# Removing ambiguity from the biological species concept

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A B S T R A C T

The biological species concept (BSC) is a common way to define species although it is ambiguous even when strictly applied. I interpret it here syntactically in four different ways and show that one of them is more suitable than previously thought. The first interpretation (fully restricted) produces discrete, non-overlapping biological species with the inconvenience of being inapplicable when there is gradual evolution of reproductive isolation. The second (cohesion relaxed) and fourth (fully relaxed) interpretation are overly unrestricted to be useful. The third interpretation (isolation relaxed) overcomes the problem of gradual evolution of reproductive isolation at the cost of recognizing non-discrete, overlapping biological species. That is, some populations are members of more than one species. Non-discreteness, however, removes hand-waving in infamous difficulties of the BSC such as those with ring species, phyletic species, and syngameons. Moreover, it lets the BSC deal with introgression with no appeal to subjectivity. Therefore, precision in terms underlying the BSC provides an objective and still natural alternative to deal with gradual evolution of reproductive isolation.

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Defining what a species is has been attempted for centuries (Mayr, 1982). Linnaeus regarded species as typological objects. Buffon included the condition of interfertility for conspecificity. Dobzhansky refined the concept by pointing to isolating mechanisms, and Mayr (1942, 1963) stated it in its well-known form: "groups of actually or potentially interbreeding natural populations [cohesion] that are reproductively isolated from other such groups [isolation]." Mayr's definition, named by him as the biological species concept (BSC), still faced a number of difficulties, however (Wheeler and Meier, 2000). In order to address those difficulties, diverse refinements (e.g., Simpson, 1961; Hennig, 1966), alternatives (e.g., Van Valen, 1976; Mallet, 1995), particularizations (e.g., Paterson, 1985), and generalizations (e.g., Templeton, 1989; de Queiroz, 1998) have been attempted giving rise to about two dozens of species concepts (Mayden, 1997), all having their own particular weaknesses (Hull, 1997). In spite of the effort, a contentious debate has prevailed which has actually reinforced "One of the most pernicious uncertainties in evolutionary biology" (Hey, 2008), known as the species problem (Hey, 2001, 2006).

However, Mayr's notion continues to play a central role (de Queiroz, 2005), especially when studying the origin of species (Coyne and Orr, 2004; Gavrilets, 2004). A primary means of

speciation is gradual acquisition of reproductive isolation, which poses unanswerable questions to the BSC such as where to delimit ring species, phyletic species, and syngameons. Indeed, gradual acquisition of reproductive isolation has urged for a relaxation of the concept so that it allows for introgression, which has the consequence of subjective gene flow thresholds to conclude heterospecificity (Coyne and Orr, 2004). I show here that removing ambiguity from the BSC lets it deal with gradual evolution of reproductive isolation with no appeal to subjectivity and with the possibility of introgression.

Mayr's BSC defines a species as a set of populations for which the cohesion and isolation conditions noted above hold. However, these conditions can be given different interpretations. I consider here two interpretations for each condition. First, both conditions can be interpreted in fully restrictive terms. In this case, the cohesion condition reads "every two populations in the set are reproductively compatible" (C1) and the isolation condition reads "every two populations, one in the set and the other one not in the set, are reproductively isolated" (I1). Second, both interpretations can be relaxed without loss of rigor. In particular, the cohesion condition can be interpreted instead as "every population in the set is reproductively compatible with at least one other population in the set" (C2) and the isolation condition as "every population outside the set is reproductively isolated with at least one population in the set" (I2). The relaxed interpretations constitute slight modifications of the restrictive ones when put in mathematical terms (see Supplementary Material). Combinations of these conditions produce four different interpretations of

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**Table 1**
Four different interpretations of the BSC

| Interpretation of the BSC | Defining conditions |
| --- | --- |
| Fully restrictive | C1 and I1 |
| Cohesion relaxed | C2 and I1 |
| Isolation relaxed | C1 and I2 |
| Fully relaxed | C2 and I2 |

the BSC (Table 1, Fig. 1). I show that the fully restrictive interpretation of the BSC is not capable of dealing with gradual evolution of reproductive isolation, while the isolation-relaxed interpretation can accomplish the task with the implication of non-discrete biological species. The other two interpretations are shown to be too unrestricted to be useful. I illustrate how isolation-relaxed biological species deal with ring species, phyletic species, and syngameons. It will then be apparent how isolation-relaxed biological species allow for introgression.

I express the above interpretations in syntactic form as well as their underlying notions (see methods online as Supplementary Material). This produces a completely formal system with five undefined signs (inheritance, immediate ancestry, potential existential quantifier, natural conditions, and reproductive sympatry) and three axioms (for time, for space, and for potentiality). I start from syntactically representing individuals and continue with syntactically defining reproduction, populations and finally species. Definitions are stated to fit standard concepts accurately; however, populations are defined in a non-standard way and are called rooted populations. A rooted population is defined as the set of individuals that can compatibly interbreed directly or immediately indirectly at a given time with a root individual, the root individual being included in the set (Fig. 2). By immediately indirectly I mean that an individual may be linked to another individual via a third individual, which allows same gender individuals to be in the same rooted population. Every individual generates thus a rooted population. The fundamental difference between rooted and standard populations is that rooted populations are defined from a root individual and not with respect to a locality. Since deciding where the limits of the locality are is frequently arbitrary, standard populations cannot often be objectively delimited. Rooted populations are delimited spatially by means of the root individual's direct or immediately indirect potential interbreeding at a given time, and temporally by the existence intervals of their members. Hence, rooted populations allow for an objective population delimitation. Thus, species are here not taken to be constituted by standard populations but by rooted populations. An important distinction that becomes evident in syntactically expressing the BSC's underlying notions is the one between potential interbreeding and reproductive compatibility. Potential interbreeding is shown to refer to the possibility of interbreeding only among sympatric individuals (see Propositions 1 and 2 in the Supplementary Material). Reproductive compatibility refers to the absence of reproductive isolating barriers and is thus shown to be meaningful among allopatric individuals (see Propositions 10 and 11 in the Supplementary Material). Hence, potential interbreeding may be taken as delimiting rooted populations while reproductive compatibility as delimiting biological species.

The BSC is typically regarded as equating conspecificity with reproductive compatibility. To see whether any of the above four interpretations of the BSC holds this view, some previous results are obtained. By defining an obligate asexual individual as one reproductively isolated from any individual (including itself, otherwise selfing could be accomplished), it is immediate that an obligate asexual individual is a member of a natural rooted population formed only by itself, and that such population
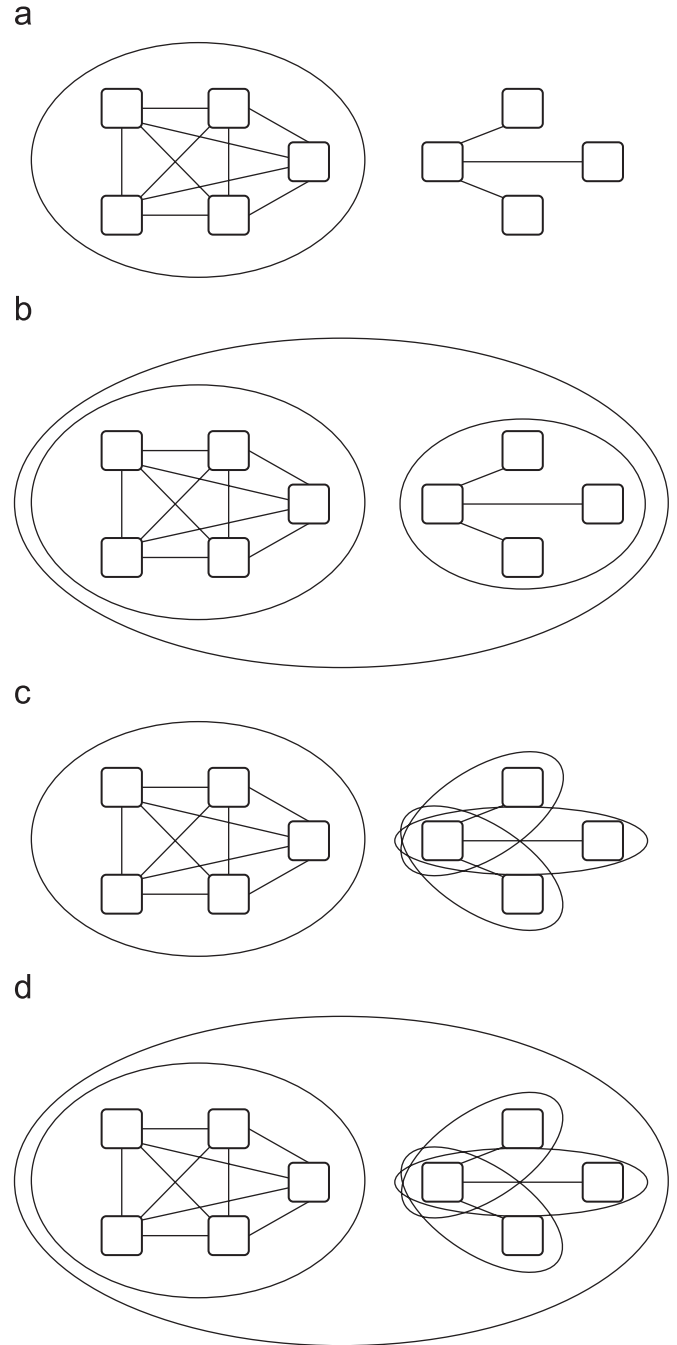


Fig. 1. Biological species in the four interpretations. Each square depicts a natural rooted population and lines connecting them indicate their reproductive compatibility. Ellipses circle biological species (a) in the fully restricted interpretation, (b) in the cohesion-relaxed interpretation, (c) in the isolation-relaxed interpretation, and (d) in the fully relaxed interpretation. In (a) populations on the right are not part of any species, in (b) and (d) species are nested since there is a whole-embracing species, and in (c) and (d) a population on the right belongs to three species.

constitutes a fully restrictive as well as an isolation-relaxed biological species. However, it is obtained that obligate asexual individuals cannot belong to any biological species under the remaining two interpretations. This raises the question of whether fully restrictive or isolation-relaxed biological species are applicable to all organisms. Indeed, this is found to be the case for isolation-relaxed but not for fully restrictive biological species. The proof of the strict universality of isolation-relaxed biological species provides with a means to derive that this interpretation
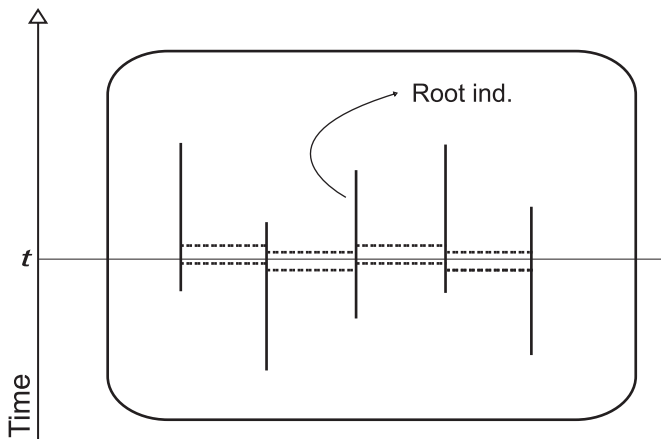
**Fig. 2.** A natural rooted population. Vertical lines indicate the existence intervals of individuals. Double broken lines indicate that the two individuals can naturally compatibly interbreed (i.e., can interbreed under natural conditions and progeny can backcross). A natural rooted population is obtained from a root individual by linking it to direct and immediately indirect mates at time *t*.

satisfies the equivalence between conspecificity and reproductive compatibility. In particular, the following are conspecificity criteria for the four interpretations.

Conspecificity criterion for fully restrictive biological species: If two different natural rooted populations are reproductively isolated, then they are heterospecific in the fully restrictive interpretation. If two different natural rooted populations are reproductively compatible and one of them belongs to a fully restrictive biological species, then they are conspecific in the fully restrictive interpretation.

Conspecificity criterion for cohesion-relaxed and fully relaxed biological species: All facultative and obligate sexual individuals are conspecific in the cohesion-relaxed and fully relaxed interpretations.

Conspecificity criterion for isolation-relaxed biological species: Two different natural rooted populations are conspecific in the isolation-relaxed interpretation if and only if they are reproductively compatible. They are heterospecific in the isolation-relaxed interpretation if and only if they are reproductively isolated.

Cohesion-relaxed and fully relaxed biological species are thus exceedingly unrestricted to be useful in the present context. On the other hand, isolation-relaxed biological species hold the usual view of equating conspecificity to reproductive compatibility although it may have been expected to be the case for fully restricted ones. Indeed, when it can be guaranteed that at least one of two populations belong to a fully restricted biological species, the fully restricted and the isolation-relaxed interpretations are equivalent. However, since not all individuals can be included in fully restricted biological species, this will not always be the case as shown below.

Means of determining reproductive compatibility can be derived from the definitions of isolating barriers and reproductive compatibility. The following criterion is obtained.

Compatibility criterion I: Two individuals are reproductively compatible if and only if, for each pair of their respective hereditary character states, there is a pair of individuals with those character states as hereditary that naturally compatibly interbreed (i.e., interbreed under natural conditions and progeny can backcross). Equivalently, two individuals are reproductively isolated if and only if they have a pair of respective hereditary character states such that no two individuals with those character states as hereditary naturally compatibly interbreed.

Compatibility criterion I is, however, dependent on complete descriptions of individuals in terms of their character states. Since complete descriptions of individuals in terms of their character states are not possible in practice, a more practicable case is attempted with the following criterion in which a superclone refers to an individual having as hereditary all the hereditary character states of another individual.

Compatibility criterion II: If two individuals have superclones that naturally compatibly interbreed, then the individuals are reproductively compatible.

This compatibility criterion indicates, more clearly than the previous one, that the compatibility of two individuals can be evaluated by testing interbreeding on other individuals. In particular, two individuals do not need to coincide in time to be compatible and their compatibility could be tested in other two individuals coexisting in time. It is to be noted that no simplifying assumptions, like character independence, are made. Hence, given possible interactions between traits making tested individuals (superclones) compatible while the untested individuals are isolated, these reproductive compatibility criteria may prove to be misfounded. An example could be if a gene in the superclone inhibits the isolating genes in the untested individuals. However, the criterion follows from the definitions of isolating barriers and reproductive compatibility which were syntactically stated to fit standard notions accurately. Therefore, if the criterion is empirically disproved, a revision of the definitions of isolating barriers and reproductive compatibility, and hence of their standard notions, would be called for. Nevertheless, all the major points in the present study are independent of the definitions used for isolating barriers and reproductive compatibility.

Finally, to explore what kind of individuals cannot be covered by the fully restrictive interpretation, it is noted that there are rooted populations such that a first one is reproductively compatible with a second one, the second one compatible with a third one, and the third one isolated from the first one; for example, in a ring species. With this it is obtained that only the instantaneous origin of reproductive isolation can produce fully restrictive biological species. Thus, the fully restrictive interpretation
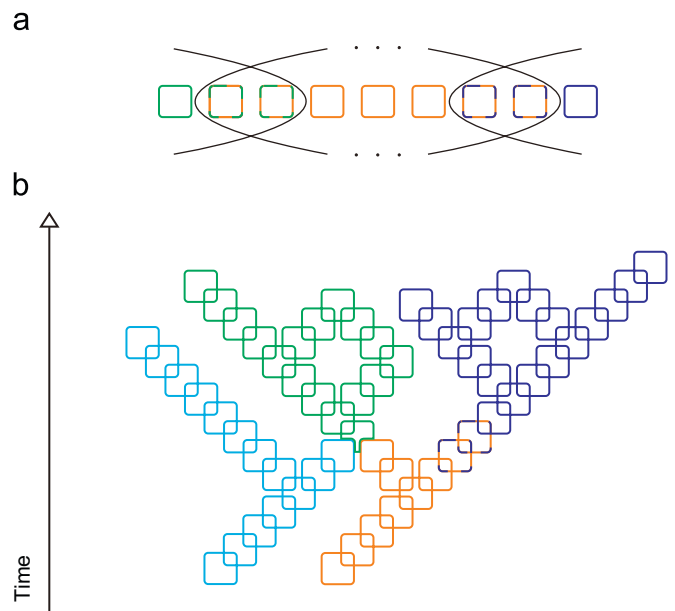


**Fig. 3.** Isolation-relaxed biological species and transitions between them. Natural rooted populations with the same color are reproductively compatible. Transitional populations have dashed lines and belong to both species. (a) Ring species have transitions with respect to space. (b) Phyletic species have transitions with respect to time. The green biological species originates instantaneously from the orange and blue ones, while the purple biological species originates gradually from the orange one.
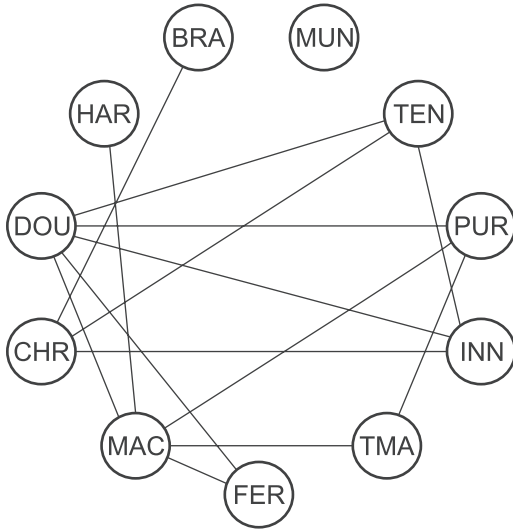
**Fig. 4.** A syngameon treated with the isolation-relaxed interpretation. The syngameon involving the Pacific North American Coast irises, series *Californicae* is redrawn with permission from Arnold (2006) which is in turn taken from Lenz (1959). Each circle represents a separate morphospecies. The species designations are as follows: BRA, *Iris bracteata*; MUN, *I. munzii*; TEN, *I. tenax*; PUR, *I. purdyi*; INN, *I. innominata*; TMA, *I. tenuissima*; FER, *I. fernaldii*; MAC, *I. macrosiphon*; CHR, *I. chrysophilla*; DOU, *I. douglasiana*; HAR, *I. hartwegii*. A line connecting two circles indicates natural hybridization between those taxa. Hence, these 11 morphospecies sort into eight highly overlapping biological species in the isolation-relaxed interpretation (Table 2). The only fully restrictive biological species formed is that of MUN.

**Table 2**
Isolation-relaxed biological species formed by the syngameon in the Pacific North American Coast irises

| Species | Members of the species |
|---------|------------------------|
| A | MUN |
| B | DOU, TEN, INN |
| C | TEN, CHR, INN |
| D | PUR, DOU, MAC |
| E | PUR, TMA, MAC |
| F | FER, MAC, DOU |
| G | MAC, HAR |
| H | CHR, BRA |

The exhaustive syntactic expression given to the BSC reveals significant subtleties that are easy to confuse. More than a drawback of the syntactic expression, this suggests that intricacies in the species notion prevent it from being properly understood without a tool that accounts for such subtleties. Verbal arguments become severely limited with such sensitivity to details. At this point formal mathematics provides an alternative.

**Appendix A. Supplementary data**

Supplementary data associated with this article can be found in the online version at 10.1016/j.jtbi.2008.09.016.

leaves uncovered rooted populations in the process of acquiring or having gradually acquired reproductive isolation. On the other hand, the isolation-relaxed interpretation sorts every rooted population into biological species, which may overlap if they are gradually acquiring or have gradually acquired reproductive isolation (Fig. 3). This offers an objective and natural way to answer taxonomic problems caused by gradualness such as ring species, phyletic species, and syngameons (Fig. 4, Table 2).

It was obtained that isolation-relaxed biological species may be overlapping, not discrete, entities. With this, there is no need to trace an arbitrary line to divide ambiguous cases such as in ring species or phyletic species. The line is traced automatically with objective population delimitation and with the conspecificity criterion for the isolation-relaxed interpretation of the BSC. There is no need to appeal to subjective gene flow thresholds. Through transitions, which may be formed by a single individual, introgression may happen. Furthermore, non-discrete biological species are consistent with abundant evidence from plants and animals (Coyne and Orr, 2004; Arnold, 2006; Mallet et al., 2007). One way to taxonomically treat transitional individuals would be as follows. Individuals belonging to more than one congeneric species receive the corresponding generic name and then the specific epithets in alphabetical order linked by a hyphen (e.g., *Quercus gambelii-grisea*.) Analogously, individuals belonging to more than one heterogeneric species receive the corresponding generic names in alphabetical order linked by a hyphen and then the specific epithets in alphabetical order also linked by a hyphen. Clearly, there will always be a supraspecific category to which transitional individuals belong uniquely.

In spite of the occurrence of transitions, largely discrete groups are commonly observed in nature (Rieseberg et al., 2006), which suggests that transitional parts of species must be relatively small when compared to non-transitional sections. It is not clear why this is so but available explanations include fast speciation rates and selection against hybrids (Coyne and Orr, 2004; Gavrilets, 2004).

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# Supplementary Material for:
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Rigorous care is taken in order to prevent details from being ignored. Importantly, this reveals significant subtleties that have caused deep confusions. The process of obtaining a syntactic formulation of the four interpretations of the biological species concept (BSC) is divided in the following sections.

1. Entities: Entities (in particular, individuals) are syntactically described as collections of character states.

2. Inheritance and ancestry: Inheritance and immediate ancestry between entities are introduced as two primitive (i.e., undefined) signs.

3. Reproduction: Reproduction of entities is introduced by defining actual and potential interbreeding. Potential interbreeding is stated in terms of a primitive sign asserting the potential occurrence of a given event (in particular, reproductive events). An axiom about

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this potential existence sign is also introduced. The system is given time order by means of a second axiom. Entities capable of inheritance are from then on termed individuals.

4. Compatibility: Reproductive isolating barriers and reproductive compatibility are defined. A fourth primitive sign is introduced for natural conditions.

5. Populations and species: Rooted population is defined and spatial ordering is introduced to the system by means of the fifth primitive sign and the third axiom. Definitions for the four interpretations of biological species are stated.

6. Results: Several consequences of the four interpretations and underlying definitions are obtained.

The first five sections are thus largely composed of definitions and hence may be skipped and used for reference when covering the sixth section. Notation used is listed at the end in the Appendix of the Supplementary Material.

# 1 Entities

The following definition describes any object as a collection of character states.

**Definition (Character, character state, entity, and existence interval).** Consider the following definitions:

1. A character is a function $c : \mathbb{C} \to X$, where $\mathbb{C}$ is a closed time interval and $X$ is a set. ($X$ may be a set of sentences, numbers, or otherwise that describe character states of the character given.)

2. A character state of the character $c$ is the value of the character at any time $t$.

3. Suppose that we have a set of characters $c_i : \mathbb{C}_i \to X_i$ indexed by $i \in A$, and that $\mathbb{E}$ is a closed time interval containing each $\mathbb{C}_i$. Then, the function

$$e : \mathbb{E} \to \wp(\bigcup_{i \in A} X_i)$$

defined by

$$e(t) = \{c_i(t) | i \in A \text{ and } t \in \mathbb{C}_i\}$$

is called entity. We say that the entity $e$ exists during the time interval $\mathbb{E}$, and that $\mathbb{E}$ is its existence interval.

4. If $e$ is an entity, then a character state, $s$, of $e$ is an element of $e(t)$ for some $t$. This is denoted by $s \in_t e$.

Thus, an individual having at time $t$ the allele $a$ in locus $A$, the genotype $b_1 b_2$ in locus $B$, and the character state $d$ for character $D$, is represented as $e(t) = \{c_1(t), c_2(t), c_3(t)\} = \{a, b_1 b_2, d\}$. Since characters are unordered, for this representation to work it is necessary to consider enough characters so that two entities are equal if and only if the objects they represent are the same. This assumes the population thinking principle (Mayr, 1976) or more explicitly that "no two things have all their properties in common" (Goodman, 1970). Note that even identical copies differ in some properties. To be sure, they differ at least in their positions in time and space. From the equality of functions, it follows that two entities are equal if and only if both their existence intervals and their character states in each instant are equal.

In the previous definition we also assume that the existence span of individuals can be represented with closed time intervals. An objection to this is that it may be more appropriate to consider these intervals as having fuzzy limits. However, this is counter-argued by noticing that an individual can be said to exist even with a slightest indication of such state. A further objection is that open time intervals might represent the existence interval of, for example, a cell.

Nevertheless, this seems intuitively bizarre. Note also that the definition considers ontogeny by letting characters change as the existence interval of the individual advances.

## 2 Inheritance and ancestry

We will use the notions of immediate ancestry and inheritance to define interbreeding and re-productive isolating barriers. These two notions are now introduced without definition, that is, as primitive signs.

**Inheritance.** Let $e_j$ and $e_{j'}$ be entities, and let $s_i$ and $s_{i'}$ be character states such that $s_i \in_t e_j$ and $s_{i'} \in_{t'} e_{j'}$. Let $(e_j, s_i)$ denote the ordered pair of $e_j$ and $s_i$. The relation $(e_j, s_i) \sqsubseteq (e_{j'}, s_{i'})$ will be read as "$e_{j'}$ inherited $s_{i'}$ from $e_j$" (the character state $s_i$ is customarily not mentioned).

**Definition (Inherited character state).** Let $s_{i'} \in_{t'} e_{j'}$. By $s_{i'} \in_{t'}^{\mathrm{i}} e_{j'}$ we denote that $e_{j'}$ inherited $s_{i'}$ from someone. We say that $s_{i'}$ is an inherited character state iff there exists an entity $e_{j'}$ such that $s_{i'} \in_{t'}^{\mathrm{i}} e_{j'}$ for some $t' \in \mathbb{E}_{j'}$.

**Immediate ancestry.** Let $e_j$ and $e_{j'}$ be entities. The relation $e_j \lessdot e_{j'}$ will be read as "$e_j$ is an immediate ancestor of $e_{j'}$".

This notation for immediate ancestry is inverted with respect to that used by Williams (1970), according to which the entity next to the small end of $\lessdot$ is the younger. The intention with this inversion is to follow the standard notation in which $x < y$ indicates that $x$ is in certain sense preceding $y$, depending on how the relation $<$ is defined. Hence, it may be clearer to think of the symbol to the left of $\lessdot$ as the ancestor, since it indeed precedes its descendants.

Ancestry is now defined.

**Definition (Ancestry).** Let $e_j$ and $e_{j'}$ be entities. We say that $e_j$ is an ancestor of $e_{j'}$, denoted by $e_j \lhd e_{j'}$, iff there exist entities $e_{j^*}, e_{j^*+1}, e_{j^*+2}, \ldots, e_{j^*+N}$ such that

$$e_{j^*} \blacktriangleleft e_{j^*+1} \blacktriangleleft e_{j^*+2} \blacktriangleleft \cdots \blacktriangleleft e_{j^*+N} \blacktriangleleft e_{j'},$$

where $e_{j^*} = e_j$. Clearly, if $N = 0$, $e_j \blacktriangleleft e_{j'}$.

Again and for the same reason, this notation is inverted with respect to that used by Williams (1970).

# 3   Reproduction

We now define interbreeding by means of reproductive events. Reproductive events are in turn defined as functions that assign to a set of parental individuals a set of their offspring. We need the two following definitions.

**Definition (Filial set).** Let $E$ be a set of entities and let $[a, b]$ be a closed time interval. The set of entities whose origin happens during the interval $[a, b]$ that are immediate descendants of all entities in $E$ will be referred to as the filial set from $E$ during $[a, b]$. Formally, the set

$$F_{[a,b]}(E) = \{e_{j'} \colon \text{entity} \,|\, \min \mathbb{E}_{j'} \in [a, b] \wedge \forall x \in E, x \blacktriangleleft e_{j'}\}$$

will be called the filial set from $E$ during $[a, b]$. The interval $[a, b]$ is determined on a case-by-case basis so that $F_{[a,b]}(E)$ includes all but solely the progeny originated in a single reproductive event.

If $F_{[a,b]}(E)$ is the filial set from $E$ during $[a, b]$, we have that $E$ is composed entirely of parents of the entities in $F_{[a,b]}(E)$. However, $E$ may not include all the parents of the entities in $F_{[a,b]}(E)$. We use the following definition to include all of them.

**Definition (Parental set).** Let $E$ be a set of entities and let $F_{[a,b]}(E)$ be the filial set from $E$ during $[a, b]$. The set of parents of a filial set will be referred to as its parental set. Formally, we will say that $E$ is the parental set of $F_{[a,b]}(E)$ iff

$$\forall e_j \left[ \left( \forall e_{j'} \in F_{[a,b]}(E), e_j \prec e_{j'} \right) \Rightarrow e_j \in E \right].$$

The two previous definitions guarantee respectively that only and all the progenitors of some filial set form its parental set. Thus, a parental set consists of a sole entity in uniparental reproduction and two entities in biparental reproduction.

Reproductive events are now defined.

**Definition (Reproductive event).** Let $E$ be a set of entities and $\mathbb{U} = \{e | e : \text{entity}\}$. A function (upsilon) $\Upsilon_{[a,b]} : A \subseteq \wp(\mathbb{U}) \to \wp(\mathbb{U})$ will be called a reproductive event iff

$$\Upsilon_{[a,b]}(E) = \begin{cases} F_{[a,b]}(E) & \text{if } E \text{ is the parental set of } F_{[a,b]}(E), \\ \varnothing & \text{if } E \text{ is not the parental set of } F_{[a,b]}(E), \end{cases}$$

where $F_{[a,b]}(E)$ is the filial set from $E$ during $[a, b]$. In such case, $\Upsilon_{[a,b]}$ will be said to occur during $[a, b]$.

The classic version of the BSC (Mayr, 1942, 1963) makes a distinction between actual and potential interbreeding. Although this distinction has long been debated (Hull, 1965; Sokal and Crovello, 1970; Mayr, 1982), we will allow for it in the present context by means of a third primitive sign. Expressed in terms of a primitive sign, the definition of potential interbreeding will not offer a practical procedure for its determination (which could be done instead in probabilistic terms). However, the meaning of the concept of potential interbreeding will be delimited as a consequence of axioms for time and space. We introduce then the following primitive sign and an axiom about it.

**Potential existential quantifier.** The sign $^c\exists$ will be read as "there can exist".

**Axiom (Of potentiality).** *"There exists $x$ such that $R$" implies that "there can exist $x$ such that $R$" but not the converse.*

We now use reproductive events and the potential existential quantifier to syntactically express actual and potential interbreeding. We define actual interbreeding, descriptively speaking, as requiring the occurrence of a reproductive event during which offspring arise, while potential interbreeding as claiming the possibility of such occurrence. Formally it is as follows.

**Definition (Actual interbreeding).** Let $E$ be a set of entities. We will say that the entities in $E$ interbreed at time $t$ during a reproductive event $\Upsilon_{[a,b]}$ iff there is an immediate descendant of them whose origin occurs at time $t$. Formally, we will say that the entities in $E$ interbreed at time $t$ during a reproductive event $\Upsilon_{[a,b]}$, denoted by $\mathscr{I}_t(E)$, iff there exists an $e_{j'} \in \Upsilon_{[a,b]}(E)$ such that $\min \mathbb{E}_{j'} = t$, where $\Upsilon_{[a,b]}$ is a reproductive event.

For the sake of simplicity, the phrase "during a reproductive event $\Upsilon_{[a,b]}$" will be dropped when possible, so the formula $\mathscr{I}_t(E)$ will usually be read as "the entities in $E$ interbreed at time $t$". When it is not necessary to make explicit the time $t$ at which interbreeding occurs, we will alternatively say that the entities in $E$ interbreed, denoted by $\mathscr{I}(E)$, iff there is a time $t$ at which the entities in $E$ interbreed.

**Definition (Potential interbreeding).** Let $E$ be a set of entities. We will say that the entities in $E$ can interbreed at time $t$ iff a reproductive event can happen during which an immediate descendant of the entities in $E$ originates at time $t$. Formally, we will say that the entities in $E$ can interbreed at time $t$, denoted by $\mathscr{CI}_t(E)$, iff there can exist a reproductive event $\Upsilon_{[a,b]}$ during which the entities in $E$ interbreed at time $t$. Alternatively, we will say that the entities in $E$ can interbreed, denoted by $\mathscr{CI}(E)$, if there is a time $t$ at which the entities in $E$ can interbreed.

A corollary and its proof illustrate the subtle difference between potential and actual interbreeding.

**Corollary.** *Actual interbreeding implies potential interbreeding, but the converse is not true.*

*Proof.* It is easy to see that $(^{c}\exists\Upsilon_{[a,b]})\mathscr{I}$ is identical with $^{c}\mathscr{I}$. Given the axiom of potentiality, we have that $\mathscr{I} \Rightarrow (\exists x)\mathscr{I} \Rightarrow (^{c}\exists x)\mathscr{I}$ but not the converse. Hence, $\mathscr{I} \Rightarrow {}^{c}\mathscr{I}$, but $^{c}\mathscr{I} \nRightarrow \mathscr{I}$. $\qquad\square$

We now focus on entities exhibiting inheritance, that is, those possessing inherited or inheritable character states. Inherited character states were already defined. The potential existential quantifier allows defining inheritable character states. Character states being either inherited or inheritable are then termed hereditary. Entities with at least one character state of this kind will be called individuals. The formal definitions are as follows.

**Definition (Inheritable character state).** Let $s_i \in_t e_j$. We will say that $e_j$ can inherit $s_i$ to someone, denoted by $s_i \, {}^{c}\in_t^{i} e_j$, iff there can exist an entity $e_{j'}$ for which there is an $s_{i'}$ such that $(e_j, s_i) \sqsubseteq (e_{j'}, s_{i'})$. We will say that a character state $s_i$ is an inheritable character state iff there exists an entity $e_j$ such that $s_i \, {}^{c}\in_t^{i} e_j$ for some $t \in \mathbb{E}_j$.

**Definition (Hereditary character state).** Let $s_i$ be a character state of an entity $e_j$ at time $t$. We will say that $s_i$ is hereditary, denoted by $s_i \in_t^{h} e_j$, iff either $s_i \in_t^{i} e_j$ or $s_i \, {}^{c}\in_t^{i} e_j$. We will say that a character state $s_i$ is a hereditary character state iff there is an entity for which it is hereditary.

From now on, we focus on the following kind of entities.

**Definition (Individual).** Let $\mathcal{I}_j$ be an entity. We will say that $\mathcal{I}_j$ is an individual iff there is a character state $s_i$ such that $s_i \in_t^{h} \mathcal{I}_j$ for some $t \in \mathbb{E}_j$.

The meaning of potential interbreeding is first delimited by showing that allochronous individuals (individuals separated in time) cannot interbreed. We will need to define reproductive adulthood and then introduce a time order to the system. Reproductive adulthood is defined as the part of the existence interval during which an individual can breed. The objection of fuzzy

limits may be raised again for the definition of reproductive adulthood; however, this is analogously rebutted by noticing that when an individual has a slightest capability of breeding, it can be said to have already reached its reproductive adulthood.

We will use the following definition.

**Definition (Potential breeding).** Let $\mathcal{I}_j$ be an individual. We will say that $\mathcal{I}_j$ can breed at time $t$ iff there is a set of individuals $I$ such that $\mathcal{I}_j \in I$ and the organisms in $I$ can interbreed at time $t$.

**Definition (Reproductive adulthood, synchrony, and reproductive synchrony).** Let $\mathcal{I}_j$ be an individual and $\mathbb{E}_j$ its existence interval. Let $\mathbb{A}_j$ be a bounded union of time intervals such that $\min \mathbb{E}_j < \inf \mathbb{A}_j$ (Remark 1). $\mathbb{A}_j$ will be called the reproductive adulthood of $\mathcal{I}_j$ iff for all $t$, we have that

$$t \in \mathbb{E}_j \cap \mathbb{A}_j \Leftrightarrow \mathcal{I}_j \text{ can breed at } t.$$

In such case, we will say that $\mathcal{I}_j$ reaches its reproductive adulthood iff $\mathbb{E}_j \cap \mathbb{A}_j \neq \varnothing$. We will say that two individuals $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ are synchronous iff $\mathbb{E}_j \cap \mathbb{E}_{j'} \neq \varnothing$. Further, we will say that two individuals $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ are reproductively synchronous at time $t$ iff they are synchronous at time $t$ having reached their reproductive adulthoods or formally, denoted by $\mathscr{T}_t^{\mathrm{r}}(\{\mathcal{I}_j, \mathcal{I}_{j'}\})$, iff $t \in (\mathbb{E}_j \cap \mathbb{A}_j) \cap (\mathbb{E}_{j'} \cap \mathbb{A}_{j'})$. Alternatively, we will say that $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ are reproductively synchronous, denoted by $\mathscr{T}^{\mathrm{r}}(\{\mathcal{I}_j, \mathcal{I}_{j'}\})$, iff $(\mathbb{E}_j \cap \mathbb{A}_j) \cap (\mathbb{E}_{j'} \cap \mathbb{A}_{j'}) \neq \varnothing$. Finally, we will say that $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ are (reproductively) allochronous iff they are not (reproductively) synchronous.

*Remark* 1. $\mathbb{A}_j$ is taken to be a bounded union because reproductive adulthood can consist of several disjoint, necessarily bounded, time intervals. The condition $\min \mathbb{E}_j < \inf \mathbb{A}_j$ is given because it is not possible for an individual to breed at the same instant it originates; necessarily, it can only do it later. $\inf$ is taken in case the time intervals of which $\mathbb{A}_j$ consists have open limits ($\inf$ exists because $\mathbb{A}_j$ is bounded).

Allochrony is sometimes used with a somewhat different meaning and the term diachrony is used instead. We use allochrony to preserve the pattern between sympatry and allopatry.

An axiom that gives time order to the system is introduced and called the axiom of origin. It states that every immediate descendant originates during the reproductive adulthood of its immediate ancestors.

**Axiom (Of origin).** *Given two individuals $\mathcal{I}_j$ and $\mathcal{I}_{j'}$, if $\mathcal{I}_j \prec \mathcal{I}_{j'}$, then $\min \mathbb{E}_{j'} \in (\mathbb{E}_j \cap \mathbb{A}_j)$.*

**Corollary.** *The immediate ancestors of a given individual are reproductively synchronous.*

*Proof.* Let $I$ be the set of the immediate ancestors of $\mathcal{I}_{j'}$. Then, by the axiom of origin, $\min \mathbb{E}_{j'} \in \bigcap_j (\mathbb{E}_j \cap \mathbb{A}_j)$, where $j$ is in a set $B$ that indexes $I$. That is, the organisms in $I$ are reproductively synchronous at least at $\min \mathbb{E}_{j'}$. □

**Proposition 1.** *If some individuals are allochronous, then they cannot interbreed.*

*Proof.* We prove that if some individuals can interbreed, then they are synchronous. Let $I$ be a set of individuals that can interbreed. Let $\Upsilon_{[a,b]}$ be a reproductive event such that $\mathcal{I}_{j'} \in \Upsilon_{[a,b]}(I)$. Hence, the individuals in $I$ are immediate ancestors of $\mathcal{I}_{j'}$. By the above corollary, such individuals are reproductively synchronous and therefore, synchronous. □

Proposition 1 helps provide potential interbreeding with some meaning by making it impossible between allochronous individuals. We will further delimit its meaning when space separation is considered.

# 4 Compatibility

Mayr used the word interbreeding to define biological species. As made explicit in the previous proposition, interbreeding cannot occur in allochrony and, as made explicit in the next section,

it cannot occur in allopatry either. In spite of this, interbreeding is intended to refer to a particular condition: "The word *interbreeding* indicates a propensity; a spatially or chronologically isolated population, of course, is not interbreeding with other populations but may have the propensity to do so when the extrinsic isolation is terminated" (Mayr, 2000). This propensity is to be understood in terms of reproductive isolating barriers (Dobzhansky, 1951; Mayr, 1963; although the word mechanisms was originally used instead, barriers may be preferable; Coyne and Orr, 2004). We now define isolating barriers and then use them to define such propensity, that is, reproductive compatibility.

We use some previous definitions. First, an indirect interbreeding relation is defined, so that same-gender individuals are not necessarily separated. We will call such relation kinship. We use this relation to define as compatible interbreeding the interbreeding in which progeny can backcross and then we make explicit its potential counterpart as follows.

**Definition (Potential kinship).** Let $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ be individuals. We will say that $\mathcal{I}_j$ can become akin to $\mathcal{I}_{j'}$ iff one of the following conditions holds:

1. $\mathcal{I}_j = \mathcal{I}_{j'}$.

2. There are sets of individuals $I_j$ and $I_{j'}$ such that $\mathcal{I}_j \in I_j$ and $\mathcal{I}_{j'} \in I_{j'}$, where the individuals in $I_j$ can interbreed, the individuals in $I_{j'}$ can interbreed, and $I_j \cap I_{j'} \neq \varnothing$. (Hence, if we have biparental reproduction the individual $\mathcal{I}_j$ can interbreed either with $\mathcal{I}_{j'}$ or with a third individual that in turn can interbreed with $\mathcal{I}_{j'}$.)

**Definition (Compatible interbreeding).** Let $I$ be a set of individuals. We will say that the individuals in $I$ compatibly interbreed at time $t$ iff the individuals in $I$ interbreed at time $t$ and one of the individuals in $I$ can become akin to one of the immediate descendants originated at time $t$ (in particular, biparental reproduction with possible backcrossing). Formally, we will say that the individuals in $I$ compatibly interbreed at time $t$ (during a reproductive event $\Upsilon_{[a,b]}$),

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denoted by $\mathscr{I}_t^c(I)$, iff

$$\left(\begin{array}{c}\exists \mathcal{I}_{j'} \\ \mathcal{I}_{j'} \in \Upsilon_{[a,b]}(I) \wedge \min \mathbb{E}_{j'} = t\end{array}\right)\left(\begin{array}{c}\exists \mathcal{I}_j \\ \mathcal{I}_j \in I\end{array}\right) \mathcal{I}_j \text{ can become akin to } \mathcal{I}_{j'}.$$

Alternatively, we will say that the individuals in $I$ compatibly interbreed (during a reproductive event $\Upsilon_{[a,b]}$), denoted by $\mathscr{I}^c(I)$, iff there is a time $t$ at which the individuals in $I$ compatibly interbreed.

**Definition (Potential compatible interbreeding).** Let $I$ be a set of individuals. We will say that the individuals in $I$ can compatibly interbreed at time $t$, denoted by $^c\mathscr{I}_t^c(I)$, iff there can exist a reproductive event $\Upsilon_{[a,b]}$ during which the individuals in $I$ compatibly interbreed at time $t$. Alternatively, we will say that the individuals in $I$ can compatibly interbreed, denoted by $^c\mathscr{I}^c(I)$, iff there is a time $t$ at which the individuals in $I$ can compatibly interbreed.

Isolating barriers are understood as "biological properties of individuals which prevent the interbreeding of populations that are actually or potentially sympatric" (Mayr, 1963). We designate here biological properties as those entailing inheritance. The word interbreeding in the just quoted definition of isolating barriers refers to interbreeding under natural conditions, otherwise breakable isolating barriers would be excluded (e.g., some behavioral isolating barriers). Natural conditions are now introduced by means of a fourth primitive sign. This allows defining natural interbreeding as interbreeding under natural conditions. Thus, we define reproductive isolating barriers as hereditary character states that when present, the individuals involved do not compatibly interbreed in nature. This definition is given for actual and not potential interbreeding because the latter excludes prezygotic isolating barriers.

**Natural conditions.** Let $I$ be a set of individuals and $[a, b]$ a closed time interval. $\mathsf{N}_{[a,b]}(I)$ will be read as "the individuals in $I$ are under natural conditions during $[a, b]$".

**Definition (Natural compatible interbreeding).** Let $I$ be a set of individuals. We will say that the individuals in $I$ naturally compatibly interbreed at time $t$ (during a reproductive event $\Upsilon_{[a,b]}$),

denoted by $\mathscr{I}_t^{\mathrm{nc}}(I)$, iff $\mathscr{I}_t^{\mathrm{c}}(I)$ and $\mathsf{N}_{[a,b]}(I)$. Alternatively, we will say that the individuals in $I$ naturally compatibly interbreed, denoted by $\mathscr{I}^{\mathrm{nc}}(I)$, iff there is a time $t$ at which $\mathscr{I}_t^{\mathrm{nc}}(I)$. The definition of potential natural compatible interbreeding (respectively, at time $t$), denoted by $^{\mathrm{c}}\mathscr{I}^{\mathrm{nc}}$ (respectively, $^{\mathrm{c}}\mathscr{I}_t^{\mathrm{nc}}$), is analogous to that of potential compatible interbreeding.

A definition for reproductive isolating barriers is now stated.

**Definition (Reproductive isolating barriers).** Let $s_i$ and $s_{i'}$ be hereditary character states. We will say that $s_i$ and $s_{i'}$ are reproductive isolating barriers to each other iff for any individuals $\mathcal{I}_j$ and $\mathcal{I}_{j'}$,

$$\left(s_i \in_t^{\mathrm{h}} \mathcal{I}_j \wedge s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'}\right) \Rightarrow \neg\mathscr{I}^{\mathrm{nc}}(\{\mathcal{I}_j, \mathcal{I}_{j'}\}),$$

for some $t \in \mathbb{E}_j, t' \in \mathbb{E}_{j'}$. This definition is now generalized for a set of individuals of any size (Remark 2). Let $S$ be a set of hereditary character states and let $I$ be a set of individuals. A function $\sigma : S \to I$ such that if $\sigma(s_i) = \mathcal{I}_j$, then $s_i \in_t^{\mathrm{h}} \mathcal{I}_j$ for some $t \in \mathbb{E}_j$, will be referred to as a hereditary-character-state function. $S$ will be said to h-correspond to $I$ iff there is a bijective hereditary-character-state function from $S$ to $I$. Hence, we will say that the character states in $S$ are reproductive isolating barriers to one another, denoted by $\mathscr{B}(S)$, iff

$$\left(\begin{array}{c} \forall I \\ S \text{ h-corresponds to } I \end{array}\right) \neg\mathscr{I}^{\mathrm{nc}}(I).$$

*Remark* 2. Such general a definition is obviously not necessary as there are no known cases of such multiparental reproduction. However, it allows for a simpler notation.

Then, we define reproductive compatibility as the condition when there are no isolating barriers between the individuals involved. It is stated as follows.

**Definition (Reproductive compatibility).** Let $I$ be a set of individuals and $S$ a set of hereditary character states. We will say that the individuals in $I$ are reproductively compatible iff they do

not have corresponding reproductive isolating barriers. Formally, if $I$ has two members, we will say that the individuals in $I$ are reproductively compatible iff

$$\neg \left( \begin{array}{c} \exists s_i, s_{i'} \\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j, s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'} \end{array} \right) \mathscr{B}(\{s_i, s_{i'}\}),$$

for some $t \in \mathbb{E}_j, t' \in \mathbb{E}_{j'}$. In general, we will say that the individuals in $I$ are reproductively compatible, denoted by $\mathscr{C}^{\mathrm{r}}(I)$, iff

$$\neg \left( \begin{array}{c} \exists S \\ S \text{ h-corresponds to } I \end{array} \right) \mathscr{B}(S).$$

We will say that the individuals in $I$ are reproductively isolated iff they are not reproductively compatible.

# 5 Populations and species

We now introduce space to the system to later define populations and then species. A spatial "order" is introduced by means of a fifth primitive sign and an axiom about it, called the axiom of sympatry. Loosely speaking, the axiom of sympatry asserts that reproductive sympatry is the remaining condition for potential interbreeding when compatible individuals coincide in time. We proceed as follows.

**Reproductive sympatry.** Let $I$ be a set of individuals and let $t \in \mathbb{E}_j$ for some $\mathcal{I}_j \in I$. $\mathsf{S}_t^{\mathrm{r}}(I)$ will be read as "the individuals in $I$ are reproductively sympatric at time $t$". Alternatively, we will say that the individuals in $I$ are reproductively sympatric iff there is a time $t$ at which they are reproductively sympatric. We will say that the individuals in $I$ are reproductively allopatric (respectively, at time $t$) iff they are not reproductively sympatric (respectively, at time $t$).

**Axiom (Of sympatry).** *Given a set of individuals $I$ and a time $t \in \mathbb{E}_j$ for some $\mathcal{I}_j \in I$,*

$$\mathscr{C}^{\mathrm{r}}(I) \wedge \mathscr{T}_t^{\mathrm{r}}(I) \wedge \mathsf{S}_t^{\mathrm{r}}(I) \Leftrightarrow {}^{\mathrm{c}}\mathscr{I}_t^{\mathrm{nc}}(I).$$

Therewith we can further delimit the meaning of potential interbreeding by means of the following proposition.

**Proposition 2.** *If some individuals are reproductively allopatric, then they cannot naturally compatibly interbreed.*

*Proof.* Let $I$ be a set of reproductively allopatric individuals. That is, $\neg \mathsf{S}_t^{\mathrm{r}}(I)$ for every time $t$ in their existence intervals. From the axiom of sympatry, $\neg \mathscr{C}\mathscr{I}_t^{\mathrm{nc}}(I)$ for any time $t$ in their existence intervals. $\qquad\square$

Therefore, potential interbreeding refers only to synchronic and sympatric individuals. That is, potential interbreeding is the one that is not accomplished for reasons other than temporal or spatial separation and reproductive isolation (e.g., by chance).

The BSC defines biological species upon the notion of population. A population is understood as a group of interbreeding individuals that share a locality in a restricted time extension, although there is much subjectivity in such notion. A notion for populations objectively extended in time and space is here used instead (a different approach with a similar objective is pursued in Pfeifer et al., 2007). We will use for this the relation of potential natural compatible kinship. Hence, we define a natural rooted population as the set of individuals that can naturally become akin at a given moment to a given individual, the individual included since kinship is reflexive. We proceed as follows.

**Definition (Potential natural compatible kinship).** Let $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ be individuals. We will say that $\mathcal{I}_j$ can naturally become compatibly akin to $\mathcal{I}_{j'}$ (respectively, at time $t$) iff the definition of potential kinship holds when "can interbreed" is replaced by "can naturally compatibly interbreed (respectively, at time $t$)".

**Definition (Natural rooted population).** Let $\mathcal{I}_j$ be an individual. The set of individuals that

can naturally become compatibly akin to $\mathcal{I}_j$ at time $t$ will be called the natural rooted population from $\mathcal{I}_j$ at time $t$ (see Fig. 2 on the main paper).

A natural rooted population is thus, loosely speaking, a group of synchronic, reproductively sympatric, and naturally compatibly interbreeding individuals.

Mayr (1942, 1963) defines biological species as "groups of actually or potentially interbreeding natural populations [cohesion] that are reproductively isolated from other such groups [isolation]." The word natural refers to populations under natural, not artificial or laboratory, conditions. This is to guarantee that breakable isolating barriers are not excluded. Having made this consideration already with the definition of natural rooted populations, we now define reproductive compatibility between natural rooted populations as the condition when two populations have respective, compatible individuals. We consider two interpretations of the cohesion condition and two for the isolation condition of Mayr's definition. Thus, four different definitions are possible. Formally, we proceed as follows.

**Definition (Reproductive compatibility between rooted populations).** Let $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ be natural rooted populations. We will say that $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively compatible iff there is a set of individuals $I$ with individuals of both $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ such that $\mathscr{C}^{\mathrm{r}}(I)$. Formally, $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively compatible iff

$$\left( \begin{array}{c} \exists I \\ I \cap \mathcal{P}_k \neq \varnothing \wedge I \cap \mathcal{P}_{k'} \neq \varnothing \end{array} \right) \mathscr{C}^{\mathrm{r}}(I).$$

We will say that $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively isolated iff they are not reproductively compatible.

**Definition (Fully restrictive biological species).** Let $\mathcal{S}$ be a set of natural rooted populations. We will say that $\mathcal{S}$ is a fully restrictive biological species iff the following conditions hold:

1. $\left( \begin{array}{c} \forall \mathcal{P}_k \\ \mathcal{P}_k \in \mathcal{S} \end{array} \right) \left( \begin{array}{c} \forall \mathcal{P}_{k'} \neq \mathcal{P}_k \\ \mathcal{P}_{k'} \in \mathcal{S} \end{array} \right) \mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively compatible (C1).

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2. $\begin{pmatrix} \forall \mathcal{P}_k \\ \mathcal{P}_k \notin \mathcal{S} \end{pmatrix} \begin{pmatrix} \forall \mathcal{P}_{k'} \\ \mathcal{P}_{k'} \in \mathcal{S} \end{pmatrix}$ $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively isolated (I1).

**Definition (Cohesion-relaxed biological species).** Let $\mathcal{S}$ be a set of natural rooted populations. We will say that $\mathcal{S}$ is a cohesion-relaxed biological species iff the following conditions hold:

1. $\begin{pmatrix} \forall \mathcal{P}_k \\ \mathcal{P}_k \in \mathcal{S} \end{pmatrix} \begin{pmatrix} \exists \mathcal{P}_{k'} \neq \mathcal{P}_k \\ \mathcal{P}_{k'} \in \mathcal{S} \end{pmatrix}$ $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively compatible (C2).

2. $\begin{pmatrix} \forall \mathcal{P}_k \\ \mathcal{P}_k \notin \mathcal{S} \end{pmatrix} \begin{pmatrix} \forall \mathcal{P}_{k'} \\ \mathcal{P}_{k'} \in \mathcal{S} \end{pmatrix}$ $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively isolated (I1).

**Definition (Isolation-relaxed biological species).** Let $\mathcal{S}$ be a set of natural rooted populations. We will say that $\mathcal{S}$ is an isolation-relaxed biological species iff the following conditions hold:

1. $\begin{pmatrix} \forall \mathcal{P}_k \\ \mathcal{P}_k \in \mathcal{S} \end{pmatrix} \begin{pmatrix} \forall \mathcal{P}_{k'} \neq \mathcal{P}_k \\ \mathcal{P}_{k'} \in \mathcal{S} \end{pmatrix}$ $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively compatible (C1).

2. $\begin{pmatrix} \forall \mathcal{P}_k \\ \mathcal{P}_k \notin \mathcal{S} \end{pmatrix} \begin{pmatrix} \exists \mathcal{P}_{k'} \\ \mathcal{P}_{k'} \in \mathcal{S} \end{pmatrix}$ $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively isolated (I2).

**Definition (Fully relaxed biological species).** Let $\mathcal{S}$ be a set of natural rooted populations. We will say that $\mathcal{S}$ is a fully relaxed biological species iff the following conditions hold:

1. $\begin{pmatrix} \forall \mathcal{P}_k \\ \mathcal{P}_k \in \mathcal{S} \end{pmatrix} \begin{pmatrix} \exists \mathcal{P}_{k'} \neq \mathcal{P}_k \\ \mathcal{P}_{k'} \in \mathcal{S} \end{pmatrix}$ $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively compatible (C2).

2. $\begin{pmatrix} \forall \mathcal{P}_k \\ \mathcal{P}_k \notin \mathcal{S} \end{pmatrix} \begin{pmatrix} \exists \mathcal{P}_{k'} \\ \mathcal{P}_{k'} \in \mathcal{S} \end{pmatrix}$ $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively isolated (I2).

Note that the only difference between C1 and C2 (as well as between I1 and I2) is that the second universal quantifier ($\forall$) is changed for an existential quantifier ($\exists$). Sometimes the following equivalent form of I2 will be used for convenience: "there is no natural rooted population outside the set that is reproductively compatible with all populations in the set".

# 6 Results

## 6.1 Universality of biological species

We now state a definition of obligate asexual individual, check the behavior of the interpretations of the BSC with asexual individuals, and show that only isolation-relaxed biological species are strictly universal (i.e., applicable to all kinds of organisms).

**Definition (Obligate asexual individual).** Let $\mathcal{I}_j$ be an individual. We will say that $\mathcal{I}_j$ is obligate asexual iff for every individual $\mathcal{I}_{j'}$ (which includes $\mathcal{I}_j$), we have that $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ are reproductively isolated.

**Proposition 3.** *If an individual is obligate asexual, then it is a member of a natural rooted population formed only by itself. In addition, such population constitutes a fully restrictive biological species as well as an isolation-relaxed biological species. However, such population cannot belong to any cohesion-relaxed or fully relaxed biological species.*

*Proof.* Let $\mathcal{I}_j$ be an obligate asexual individual. Thus, $\mathcal{I}_j$ is reproductively isolated of any $\mathcal{I}_{j'}$. From the axiom of sympatry, it follows that $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ cannot naturally compatibly interbreed at any time $t$. Thus, $\mathcal{I}_j$ cannot naturally become compatibly akin to any $\mathcal{I}_{j'} \neq \mathcal{I}_j$. Therefore, from the definition of potential natural compatible kinship, $\mathcal{I}_j$ can only naturally become compatibly akin to itself and thus $\{\mathcal{I}_j\}$ is the natural rooted population from $\mathcal{I}_j$ at any $t \in \mathbb{E}_j$. Now consider $\{\{\mathcal{I}_j\}\}$. Since there are no two different natural rooted populations in $\{\{\mathcal{I}_j\}\}$, the antecedent of C1 is false and thus C1 follows. Since $\mathcal{I}_j$ is obligate asexual, I1 and I2 also follow. Therefore, $\{\{\mathcal{I}_j\}\}$ is a fully restrictive and an isolation-relaxed biological species. Clearly, since $\mathcal{I}_j$ is obligate asexual, C2 does not hold for any set of natural rooted populations containing $\{\mathcal{I}_j\}$ and hence $\{\mathcal{I}_j\}$ cannot belong to any cohesion-relaxed or fully relaxed biological species. $\qquad\square$

As seen in the previous proposition, obligate asexual individuals are not covered by the

cohesion-relaxed or the fully relaxed interpretation of the BSC. It will be seen in section 6.4 that although fully restricted biological species include asexuals, they exclude some other kind of organisms. However, the isolation-relaxed interpretation can be shown to be fully inclusive. We use the following hypothesis that is guaranteed on a biological basis (Remark 3).

*Remark* 3. This hypothesis would be required only if the number of natural rooted populations were by far unrealistically large: of a much larger size than the cardinality of the set of real numbers. The hypothesis can thus be safely dropped but I use it for the sake of generality of the universality proposition obtained below.

**Hypothesis.** *The class of all natural rooted populations is a set.*

It will be useful to say that $x_1$ is included in $x_I$ when $x_1 \in x_2 \in \cdots \in x_I$ for some $x_i$ $(i = 2, \ldots, I - 1)$.

**Proposition 4.** *For any individual, there is at least one isolation-relaxed biological species in which it is included.*

*Proof.* Let $\mathcal{I}^*$ be an individual and let $\mathcal{P}^*$ be the natural rooted population from $\mathcal{I}^*$ at time $t$ (such population always exists because the potential natural compatible kinship relation is reflexive). We prove that there exists an isolation-relaxed biological species $\mathcal{S}^*$ such that $\mathcal{P}^* \in \mathcal{S}^*$.

Let $\mathbb{P}$ be the class of all natural rooted populations. Given the above hypothesis, $\mathbb{P}$ is a set. Let $\wp(\mathbb{P})$ be well ordered. Note that this induces a well ordering in $\mathbb{P}$. We define by transfinite recursion the function $\epsilon$ as:

1. $\epsilon(0) = \{\mathcal{P}^*\}$.

2. $\epsilon(\alpha + 1) = \epsilon(\alpha) \cup \{\mathcal{P}_\alpha\}$, with $\mathcal{P}_\alpha$ reproductively compatible with all $\mathcal{P} \in \epsilon(\alpha)$, being $\mathcal{P} \neq \mathcal{P}_\alpha$, for all $\alpha \in \mathrm{OR}$ where $\mathrm{OR}$ is the class of all the ordinal numbers. If there is no such $\mathcal{P}_\alpha$, let $\epsilon(\alpha + 1) = \epsilon(\alpha) \cup \varnothing = \epsilon(\alpha)$.

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3. If $\alpha$ is a limit ordinal, let $A_\alpha$ be the set of $\mathcal{P} \in \mathbb{P}$ such that $\mathcal{P} \notin \bigcup_{\beta < \alpha} \epsilon(\beta)$ and $\mathcal{P}, \mathcal{P}'$ :
   rep. comp. for all $\mathcal{P}' \in \bigcup_{\beta < \alpha} \epsilon(\beta)$. Thus, $\epsilon(\alpha) = \bigcup_{\beta < \alpha} \epsilon(\beta) \cup \{\min A_\alpha\}$. If $A_\alpha = \varnothing$, let
   $\epsilon(\alpha) = \bigcup_{\beta < \alpha} \epsilon(\beta)$.

Let $\mathcal{S}^* = \bigcup_{\alpha \in \mathrm{OR}} \epsilon(\alpha)$. From the definition of $\epsilon$, every pair in $\mathcal{S}^*$ is reproductively compatible, that is, C1 follows. Since $\epsilon$ exhausts all natural rooted populations, there is no $\mathcal{P}_k \notin \mathcal{S}^*$ that is reproductively compatible with all $\mathcal{P}_{k'} \in \mathcal{S}^*$, that is, I2 also follows. Therefore, $\mathcal{S}^*$ is an isolation-relaxed biological species with $\mathcal{P}^* \in \mathcal{S}^*$. $\qquad\square$

The above proof describes a way to construct an isolation-relaxed biological species. It is by starting with any natural rooted population and adding subsequent populations compatible with all the previously added ones. Thus, an isolation-relaxed biological species is not built as a block in which any individual exhibiting the defining properties of the species immediately belongs to it. Instead, it is built as a chain whose links are added each at a time depending on their reproductive compatibility.

## 6.2   Operationality of biological species

We now state definitions of conspecificity and heterospecificity, and derive criteria for such conditions for the four interpretations.

**Definition (Conspecific and heterospecific natural rooted populations).** Let $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ be natural rooted populations. We will say that $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are conspecific in a given interpretation iff there exists a biological species $\mathcal{S}$ in the interpretation such that $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are in $\mathcal{S}$. We will say that $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are heterospecific in a given interpretation iff they are not conspecific in the interpretation, that is, for all biological species $\mathcal{S}$ in the interpretation, if $\mathcal{P}_k \in \mathcal{S}$, then $\mathcal{P}_{k'} \notin \mathcal{S}$.

**Proposition 5 (Con/heterospecificity criterion for fully restricted biological species).** *If two different natural rooted populations are reproductively isolated, then they are heterospecific*

*in the fully restricted interpretation. If two different natural rooted populations are reproductively compatible and one of them belongs to a fully restricted biological species, then they are conspecific in the fully restricted interpretation.*

*Proof.* Let $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ be different, reproductively isolated natural rooted populations. From C1, $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are not conspecific in the fully restricted interpretation. Now, let $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ be different, reproductively compatible natural rooted populations and let $\mathcal{P}_k \in \mathcal{S}$, where $\mathcal{S}$ is a fully restricted biological species. From I1, it is not possible that $\mathcal{P}_{k'} \notin \mathcal{S}$. $\square$

**Proposition 6 (Conspecificity criterion for cohesion-relaxed and fully relaxed biological species).** *All facultative and obligate sexual individuals are conspecific in the cohesion-relaxed and the fully relaxed interpretations.*

*Proof.* Let $\mathcal{S}$ be the set of natural rooted populations that are not isolated from all other populations (that is, the set of populations with facultative or obligate sexual individuals). Hence, C2 holds for $\mathcal{S}$. Since the only populations outside of $\mathcal{S}$ are singletons of obligate asexuals, both I1 and I2 hold for $\mathcal{S}$. Therefore, $\mathcal{S}$ is a cohesion-relaxed and a fully relaxed biological species. $\square$

**Proposition 7 (Con/heterospecificity criterion for isolation-relaxed biological species).** *Two different natural rooted populations are conspecific in the isolation-relaxed interpretation if and only if they are reproductively compatible.*

*Proof.* Let $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ be different natural rooted populations such that $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are in $\mathcal{S}$, being $\mathcal{S}$ an isolation-relaxed biological species. From C1, $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively compatible. On the other hand, let $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ be different reproductively compatible natural rooted populations. Use $\epsilon$ with $\epsilon(0) = \{\mathcal{P}_k, \mathcal{P}_{k'}\}$ to obtain an isolation-relaxed biological species. $\square$

We now derive criteria for reproductive compatibility. Proofs are for the case of biparental reproduction, that is, the case in which the set of individuals $I$ has two members. Proofs for the general case of multiparental reproduction are analogous but are obviated.

**Proposition 8 (Compatibility criterion I).** *Two individuals are reproductively compatible if and only if, for each pair of their respective hereditary character states, there is a pair of individuals with those character states as hereditary that naturally compatibly interbreed.*

*Proof.* Let $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ be individuals. By definition, $\mathscr{C}^{\mathrm{r}}(\{\mathcal{I}_j, \mathcal{I}_{j'}\})$ is

$$\neg \begin{pmatrix} \exists s_i, s_{i'} \\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j, s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'} \end{pmatrix} \mathscr{B}(\{s_i, s_{i'}\}),$$

which is also by definition

$$\neg \begin{pmatrix} \exists s_i, s_{i'} \\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j, s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'} \end{pmatrix} \begin{pmatrix} \forall \mathcal{I}_{j*}, \mathcal{I}_{j**} \\ s_i \in_{t*}^{\mathrm{h}} \mathcal{I}_{j*}, s_{i'} \in_{t**}^{\mathrm{h}} \mathcal{I}_{j**} \end{pmatrix} \neg \mathscr{I}^{\mathrm{nc}}(\{\mathcal{I}_{j*}, \mathcal{I}_{j**}\}),$$

which is equivalent to

$$\begin{pmatrix} \forall s_i, s_{i'} \\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j, s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'} \end{pmatrix} \begin{pmatrix} \exists \mathcal{I}_{j*}, \mathcal{I}_{j**} \\ s_i \in_{t*}^{\mathrm{h}} \mathcal{I}_{j*}, s_{i'} \in_{t**}^{\mathrm{h}} \mathcal{I}_{j**} \end{pmatrix} \mathscr{I}^{\mathrm{nc}}(\{\mathcal{I}_{j*}, \mathcal{I}_{j**}\}),$$

for some $t \in \mathbb{E}_j, t' \in \mathbb{E}_{j'}, t^* \in \mathbb{E}_{j*}, t^{**} \in \mathbb{E}_{j**}$. $\qquad\square$

The next compatibility criterion uses the following definition.

**Definition (Superclone and clone).** Let $\mathcal{I}_j$ and $\mathcal{I}_{j*}$ be individuals. We will say that $\mathcal{I}_{j*}$ is a superclone of $\mathcal{I}_j$, denoted by $\mathcal{I}_{j*} \sqsupseteq \mathcal{I}_j$, iff

$$\begin{pmatrix} \forall s_i \\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j \end{pmatrix} s_i \in_{t*}^{\mathrm{h}} \mathcal{I}_{j*},$$

for some $t \in \mathbb{E}_j, t^* \in \mathbb{E}_{j*}$. We will say that $\mathcal{I}_{j*}$ is a clone of $\mathcal{I}_j$, denoted by $\mathcal{I}_{j*} \simeq \mathcal{I}_j$, iff $\mathcal{I}_{j*} \sqsupseteq \mathcal{I}_j$ and $\mathcal{I}_j \sqsupseteq \mathcal{I}_{j*}$.

**Proposition 9 (Compatibility criterion II).** *If two individuals have superclones that naturally compatibly interbreed, then the individuals are reproductively compatible.*

*Proof.* Let $\mathcal{I}_j$ and $\mathcal{I}_{j'}$ be individuals with superclones that naturally compatibly interbreed. That is, there exist $\mathcal{I}_{j^*}$ and $\mathcal{I}_{j^{**}}$ such that

$$\left(\begin{array}{c}\forall s_i\\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j\end{array}\right) s_i \in_{t^*}^{\mathrm{h}} \mathcal{I}_{j^*} \wedge \left(\begin{array}{c}\forall s_{i'}\\ s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'}\end{array}\right) s_{i'} \in_{t^{**}}^{\mathrm{h}} \mathcal{I}_{j^{**}} \wedge \mathscr{I}^{\mathrm{nc}}(\{\mathcal{I}_{j^*}, \mathcal{I}_{j^{**}}\}),$$

for some $t \in \mathbb{E}_j, t' \in \mathbb{E}_{j'}, t^* \in \mathbb{E}_{j^*}, t^{**} \in \mathbb{E}_{j^{**}}$. Reorganizing this, there exist $\mathcal{I}_{j^*}$ and $\mathcal{I}_{j^{**}}$ such that

$$\left(\begin{array}{c}\forall s_i, s_{i'}\\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j, s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'}\end{array}\right) (s_i \in_{t^*}^{\mathrm{h}} \mathcal{I}_{j^*}, s_{i'} \in_{t^{**}}^{\mathrm{h}} \mathcal{I}_{j^{**}}) \wedge \mathscr{I}^{\mathrm{nc}}(\{\mathcal{I}_{j^*}, \mathcal{I}_{j^{**}}\}),$$

for some $t \in \mathbb{E}_j, t' \in \mathbb{E}_{j'}, t^* \in \mathbb{E}_{j^*}, t^{**} \in \mathbb{E}_{j^{**}}$. This implies that

$$\left(\begin{array}{c}\forall s_i, s_{i'}\\ s_i \in_t^{\mathrm{h}} \mathcal{I}_j, s_{i'} \in_{t'}^{\mathrm{h}} \mathcal{I}_{j'}\end{array}\right) \left(\begin{array}{c}\exists \mathcal{I}_{j^*}, \mathcal{I}_{j^{**}}\\ s_i \in_{t^*}^{\mathrm{h}} \mathcal{I}_{j^*}, s_{i'} \in_{t^{**}}^{\mathrm{h}} \mathcal{I}_{j^{**}}\end{array}\right) \mathscr{I}^{\mathrm{nc}}(\{\mathcal{I}_{j^*}, \mathcal{I}_{j^{**}}\}),$$

for some $t \in \mathbb{E}_j, t' \in \mathbb{E}_{j'}, t^* \in \mathbb{E}_{j^*}, t^{**} \in \mathbb{E}_{j^{**}}$. $\square$

## 6.3 Dimensionality of biological species

We use two empirical assertions to show that unlike interbreeding, reproductive compatibility is not by necessity impossible between individuals separated in time or space. The empirical assertions say that there are at least two individuals separated in time or space that have two corresponding superclones that naturally compatibly interbreed. Verifying this is straightforward as it suffices to do it for any two individuals slightly separated in time or space. The empirical assertions are stated for the general case of multiparental reproduction.

**Empirical assertion 1.** *There exists a set of allochronic individuals with corresponding superclones that naturally compatibly interbreed.*

**Proposition 10.** *Allochrony does not imply reproductive isolation.*

*Proof.* Let $I_j$ be a set of allochronic individuals with corresponding superclones that naturally compatibly interbreed. Let $I_{j^*}$ be the set of superclones of the individuals in $I_j$ that naturally

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compatibly interbreed. From compatibility criterion II, the individuals in $I_j$ are reproductively compatible. $\qquad\square$

**Empirical assertion 2.** *There exists a set of reproductively allopatric individuals with corresponding superclones that naturally compatibly interbreed.*

**Proposition 11.** *Reproductive allopatry does not imply reproductive isolation.*

*Proof.* Let $I_j$ be a set of reproductive allopatric individuals with corresponding superclones that naturally compatibly interbreed. Consider the set $I_{j*}$ of superclones of the individuals in $I_j$ that naturally compatibly interbreed. $\qquad\square$

## 6.4  Discreteness of biological species

We now introduce the two tempos in which species arise, that is, instantaneously or gradually, by means of two empirical assertions. We then conclude that isolation-relaxed biological species are not necessarily discrete and that fully restrictive ones cannot be produced gradually, only instantaneously. This makes fully restrictive biological species non-existent when there is gradual evolution of reproductive isolation. We use the following definition.

**Definition (Immediately-ancestral natural rooted population).** Let $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ be natural rooted populations. We will say that $\mathcal{P}_k$ is immediately ancestral to $\mathcal{P}_{k'}$, denoted by $\mathcal{P}_k \lessdot \mathcal{P}_{k'}$, iff there exist $\mathcal{I}_j \in \mathcal{P}_k$ and $\mathcal{I}_{j'} \in \mathcal{P}_{k'}$ such that $\mathcal{I}_j \lessdot \mathcal{I}_{j'}$.

**Empirical assertion 3.** *Evolution of reproductive isolation may be instantaneous, that is, there exist natural rooted populations $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ such that $\mathcal{P}_k \lessdot \mathcal{P}_{k'}$ that are reproductively isolated.*

**Empirical assertion 4.** *Evolution of reproductive isolation may be gradual, that is, there exist natural rooted populations $\mathcal{P}_k, \mathcal{P}_{k'}, \mathcal{P}_{k''}$ such that $\mathcal{P}_k, \mathcal{P}_{k'}$: rep. comp., $\mathcal{P}_{k'}, \mathcal{P}_{k''}$: rep. comp., and $\mathcal{P}_k, \mathcal{P}_{k''}$: rep. isol.*

With empirical assertion 4 the conspecificity relation is not transitive for the isolation-relaxed interpretation (as noted by Kornet, 1993 and Kornet et al., 1995) as shown as follows.

**Definition (Transition).** Let $\mathcal{S}_l$ and $\mathcal{S}_{l'}$ be different biological species in either interpretation. $\mathcal{S}_l \cap \mathcal{S}_{l'}$ will be called a transition iff it is non-empty.

**Proposition 12.** *There exist transitions in the isolation-relaxed interpretation.*

*Proof.* Let $\mathcal{P}_k, \mathcal{P}_{k'}, \mathcal{P}_{k''}$ be natural rooted populations such that $\mathcal{P}_k, \mathcal{P}_{k'}$: rep. comp., $\mathcal{P}_{k'}, \mathcal{P}_{k''}$: rep. comp., and $\mathcal{P}_k, \mathcal{P}_{k''}$: rep. isol. From the conspecificity criterion for isolation-relaxed biological species, $\mathcal{P}_k, \mathcal{P}_{k'}$: conspecific, $\mathcal{P}_{k'}, \mathcal{P}_{k''}$: conspecific, and $\mathcal{P}_k, \mathcal{P}_{k''}$: heterospecific in this interpretation. Thus, there are isolation-relaxed biological species $\mathcal{S}_l$ and $\mathcal{S}_{l'}$ such that $\mathcal{P}_k, \mathcal{P}_{k'} \in \mathcal{S}_l$ and $\mathcal{P}_{k'}, \mathcal{P}_{k''} \in \mathcal{S}_{l'}$, but $\mathcal{P}_{k''} \notin \mathcal{S}_l$ and $\mathcal{P}_k \notin \mathcal{S}_{l'}$. Therefore, $\mathcal{S}_l$ and $\mathcal{S}_{l'}$ are different and $\mathcal{P}_{k'} \in \mathcal{S}_l \cap \mathcal{S}_{l'}$. $\square$

**Proposition 13.** *Only the instantaneous origin of reproductive isolation can produce fully restrictive biological species.*

*Proof.* We prove two things: (1) A transition in the isolation-relaxed interpretation is not contained in any fully restrictive biological species, and (2) A natural rooted population reproductively compatible with populations in a transition in the isolation-relaxed interpretation does not belong to any fully restrictive biological species.

Let $T$ be a transition in the isolation-relaxed interpretation. (1) Suppose that $T \subseteq \mathcal{S}$ where $\mathcal{S}$ is a fully restrictive biological species. From the above proposition, there exist $\mathcal{P}_k, \mathcal{P}_{k'}$ reproductively compatible to some $\mathcal{P} \in T$ that are reproductively isolated from each other. From the conspecificity criterion for fully restrictive biological species, $\mathcal{P}_k, \mathcal{P}_{k'} \in \mathcal{S}$, but they are reproductively isolated which is contradictory.

(2) Let $\mathcal{P}_k \notin T$ be reproductively compatible with a $\mathcal{P} \in T$. Then, there is a $\mathcal{P}_{k'}$ reproductively compatible with $\mathcal{P}$ but reproductively isolated from $\mathcal{P}_k$. Suppose $\mathcal{P}_k \in \mathcal{S}$, where $\mathcal{S}$

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is a fully restrictive biological species. From the conspecificity criterion for fully restrictive biological species, $\mathcal{P} \in \mathcal{S}$ and again by this conspecificity criterion $\mathcal{P}_{k'} \in \mathcal{S}$. However, $\mathcal{P}_k$ and $\mathcal{P}_{k'}$ are reproductively isolated which is contradictory. $\qquad\square$

# Appendix: Notation

## Table A1. Usage of typefaces

| Typeface | As in | Refers to |
|---|---|---|
| Double-struck | $\mathbb{E}$ | Time intervals or their union |
| MathCal | $\mathcal{I}$ | Biological entities |
| Sans-serif | $\sqsubset$ or $\mathsf{N}$ | Primitive signs |
| Script | $\mathscr{I}$ | Non-primitive assertions |
| Double-struck sans-serif | $\mathbb{U}$ | Whole-embracing collections, such as the class of all entities |

## Table A2. Set theory notation

| Symbol | Meaning |
|---|---|
| $x_1 \in x_2 \in \cdots \in x_I$ | $x_1$ is included in $x_I$ |
| $\wp(x)$ | The power set of $x$ |
| $(\exists x)\mathscr{A}$ | There exists an $x$ such that $\mathscr{A}$ holds |
| $\mathscr{A}(x)$ | The assertion $\mathscr{A}$ made on $x$ |
| $\begin{pmatrix} \exists x \\ \mathscr{A} \end{pmatrix}\mathscr{B}$ | There exists an $x$ for which $\mathscr{A}$ holds such that $\mathscr{B}$ also holds |
| $\begin{pmatrix} \forall x \\ \mathscr{A} \end{pmatrix}\mathscr{B}$ | For all $x$ such that $\mathscr{A}$ holds, we have that $\mathscr{B}$ also holds |
| $\begin{pmatrix} \exists x, y \\ \mathscr{A}, \mathscr{B} \end{pmatrix}\mathscr{C}$ | There exist $x$ and $y$ for which $\mathscr{A}$ and $\mathscr{B}$ hold such that $\mathscr{C}$ also holds |
| $\begin{pmatrix} \forall x, y \\ \mathscr{A}, \mathscr{B} \end{pmatrix}\mathscr{C}$ | For all $x$ and $y$ such that $\mathscr{A}$ and $\mathscr{B}$ hold, we have that $\mathscr{C}$ also holds |

## Table A3. Notation of biological assertions

| Symbol | Meaning |
|---|---|
| $s \in_t e$ | $s$ is a character state of $e$ at time $t$ |
| $s \in_t^{\mathrm{i}} e$ | $s$ is a character state of $e$ at time $t$ that is inherited |
| $s\ ^{\mathrm{c}}\!\in_t^{\mathrm{i}} e$ | $s$ is a character state of $e$ at time $t$ that is inheritable |
| $s \in_t^{\mathrm{h}} e$ | $s$ is a character state of $e$ at time $t$ that is hereditary |
| $(e_j, s_i) \sqsubseteq (e_{j'}, s_{i'})$ | $e_{j'}$ inherited $s_{i'}$ from $e_j$ |
| $e_j \lessdot e_{j'}$ | $e_j$ is an immediate ancestor of $e_{j'}$ |
| $\mathsf{N}_{[a,b]}(I)$ | The individuals in $I$ are under natural conditions during $[a, b]$ |
| $\mathsf{S}_t^{\mathrm{r}}(I)$ | The individuals in $I$ are reproductively sympatric at time $t$ |
| $\mathscr{I}_t(I)$ | The individuals in $I$ interbreed at time $t$ |
| $\mathscr{I}(I)$ | The individuals in $I$ interbreed |
| $^{\mathrm{c}}\mathscr{I}(I)$ | The individuals in $I$ can interbreed |
| $\mathscr{I}^{\mathrm{c}}(I)$ | The individuals in $I$ compatibly interbreed |
| $\mathscr{I}^{\mathrm{nc}}(I)$ | The individuals in $I$ naturally compatibly interbreed |
| $^{\mathrm{c}}\mathscr{I}^{\mathrm{nc}}(I)$ | The individuals in $I$ can naturally compatibly interbreed |
| $\mathscr{T}^{\mathrm{r}}(I)$ | The individuals in $I$ are reproductively synchronous |
| $\mathscr{B}(S)$ | The character states in $S$ are reproductive isolating barriers to one another |
| $\mathscr{C}^{\mathrm{r}}(I)$ | The individuals in $I$ are reproductively compatible |

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