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The Species Problem in Artificial Life

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***Abstract*- This paper deals with the Species Problem in an ALife approach. We present the problem and identify three paradigmatic species concepts that permit different operationalizations. We use the FATINT system to test and compare them in a fully embedded, agent based environment with complete information about lineages, individual phenotypes and reproduction capabilities. We find that under mild conditions (we propose to call them the Darwin condition) the different species concepts tend to yeld similar or identical categorizations. We outline further studies using different models, various species concepts, and new testable hypotheses.**

I. INTRODUCTION

Do species exist? This perennial question was fond to both Aristotle and Darwin, who gave different answers. Dogs bark and cats meow, dogs get dogs, and cats get cats, and never the other way around. Why is this? Aristotle said this is because dogs and cats are categories or natural kinds. Darwin said this is because cats and dogs are continuous variants so that nothing between them survived – but could. Ever since Aristotle (and Darwin) species presented a problem. This paper investigates the species problem using ALife tools to flesh out the question, in particular, to test if radically different species concepts give radically different practical answers to the old question as to what a species is.

II. THE PROBLEM

Are species concepts real? The modern Species Problem (SP) has its roots in Evolutionary Synthesis (ES) in biology and consists of two interrelated questions: (1) What is the appropriate definition of the concept of species, (2) how to delineate species taxa, i.e. particular species [1]. In response to the most influential proposal, the so-called Biological Species Concept [2], a huge variety of alternative definitions were thrown in, resulting in an extensive polemy. No less than 22 different species concepts are explicable from contemporary literature [3], [4] (Table 1).

The difficulty of the task of finding general criteria for both the concept and the delimitation of taxa is generally recognized as a long-term implication of ES [5], [6], [7]. The evolutionary turn introduced the Biological Species Concept, but the term, historically, was shared by systematics as well, serving in the latter as a tool for classifying biological diversity. Now systematics had to deal with the new, theory-laden approach to species („new systematics"). Reconciling the different epistemological roles, i.e. the functions to explain the existence (and nature) of species, and that of reconstructing taxa on the same basis, has proven to be a goal almost impossible to achieve.

TABLE 1.
SPECIES CONCEPTS EXPLICABLE FROM CONTEMPORARY LITERATURE, AFTER MAYDEN 1997.

Acronym	*Name/criterion*	*Acronym*	*Name/criterion*
ASC	Agamospecies concept	**GCD**	Genotypic Cluster Definition
BSC	Biological Species Concept	**HSC**	Hennigian Species Concept
CSC	Cladistic Species Concept	**ISC**	Internodal Species Concept
CoSC	Cohesion Species Concept	**MSC**	Morphological Species Concept
CpCS	Composite Species Concept	**NdSC**	Nondimensional Species Concept
ESC	Ecological Species Concept	**PSC**	Phenetic Species Concept
ESU	Evolutionary Significant Unit	**PhSC**	Phylogenetic Species Concepts
EvSC	Evolutionary Species Concept	**PtSC**	Polythetic Species Concept
GCC	Genealogical Concordance Concept	**RCC**	Reproductive Competition Concept
RSC	Recognition Species Concept	**SSC**	Successional Species Concept
GSC	Genetic Species Concept	**TSC**	Taxonomic Species Concept

As a consequence, treatments of the SP often proceed by reconsidering the relationship between questions (1) and (2). One of the most influential approaches is that of Mayden [3] who argues that the underlying cause of the SP lies in the fact that no species concept (SC) has met all the measures of adequacy to date: a) being operational, b) being applicable, c) being general, and d) possessing an explanatory power. Evaluating the 22 concepts against these dimensions, Mayden set up a hierarchy of SCs, where most concepts are operational

„proxies” to a most general theoretical evolutionary concept (EvSC). Another often quoted SC taxonomy is that of Wilkins [8] (Table 2.). He utilizes many distinctions that emerged in the SP debate. The most general of these is to distinguish between species as a (theoretical) concept, and as a category (or rank) of systematics. In this taxonomy, concepts are divided into horizontal and vertical lines (depending on wether or not they operate across generations), and further divided by the unifying feature (grouping criterion) of the corresponding concepts. We can approximate these categories (and demonstrate the four adequacy measures) by exposing three paradigmatic examples: the biological (BSC), the cladistic (CSC) and the phenetic (PSC) species concepts.

TABLE. 2.
TAXONOMY OF SPECIES DEFINITIONS IN WILKINS 1997

1st level distinction	*2nd level distinction*	*Terminal nodes*	*Unifying concept*	*Example*
Species Concepts (SCs)	Horizontal SCs (HSCs)	Reproduct. HSCs (RHSCs)	Reproductive ‘reach’ of conspecifics	BSC
		Ecological HSCs (EHSCs)	Similar ability to use ecological resources	ESC
	Vertical SCs (VSCs)	Process VSCs (PVSCs)	Descendency (...), speciation	EvSC
		Historical VSCs (HVSCs)	Historical record	PhSC
Taxonom. Units (TU)	Ontological TUs (OTUs)	Metaphysical OTUs (MOTUs)	Philosophical ontology	Species as individuals
		Causal OTUs (COTUs)	Causal relations between members	Most species concepts above
	Epistemic TU (ETU)	Morphological ETUs (METUs)	Similarity of member form	Linné; Opertainoal Taxonomic Unit, OTU
		Dynamic ETUs (METUs)	Similarity of member behaviour	Game Theoretic strategy (Maynard Smith)

1. The BSC. Although refined many times since its introduction (cf. [9]), the main feature (or grouping criterion) of the BSC has remained unchanged. On the BSC, a species corresponds to a maximal group of potentially interbreeding organisms (a „Mendelian” population) that are reproductively isolated from other organisms. The definition translates to this formal structure (where *U* is the universe of individuals, *IB* is the relation of interbreeding, *IB** its transitive closure defined to be an equivalence relation, *x/IB** is an equivalence class by *IB** of which *x* is an element, and BSC is the set of equivalence classes derived from *IB**):

$$\left\langle U, IB, IB^*, BSC \right\rangle, IB \subset U^2, BSC \propto \left\{ x / IB^* \,\middle|\, x \in U \right\}. \qquad (1)$$

BSC is a horizontal (or synchronous) concept, applicable only to co-existing organisms; it is based on interbreeding relations (RHSC, see Table 2.). The concept is not fully operational: testing for *potential* interbreeding is problematic in nature [10]. Nor is it clearly applicable: empirical results show that interbreeding (the transitive closure) is not an equivalence relation, as the case of the so-called ring species[1] shows; it follows that applying these criteria does not necessarily result in a clear taxonomic structure. Since asexual species (agamospecies) also exist, BSC suffers the lack of generality as well. However, the concept has a strong theoretical background (inspired by population genetics), and, therefore, good explanatory power.

2. The CSC. On the Cladistic Species Concept, a species is a (minimal) lineage of populations delineated by two branching events („points”) on the phylogenetic tree [11]. The grouping criterion in this family of concepts is the ancestral-descendant relation (*AD*). The concept is vertical, as it does not exclude organisms existing in different time-frames. The CSC, in this general form, is not operational. Systematic practice translates it to a phenetic method that concentrates on characters distinguished by the *theory* of cladistics. It is, therefore, a strongly theory-laden concept. The main problem however is related to the applicability dimension. The ancestral-descendant relationship does not, by itself, split the ‘tree of life’ into species: genealogical links collect every living organism in a single class. This means that branching events in the tree (monophyletic origin of taxa) cannot be unequivocally identified on the basis of genealogical relation alone. Vertical concepts usually require a somewhat arbitrary auxiliary criterion of ranking. In a Darwinian manner, we might add a *time*-based ranking (T, <) to monophyly-based concepts. (This is a natural choice as ancestral-descendant relations inherently contain an element of succession.) The ranking can then be used to divide the tree into species taxa and to separate them from more or less inclusive lineages. In a certain time-frame, the appropriate genealogy-based relation is an equivalence relation with mutually exclusive classes (distinct lineages in the given time-frame):

$$\left\langle U, AD, AD^*, \left\langle T, < \right\rangle, f, CSC^* \right\rangle, \qquad (2)$$

$$AD \subset U^2, \qquad (3)$$

$$CSC^*\left[t_1 \ldots t_{1<N}\right] \propto \{ x / \left(AD^* \setminus \bigcup_{y=1}^{N} f\left(t_y\right) \right) \big| \, x \in U \}, \qquad (4)$$

where *AD* is the ancestral-descendant relation, *AD** is its transitive and symmetric closure, $\left\langle T, < \right\rangle$ is the ordered set of time-points, *f* a function that assigns to each time-point *t* a set of organisms from *U*. CSC* is the modified CSC, referring to equivalence classes in the sub-structure of *AD** restricted to the selected time-interval $\left[t_1 \ldots t_{1<N}\right]$.

3. The PSC. On the phenetic concept, a species is a cluster of similar organisms delimited with the aid of some statistical clustering method. Clustering is based on a huge number of

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[1] Cf. e.g. http://en.wikipedia.org/wiki/Ring_species

characters of organisms. The PSC is non-dimensional (neither horizontal nor vertical), and, for many authors, it is not a concept but a device for operationalizing other concepts. In the Wilkins-tree, it is a Taxonomic Unit (TU), not a Species Concept (SC). It is unique, however, in not selecting among characters (as any operationalized theoretical concept, like the CSC, would do). Hence, the PSC is operational, applicable and general, but lacks theory or explanatory power. Proponents argue that since it is theory-neutral, it does not impose any *a priori* bias on the recognition of the „natural system" of species [10]. The main objection stands on the same grounds: the resulting classification is sensitive to the clustering method, the chosen thresholds of difference/ similarity, and the selection of characters.

In [12] Soós discusses further species concepts and their problems in the context of the interdisciplinary species problem (ISP).

III. MATERIAL AND METHOD

Artificial Life (AL) offers itself as a powerful tool for testing species concepts. Natural data sets are necessarily incomplete, while data sets in AL models are complete. Using a combination of bioinformatics and AL techniques, lineages, property spaces, and interacting or non-interacting populations can be fully analyzed and the operational consequences of various species definitions can be studied.

Despite a few earlier works on species in ALife systems (such as Clement on phylogenetic trees [13] or Wilke *et al.* on quasispecies [14], [15]) this methodology is largely untested. In order to address the problem, we performed experiments in the FATINT system using mostly 1 or 2 species.

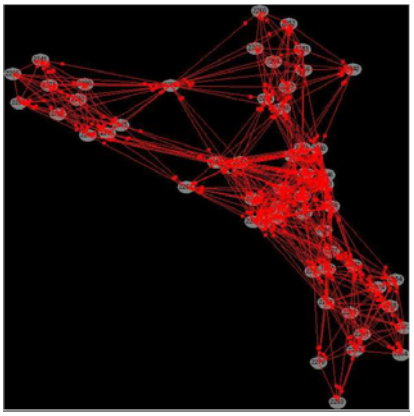

Fig. 1. Sample Fruchterman-Reingold (FR) plot of a single species on BSC. Lines represent possible reproduction events.

A. The Model.

FATINT is a fully embedded agent based simulation of an artificial ecosystem for evolutionary studies [16], developed in the Java-based RePast environment ([17], [18]) at Eötvös University.[2] Descriptions of this subsection refer to the work of Kampis and Gulyás [19], [20], [21], [22]. The model uses similarity-based genderless sexual reproduction (no separate sexes), where the probability of offsprings is given as $M_{const} + (M_{limit} - d) \cdot M_{slope}$ (for $d<M_{limit}$); d is (dis)similarity defined by the Euclidean distance between phenotype vectors represented as n-tuples. The purpose of the system is to study the emergence of new species in an interaction-based model combined with phenotype plasticity: n-vectors are allowed to change under specific conditions.

The model exists in several versions. Here we use the one with a metric similarity and a global dimension change operator for phenotype effects. This is a crude model of phenotype-driven speciation based on horizontal adaptation (such as cultural learning or a global enactment of hidden phenotype properties such as in sudden climate change). A more realistic spectrum of phenotype-induced transitions would include individual point mutations, phenocopies, and various epigenetic changes [23].

B. Behavior of the model

Without phenotype changes the model shows stable convergence into a single emergent species with a self-organized center defined by several contingencies (such as randomization and other parameters). If phenotype change is allowed (or introduced by hand), then formerly stable species may split into several new stable species.

In the current version we observe an implicit resource competition due to density-dependent side effects (called "hypercompetition" – the term reflects the resulting higher than linear growth rate). As a result, multiple species tend not to coexist for more that 400-600 overlapping generations.

In the current study, experiments were performed on minimal digital organisms, having only 5 focal phenotype traits (n=5) and a trivial ontogeny (a 1-1 mapping bw. genes and phenotype traits). The interpretation is that other genes serve basic metabolism but do not participate in the definition of sexual phenotype and hence in the mating success, which is the selective force in our model. Besides simplicity, the minimalist choice was motivated by the fact that earlier works describe experiments using the same settings [19], [21], [22]. Unless indicated otherwise, all original parameter values were kept (for details see the cited publications), including an extreme mutation rate of $P_{mutation} = 0.1$ (discussed therein). A typical run starts with 1,000 agents. Species tend to consist of 50-100 members. Time denotes discrete, overlapping generations.

C. Methods.

We introduce the following natural definitions.

<u>BSC</u>.

We define a species on BSC at time T as a connected network of agents with $d<M_{limit}$. (Fig. 1.) This operationalizes the notion of reproductive ability/isolation. Disconnected graphs correspond to multiple species. The topology and geometry of the resulting net reveals the internal species structure. In particular, on BSC, speciation events appear as subgraph disconnection events. <u>Realization.</u> BSC is realized using a variant of Kruskal's minimum spanning tree algorithm

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[2] Home page: http://hps.elte.hu/~kampis/EvoTech/ET.html

[24]. Note that this is equivalent to agglomerative hierarchical clustering with single linkage [25].

CSC.

A species is the historical envelope of past reproduction events in a given lineage between T0 and T. Two individuals in T belong to different species if the two envelopes do not intersect. _Realization._ CSC is realized using network components analysis with component size ≥ 2 applied to lineages traced back to individuals born no earlier than T0 in a history dump up to T. For comparisons, species are narrowed down to members of components alive at T.

PSC.

We define a PSC species as a cluster in phenotype space, characterized with a clustering constant $d_{cluster}$. We want to express $d_{cluster}$ as a ratio to M_{limit}. The choice is motivated by the fact that here (because of the FATINT reproduction rule) both BSC and PSC are metric based and $d_{cluster}$ links the two. (For $d_{cluster}$=1 we ask about clusters of size M_{limit}). Different values of $d_{cluster}$ usually yield different clusters. Hence, of special interest are sweeps using various values. _Realization._ PSC partitions are clusters formed using agglomerative hierarchical clustering with complete linkage [25].

BSC, CSC and PSC define different classifications over simulated populations. In each case, we assign a single label to every individual. The label is an integer identifier of the species to which the given individual belongs. Pairwise comparisons of clusters are then performed by calculating the Rand-index (R), a standard method for comparing classifications, see Appendix [26]. The Rand index has a value between 0 and 1. The value 0 indicates that the two data clusters do not agree on any pair of points and 1 indicates that the data clusters are exactly identical. Calculations were performed in the R statistical program package[3] which was successfully applied to philogenetic comparisons before [27].

Visualization was performed using RePast (Fruchterman-Reingold, FR, clustering of populations at T) and Pajek functions (FR, clustering of populations in T0-T).

IV. EXPERIMENTS AND RESULTS

The study of the above species concepts and their differences will be most interesting for dynamic or emergingy species and/or stable species in transition. In this paper we report three different treatments.

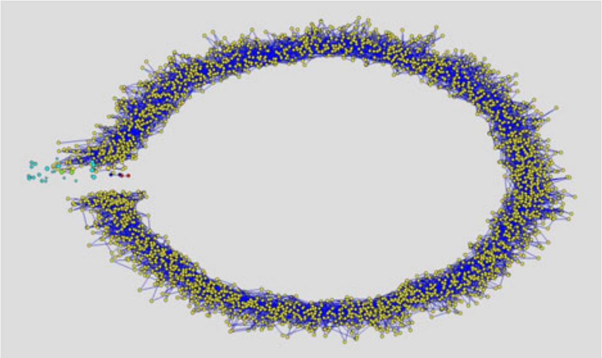

Fig.2. Circular FR plot of partitions of CSC under T1 in the interval T0=0 to T=644. The picture shows one giant, connected lineage, and several small, isolated components (on the left).

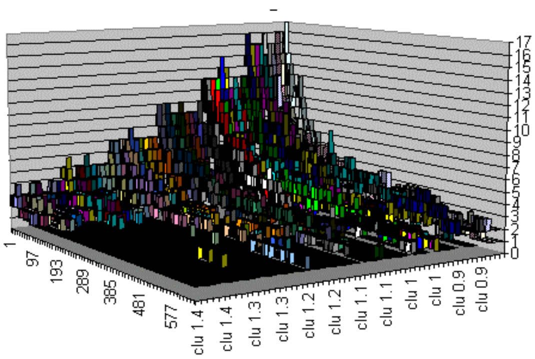

Fig. 3. Clusters against time. Convergence to (typically) one PSC cluster under T1 for $d_{cluster} \geq 1$. The Figure summarizes 60 runs, 10 for 6 random seeds each, from $d_{cluster}$ = 0.9 to 1.4 . Time goes left to right, the clustering constant increases right to left. Vertical axis shows number of clusters.

A. *Treatment T1*

No treatment (basic convergence to a single species without phenotype change). The interval T0=0 to T=644 was tested using different random seeds and clustering constants (Fig. 3.). We computed R once for every value of $d_{cluster}$ and found R=1 for all comparisons of PSC (for $d_{cluster} \geq 1$), BSC and CSC for T0=100 to T=644. For $d_{cluster} < 1$ the number of CSC clusters radically increases.

To further examine this situation we tested T0-T=0-1,500 with 10 different random seeds for $d_{cluster}$=0.5. We found that there is a ubiquitous convergence to a single PSC cluster at T=1,500 with R = 1 for all pairwise comparisons in each run (Fig. 4.).

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[3] http://www.r-project.org/

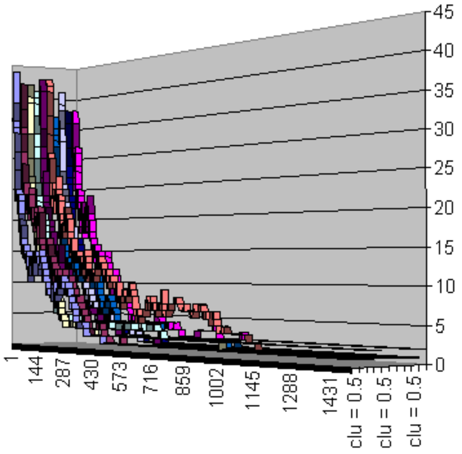

Fig.4. CSC time plot in the interval T0-T=0-1,500 for $d_{cluster}$=0.5 using 10 different random seeds, yielding one surviving cluster. Vertical axis shows number of clusters, time goes left to right.

B. *Treatment T2.*

Speciation experiments ($P_{mutation}$ = 0.001). A new global phenotype dimension was added by hand at T=475. Sample runs use T0=0 to T=1,000, 7 random seeds. In 5 of the 7 runs 2 BSC species emerged (Fig. 5.). In three cases of the 5, the second species went extinct between T=650 and T=980.

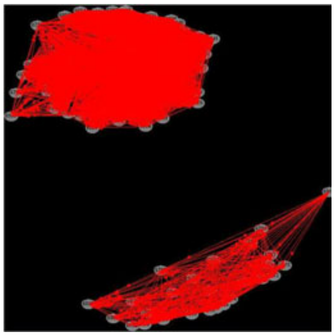

Fig. 5. Sample FR plot on BSC at T=550 in treatment T2.

Despite the above differences in the speciation dynamics, we obtained the following highly uniform results in T2 (Table 3.). Rows correspond to different random seeds, here *#comp* is the number of BSC graph components at T=1,000.

TABLE 3.
SPECIES COMPARISONS IN T2.

# comp.	PSC vs. BSC	PSC vs. CSC	BSC vs. CSC
2	R = 1.0	R = 1.0	R = 1.0
2	R = 1.0	R = 1.0	R = 1.0
1	R = 1.0	R = 1.0	R = 1.0
1	R = 1.0	R = 1.0	R = 1.0
2	R = 1.0	R = 1.0	R = 1.0
2	R = 1.0	R = 1.0	R = 1.0
2	R = 1.0	R = 1.0	R = 1.0

A further study using the same runs reveals a hidden structure in T0-T = 475-550, 515-550, and 550-1,000 (i.e., around the artificial speciation event and afterwards; the FR plot part of the FATINT GUI shows speciation to be over by T=550). As expected, results (Table 4.) indicate low values of R around speciation (Fig.6.) and increasing values ending with R=1 later.

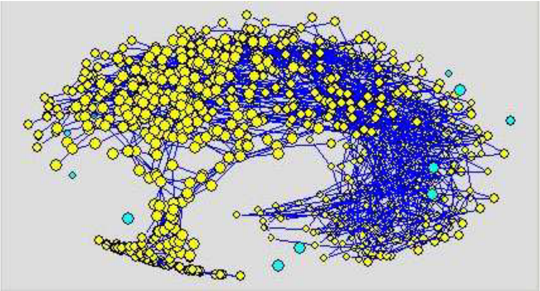

Fig. 6. FR plot of CSC partitions (nodes with different colors) during the speciation process T0=450 to T=550 in T2. The picture shows one single lineage but with a divided connectivity structure that reflects the temporal branching of the lineage.

TABLE 4.
THE STRUCTURE OF A SPECIATION EVENT IN T2.

Time interval	PSC vs. BSC	PSC vs. CSC	BSC vs. CSC
450-550	R = 0.716	R = 0.356	R = 0.640
515-550	R = 0.716	R = 0.716	R = 1.0
550-1000	R = 1.0	R = 1.0	R = 1.0

C. *Treatment T3*

Autonomous speciation experiments. Sample runs with $p_{newslot}$=0.001 in T0=0 to T=1071. The nonzero value of this parameter introduces random phenotype change events, which then induce potential speciation events. The high value applied permits several speciation events and speciation bursts within a single run (Fig. 7.) We present how this influences species comparisons in Table 5.

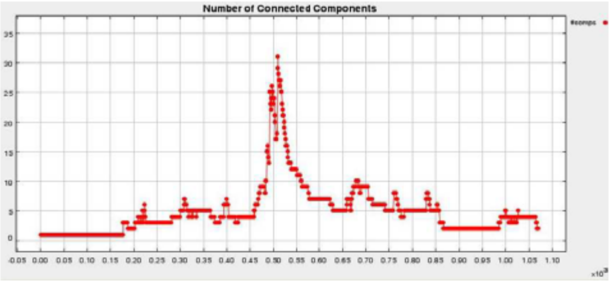

Fig. 7. Sample run in T3, number of BSC species shown in T0=0 to T=1071. Random speciation burst at T=500, later extinctions.

In Table 5., here is a strong correlation between PSC and BSC, independent of the time-frame of analysis. However, CSC only yields high R-index values for short time-windows both with PSC and BSC. (Further analysis is provided in the next section.) Table 6. summarizes the same treatment and results using 7 random seeds over the period T0=100 to T=1071. Here *#comp* is the number of CSC components in the given interval. Column averages are R_{avg} = 0.791, 0.305 and 0.513, respectively.

TABLE 5.
THE SAMPLE RUN OF FIG. 7. AT SPECIATION BURST.

Time interval	PSC vs. BSC	PSC vs. CSC	BSC vs. CSC
800-1071	R = 0.788	R= 0.788	R = 1.0
500-1071	R = 0.788	R= 0.788	R = 1.0
100-1071	R = 1.0	R= 0.423	R = 0.634

TABLE 6.
RESULTS IN T3 USING DIFFERENT RANDOM SEEDS (LISTED IN DIFFERENT ROWS)

# comp.	PSC vs. BSC	PSC vs. CSC	BSC vs. CSC
4	R = 0.578	R= 0.127	R = 0.549
4	R = 0.900	R= 0.174	R = 0.273
1	R = 0.217	R= 0.217	R = 1.0
5	R = 0.940	R= 0.509	R = 0.568
3	R = 0.954	R= 0.729	R = 0.775
6	R = 0.951	R= 0.156	R = 0.205
4	R = 1.0	R= 0.222	R = 0.222

V. DISCUSSION

A. *General*

Our results show that, expressed briefly, species do exist in a very strong sense (as far as generalizable from our model). This strong sense of existence includes compatibility, or even coincidence of various species definitions, which yield different operational characterizations. In other words, what we find is that autonomous population dynamics under changing selection conditions tends to regulate co-reproductive aggregates in such a way that the latter behave in ways that simultaneously satisfy various species intuitions.

B. *Understanding the measures*

It follows from the definitions that even under comparable conditions (e.g. $d_{cluster}$=1), BSC and PSC may yield radically different results, despite their 'common' origin in FATINT where both phenotype clusters (PSC) and reproduction rates (BSC) are based on metric similarity. On the other hand, PSC defines a hypersphere of diameter $d_{cluster}$, whereas BSC a graph where no individual edge can be 'longer' than M_{limit}. (So we can imagine a 100-member BSC species 'streched' to $100d_{cluster}$.) In BSC to PSC comparisons, therefore, we expect that the R index will depend on the 'compactness' of the species: the smaller the diameter in n-space, the more likely BSC and PSC to coincide.

We must appreciate, on the other hand, that CSC and BSC automatically coincide at T and short intervals around it. The difference between CSC and BSC is a rough estimate of how many past reproduction events lead "outside" the BSC species existing at T. Longer intervals that include speciation events are prime candidates for large differences. (Imagine a single BSC species splitting into two in T0-T. By definition, CSC yields one species in T0-T and BSC two at T). Following this argument, a good coincidence of CSC with BSC is expected to indicate the stability of a given composition of species with respect to their 'types': the two classifications collapse into one if (in the studied interval) every species behaves as an immutable, true Aristotelian category where no historical chain of reproduction events leads outside (i.e. branches off) the reproductive closure that exists at the present.

Note that our current CSC definition excludes one-member lineages, i.e. agents without offspring. A consequence is that 'monster' organisms that do not (or cannot) ever reproduce with any others are not part of our comparisons. (A simple test shows their proportion to be negligible.) Our choice does not influence generality and makes comparisons more systematic by eliminating random noise.

Values of R=1 imply complete identity. However, we must understand that R=1 at T does not directly imply R=1 at any other T'≠T. In particular, the classification based on CSC highly depends on the choice of T, as CSC counts 'backwards' in time. If, for instance, only one of previous two lineages survives at T, then R (by CSC's 'dropping' the extinct line) may be significantly higher at T than for T'<T where both species exist.

C. *The D Condition and taxonomic realism*

In our experiments we observe that emergent species tend to show a self-organized dynamics towards higher 'compactness' and towards the emergence of well-defined 'types' both in the relaxation (T1) and in speciation (T2) situations. By the above words we mean:

Compactness: all individuals clearly belong to species, which are widely separated and lack transitory characters that would temporarily link them. In particular, lineages that originate at characters inside the same phenetic cluster typically end up in the same reproductive cluster (cross-measure closure property).

Being 'Typed': members of a lineage (or a reproductive cluster) share certain characters, and any organism with the same characters predictably belongs to the same lineage. In particular, randomly chosen members of a species can represent the species both at a given time and in a historical time frame (prototype property).

In the above condition, different measures give the same classification and resulting clusters 'look like true species'.

We suggest to call this important condition the *D condition* after Darwin, who famously foresaw the reconciliation of the individual variation based notion of species (introduced by him) with a taxonomic and an evolutionary species concept – it appears that our D condition faithfully parallels his expectations.

Our results related to the D condition can be interpreted as an argument for taxonomic realism in the current era of the anti-essentialist species concepts (such as BSC, CSC, etc.) of the Evolutionary Synthesis (ES). At the same time, the finding that the extensional equivalence of the various concepts (CSC, BSC, PSC) depends on various circumstances (such as the rate and dynamics of the evolution process), and that they, nevertheless, generate well individuated groups, is advantageous for views like the "eliminative pluralism" of Ereshefsky [28]. On this view, (1) there is no unique species category, but (and because) (2) there are different, potentially coinciding categories that nevertheless do not individuate species on any single, common ground.

D. *Analysis of the results*

T1 delivers our basic result. A species, left undisturbed, shows important convergence properties: it tends to converge to the D condition. Values of R=1 at T=644 (with $d_{cluster} \geq 1$) are only possible if the 'diameter' of the species is around M_{limit}. On the other hand, R=1 for $d_{cluster}$ = 0.5 at T=1,500 means that the same 'diameter' will be around the half of the 'reproduction hypersphere' available for the species by that time, yielding an inevitable BSC = PSC. This also explains why CSC ultimately coincides with the other two SC's: the only surviving lineage (and here only backward lineages count) is in the same hypersphere as BSC and never leaves that. (We may add that although a random drift of the species' hypersphere was described in Kampis and Gulyas 2004, this does not change the above situation; here, again, the cue is that lineages are defined relative to the present time and meander together with the species based on the present.)

The interpretation of the findings of T2 can be based on the same observation that the common point of reference for all three measures (BSC, PSC, and CSC) is the end point T=1,000, which is a time stamp in the simulation distant enough from the (successful or unsuccessful) speciation event at T=475. So PSC has time to converge to BSC, just as in T1, and CSC likewise, to drop non-surviving lineages. During the speciation event the species extends in all directions before it breaks (T0-T=450-550) and starts converging into typically two lineages (T0-T= 515-500). Note that comparisons in T2 are insensitive to whether 1 or 2 species prevail in the end. This shows that the familiar T1-type convergence takes places in dynamically emerging species as well.

T3 gives a notoriously bad agreement of comparisons. This is understandable and mainly a consequence of the behavior of CSC. Despite the short relaxation times between the forced random speciation events on T3, PSC and BSC generally tend to produce a good matching at the time of the test, whereas CSC yields a poor match to both of them, unless the population collapses to one single species (analysis shows that when this happened it was just before the time of the test). The noted difference must be due to past speciation events that link organisms at T on CSC but leave them separate on BSC (a "fork"). Under the extremely fast speciation circumstances of T3, in the interval of T0-T=100-1,071 there was an average of 10 speciation events in a lineage of ca. 10-20,000 agents.

As expected from the above discussion, the picture should be radically different if the time frames are shrunk in T3. Indeed, for the intervals 800-1,071 and 500-1,071, in the presented sample run we see that the burst around T=500 dies out (R=1 bw. BSC and CSC), and this implies necessarily higher values for the other two available comparisons as well.

Paradoxically, CSC is necessarily "blind" to speciation events, which is taken into consideration in the applied cladistic definitions of biological taxonomy. Although the *a priori* use of the criterion of monophyly is questionable, as it is theory laden, our results show that under the condition of rare speciation events (i.e. where there is enough time for T1-like relaxation), both BSC or PSC markers can be safely used for the definition of a suitable time window for CSC classifications between distant speciation events. This completes our discussion on the D condition and T1-type processes.

E. *Further work.*

Recalling that BSC is a notion of reproductive isolation (and hence, indirectly, of niche segregation), and that PSC classiffications are based on phenotype similarity (such as morphology), we may reformulate our results in a hypothesis that the phenotype is a good prediction of ecological function only at species equilibrium. A more precise formulation and the testing of this hypothesis is left to future work.

Clearly, our results have implications to species concepts not directly tested in our experiments, such as those listed in Table 1. Two further species concepts of immediate importance are the quasispecies concept and Wittgenstein's 'family resemblance' notion (i.e. disjunctive class definition). Discussion of these or further experiments go beyond the scope of the present paper.

VI. CONCLUSIONS

We studied three paradigmatic species concepts in the FATINT ALife system where species exist as emergent, self-organized entities. We found that despite an inevitable effect of temporal dynamics on the comparisons, different species measures tend to yield similar or identical classifications if there is enough time for natural selection to operate. Under these circumstances (the Darwin condition) species tend to converge into compact unities characterized by a dominant type. This paper is a first step in the exploration of the existence and coexistence of species under various definitions and the operational conditions of ALife systems. We proposed a few items of further study and a hypothesis.

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APPENDIX

Given a set of n objects $S = \{O_1, ..., O_n\}$ and two data clusters of S, to be compared, $X = \{x_1, ..., x_R\}$ and $Y = \{y_1, ..., y_S\}$, where the different partitions of X and Y are disjoint and their union is equal to S; we compute the following values:

- a is the number of elements in S that are in the same partition in X and in the same partition in Y,
- b is the number of elements in S that are not in the same partition in X and not in the same partition in Y,
- c is the number of elements in S that are in the same partition in X and not in the same partition in Y,
- d is the number of elements in S that are not in the same partition in X but are in the same partition in Y.

Intuitively, one can think of $a+b$ as the number of agreements between X and Y and $c+d$ the number of disagreements between X and Y. Then, the Rand index, R, is defined as:

$$R=\frac{a+b}{a+b+c+d}=\frac{a+b}{\binom{n}{2}}. \quad (5)$$

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