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2 **Species are, at the same time, kinds and individuals:**  
3 **a causal argument based on an empirical approach**  
4 **to species identity**

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8 **Abstract**

9 After having reconstructed a minimal biological characterisation of species, we  
10 endorse an “empirical approach” based on the idea that it is the peculiar evolutionary  
11 history of the species at issue—its peculiar origination process, its peculiar metapopulation  
12 structure and the peculiar mixture and strength of homeostatic processes  
13 vis à vis heterostatic ones—that determine species’ identity at a time and through  
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15 in settling the individuals versus kinds dispute. In particular, while conceptual arguments  
16 have been proposed to show that species can be equally *treated* as individuals  
17 and kinds because mereology’s and set-theory’s languages are inter-translatable, we  
18 advance instead a causal argument to sustain the claim that each species is both a  
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22 **1 Sexual species from a biological point of view**

23 A longstanding disagreement about what species are persists. A glance at the literature  
24 on the so-called “species problem” reveals that more than twenty concepts of  
25 species have been, and still are, employed (Stamos 2003; Wilkins 2009; Richards  
26 2010; Ereshefsky 2010). A way to overcome this disagreement is to make reference  
27 to the distinction between a very general species concept (capturing what all species  
28 concepts have in common) and different operational criteria (de Queiroz 2005a, b,

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29 2007) or standards of application (LaPorte 2007).<sup>1</sup> For instance, de Queiroz argues AQ1  
30 that a general concept of species can be singled out because "...virtually all contem-  
31 porary definitions of the species category are based on a common general concept of  
32 species: the concept of species as (segments of) metapopulation lineages" (de Quei-  
33 roz 2005a: p. 6602). According to this view, to be segments of separately evolving  
34 metapopulation lineages is the only essential property for being a species. All the  
35 other properties identified by species concepts are contingent in the sense that they  
36 not only are typically acquired at different times during the speciation process (e.g.,  
37 two lineages can become phenotypically distinguishable before developing repro-  
38 ductive barriers), but also in the sense that they might or might not be acquired dur-  
39 ing the course of the history of the metapopulation lineage. Making mainly refer-  
40 ence to de Queiroz' version of the general species concept, the question to which our  
41 contribution tries to give an answer is twofold: first, what follows from endorsing a  
42 general species concept concerning the identity of species taxa (i.e., their criteria of  
43 diachronic and synchronic identity)? And, secondly, what is their metaphysical statu-  
44 s (i.e., which kind of entities they are)?

45 In order to answer the above questions, we firstly need to examine the concept of  
46 metapopulation and the related concept of Mendelian population more closely.

47 Metapopulation structure and dynamics, depending on the actual historical and  
48 geographical relations among the species subpopulations, play a fundamental role  
49 in determining species' identity. According to Levins (1970), who firstly introduced  
50 the term, a metapopulation consists of several spatially discrete local populations  
51 connected through migration and recolonization. The cohesiveness of the metapopu-  
52 lation as well as its vulnerability to extinction depends on its structure and dynam-  
53 ics (i.e., the size and interactions between the constituent populations) which varies  
54 from species to species.

55 The components of metapopulations are Mendelian populations. The concept of  
56 Mendelian population was originally elaborated by Wright (1931) and Dobzhansky.  
57 The latter defined a Mendelian population as a reproductive community of sexual  
58 and cross-fertilizing individuals sharing a common gene pool (Dobzhansky 1950:  
59 p. 405). Two features of Mendelian populations should be highlighted. Firstly, the  
60 attainment of reproductive isolation between genetically diverging populations is  
61 "the essence of biological speciation" (Dobzhansky 1950: p. 415). Secondly, the ori-  
62 gin and maintenance of isolating mechanisms are two different processes, the first  
63 leading to divergence of lineages, the second to the maintenance of the species' gene  
64 pool (Mayr 1988: p. 433).

65 It might be tempting to identify species with gene pools (Ridley 2004: p. 345).  
66 But this identification is problematic. Stamos (2003: p. 195), for instance, argues  
67 that if a species "literally *is* a protected gene pool", then it also cannot "literally *be*"  
68 a group of interbreeding natural populations, on pain of contradiction. Additionally,

<sup>1</sup> Even though the general species concept is quite agreed upon when species of sexually reproducing organisms are at stake, its applicability to asexual species has been questioned (see for instance Doolittle and Zhaxybayeva 2009; and see Samadi and Barberousse 2006 for a possible way to overcome this problem).

69 identifying species with gene pools would imply a very strong reductionist position  
70 at odds with the metapopulation approach, which makes reference to interactions  
71 among populations, such as migration and colonization, without reducing them at  
72 the genetic level. Accordingly, we prefer to speak of *characterization* rather than  
73 *identification*. Moreover, we would not like to dismiss, in principle, the possibil-  
74 ity that both phenotypic properties and non-genetically inherited properties might  
75 be relevant for species characterisation. Concerning phenotypic properties, con-  
76 sider the following example. Seasonal polyphenism (either/or phenotypes elicited  
77 by environmental induction, e.g., temperature) in many butterfly species can lead to  
78 fixation of alternative phenotypes in geographically isolated populations. The pat-  
79 tern of evolution is first the production of alternative phenotypes with same genetic  
80 basis by developmental plasticity and then reproductive isolation, causing speciation  
81 (West-Eberhard 2003, p. 532). In this case, characteristic phenotypes of species are  
82 relevant for speciation. Concerning non-genetically inherited properties, it has been  
83 argued that, for instance, epigenetic inheritance may be important for adaptation,  
84 especially when the available genetic variation is scarce, because it might enable  
85 survival in dynamic environments (e.g., climate change effects) *before* genetic adap-  
86 tation evolves (Burggren 2016). If so, then non-genetically inherited properties may  
87 guarantee the persistence over time of a species.

88 For these reasons, we propose to replace the gene pool concept with the more  
89 comprehensive concept of *gene-phenone pool*. Mayr (1970: p. 417) defined the gene  
90 pool as “The totality of the genes of a given population existing at a given time.”  
91 Analogously, we define the concept of gene-phenone pool as the totality of the genetic  
92 and phenotypic properties of a given population or metapopulation existing at a  
93 given time.<sup>2</sup> The concept of gene-phenone pool provides a genetic and phenotypic  
94 characterization of sexual species that complements the ecological characterization  
95 provided by the metapopulation concept. Importantly, notice that the metapopula-  
96 tion structure and dynamics (i.e., the size and migration and colonization patterns of  
97 the populations that make up the metapopulation) co-determine the nature and the  
98 formation of the gene-phenone pool of the species (e.g., a migration from one popu-  
99 lation to another population of the same metapopulation can be a means through  
100 which gene flow occurs in the metapopulation).

101 To sum up, despite the multiplicity of species concepts, a *minimal characterisa-*  
102 *tion* on what sexually reproducing species are can be pointed out:

103 (MC) Species of sexually reproducing organisms are segments of metapopula-  
104 tion lineages whose constituents are Mendelian populations characterized by  
105 their own gene-phenone pool.

<sup>2</sup> It is important to emphasise that the concepts of gene pool and gene-phenone pool could be defined by taking into consideration the extant organisms of the species—like Mayr does—or by taking into account all its past, present and future members. This latter characterization clearly shows the indefiniteness of the concepts of gene pool and gene-phenone pool. Furthermore, it is also important to note that, unlike Mayr, we prefer to use the term “genetic property” in order to define the concept of gene-phenone pool; the reason is that this latter term is more general and neutral as it might also refer to sequences of DNA with not yet known functional role in development.

106 Three clarifications are in order. First, whether the populations of a metapopulation  
107 are Mendelian populations or not is an open empirical issue (E.O. Wilson 1975: p.  
108 51). Here, for simplicity, we assume that all the populations in a segment of a meta-  
109 population lineage are Mendelian populations. Second, it is tempting to merge the  
110 two concepts of metapopulation and Mendelian population—which are in fact very  
111 close—and claim that a species is the largest Mendelian population, as Dobzhansky  
112 did (1950: p. 406). We prefer to maintain the concepts separated. There are cases in  
113 which as a matter of fact a species is a Mendelian population without being a meta-  
114 population: think of the only extant population of a critically endangered species  
115 localised in a small territory; it is highly likely that, in the past, this species exhib-  
116 ited a metapopulation structure (i.e., being constituted of geographically distributed  
117 Mendelian populations) and that its present status is the result of its past metapopu-  
118 lation dynamics. So, in order to be able to account for past metapopulation dynamics  
119 that have played a fundamental role in determining the identity of a species, it is  
120 methodologically useful to keep the concepts separated. Third, it should be noted  
121 that the minimal characterization sketched provides a two-level definition making  
122 reference, on the one hand, to the genetic and phenotypic level (through the concept  
123 of gene-phenotype pool) and, on the other hand, to the ecological level (through the con-  
124 cept of metapopulation). Whether the two levels could be reduced to each other is an  
125 issue we are not going to consider in this article.

## 126 2 The identity of species

127 Given the minimal characterisation of species articulated in the previous section, we  
128 can proceed to answer the first part of our twofold metaphysical question concern-  
129 ing species' identity. We suggest that the identity of a species is determined by the  
130 limits of the relevant metapopulation lineage segment and the relative cohesiveness  
131 of its gene-phenotype pool. As it will become clear, we do not endorse the view that it  
132 will inevitably be possible to clearly determine the limits of the segment and the  
133 level of cohesiveness required to be a species. Nonetheless, in principle the determi-  
134 nation of the limits of the segment is possible by making reference to the nature of  
135 the relevant speciation process, while the determination of relative cohesiveness of  
136 the gene-phenotype pool is possible by making reference to the metapopulation dynam-  
137 ics and the biological processes producing and maintaining lineage cohesiveness or,  
138 conversely, generating divergence among lineages. It is for this reason that the con-  
139 cepts of Mendelian population characterized in terms of gene-phenotype pool and meta-  
140 population are useful epistemological tools to answer the identity question.

141 The MC suggests that only by knowing the speciation process, the peculiar meta-  
142 population dynamics and the distinctive gene-phenotype pool it becomes possible to rec-  
143 ognize a particular segment of a lineage as a species and, furthermore, as *that* par-  
144 ticular species. This is the core message of the empirical approach we endorse. Since  
145 the speciation process, the metapopulation dynamics and the distinctive gene-phenotype  
146 pool differ in each species case, every single species taxon should be considered as  
147 an entity on its own. In order to show this, consider a species with its own metapopu-  
148 lation structure. Each species underwent its peculiar speciation process, has its own

149 peculiar history and is characterised by its unique metapopulation structure (i.e., a  
150 given sequences of generations of Mendelian populations over time) and dynam-  
151 ics (migrations and colonisations). Moreover, the ties that keep together, on the one  
152 hand, the members of Mendelian populations and, on the other hand, the Mendelian  
153 populations of the metapopulation, can be of different type in different species. For  
154 instance, the members of one species might be kept phenotypically homogeneous  
155 by stabilising selection while the members of another might be kept phenotypically  
156 homogeneous by the curtailment of mutation through processes enhancing genomic  
157 stability (e.g., DNA editing) or by developmental homeostasis (i.e., a process that  
158 canalises the development of the organisms of the species). Additionally, the devel-  
159 opmental and evolutionary processes keeping together the members of Mendelian  
160 populations as well as the Mendelian populations of the metapopulation may also  
161 display different strengths at different times of a species life. For instance, gene con-  
162 servation through stabilising selection might be stronger in different phases of the  
163 life of the species (see Sect. 3.3).

164 In our view, each sexual species is thus identified, first, by its peculiar speciation  
165 process; second, by the specific combination of the *types* of processes maintaining  
166 its cohesion (see Sect. 3.2); and third, by the specific *strength* of such maintenance  
167 processes (see Sect. 3.3). Accordingly, we propose that a species' identity is deter-  
168 mined by its *integrating principle* (Colless 2006), which is constituted by two sorts  
169 of processes:

- 170 (i) *Origination processes*, i.e., the kind of processes through which the species  
171 originated or, put in other words, that allow us to identify the limits of the  
172 metapopulation lineage segment at issue;
- 173 (ii) *Homeostasis processes*, i.e., the processes maintaining lineage cohesiveness  
174 or, in other words, in virtue of which a species persists over time, in spite of  
175 the changes it undergoes, as one and the same species.

176 Given the contingency of the historical process a species undergoes (represented  
177 by, e.g., its geographical separation, its history of mutation, its metapopulation  
178 dynamics), it seems clear that every species has a peculiar history that leads in pecu-  
179 liar ways (i.e., through the causal action of a peculiar mixture of evolutionary pro-  
180 cesses) to the formation and maintenance of its distinctive gene-phenon pool.

### 181 3 Sexual species from a metaphysical point of view

182 The perspective sketched so far takes as departure point the general concept of spe-  
183 cies put forward by de Queiroz, i.e., a definition of the species *category*, and then—  
184 adopting the empirical stance suggested by the MC —moves to consider species  
185 *taxa* and their identity conditions. We would now like to argue that this empirical  
186 approach may help in settling the *vexata quaestio* whether species taxa should be  
187 conceived as individuals (SAI) or as kinds, more specifically as a peculiar sort of  
188 natural kinds defined on the basis of homeostatic property clusters (HPC), answer-  
189 ing the second part of the twofold metaphysical question articulated in Sect. 1. De



190 Queiroz (1999: p. 67 ff.) pointed out that the general species concept *is compatible*  
191 *with conceptualizing* species as either individuals or classes. We shall defend  
192 a stronger metaphysical claim, namely, that species *are* individuals and kinds at  
193 the same time.<sup>3</sup> More specifically, we shall argue that the fact that species are indi-  
194 viduals and kinds at the same time *causally follows* from the minimal characteriza-  
195 tion given above. Our argument proceeds as follows. In Sect. 3.1 we illustrate the  
196 main conceptual arguments that have been proposed to show that species can be  
197 equally treated as individuals and as kinds. These arguments are typically based on  
198 the inter-translatability of the two respective languages (i.e., mereology's and set-  
199 theory's languages). In Sect. 3.2, we take things a step further by arguing that the  
200 issue concerning the metaphysical status of biological species is not to be solved by  
201 uncovering whether the relationships between individual organisms and the species  
202 they belong to are set-theoretical or rather mereological, but by understanding their  
203 biological nature. Finally, in Sect. 3.3 we shall highlight that, as we have anticipated  
204 in Sect. 2, species' identity through time also depends on the *strength* of homeo-  
205 static processes. In fact, homeostatic processes maintaining species integrity (i.e.,  
206 the integrity of its gene-phen pool) clash with the processes creating (heterogenic)  
207 and maintaining (heterostatic) genetic and phenotypic variation (Ereshefsky and  
208 Matthen 2005). In case the latter prevail, the integrity of the species might be com-  
209 promised, possibly leading to speciation.

### 210 3.1 SAI versus HPC

211 According to SAIsts (Ghiselin 1974; Hull 1978; Eldredge and Gould 1972; Brogaard  
212 2004)<sup>4</sup> species taxa are to be treated as spatio-temporally localized individuals,  
213 made up of parts (i.e., organisms) related by descent. The relation between organ-  
214 isms, populations and species taxa would then be construed as a part-whole rela-  
215 tion (i.e., a mereological relation) instead of a class-membership relation (i.e., a set-  
216 theoretical relation), thus avoiding—at least according to Ghiselin (1974)—intrinsic  
217 essentialism. It should be noted that there are two *prima facie* incompatible ways to  
218 characterise the SAI thesis. SAI might be seen as (a) a mereological thesis according  
219 to which species are spatio-temporally localized individuals (concrete particulars)  
220 made up of causally related parts (i.e., organisms). An advocate of this version of  
221 SAI is Ghiselin (1974: p. 536), who claims of taking the term “individual” in its  
222 logical sense—i.e., “not a synonym for ‘organism’”—but rather as merely designat-  
223 ing concrete particulars as opposed to abstract entities such as sets or classes. Oth-  
224 erwise, SAI might be characterised as (b) the thesis that species are “organismal” in  
225 the sense of displaying organism-like properties such as a certain level of functional  
226 integration. Hull (1976, 1978) sometimes seems to endorse this version of SAI:  
227 “they [species] possess all the characteristics of individuals—that is, if organisms  
228 are taken to be paradigm individuals” (Hull 1976, p. 174). In this article, we shall

3FL01 <sup>3</sup> de Queiroz (1995) admits the same possibility, on the basis of mainly semantic considerations.

4FL01 <sup>4</sup> The historical roots of the thesis are much older, going back at least to Buffon (Gayon 1996).

229 consider the mereological thesis as our main target. Notice, however, that the two  
230 theses are different but not incompatible. One way to understand the relationships  
231 between these two characterisations is through genidentity (Hull 1992). Genidentity  
232 (see below in this section) is in this sense both a mereological relationship and an  
233 account of organismality. In the first sense, organisms are the states of the biological  
234 trajectory of the genealogical lineage, while in the second sense species are cohesive  
235 units of organisms analogous to the cohesive units of cells constituting multicellular  
236 organisms.

237 In our view, (b) might be seen as a particular case of (a): under certain conditions,  
238 the causal relations connecting the parts of a species might become tighter and being  
239 of the relevant type as to consider a certain species (or a temporal part of it) as an  
240 organism-like entity. If organismality is a matter of degree and has to do with the  
241 balance between cooperation and competition, when competition among the parts of  
242 a species is higher than cooperation, the species will be less organism-like, and vice  
243 versa (Queller and Strassman 2009).

244 The major rival of the individuality view is HPC (endorsed in different versions  
245 by authors like Boyd 1999; Wilson et al. 2007; Brigandt 2009).<sup>5</sup> The core idea of  
246 the HPC view is that species are to be treated as natural kinds whose members share  
247 some of the properties included in a cluster, or a “family” (Boyd 1999: p. 143) of  
248 properties exhibiting some degree of correlation (i.e., typically co-instantiation).  
249 Each species member possesses several of these properties, though usually not all  
250 of them, and none of them must necessarily be shared by all the members of the  
251 kind (thus overcoming the problems of traditional essentialism).<sup>6</sup> Moreover, unlike  
252 traditional kinds, HPC kinds can account for the fact that a species is a historical  
253 entity by recognizing historical relations (e.g., the relation of descent) as one type  
254 of homeostatic mechanism at the basis of the clustering.<sup>7</sup> The family of properties is  
255 indeed “contingently clustered in nature” (Boyd 1999: p. 143) in the sense that these  
256 phenotypic or genetic features co-occur in an important number of cases in virtue of  
257 underlying causal processes (i.e., homeostatic processes) that tend to maintain their  
258 co-occurring presence.<sup>8</sup>

259 A third metaphysical position concerning specieshood is worth mentioning for  
260 its closeness to that hereby defended, namely that species are historical entities.

5FL01 <sup>5</sup> An alternative account taking Boyd’s HPC view as a departure point has been recently offered by  
5FL02 Slater (2013, 2015), who suggests replacing the notion of homeostatic property clusters with the notion  
5FL03 of *stable* property clusters (SPC).

6FL01 <sup>6</sup> Whether all the extant (or even past and future) organisms of a species actually share a set of intrinsic  
6FL02 properties remains an open empirical issue that cannot be settled philosophically (Devitt 2008; Barker  
6FL03 2010).

7FL01 <sup>7</sup> We characterise a cluster in terms of intrinsic and relational properties. Wilson et al. 2007 argue that  
7FL02 a cluster consists of both kinds of properties for the reason that “... the features that promote cohesion  
7FL03 within a species [i.e., that keep the cluster homeostatic] are typically relational properties of conspecif-  
7FL04 ics....” Our argument does not depend on privileging relational over intrinsic properties.

8FL01 <sup>8</sup> It is interesting to note that no definite list of homeostatic mechanisms has been provided. In our opin-  
8FL02 ion, the reason for this omission is simply that homeostasis is species-dependent: the homeostatic mecha-  
8FL03 nisms at play depend on the peculiar speciation process and metapopulation structure and dynamics and  
8FL04 thus may vary over time and/or space.

261 According to Ereshefsky (2014: p. 714), a species' identity "is not determined by its  
262 intrinsic properties or its origin, but by its unique evolutionary path". A similar view  
263 was already defended by Hull (1992), who argued that genidentity is the only avail-  
264 able criterion of individuality for supra-organismal aggregates such as species. The  
265 genidentity criterion can be characterised as the thesis that an object can be indi-  
266 viduated through time not by retention of intrinsic properties but because of its con-  
267 tinuous historical relationship to its previous states in the context of its life history  
268 trajectory. Genidentity is thus a historical relation purely characterisable in terms of  
269 the causal relationship between the various life history states of the object. From this  
270 perspective, it follows that the organisms constituting a species do not belong to it  
271 because they share intrinsic properties. Thus, the historical identity of a species can  
272 only be grounded on its unique evolutionary origin and on the phylogenetic relation-  
273 ship that its constituent organisms have with such origin as spatio-temporal parts of  
274 that genealogical nexus (i.e., a genidentity relationship). Thus, Hull's and Ereshef-  
275 sky's positions are similar in the sense that both consider species as path-dependent  
276 historical entities, while they significantly differ because species' origin is not taken  
277 as part of the identity criterion by Ereshefsky. Unlike Ereshefsky, we shall consider  
278 the biological nature of the origination process as a crucial ingredient for the iden-  
279 tity of species.

280 HPC and SAI have usually been presented by their respective supporters as onto-  
281 logically incompatible. For instance, in reviewing Dupré's (1995) book, Wilson  
282 (1996: p. 310) pointed at the fact that it is "an absurdity" to say "that one and the  
283 same thing is a natural kind and an individual" since "individuals and kinds belong  
284 to fundamentally different ontological categories".

285 Wilson's view is not universally shared. In fact, the supposed ontological incom-  
286 patibility between kinds and individuals has been treated by many authors with a  
287 certain dose of scepticism. Some have argued that the issue matters more to phi-  
288 losophers rather than to biologists (Assis and Brigandt 2009), and others have raised  
289 doubts concerning its significance. Hull himself, in the conclusion of his paper on  
290 SAI (Hull 1976), mentioned that "perhaps the distinction between individuals and  
291 classes is too crude", and Boyd (1999: p. 162 ff.) suspected that the incompatibility  
292 issue might have been somehow inflated in the literature. Moreover, Okasha (2002:  
293 p. 193) claimed "that it is largely a matter of convention whether species are con-  
294 ceptualized as individuals, kinds or historical entities", echoing Dupré (1995: p.  
295 43) who wrote that: "in some contexts species are treated as individuals, in others  
296 as kinds". The argument usually brought in favour of the consistency between the  
297 two views may be called "the argument from inter-translatability": "An organism  
298 is 'a part of a species-individual' on SAI, while the HPC view has to conceptual-  
299 ize this organism as 'a member of a species-natural-kind', and translate any talk  
300 about organisms accordingly (and vice versa for SAI)." (Brigandt 2009: p. 85) This  
301 argument avoids taking a stance on what species are, both from a metaphysical  
302 and a biological point of view, effectively considering the issue merely conceptual  
303 or linguistic: a certain portion of the biological realm can be conceptualized and

304 described in mereological terms as well as in set-theory terms.<sup>9</sup> In fact, the main  
305 difference between the two ways of speaking is that mereology is not committed  
306 to the existence of abstract entities—such as classes or sets—, while set-theory is  
307 (this does not mean that mereology is committed to concreta instead: the whole can  
308 be as concrete as the parts, and the parts can be as abstract as the whole—see Varzi  
309 2016). But this difference does not seem to play any substantial role in the case of  
310 biological species. In speaking of species taxa as kinds, what we are interested in  
311 is not abstract entities but, rather, their concrete members with their properties. For  
312 instance, by saying that “species evolve” we are not aiming to say that there is an  
313 abstract entity—a class—that evolves (abstract entities cannot evolve by definition).  
314 What we might mean is that, over time, the frequency of a certain phenotype (i.e., a  
315 property of individual organisms, namely the members of the species at issue) has  
316 increased or decreased in the population of reference.<sup>10</sup> The very same point can be  
317 expressed in terms of parts (Okasha 2002; LaPorte 2004; Brigandt 2009).

318 The intertranslatability argument states that the two languages—mereology’s  
319 and set-theory’s—have an equivalent expressive power or, conversely, that the same  
320 portion of reality can be equally well described by means of the two different lan-  
321 guages. On the contrary, we shall argue that SAI and HPC could be closer than it  
322 seems at a first glance also in virtue of biological considerations. In the next section,  
323 we argue that the empirical approach provides a biological foundation for the inter-  
324 translatability argument. Our argument is not an entirely new one. It is close, under  
325 some respects, to Rieppel’s (2007, 2009) and LaPorte’s (2004), according to whom  
326 species are both kinds and individuals: “where there are properties, there are natural  
327 kinds. ... As long as it is admitted that talk about species have causally grounded  
328 properties, it also has to be admitted that talk about species as individuals can be  
329 translated into talk about species as natural kinds (LaPorte 2004)” (Rieppel 2007:  
330 p. 378). But it has two important differences. First, we do not endorse Rieppel’s  
331 conclusion that the fact that species are kinds means that they are “single members  
332 of their own specific natural kinds”, i.e. “complex wholes (particulars, individuals)  
333 that instantiate a specific natural kind” (Rieppel 2007: p. 373), for we see no reason  
334 in considering each species as a *member of its own kind*, which would multiply enti-  
335 ties unnecessarily. What we do claim is that each species is both a kind (i.e., a class  
336 whose members share some properties included in a cluster) and an individual. Of  
337 course, this implies a conflation of the distinction between kinds and individuals; we  
338 accept this implication, seeing it as a low price to pay.

9FL01 <sup>9</sup> We use the terms “class” and “set” as synonymous and as intensionally defined.

10FL01 <sup>10</sup> This is called, by Kitcher (1984), “The fallacy of incomplete translation”. Kitcher reconstructs the  
10FL02 argument in favour of SAI as follows: Sets cannot evolve; species evolve; hence species are not set. In  
10FL03 the argument, “species evolve” is, according to Kitcher, left untranslated. To complete the translation, we  
10FL04 need to consider that a species, set-theoretically conceived, is a union of subsets—or *stages*. A stage is  
10FL05 the set of organisms belonging to the species which are alive at a given time. Accordingly, the complete  
10FL06 translation of “species evolve” would be something like: the frequency of the distribution of (genetic  
10FL07 or genetic plus phenotypic) properties at one stage will differ from the frequency of the distribution of  
10FL08 (genetic or genetic plus phenotypic) properties at a later stage. Proceeding in this way, Kitcher argues,  
10FL09 claims about the evolutionary behaviour of species—such as for instance speciation or extinction—may  
10FL010 be easily expressed in set-theoretical terms.

339 Consider that the master argument provided by SAIsts in favour of their view is  
340 the following: species evolve; abstract entities (such as kinds) are atemporal enti-  
341 ties, thus they cannot evolve; then, species are not kinds. But, as Kitcher (1984) and  
342 LaPorte (2004) have shown, abstract entities can be made compatible with evolu-  
343 tion once the fallacy of incomplete translation is recognized. The metaphysical dis-  
344 tinction lying behind the argument is that between abstract and concrete entities,  
345 whereas abstract entities are identified with sets or classes, and concrete entities  
346 with individuals or particulars. However, such identification is questionable: just as  
347 there might be *abstract* individuals (such as, for instance, numbers), there might be  
348 *concrete* kinds, i.e., either a kind may be identified with its members or with its  
349 defining properties, where these properties are understood as concrete particulars  
350 (i.e., individualized properties).

351 Moreover, as Reydon (2009) has argued, Rieppel's reconciliation between kinds  
352 and individuals is merely an epistemological, not a metaphysical argument. Our  
353 position is a stronger one: species are at the same time kinds and individuals in a  
354 metaphysical (and biological) sense, and not only because *conceiving* them as such  
355 is required by different kinds of biological explanations, or allowed by the inter-  
356 translatability of sets-talk and part-whole talk. The fact that species taxa are both  
357 kinds and individuals is a consequence—so we argue—of the way in which some  
358 lineage segments originate, evolve, and become extinct.

### 359 3.2 A causal argument for compatibility

360 The empirical approach addresses the question concerning the metaphysical sta-  
361 tus of species taxa in these terms: each species is at the same time an individual  
362 and a kind individuated by its characteristic origination process, its characteristic  
363 gene-phenome pool and its characteristic metapopulation structure and dynamics. The  
364 twofold metaphysical status of species taxa depends on this biological characteriza-  
365 tion, rather than on purely linguistic or conceptual considerations. The reason is that  
366 organisms participate in species-specific biological processes, and this participation,  
367 as well as those processes, is what makes them both parts of wholes and members of  
368 classes. This participation is causally primary since, without it, there would simply  
369 be no species at all, and hence it should inform the metaphysical analysis of species  
370 *in so far as* they are biological entities. Certain species-specific causal relations hold  
371 among the organisms that make a species (e.g., relations of descent or reproduction),  
372 as well as between those organisms and the species (e.g., relations of part-hood or  
373 membership). When those relations hold, an entity which is at the same time an  
374 individual and a kind is what we are dealing with. For instance, consider common  
375 descent. Organism *a* is part of the whole/species *S* when it is genealogically related  
376 to another organism *b*, where *b* is a recognised part of *S*; and, at the very same time,  
377 that same organism *a* is a member of class/species *S* because it shares *n* properties  
378 of the cluster *C* characterising *S* with *b*, where *b* is a recognised member of *S*. Now  
379 note that this is the twofold outcome of one and the same process that emphasises  
380 different causal relationships, i.e., being genealogically related and sharing genetic  
381 and phenotypic properties. Yet, ultimately, both relationships involve material



382 inheritance: common descent is both the causal process linking part  $a$  and part  $b$   
383 of  $S$  and the causal process making member  $a$  genetically and phenotypically simi-  
384 lar to member  $b$ . To put it in other words: if species are biological entities, then an  
385 organism  $a$  is a part of individual/whole  $S$  because it stands in a particular biological  
386 relationship with  $S$  which happens to be mereological. Equally, if organism  $a$  is a  
387 member of class  $S$ , it is because it stands in a particular biological relationship with  
388  $S$  which happens to be set-theoretical. Thus, mereological and set-theoretical rela-  
389 tions should be, in the case of things like biological species, interpreted biologically  
390 because they are biologically realised.

391 The putative incompatibility between the individuality and HPC kind theses  
392 highlighted in Sect. 3.1 stems from the fact that, *prima facie*, they seem to identify  
393 species' part-hood and membership conditions differently. In the case of the indi-  
394 viduality thesis, in order to characterise part-hood conditions explicit reference to  
395 the causal relations between parts is needed. Conversely, in the case of the HPC kind  
396 thesis, the characterisation of membership conditions makes reference to the genetic  
397 and phenotypic properties of the relevant cluster (see footnote 8). But this difference  
398 is spurious. In fact, causally speaking the two theses both make reference to specific  
399 causal relations and interactions between organisms in terms of their participation  
400 in causal processes. Causally speaking, the individuality thesis claims that an indi-  
401 vidual is a whole made of parts; parts are causally related to other parts because  
402 they participate in specific causal processes, where these causal processes make the  
403 whole individual-like; for instance,  $a$  is part of the whole/species-as-individual  $S$  if  
404 it is causally related (e.g., by reproduction or descent) to another part  $b$  of  $S$ . The  
405 specific causal relationship between  $a$  and  $b$  contributes to make  $S$  a cohesive whole.  
406 In the HPC case, a kind has members and its members are identified by property  
407 clusters; members are causally related to other members because they participate in  
408 homeostatic processes, where these causal processes make the participating mem-  
409 bers genetically and phenotypically similar and the relative species kind-like; for  
410 instance,  $a$  is member of the species-as-HPC-kind  $S$  if it shares a subset of the prop-  
411 erties of the cluster  $C$  that characterises species  $S$  with  $b$ .

412 When a causal approach is endorsed, we can see that the two main putative dif-  
413 ferences between the two views are apparent. The first is a difference in emphasis:  
414 while the individuality thesis stresses the causal participation of the organisms of  
415 the same species in specific causal processes, the HPC kind thesis might be inter-  
416 preted as stressing the similarity between those organisms; however, their similarity  
417 is *determined* by their participation in causal processes, i.e., similarity is the causal  
418 effect of such participation. To strengthen this point, consider again the metapopu-  
419 lational structure of a species. If you look at the sequence of Mendelian populations  
420 through time, it is clear that what keeps together the successive generations of popu-  
421 lations are causal relations such as reproduction and descent. But if you look at the  
422 metapopulation at time  $t$  (i.e., if you consider just one generation), what catches the  
423 eye is the similarity among the organisms that compose the species (since gene flow  
424 and descent are inter-generational processes). The second apparent difference stems  
425 from the fact that certain causal processes might render a species individual-like  
426 while others might make it kind-like. But even in this case the difference is spurious.  
427 What needs to be understood is the nature of the causal relations and interactions

428 between the organisms of a lineage in terms of their participation in causal pro-  
429 cesses. It is highly probable that the homeostatic processes keeping the members  
430 of species genetically and phenotypically homogeneous are different (e.g., develop-  
431 mental and genetic homeostasis in the case of one species and genetic drift, direc-  
432 tional selection and adaptive introgression in the case of another); accordingly, dif-  
433 ferent species may be individual-like and kind-like in virtue of different processes.  
434 This species-specificity and uniqueness was already highlighted by Mayr (1963)  
435 when referring to “species-specific homeostatic mechanisms”. Our point is that it is  
436 not possible that a single species with a specific origin, life history, metapopulation  
437 structure and gene-phen pool is individual-like because of the causal contribution  
438 of a set of biological processes  $x$  and kind-like because of the causal contribution of  
439 a different set of biological processes  $y$ . *We here argue that if these causal processes*  
440 *render the species individual-like, then they also render it HPC-kind-like and vice*  
441 *versa. On the one hand, the various parts of a species are kept together tightly by*  
442 *means of their causal relations and through their participation in specific biologi-*  
443 *cal processes that make the whole cohesive, integrated and individual-like. On the*  
444 *other hand, the cluster of co-occurring genetic and phenotypic properties partially*  
445 *shared by the members of the species-as-kind is kept together as a homeostatic clus-*  
446 *ter through the action of the very same specific biological processes.*

447 Ultimately, we argue that, because the same processes cause a species to be both  
448 individual-like and kind-like, that entity is both an individual and a kind. The con-  
449 trast between SAI and HPC can then be read as occurring at an epistemological  
450 rather than at an ontological level. As a matter of fact, SAI and HPC look at the  
451 same biological reality from two alternative perspectives, i.e., they are describing  
452 two sides of the same coin: the cohesiveness of biological species as wholes and the  
453 compactness of their gene-phen pools. For instance, processes like developmen-  
454 tal and genetic homeostasis, made possible by reproduction, equally make a species  
455 individual-like and kind-like at the same time. Some advocates of the individuality  
456 thesis (e.g. Hull 1978; Gould 2002: chapter 8) argued that these homeostatic pro-  
457 cesses render the species cohesive like an individual (and unlike a kind). But also  
458 note that the effect of these processes is homeostatic in the sense that they main-  
459 tain the species’ gene-phen pool stable; that is, the processes rendering the species  
460 a cohesive individual are also those maintaining the stability of its distinctive and  
461 characterising HPC. The reason is obvious: developmental homeostasis canalises  
462 the development of the organisms of the species by making them phenotypically  
463 uniform, while genetic homeostasis (i.e., stabilising selection eliminating less fit  
464 hybrids and “deviant” organisms) has an equivalent genetic effect.

465 The inter-translatability argument states that individual-talk and kind-talk are  
466 inter-translatable. The argument from causality we have here proposed shows that  
467 the two metaphysical views are consistent on the basis of making reference to the  
468 same biological processes. Thus, as far as sexual species are concerned, the argu-  
469 ment from causality supports the inter-translatability argument that each species can  
470 be treated as both an individual and as an HPC kind on the basis of the metaphys-  
471 ical thesis that each species is, at the same time, an individual and an HPC kind.  
472 We therefore argue that there is a fact of the matter concerning the question of the  
473 metaphysical status of sexual species: it is not a matter of convention to treat sexual

474 species as individuals or as kinds, but it is rather a matter of looking at the causal  
475 processes determining species' identity.

### 476 3.3 Individuality and kindness are a matter of degree

477 In this section we characterize our position in more detail and evaluate the implied  
478 corollary that both individuality and kindness may come in degrees. In Sect. 2 we  
479 observed that there might be a difference not only in the kind of homeostatic pro-  
480 cesses at play, but also in the homeostatic *strength* of the processes. As a conse-  
481 quence of this, a species might be more individual-like (i.e., a more or less cohesive  
482 whole) and more kind-like (i.e., a more "natural" cluster sensu Boyd) at time  $t$  and  
483 less at (past or future) time  $t_n$  and vice versa. The reason (also highlighted by Slater  
484 2015: p. 393) is the following. Evolutionary processes such as, for instance, selec-  
485 tion and drift can be homogenizing forces in specific circumstances, but not gener-  
486 ally. It is again a contingent matter depending on the peculiar history and present  
487 status of the metapopulation whether evolutionary processes will have a homogeniz-  
488 ing rather than a disruptive effect. It is useful to think of this dynamic as a clash  
489 between the homeostatic processes that maintain species integrity (i.e., its genetic  
490 and phenotypic uniformity) and the processes creating (heterogenic) and maintain-  
491 ing (heterostatic) genetic and phenotypic variation. Thus, we suggest that individu-  
492 ality and kindness come in degrees, depending on the strength of homeostasis and  
493 on the prevalence of homeostasis *vis à vis* heterostasis.

494 In order to show this, let us consider an example concerning our species. Mayr  
495 argued that species' homeostasis is often characterized by inertia:

496 ... owing to the hundreds or thousands of generations that have undergone pre-  
497 ceding selection, a natural population will be close to the optimal genotype...  
498 All the mutations of which this genotype is capable and that could lead to an  
499 improvement of this standard phenotype have already been incorporated in  
500 previous generations. (Mayr 2001: 50)

501 However, homeostatic inertia can be eclipsed. For instance, consider the evolution of  
502 lactose tolerance. In this case, mutation acts as a heterogenic process: several muta-  
503 tions associated with the expression of the lactase gene allowing humans to process  
504 lactose occurred in different geographic areas in the last 10.000 years or so (Tishkoff  
505 et al. 2007). Given the existence of heterogenesis, with what frequency does heter-  
506 ostasis happen? The chief reason for thinking that heterogenesis does not usually  
507 translate into stable polymorphisms is that selection is assumed to mostly fix one  
508 variant, i.e., to be stabilising (West-Eberhard 2003: p. 6 ff.). But the frequency of  
509 stabilising selection compared to other forms of selection depends on the constancy  
510 of the developmental and evolutionary environments in which the species lives. As  
511 a matter of fact, in the case of lactose tolerance, directional selection has been act-  
512 ing as a heterostatic process: the lactose tolerance mutations have spread, partially  
513 disrupting the homeostatic inertia of our species, with a significant subpopulation of  
514 contemporary humans lactose tolerant. The present human dimorphism exhibits the  
515 underlying genetic variation at the metapopulation level and the evolution of lactose



516 tolerance that is currently taking place. Obviously, we are not here arguing that this  
517 is an impending case of sympatric speciation with the lactose-tolerant and intolerant  
518 human populations slowly diversifying and separating as distinct lineages. What we  
519 claim is rather that the maintenance of the present dimorphism or the eventual fixa-  
520 tion of the lactose tolerant phenotype (in one of its known genetic variants or others)  
521 will depend on the present and future status of the human metapopulation and the  
522 relative strength of different evolutionary forces. In a scenario in which, in differ-  
523 ent ecological and social settings, the lactose tolerant and lactose intolerant traits  
524 maintain fitness-enhancing properties (respectively an environment where domesti-  
525 cated cattle are abundant, milk extraction techniques are sufficiently refined etc. vs.  
526 an environment with increasing availability of milk substitutes, not enough cattle  
527 to meet population needs etc.) disruptive selection might act as a heterostatic force.  
528 Conversely, given a change in this setting (e.g., the increasing fitness of the lactose  
529 tolerant phenotype due, for instance, to the rising importance of milk and dairy con-  
530 sumption on a planet devastated by underproduction of alternative food resources, or  
531 enhanced immunity to zoonotic diseases transmitted by cattle), directional selection  
532 might act as a homeostatic force.

533 Besides this speculation, the example shows that homeostasis is counterbal-  
534 anced by a number of context-relative and species-specific heterogenic and hetero-  
535 static forces and that the prevalence of these forces determines the conditions for  
536 speciation. In particular, the example shows that the existence of polymorphisms  
537 is an important—though per se insufficient—condition for sympatric speciation. It  
538 is insufficient because a heterostatic force must be at play to disrupt homeostasis  
539 and actually diversify the lineage. When polymorphisms are available, for instance,  
540 disruptive selection can act as a heterostatic force. Indeed, as Mallet (1995: p. 299)  
541 argued, “To understand speciation, we need to understand when disruptive selection  
542 can outweigh gene flow between populations.” Ultimately, it is a contingent matter  
543 depending on the peculiar history and present status of a species whether specific  
544 developmental and evolutionary processes will have a homogenizing rather than a  
545 disruptive effect.

546 The example above is also meant to show that heterostasis renders simultaneously  
547 the species less individual-like (by making it less cohesive) and less HPC kind-like  
548 (by making its distinctive homeostatic cluster less homogeneous). Starting with the **AQ2**  
549 issue of individuality, the notion of species cohesion might be interpreted, follow-  
550 ing Barker and Wilson (2010, pp. 64–65), in at least two ways: as response cohe-  
551 sion, when its component organisms respond as a unit to some kind of intervention  
552 (causal interaction among them is not required, they may respond similarly but inde-  
553 pendently), or as integrative cohesion (i.e., when the causal interactions between  
554 *most or all* of the organisms make it function as a whole). Barker and Wilson argue  
555 that, typically, biological species only display the first kind of cohesion—i.e., by  
556 responding as a unit to evolutionary pressures—but lack integrative cohesion. Thus,  
557 according to them, species cannot be considered individuals because, being “gappy”  
558 entities (for instance in the sense that their members are physically separated), *most*  
559 *or all* species members are unable to causally interact appropriately in order to  
560 achieve integrative cohesion (for instance, because certain behaviours may preclude  
561 gene flow). At the same time, they admit that “response cohesion comes in degrees”.

562 We suggest the same applies to integrative cohesion, with the consequence that also  
563 individuality comes in degrees, resulting in species whose individuality is more  
564 or less “organismal” (recall the distinction between the two formulations of SAI  
565 sketched in Sect. 3.1).

566 Consider also that gene flow might not be the only means to achieve integrative  
567 cohesion. At least Eldredge and Gould (1972), Templeton (1989) and Mallet (1995)  
568 have maintained that species can evolve as cohesive units even in the absence of sig-  
569 nificant gene flow. For instance:

570 The coherence of a species, therefore, is not maintained by interaction among  
571 its members (gene flow). It emerges, rather, as an historical consequence of the  
572 species’ origin as a peripherally isolated population that acquired its power-  
573 ful homeostatic system ... if ... stability is an inherent property both of indi-  
574 vidual development and the genetic structure of populations, then its power  
575 is immeasurably enhanced, for the basic property of homeostatic systems, of  
576 steady states, is that they resist change by self-regulation. (Eldredge and Gould  
577 1972: 114)<sup>11</sup>

578 The origination process of our species provides an illustration of the Eldredge’s and  
579 Gould’s point. An accredited hypothesis postulates an allopatric cladogenetic sce-  
580 nario whereby an estimated population of 10.000 organisms represented the ances-  
581 tral population of *H. sapiens* (Relethford 2008). Supposing that ancestral humans  
582 were tightly interacting so as to constitute an organism-like functional system, this  
583 might represent a case of integrative cohesion whereby all original parts are suffi-  
584 ciently interconnected as to constitute a strongly individual-like whole. This putative  
585 lack of original gappines was then protected by developmental and genetic homeo-  
586 stasis. Thus, whether a species displays integrative cohesion depends on the par-  
587 ticular species and on the particular moment of its history taken into consideration.  
588 Not every species is gappy, and their gappiness might increase (or decrease) through  
589 time.

590 Notice that the cohesion Eldredge and Gould hypothesise would also imply  
591 genetic and phenotypic uniformity (genetic uniformity is the outcome of genetic  
592 homeostasis and phenotypic uniformity is the outcome of developmental homeo-  
593 stasis). Secondly, species’ cohesion might change through time, passing from being  
594 integrative to being merely responsive, or even weaker (and vice versa). This means  
595 that, passing to the issue of kindness, also genetic and phenotypic homogeneity  
596 comes in degrees, in parallel with individuality.

597 HPC-kindness is the result of exactly the same biological conditions we have  
598 stressed so far: the prevalence of homeostatic, homogenising and cohesive pro-  
599 cesses over heterogenic and heterostatic ones. If the former prevail, the cluster will  
600 be more tightly knit. We thus suggest that when homeostatic processes prevail over  
601 heterostatic ones, the species will be concomitantly a whole whose parts are more

<sup>11</sup> It may be objected that the kind of cohesiveness Elredge and Gould are talking about here is respon-  
siveness cohesion. However, their reference to a homeostatic *system* implies the existence of a *causal*  
interactions among the members of the population beyond gene flow.

602 cohesive (hence, more organism-like) and a cluster whose characterizing properties  
603 are more tightly knit (hence, more natural sensu Boyd, as an HPC kind). Conversely,  
604 when heterostatic processes prevail, the conditions leading to potential speciation  
605 would emerge. One outcome of the prevalence of heterostatic processes could be  
606 illustrated by the evolution of our species: migrations out of Africa, interbreeding  
607 with other hominin species, colonization of various continents, etc. have concomi-  
608 tantly rendered our species an increasingly less cohesive whole and a less pheno-  
609 typically uniform cluster. A different outcome of the prevalence of heterostatic pro-  
610 cesses might result in speciation. The prevalence of heterostatic processes might  
611 have the consequence that the cohesive individual would ultimately cease to exist as  
612 such (for instance, when it will “become” two individuals), and the cluster would be  
613 increasingly disjointed and reflect increasing multi-modality in phenotypic expres-  
614 sion, until its ultimate disintegration (in the sense that two different clusters will  
615 be eventually needed to characterise two different species). For example, the exist-  
616 ence of significant polymorphisms (e.g., of non-neutral variants) renders simulta-  
617 neously the species-individual less organism-like (because, for instance, disruptive  
618 selection might lead to diversification of the lactose-tolerant and intolerant human  
619 populations) and its distinctive homeostatic cluster less homogeneous (because, for  
620 instance, the human metapopulation is characterized by dimorphism concerning lac-  
621 tose tolerance).

622 It might be objected that in some cases the existence of polymorphisms might  
623 make the species more organism-like, for example, through the division of labour  
624 among the parts (think of the different castes seen in ant and termite colonies).<sup>12</sup> If  
625 this is the case, then some processes seem to generate a less tightly-knit and more  
626 disjointed HPC kind while simultaneously generating a more cohesive individual.  
627 Even though we concede that this might happen, we would also like to stress that  
628 nonetheless the differentiated parts display both a certain, general, level of similarity  
629 and a stronger level of similarity “locally”, that is, between the members of the dif-  
630 ferent castes (i.e., the higher-level parts/members) of the species.

631 To conclude, at different moments of its history, a species might be more an  
632 individual (i.e., more organism-like) or more natural an HPC kind than at other  
633 moments. What makes sexual species individuals also concomitantly makes them  
634 HPC natural kinds. Whether the same holds for asexual species (in case they were  
635 considered species at all) remains an open question.

## 636 4 Conclusion

637 We have argued that our empirical approach vindicates the ecumenical stance that  
638 species are at the same time individuals and HPC kinds. The starting point of our  
639 argument is the general species concept, which captures what all species concepts  
640 have in common, i.e., that species are segments of metapopulation lineages. We  
641 then articulated in more detail the concept of metapopulation, ending up with what

<sup>12</sup> We thank a reviewer for raising this objection.

642 we called a “minimal characterization” of species. Then, adopting the empirical  
643 stance that seems to be required by the minimal characterization (namely that only  
644 by considering the species-specific origination process, metapopulation dynamics  
645 and gene-pene pool it is possible to recognize a particular segment of a lineage as  
646 a species and, furthermore, as *that* particular species), we have moved to consider  
647 species taxa and their identity conditions over time. By looking at the biological  
648 processes that led to the origin of new species, to those impinging on their life histo-  
649 ries, to those affecting their metapopulation dynamics and creating their metapopu-  
650 lation structures and, finally, to the homeostatic and heterostatic processes affect-  
651 ing their history, we believe the metaphysical issue concerning the nature of species  
652 could also be settled. One possible outcome of our analysis could be that, given the  
653 uniqueness of the biological processes punctuating every species’ life history, some  
654 form of ontological pluralism should be endorsed: perhaps some sexual species are  
655 individuals and others HPC kinds. However, we excluded that outcome on the basis  
656 of our causal argument: because the biological processes at the basis of the individu-  
657 ality and kindness of a species are the same, what shall be concluded is that species  
658 taxa are *at the same time* both individuals and HPC kinds. Being an individual, it is  
659 identifiable in terms of mereological relationships. Being a kind, it is characterizable  
660 in terms of an HPC cluster, however formed and maintained.

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