohesion is also a systemic manifestation, wherein cohesive species respond to environmental pressures as a whole, exhibit consistent responses to the environment, and maintain a certain identity through genetic similarity. The relationship between organisms and the environment is dynamic, and the mutual influence between organisms and the environment alters both the offspring of organisms and the environment itself. In this sense, organisms and the environment are interdependent and form part of a cross-temporal feedback relationship (also known as a "reciprocal causal relationship") (Neto, 2016). Regarding species, in order to respond similarly to external stimuli, organisms of the same species must be similar to one another-these organisms share many common characteristics (Barker and Wilson, 2010). When a species' response to the environment becomes inconsistent due to geographical isolation, gene immobility, or other factors—that is, when cohesion is disrupted—species differentiation occurs, and new species begin to form. For example, the Darwin's finches in the Galápagos Islands descended from a common ancestor——a species of finch from South America. However, as they migrated to different islands, they evolved distinct characteristics. On islands with hard seeds, birds possessing large, robust beaks were better equipped to survive and reproduce. Conversely, on insect-rich islands, those with slender, pointed beaks could more effectively access nectar and cactus fruits.

5.3 The continuous reproduction of species forms a divergent trend

5.3.1 Reproduction of the fittest

Species undergo natural selection, sexual selection, and other processes, but not all mutated offspring can survive for extended periods. The blind branches generated during evolution are mercilessly eliminated by nature. The fittest continue to reproduce, and advantageous genes perpetuate their own structure. Following a single maternal body, there emerge more maternal bodies that reproduce offspring at an exponential rate. Although only a small number can survive under environmental constraints and may even face extinction, the ideal reproductive trend remains one of diffusion or divergence. The continuous reproduction of species generates both greater similarity—genetic similarity—and greater variability—genetic variability.

5.3.2 Similarity

Offspring and parents exhibit similarities during the adult stage, and within the same generation, there are similarities across the reproductive, juvenile, and adult stages. Overall, these offspring display similarity among small individuals and form a natural class when compared horizontally. In a natural state, it is impossible for one species to reproduce another species with heterogeneity. If such a situation were to occur, the SAC theory could not be established. Therefore, the divergent trend of species—expanding the number of organisms—was initially evaluated by the horizontal judgment of the SAC theory regarding this outcome. The replication of organisms is not identical replication but rather similar replication and approximate replication. Thus, the "class" in SAC theory refers to similarity (allowing some differences), not isotropy (not allowing any differences), and shared attributes are utilized in this sense.

5.3.3 Exceptional circumstances

The SAC theory is not applicable to the divergence of all species, and there are always exceptions in species. For example, there are "dwarf males" in barnacles and anglerfish, whose female and male appearances differ greatly. If judged by "overall similarity", they will be classified as different species (Godfrey-Smith, 2014, p.101). Thus maybe this depends on the granularity of the description of subspecific structures which compose a species as individual (and descriptive class). In addition, some special organisms such as hydroids can fuse with each other to form new biological entities, while some organisms can split into two during the reproductive process, as well as the bottleneck period of reproduction and embryo separation, making it difficult to define identity and similarity. Some special species can only apply the SAI theory. The SAC theory is at least limited in its scope of application here, even if it has not failed.

5.4 Conversely, species that trace back are constantly converging

5.4.1 Tracing the cause

The method of tracing the origin of species can be adopted. From the perspective of homology, organisms form phylogenetic relationships, such as the forelimbs of animals and the wings of birds, which are homologous. "Homology is a relation of correspondence, not, as some authors have claimed, of similarity. When we homologize we are tracing lineages of organs, and the lineages are historical units (Ghiselin, 1981)" Homology suggests that species have diverged in their evolutionary paths and provides a

foundation for constructing phylogenetic trees. Darwin's theory of a common ancestor posits that different species descended from a shared ancestor, a hypothesis that has been substantiated by scientific evidence.¹⁰ Throughout the history of life on Earth, tracing species back in time reveals fewer species, with their traits becoming increasingly similar. In the early stages of life's emergence, only replicating molecules existed within the "organic soup" predating the existence of distinct species.

5.4.2 Convergence

Excluding factors such as lateral gene transfer, gene embedding, and species lineage merging, in the general common ancestor model, from the near group to the distant ancestor, there is a continuous convergence toward a minority population, a minority group, or even a single organism. For example, all birds and crocodiles share a common ancestor that lived about 250 million years ago as a primitive archosaur reptile; humans, mushrooms and bacteria can be traced back to a common ancestor, known as "Lucia" 12. This convergence trend suggests that the causal integration of species is deeply rooted in history, inherent, and progressively refined. However, convergence does not imply the unification of all aspects of life or laws; it merely indicates a shared origin. The tracing of species through convergence validates the SAI theory. Convergence provides a clearer elucidation of the identity, integration, and evolutionary history of species, offering a comprehensive representation and profound description of species. Tracing convergence and reproductive divergence represent opposite perspectives: converging toward ancestors and diverging toward descendants.

5.5 The formulation and explanation of the equation

In summary, the above argument can be succinctly expressed as:

SAI = SAC + Process/Lineage Relationship

+ Systematicness/Causal Integration

This equation is a novel conceptual framework. Consider Homo sapiens as an example:

On the left side of the equation: *SAI* — the Homo sapiens species as a whole has an origin (differing from Homo heidelbergensis), a duration (up to the present), and a potential future extinction. As an evolutionary individual, it has participated in cultural and technological evolution, adapting to environmental changes.

On the right: *SAC*—Homo sapiens share a range of morphological and genetic traits, such as brain size, upright walking, and language ability, which make it easy to identify members of Homo sapiens.

On the right: *Process/Lineage Relationship*——DNA analysis and fossil records show all Homo sapiens share a common ancestor (in Africa around 200,000 years ago) and are connected through reproductive relationships into a continuous lineage.

On the right: *Systematicness/Causal Integration*——Homo sapiens diverged into different races due to different environments.

This equation demonstrates that the SAI theory encompasses and surpasses the SAC theory, with "process/lineage relationship + systematicness/causal integration" constituting the core aspect of species individualism that SAC is unable to account for. The explanatory capacity of SAC theory is constrained, as its definitions and criteria for classification reflect only a specific dimension or link of species, inherently excluding a range of complex scenarios associated with species. This limitation has led to the emergence of the SAI theory. Ultimately, the SAI theory serves as a framework for scholars to interpret species phenomena, with its rationality rooted not merely in offering a different perspective but in its superior unifying strength and explanatory power. Our overall understanding of species can basically be incorporated into this equation. This equation helps to explain the role of natural selection at the species level (species selection), as well as the problem of the traditional concept of "class" (such as intraspecific variation and evolutionary change).

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

LX: Writing – original draft, Writing – review & editing. RL: Writing – review & editing.

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¹⁰ Contemporary molecular biology has established that all organisms utilize the same genetic code. The genetic code consists of a set of rules by which information encoded in genetic material (DNA or RNA) is translated into proteins, with codons of three nucleotides each specifying amino acids during protein synthesis. The genetic code exhibits remarkable universality across all organisms, and biochemical studies demonstrate a high degree of molecular consistency among living beings, thereby providing strong support for Darwin's hypothesis.

¹¹ The concept of the "organic soup" was introduced by G. C. Williams in his 1974 book *Adaptation and Natural Selection*, referring to the early Earth's oceans, which were chemically complex environments where molecules likely emerged through self-catalytic processes.

¹² After Luca, the earliest split in the tree of life was the separation of bacteria and archaea. Later, a branch of archaea entered into endosymbiosis with bacteria, giving rise to eukaryotes (all life that is not bacteria or archaea, including humans, mushrooms, and plants).

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