Scientific Explanation as Ampliative, Specialized Embedding: The Case of Classical Genetics[1]

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Abstract
Explanations in genetics have intriguing aspects to both biologists and philosophers, and there is no account that satisfactorily elucidates such explanations. The aim of this article is to analyze the kind of explanations usually given in Classical (Transmission) Genetics (**CG**) and to present in detail the application of an account of explanation as ampliative, specialized nomological embedding to elucidate the such explanations. First, we present explanations in **CG** in the classical format of inferences with the explanans as the premises and the explanandum as the conclusion and compare them with explanations in other paradigmatic explanatory fields such as Classical Mechanics. Second, we summarize the main aspects discussed in the literature with regard to the peculiarities of genetic explanations. Third, we introduce the account of scientific explanation as ampliative, specialized nomological embedding making use of Sneedian structuralism, in particular the notions of theory-net, fundamental law or guiding principle, specialization, and special laws. Finally, we apply this account to the case of **CG** and show that this analysis sheds light on the intriguing aspects of genetic explanations and removes most of their alleged oddities.

Keywords: Classical Genetics, laws, explanation, structuralism, models, embedding

1. Introduction

Explanations in biology have aspects that look intriguing to both biologists and philosophers. A well-known reading of explanation in biology summarizes the main problems thus (Braillard & Malaterre, 2015, p. 9): “These [four main] problems are related to (1) whether natural laws exist in biology, (2) whether causation plays a specific

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explanatory role in biology, (3) whether other forms of explanation – e.g., functional or teleological – are also needed, and (4) whether the recent mechanistic type model of explanation that brings together some form of law-like generalizations and of causation fulfills all expectations". With regard to genetics, two main aspects discussed in the literature on explanations in Classical Genetics (**CG**) are the presence/absence of laws in their explanantia (cf., e.g., Smart, 1963; Ruse, 1970; Rosenberg, 1994, 2001; Brandon, 1997), and the alleged not fully causal (functional or other) nature of such explanations (cf., e.g., Schaffner, 1993; Waters, 1998).

With regard to the use of laws, the main objection comes from those who deny the existence of laws in biology in general, and in genetics in particular. As for the non-existence of laws in biology in general, the main reasons provided for such a view are the locality or non-universality of generalizations in biology (Smart, 1963) and their alleged contingency (Beatty, 1995). With respect to the existence of laws in genetics in particular, we must distinguish the claim that there are no laws in **CG** at all, which is hardly tenable given at least Mendel's so-called laws, and the more commonly asserted and discussed claim that there are no fundamental and/or general nomological principles in genetics (see Lorenzano, 2006, 2007, for a discussion).

As for the non-universality of biological generalizations, we contend that universality is too demanding a condition. What matters is not strict universality but rather the existence of at least non-accidental, counterfactual-supporting generalizations, whose presence in biology we think is hardly deniable, though generally they are more domain restricted and ceteris paribus dependent than in other more fundamental fields such as mechanics or thermodynamics. Many philosophers of biology, and of physics as well, accept a broader sense of lawhood that does not require non-accidental generalizations to be universal and exceptionless in order to qualify as laws (Carrier, 1995; Mitchell, 1997; Lange, 1995, 2000; Dorato, 2005, 2012; Craver & Kaiser 2013; Lorenzano, 2014). Our minimal characterization of laws as *counterfactual-supporting regularities* is similar to the one defended in Dorato (2012), and it is also compatible with some proposals about laws in biology in particular, such as the "paradigmatic" (Carrier, 1995) and "pragmatic" (Mitchell, 1997) ones. As for genetics specifically, some authors who argue that there are no laws in **CG** in a strict sense (see e.g. Kitcher, 1984; Darden, 1996, against fundamental laws in **CG**) at the same time give an account of explanation in **CG** that involves nomological patterns (Kitcher, 1989, 1993), thus involving nomological regularities, i.e. non-accidental, counterfactual-supporting regularities in a broad sense. All we need, in this regard, is the acceptance that **CG** makes use of regularities with counterfactual force, irrespective of whether this modal force is, in turn, explained in causal or other terms. Whether one wants to call these non-accidental, domain-restricted generalizations "laws" is a terminological issue into which we will not enter here. What matters is that, regardless of what we call them, these non-accidental generalizations play a key role in **CG** explanations.

One may argue that, even accepting the existence of nomological, counterfactual-supporting regularities in genetics, genetic explanations are not nomological because (*contra* e.g. Kitcher, 1984) they simply do not include such regularities in their explanantia. Genetic explanations, the objection goes, are causal, or functional, or teleological, or mechanistic, etc., all in a sense that does *not* require nomological regularities. We do not think this objection is sound. As has been argued, mechanistic explanations, for instance, require or involve laws (cf. e.g. Leuridan, 2010; Craver &

Kaiser 2013); and similar considerations apply to functional, teleological, or even causal explanations.[2] We are not going to enter into, or even review, these debates, but rather we will proceed by exemplification. We first present some paradigmatic explanations in **CG** in a standard inferential manner, and then we will reconstruct them in a model-theoretic format that makes manifest the fact that these explanations make essential use of counterfactual-supporting generalizations, thus qualifying as nomological explanations in a model-theoretic sense explicated in detail within the Sneedian-structuralist meta-theoretical framework via the notion of ampliative, specialized embedding (**ASE**).

The scope of this work is confined to "the heart" of Classical Genetics, namely "the theory of *transmission genetics*" (Kitcher, 1984), thus leaving aside the other subtheories that grow out of this theory like the theory of *gene mapping* (Kitcher, 1984; Weber, 1984) and the *theory of mutation* (Kitcher, 1984) as well as other "investigative strategies (such as the 'genetic approach')" (Waters, 2004); thus 'Classical Genetics' must be read in this way in what follows. Nevertheless, although our elucidation does not deal with explanations in contemporary *molecular* genetics, we claim, without argument here, that a similar analysis can be applied to contemporary molecular biology, as it has successfully been applied to other fields in biology (see e.g. Díez & Lorenzano, 2013, 2015, for Natural Selection; Alleva et al., 2017, for Allosterism; Lorenzano, 2014, for Population Genetics; Lorenzano & Díaz, 2020, for Population Dynamics; Díez & Suárez, 2021, for Systems Biology). We also believe that the value of this case study is not merely historical, nor simply that of applying an account of explanation to a new biological case, but that it also sheds some light on some issues in contemporary biology practices that still use Classical Genetics in laboratory and field work.[3]

2. Some paradigmatic explanatory patterns in Classical Genetics

Classical Genetics is a theory about hereditary trait transmission, in which several traits, characteristics or characters (phenotype) of individuals are transmitted across generations. **CG** uses the following basic conceptual framework: *individuals*, being parents or progeny, and their sets or *populations* that make up *families*, that is, populations connected by bonds of common descendent; *traits*, *characteristics*, *characters* or *appearances* (*APP*) that are *possessed by* individuals; individuals that *mate* (*MAT*) and produce *progeny*, which also possess certain *traits*/*characters*, and where numerical ratios, proportions or relative frequencies in the *distribution* (*DIST*) of those characters in the progeny are distinguished. We can represent this graphically as in Fig. 1 – where the

[2] In a broadly, though admittedly not universally, accepted account according to which causation is a relation between particular events *in virtue of* such events exemplifying general types involved in counterfactual-supporting regularities.

[3] It is not the aim of this paper to carry out a historical and systematic analysis of the relationship between Classical Genetics and Molecular Genetics. However, we would like to point out that, with the emergence of Molecular Genetics, Classical Genetics was neither displaced, replaced nor reduced, and that, at present, explanations provided by Classical Genetics for certain hereditary patterns (e.g. those mentioned in Section 2) are still considered valid.

rectangles represent **CG**'s base sets or "ontology" and the arrows represent **CG**'s functions defined over them:

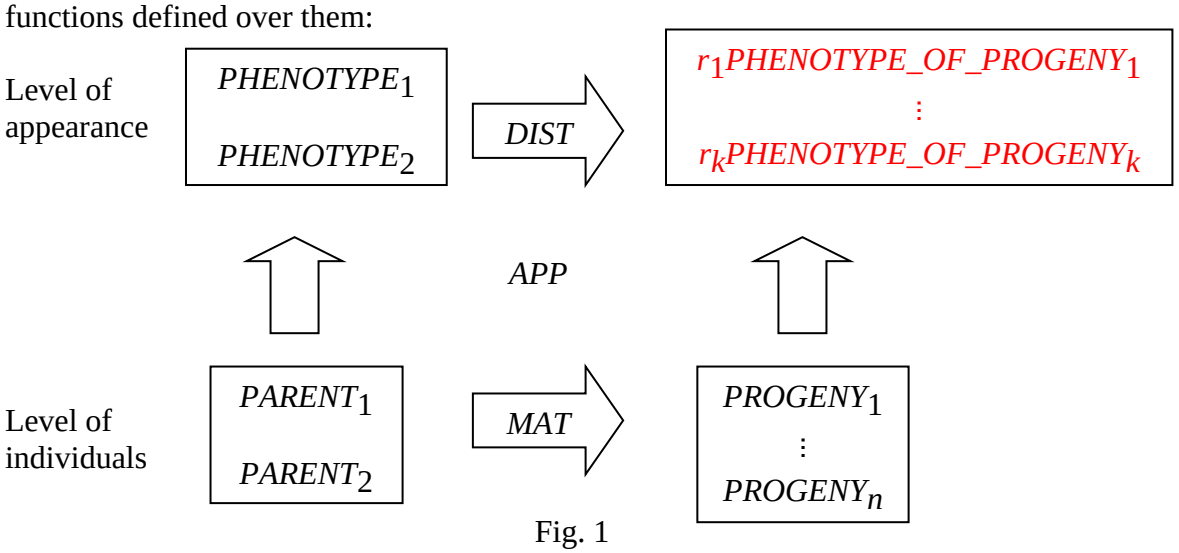

Fig. 1

In order to account for the distributions of the characters in the progeny (i.e., for the relative frequencies) the following parameters have to be theoretically postulated:

(i) appropriate types and numbers of factors or genes (genotype),
(ii) the way in which they are distributed or combined in the progeny (*COMB*) (as expected or theoretical probabilities),
(iii) the specific relationship (*DET*) in which they are with the characters of the individuals.

Graphically:

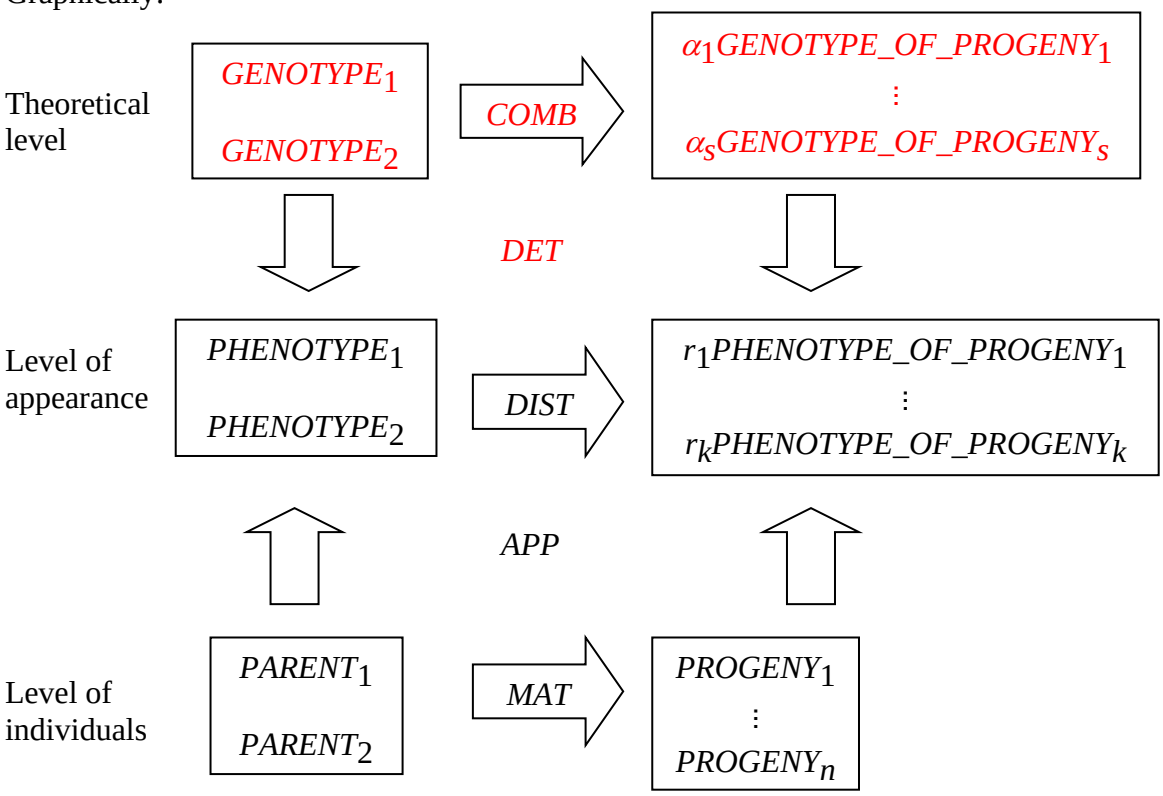

Fig. 2

Let us see some paradigmatic examples of explanation in **CG**, as they are usually presented in scientific articles, monographies and textbooks. The components related in Figs. 1 and 2 can be identified in every given example of explanation in **CG**. We start with the case of the color of pea seed albumin: pea plants belonging to the first filial generation, with yellow seed coats, which are self-fertilized and produce offspring having a ratio of 3:1 of yellow seed coats (¾) and green seed coats (¼). These pea plants (i) are heterozygous with respect to factors for seed coat color, (ii) combinations of their factors in offspring are equiprobable, and (iii) factors for a yellow seed coat are dominant over factors for a green seed coat (see [Mendel, 1865, pp. 9-12] for the original explanandum; Sinnott & Dunn, 1925, pp. 40-41, 45-50, for a standard **CG** explanation of such an explanandum; and Hartwell et al., 2017, pp. 21-24, for a current presentation of it; here and in the following examples we use square brackets to refer to the original source of the explanandum phenomenon, and normal references to refer to its standard **CG** explanation, past and present). Let us summarize this and the following explanations in the classical format of arguments with the explanans as the premises and the explanandum as the conclusion:[4]

Pea Seed Color:

Plants that

(1) (i) belong to the first filial generation, (ii) with yellow seed coats,
(2) are self-fertilized and produce offspring,
(3) (i) are heterozygous with respect to factors for seed coat color, (ii) whose combinations of factors are equiprobable, and (iii) where factors for yellow seed coat are dominant over factors for green seed coat

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Have

(4) ¾ of offspring with yellow seed coat and ¼ with green seed coat (a ratio 3:1)

A similar form applies to the explanation of some flower colors, such as the *Mirabilis jalapa* (see [Correns, 1905, p. 18]; Morgan et al., 1915, pp. 27-28; Brooker, 2018, p. 82):

Four O'Clock (Mirabilis jalapa or Marvel of Peru) Flower Color:

Plants that

(1) (i) belong to the first filial generation, (ii) with pink flowers,
(2) are self-fertilized and produce offspring,

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[4] The conclusion follows due to join action of all the premises; notice in particular the crucial role of (3) that implies that, given the dominance of the factors that determine yellow character, three of the four combinations of the two factors express the yellow character. The same applies to the following, less straightforward examples. As we will emphasize below, (3) specifies the particular parameters for transmission and determination of characters by factors for the case in point.

(3) (i) are heterozygous with respect to factors for flower color, (ii) whose combinations of factors are equiprobable, and (iii) where factors for red flower color are incompletely dominant over factors for white flower color

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Have

(4) ¼ of offspring with red flowers, ½ with pink, and ¼ with white (a ratio 1:2:1)

This kind of explanation also applies to combinations of characters considered together, such as the pair, color and form of pea seeds (see [Mendel, 1865, pp. 19-21]; Sinnott & Dunn, 1925, pp. 63-69; Klug et al., 2019, pp. 42-43):

Pea Seed Color & Pea Seed Form:

Plants that

(1) (i) belong to the first filial generation, (ii) with yellow seed coat and round seeds, (2) are self-fertilized and produce offspring

(3) (i) are heterozygous with respect to factors for seed coat color and for seed form, (ii) whose combinations of factors are equiprobable, and (iii) where factors for yellow seed coats are dominant over factors for green seed coats and factors for round seeds are dominant over factors for wrinkled seeds

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Have

(4) $^{9}/_{16}$ of offspring with yellow seed coats and round seeds, $^{3}/_{16}$ of offspring with yellow seed coats and wrinkled seeds, $^{3}/_{16}$ of offspring with green seed coats and round seeds, $^{1}/_{16}$ of offspring with green seed coats and wrinkled seeds (a ratio 9:3:3:1)

Or three characters, such as pea seed color and form, and pea flower color (see [Mendel, 1865, pp. 21-22]; Sinnott & Dunn, 1925, pp. 72-74; Hartl & Cochrane, 2019, pp. 89-91):

Pea Seed Color, Pea Seed Form & Pea Flower Color:

Plants that

(1) (i) belong to the first filial generation, (ii) with yellow seed coats, colored flowers and round seeds,

(2) are self-fertilized and produce offspring

(3) (i) are heterozygous with respect to factors for seed coat color, for flower color and for seed form, (ii) whose combinations of factors are equiprobable, and (iii) where factors for yellow seed coats are dominant over factors for green seed coats, factors for colored flowers are dominant over factors for white flowers and factors for round seeds are dominant over factors for wrinkled seeds

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Have

(4) $^{27}/_{64}$ of offspring with yellow seed coats, colored flowers and round seeds, $^{9}/_{64}$ of offspring with yellow seed coats, colored flowers and wrinkled seeds, $^{9}/_{64}$ of offspring with yellow seed coats, white flowers and wrinkled seeds, $^{9}/_{64}$ of offspring with green seed coats, colored flowers and wrinkled seeds, $^{3}/_{64}$ of offspring with yellow seed coats, white flowers and wrinkled seeds, $^{1}/_{64}$ of offspring with green seed coats, white flowers and wrinkled seeds (a ratio 27:9:9:9:3:3:3:1)

The explanandum may also involve traits which are not discrete but continuous, as in the case of the kernel color in wheat (see [Nilsson-Ehle, 1908, pp. 268-270]; Sinnott & Dunn, 1939, pp. 125, 127-128; Pierce, 2019, pp. 58-60):

Wheat Kernel Color:

Plants that

(1) (i) belong to the first filial generation, (ii) with red kernels,

(2) are self-fertilized and produce offspring

(3) (i) are heterozygous with respect to factors for kernel color in wheat, (ii) whose combinations of factors are equiprobable, and (iii) where the two pairs of factors are for kernel color have a cumulative effect, but only with one factor in each pair determining pigment

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Have

(4) offspring with kernels ranging from purple (very dark) to white in a transitional continuous way (through dark-red, red and light red kernels)

Although peas and other vegetables became the most well-known paradigmatic examples, other paradigmatic explanations in **CG** are of complicated animal traits, as in the case of the comb form of fowls (see [Bateson & Punnett, 1904, pp. 109-110]; Morgan et al., 1915, pp. 216-219; Snustad & Simmons, 2012, pp. 72-73):

Fowl Comb Form:

Fowls that

(1) (i) belong to the first filial generation, (ii) with walnut-shaped comb,

(2) mate and produce offspring

(3) (i) are heterozygous with respect to both pairs of factors for comb form, (ii) whose combinations of factors are equiprobable, and (iii) where the walnut comb depends on the presence of two dominant factors, one of these genes alone produces the rose-shaped comb, the other alone produces the pea-shaped comb, and the combination of the recessive alleles of these factors produces the single type of comb

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Have

(4) $^{9}/_{16}$ of offspring with a walnut-shaped comb, $^{3}/_{16}$ of offspring with a rose-shaped comb, $^{3}/_{16}$ of offspring with a pea-shaped comb, and $^{1}/_{16}$ of offspring with a single comb (a ratio 9:3:3:1)

All the previous cases satisfy the so-called "Mendel's Second Law", or "Law of Independent Assortment", but **CG** also explains cases of two or more characters considered together in which the numerical proportions in the second filial generation were completely different from the usual proportions (e.g. the 9:3:3:1 proportion for cases of two characters considered together), as in the case of pea flower color and pollen grain length (see [Bateson, Saunders & Punnett, 1906, p. 238]; Sinnott & Dunn, 1925, pp. 151-153; Brooker, 2018, p. 128):

Pea Flower Color & Pea Pollen Grain Length:

Plants that

(1) (i) belong to the first filial generation, (ii) with purple flowers and long pollen grains,

(2) are self-fertilized and produce offspring

(3) (i) are heterozygous with respect to factors for flower color and for pollen grain length, (ii) whose combinations of factors are not equiprobable (purple flower color and long pollen grains that enter together come out together more frequently than expected for independent assortment of purple-red and round-long), and (iii) where factors for purple

flowers are dominant over factors for red flowers and factors for long pollen grains are dominant over factors for round pollen grains

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Have

(4) $^{7}/_{16}$ of offspring with purple flowers and long pollen grains, $^{1}/_{16}$ of offspring with purple flowers and round pollen grains, $^{1}/_{16}$ of offspring with red flowers and long pollen grains, $^{7}/_{16}$ of offspring with red flowers and long pollen grains (a ratio 7:1:1:7)

These are some paradigmatic examples of explanations in **CG**. Before proposing a deeper reconstruction, let us briefly show that their superficial inferential structure looks similar to other standard, non-intriguing explanations in, for instance, Classical Mechanics (**CM**).

In **CM** we explain, for instance, Galileo's free fall regularities, or Kepler's laws of planetary motion, or a pendulum's trajectory, etc., by certain initial conditions, together with a specific application of Newton's Second Law and certain other empirical assumptions. For instance, if we reconstruct the **CM** explanation for Galileo's free fall law, we obtain the following argument:

Earth Free Fall:

If

(1) no friction

(2) zero initial velocity

(3) $m \cdot g = m \cdot d^2s/dt^2$

Then

(4) $s = 1/2\ gt^2$

in which (4) logically/mathematically follows from (1)-(3).

Likewise, in the paradigmatic Earth–Sun case, in which the explanandum, i.e. the Earth's spatio-temporal trajectory around the Sun that is actually measured, logically follows from the explanans, namely, the mechanical model that includes masses and forces and is defined by certain specific mechanical laws.

Earth-Sun System:

If

(1) (i) the Earth is at such a time in such position and (ii) the Sun is at such a time in such a position

(2) (i) the Earth's mass is such-and-such and (ii) the Sun's mass is such-and-such

(3) (i) only the gravitational force of the Sun is acting on the Earth and (ii) the gravitational force of the Earth acting on the Sun is negligible

(4) $m \cdot d^2s/t = G(m \cdot m'/s^2)$

Then

(5) the Earth's spatio-temporal trajectory around the Sun is such-and-such

in which (5) logically/mathematically follows from (1)-(4).

These two paradigmatic **CM** explanations show a crucial feature that will play an essential role in the explication of unified explanations below, namely that the premises in the explanans include, together with antecedent conditions, a nomic generalization that is a particular version, a specification, of the fundamental mechanical law $F = m \cdot a$. In the

Earth Free Fall case, (1) and (2) are antecedent conditions, while (3) is the particular application of **CM**'s fundamental law; whereas in the case of the *Earth–Sun System*, (1), (2) and (3) are antecedent conditions, and (4) is the particular application of the same fundamental law of **CM** for the specific explanandum. We will see that a similar structure is present in genetic explanations when correctly understood. In the next section we introduce the main metatheoretical notions through the example of Classical Mechanics, and in Section 4 we apply them to Classical Genetics. With these tools to hand, we present the **ASE** account in Section 5, and apply it to **CG**.

3. Fundamental Law/Guiding Principle-Based Theories

It is our claim that, in order to fully understand the deep structure of genetic explanations, and clarify their alleged intriguing aspects, it is necessary to understand the structure of **CG** as a unified theory guided by a general principle. This idea of unified, guiding principle-driven theories was initially implicit in Kuhn's philosophy of science and later made explicit by Sneedian structuralism. The Kuhnian idea is connected to his notion of *generalization-sketches* that he exemplifies with Newton's Second Law and its role in Classical Mechanics. Biology and physics in general, and **CG** and **CM** in particular, have notable differences, and in some important respects (e.g. locality, domain specificity, and the non-strictness of their non-accidental generalizations) some biological theories are more similar to theories in the human and social sciences. Nevertheless, the comparison with **CM** is particularly useful here as it highlights features that are independent of these differences, and that we believe are relevant for understanding the intriguing aspects of **CG** explanations. These features, i.e. the hierarchical and guiding principle-driven nature of unified theoretical explanations, are particularly well exemplified by **CM**; thus, this comparison is useful, other differences notwithstanding.

The general Kuhnian idea is that highly unified theories explain/account for specific applications/exemplars by developing "specific laws" for specific applications: specific laws that are the specific versions that a general principle takes for the specific phenomenon to hand. In Kuhn's words:

> […] generalizations [like $f = ma$…] are not so much generalizations as generalization-sketches, schematic forms whose detailed symbolic expression varies from one application to the next. For the problem of free fall, $f = ma$ becomes $mg = md^2s/dt^2$. For the simple pendulum, it becomes $mg\text{Sin}\theta = -md^2s/dt^2$. For coupled harmonic oscillators it becomes two equations, the first of which may be written $m_1d^2s_1/dt^2 + k_1s_1 = k_2(d + s_2 - s_1)$. More interesting mechanical problems, for example the motion of a gyroscope, would display still greater disparity $f = ma$ and the actual symbolic generalization to which logic and mathematics are applied. (Kuhn, 1974, p. 465)

This Kuhnian idea has been elaborated in detail by meta-theoretical Sneedian structuralism through the notions of *specialization* and a *theory-net*, and it has been applied to several sufficiently robust and unified theories (see, among others, Balzer, Moulines & Sneed, 1987, 2000; Stegmüller, 1986).

Most theories are strongly hierarchical systems – forming a kind of net – including laws with very different degrees of generality within the same conceptual setting. Usually there is a single fundamental law or guiding principle 'at the top' of the hierarchy, and a vast array of special laws which apply to specific situations.[5] Very briefly, we can mention five characteristics or criteria for a statement to be considered a fundamental law/guiding principle in the structuralist sense (Lorenzano, 2006, 2007):

1) *Cluster or synoptic character*. This means that a fundamental law should include: "*all* the relational terms (and implicitly also all the basic sets) and, therefore, at the end, *every fundamental concept* that characterize such a theory" (Moulines, 1991); "several of the magnitudes", "diverse functions", "possibly many theoretical and non-theoretical concepts" (Stegmüller, 1986); "almost all" (Balzer, Moulines & Sneed, 1987).
2) *Applicability to every intended application*. It is not necessary that fundamental laws have unlimited scope, applying every time, everywhere to everything. Rather, their universal applicability is relativized to the phenomena/applications intended by the theory's users: the set of intended applications of the theory (Stegmüller, 1986). This application is an "aim", for the theory may fail in a particular phenomenon (e.g. Mercury's perihelion); actually, to be an intended application of the theory is precisely for there to be an intention to account for something by (a specific specialization of) the guiding principle.
3) *Quasi-vacuous character*. Fundamental laws are highly abstract and schematic, and contain essential occurrences of **T**-theoretical terms, which in a structuralist sense are terms whose extension can only be determined through the application of a theory's fundamental law(s)[6] so that they can resist possible refutations, but which nevertheless acquire specific refutable empirical content through the (non-deductive) process of specialization (Moulines, 1978/1984).
4) *Systematizing or unifying role*. Fundamental laws allow us to include diverse applications within the same theory since they provide a guide to and a conceptual frame for the formulation of other laws (the so-called 'special laws'), which are introduced to impose restrictions on the fundamental laws and thus for them to apply to particular empirical systems (Moulines, 1978/1984).
5) *Modal import*. Fundamental laws express non-accidental regularities, are able to give support to counterfactual statements (if they are taken together with their specializations within a theory-net), even when they are context sensitive and have a domain of local application, they are *necessary in their area of application* (Lorenzano, 2006, 2007, 2020; Díez & Lorenzano, 2013).

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[5] It is worth mentioning that the term 'fundamental law' is here used in a different sense from the classical one, i.e. as a true strict universally quantified conditional statement, see e.g. Hempel & Oppenheim 1948.

[6] For a standard presentation of the structuralist criteria of **T**-theoreticity, see Balzer, Moulines & Sneed (1987). For a discussion of different criteria of theoreticity – either linguistic or model-theoretic –, a comparison of both ways of presentation of criteria – including the model-theoretic structuralist criteria of **T**-theoreticity –, and a proposal of definitions of theoreticity and pre-theoreticity, see Schurz (2014).

Fundamental laws/guiding principles are thus "programmatic" or heuristic in the sense that they tell us the kind of things we should look for when we want to explain a specific phenomenon. But, as mentioned before, taken in isolation, without their specializations, empirically they say very little. They can be considered, when considered alone, "empirically non-restricted" in the sense that in order to be tested/applied they have to be specialized ("specified"). These specific forms adopted by the fundamental laws are the so-called "special laws". It is worth emphasizing that this top-down specialization relationship is *not* one of implication or derivation: laws lower down are specific versions of top ones, i.e. they specify some functional dependences that are left partially open in the laws higher up in the tree.

The resulting structure of a theory may be represented as a net, where the nodes are given by the different theory-elements, and the links represent different relations of specialization (see Fig. 3).

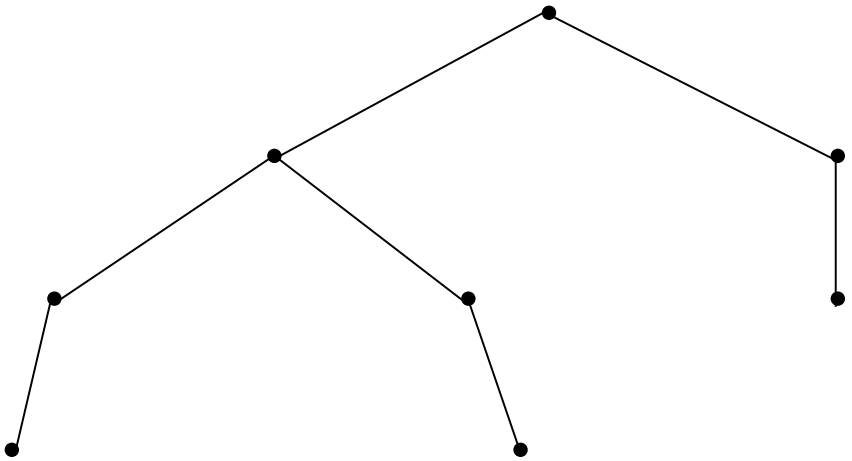

Fig. 3

For instance, the theory-net of Classical Mechanics (**CM**) has Newton's Second Law as the top unifying nomological component, i.e. as its Fundamental Law or Guiding Principle (Balzer & Moulines, 1981; Moulines, 1978/1984; Balzer, Moulines & Sneed, 1987). It can be read as following:

CMGP: For a mechanical trajectory of a particle with mass *m*, the change in quantity of movement, i.e. $m \cdot a$, is due to the combination of the forces acting on the particle.

As already mentioned, fundamental laws/guiding principles are programmatic/heuristic in the sense that they tell us *the kind of things* we should look for when we want to explain a specific phenomenon. In the case at hand, Newton's Second Law can be heuristically read as follows: "When mass particles change their velocity, look for forces that when added together account for the change in motion."

The **CM** guiding principle at the top becomes specialized as we move down, opening up different branches for different phenomenon *explananda*. This specification/branching

is reconstructed in different steps. First, there are symmetry forces, space-dependent forces, velocity-dependent forces, and time-dependent ones; then, e.g., the space-dependent branch specializes into direct and indirect space-dependent; the direct space-dependent branch in turn into linear negative space-dependent and…; the indirect space-dependent branch specializes into inverse-square and…. At the bottom of every branch, we have a completely specified law that is the version of the guiding principle for the specific phenomenon in question: pendula, planets, inclined planes, etc. (Kuhn's "detailed symbolic expressions").

The theory-net of **CM** looks (at a certain historical moment) as follows (though only some, simplified, terminal nodes are shown here, this suffices for our present exemplification concerns):

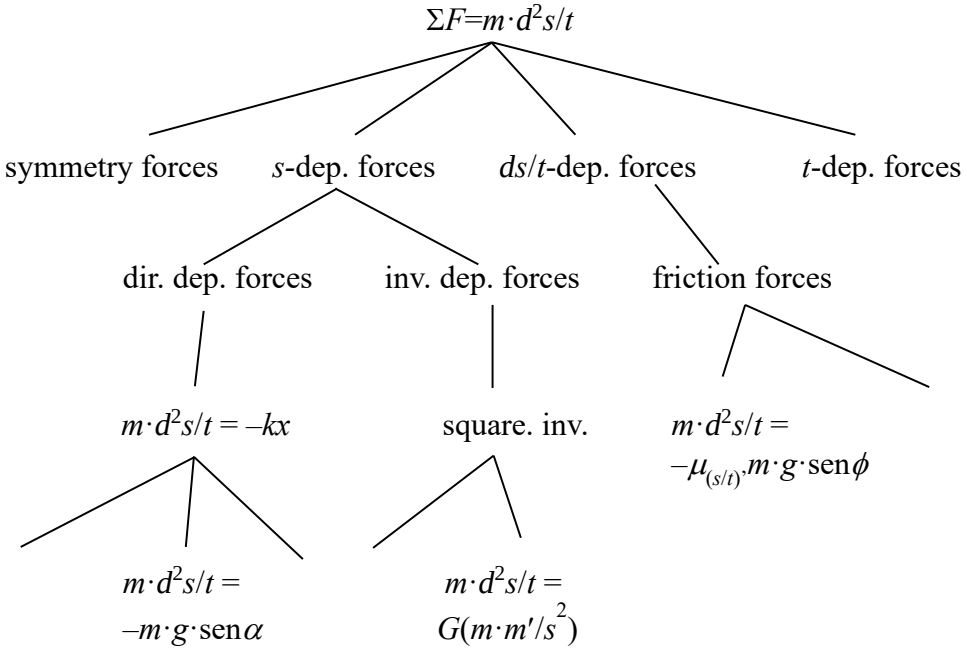

Fig. 4

4. Application to Classical Genetics

It is our claim that explanations in Classical Genetics follow a general pattern similar to that followed by explanations in Classical Mechanics. In all the paradigmatic examples of explanation in **CG** presented in Section 2, among the premises, together with antecedent conditions (initial conditions plus other empirical assumptions) – premises (1)-(2) – we can identify a specific law for the *explanandum* in each case – premise (3). It can be shown (Lorenzano, 2006, 2007) that, although in the superficial presentation of specific **CG** explanations only specific laws appear, there is a guiding principle implicitly working in such explanations: as in **CM**, in **CG** the specific law present in the explanans is the particular application/specialization of a general, fundamental guiding principle for the *explanandum* in each case. Yet, and in contrast to **CM** where the guiding principle is explicitly formulated in papers and textbooks, it is worth noting that in **CG** the

fundamental law/guiding principle is not made explicit in standard literature but only implicitly assumed in case studies. The Fundamental Law/Guiding Principle of Classical Genetics – which is diagrammatically depicted by Fig. 2 – implicitly presupposed in specific **CG** explanations, reads in an intuitive way as follows:

CGGP: The statistical communality of characters/phenotypes between parents and progeny (given by characters/phenotypes distributions in the progeny) is due to (i) the presence in parents of factors/genes, (ii) the transmission of those factors from parents to progeny, and (iii) a determining relation between specific factors and specific characters, so that factor distributions "match"/"fit" (in some manner to be specified) distributions of characters.

As mentioned above, fundamental laws/guiding principles are programmatic or heuristic in the sense that they tell us *the kind of things* we should look for when we want to explain a specific phenomenon. In the case of **CG** fundamental law/guiding principle, its heuristic character can be read as follows: "When confronted to specific statistical distribution of specific parental characters (phenotype) in offspring, look for factors (genes) responsible for the characters that combine in a specific manner in parents so that they "match"/ "fit" the distribution of characters in offspring". Thus, in every specific case we have to look for specific factors/genes and discover the specific way they combine in reproduction (genotype distribution) that accounts for the phenotype distribution in offspring.

This specific way genes combine in reproduction that accounts for phenotype distributions, is expressed by specifying the following parameters:

(i) the number of pairs of factors or genes involved (either one or more),
(ii) how the parental factors or genes are distributed in the progeny (with combinations of factors or genes with the same probability or not), and
(iii) the way in which factors or genes are related to the characters (with complete or incomplete dominance, codominance or epistasis).

When these three types of specifications are made, *terminal special laws* are obtained. These are what we find in specific **CG** explanations. Thus, as in other robust unified theories, particular **CG** explanations of particular *explananda* include specific versions/ applications of this "law". As our examples in Section 2 show, we have a specific version/application of **CGGP**, i.e. a special law, for each type of paradigmatic example. For instance, for the *Pea Seed Color* case, we have premise (3) stating that (i) plants belonging to the first filial generation are heterozygous with respect to the pair of factors responsible for seed coat color, (ii) combinations of their factors in offspring are equiprobable, and (iii) factors for a yellow seed coat are dominant over factors for a green seed coat. Or, in the *Wheat Kernel Color* case, premise (3) states that (i) plants belonging to the first filial generation are heterozygous with respect to factors for kernel color in wheat, (ii) whose combinations of factors are equiprobable, and (iii) in which two pairs

of factors for kernel color have a cumulative effect, but only one factor in each pair determines pigment.[7]

It is worth noting that the **CG** fundamental law/guiding principle is implicitly assumed by the scientific community as *a guide for dealing* with the plethora of empirical situations/applications/*explananda* that geneticists face. This is what we mean when we say that the **CG** fundamental law/guiding principle guides the process of specialization, determining the ways in which it must be specified to obtain special laws.

It is easy to see that **CGGP** has all the characteristics of guiding principles we mentioned above.

First, **CGGP** can be seen as a *synoptic* law establishing a substantial connection between the most important genetics terms in a single, complex statement: it connects all the terms, both the **CG**-theoretical ones (the set of factors or genes, the distributions of probability of the genes in the progeny and the postulated relations between genes and characters) and the **CG**-non-theoretical ones, which are previously empirically accessible (individuals, the set of characters, the assignment of characters to individuals and of progeny to parental individuals, and the relative frequencies of characters observed in the progeny).

Second, **CGGP** is *implicitly accepted as valid in every intended application of the theory* by the community of classical geneticists.

Third, **CGGP** is *highly schematic* and *general* and it possesses so *little empirical content* that it is irrefutable *taken in isolation* (i.e. it has a "*quasi-vacuous*" character). To examine the empirically determined relative frequency of the characters and the theoretically postulated distribution of genes, and to set out coefficients in the distribution of characters and of genes to fit data, *without introducing any kind of further restriction*, is empirically empty.

Nevertheless, fourth, as we would expect in the case of any fundamental law/guiding principle, despite being irrefutable taking alone, it *provides a conceptual framework* within which *all special laws can be formulated as specializations*; that is, special laws with a limited domain of application associated with specific empirical claims can be seen as particular, testable and, eventually, refutable hypotheses, which enable the application/explanations of classical genetics for particular *explananda*, with all such explanations being unified under the **CG**GP umbrella.

And fifth, **CGGP** expresses a *non-accidental regularity* that is *able to give support to counterfactual statements* via its specializations, no matter how context-sensitive0 or

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[7] Actually, in the formulation we made of the premise (3) in the **CG**-explanations above (Section 2), although it is clear that such premise includes the specification of parameters (i), (ii) and (iii) of **CGGP** for (deriving) the explanandum in point, the nomological aspect is less transparent. Premises (3) as formulated above may not look like special "laws", since they specify such parameters but without explicitly adding "and these are responsible of the phenotype data in point". Nevertheless, it is clear that they have to be read as implicitly saying so, for (as we emphasized in fn. 4) from them (and the initial conditions stablished in the other premises) one can infer the phenotypic distribution. Since this implication is "general" (do not apply just to a single event but to a type of phenotypic explananda) and "counterfactual-supporting" (it has modal import), we think it has all the elements for considering it lawful (in the minimal sense mentioned above).

domain restricted; this is the minimal, yet sufficient, sense in which we can talk of the modal import of specific **CG** models.

Thus, according to the present proposal, and just as is the case of any other robust unified theory such as Classical Mechanics, **CG** can also be better analyzed as a theory-net, which has the following structure (see Lorenzano, 1995, 2000; and Balzer & Lorenzano, 2000, for full details):

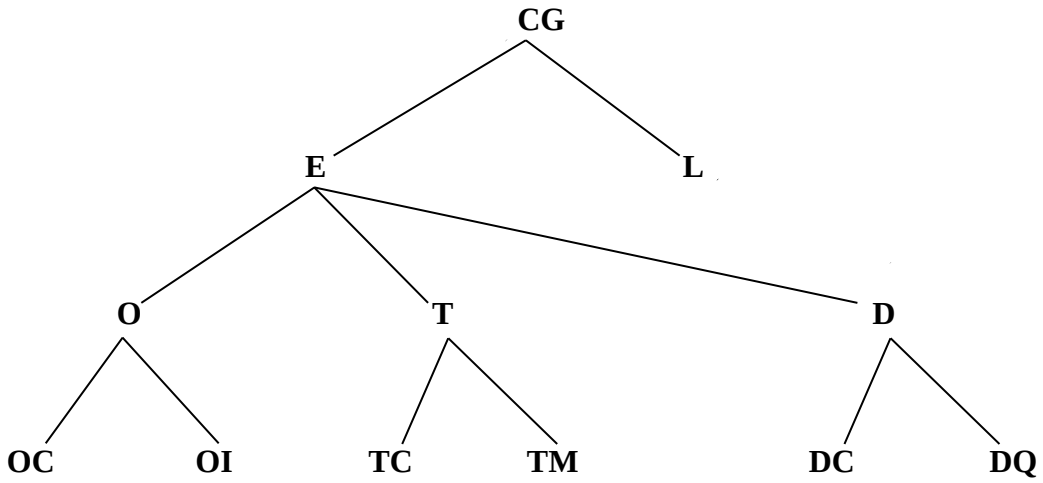

Fig. 5

At the first level of specialization of the **CG** theory-net, we have either that all combinations of factors have equal probabilities (**E**) or that not all the combinations of factors are equally probable, i.e. that "linkage" takes place (**L**). *Pea Flower Color & Pea Pollen Grain Length* from Section 2 is a case of the latter. We can then further specialize **E**. So, at a second level of specialization of the **CG** theory-net, we can consider either that just one pair of factors is involved in the determination of the characters, and that there are four different possible combinations of factors (**O**), or that two pairs of factors are involved in the determination of the characters, and that there are then sixteen different possible combinations of factors (**T**), or that three pairs of factors are involved in the determination of characters, and so there are sixty-four different possible combinations of factors (**D**). At a third level of specialization of the **CG** theory-net we reach the level of terminal specializations. If **O** is further specialized, we can have either a case of complete dominance (**OC**), like *Pea Seed Color* from Section 2, or a case of incomplete dominance (**OI**), like *Mirabilis Jalapa Color* from Section 2. If **T** is further specialized, we can have either a case of complete dominance (**TC**), like *Pea Seed Color & Pea Seed Form* from Section 2, or a case of multifactorial inheritance (**TM**), like *Fowl Comb Form* from Section 2. If **D** is further specialized, we can have either a case of complete dominance (**DC**), like *Pea Seed Color, Pea Seed Form & Pea Flower Color* from Section 2, or a case of quantitative characters (**DQ**), like *Wheat Kernel Color* from Section 2.

5. Scientific explanation as ampliative, specialized embedding

We contend that these traits of **CG** explanations are not explicated by any specific account of scientific explanation that is dominant in the literature: mechanistic, manipulativist (or any other specific causal account), functional, teleological, unificationist, or concerning statistical relevance. The main account currently applied in biology, the mechanistic account, does not square with **CG**, since the *classical* relation between genes/factors and phenotypes is not mechanistic in any non-ad hoc way. Other causalist accounts, such as manipulativism, may fit *some* aspects of **CG** explanations well, but remain silent on other aspects/components, such as gene distributions. Unificationism does not specify the unifying, guiding principle-driven structure of the theory. Functional and teleological accounts do no better. We propose to explicate **CG** explanations as a particular case of a very general account of empirical explanations as ampliative, specialized embeddings (**ASE** account) as elaborated in Díez (2014), developing some structuralist model-theoretic ideas (as we will see, this analysis does not presuppose that all explanations are causal, so the causal component, if philosophers of **CG** agree it is always present, may be added later).

The basic idea of this account is quite simple: Explaining a phenomenon (represented by a model of data) consists of embedding it into a nomic pattern within a theory-net, i.e. embedding the phenomenon (the model of data) into some branch of a theory-net (i.e. into some model present in a theory-net).[8] (cf. Balzer, Moulines & Sneed, 1987; Bartelborth, 1996a, b; Forge, 2002; Díez, 2002, 2014).

Here explanandum and explanans are certain kinds of models/structures, the former being the data model, *DM*, we want to explain; the latter, the theoretical model, *TM*, defined by certain laws and, when needed, initial conditions. Let $DM = \langle D_1,..., D_n, f_1,..., f_n \rangle$ be the explanandum: a data model consisting of several domains of entities and certain functions defined on them; and $TM = \langle D_1,..., D_m, g_1,..., g_m \rangle$, the theoretical model ($m \geq n$, more on this later). For instance, in the paradigmatic Earth–Moon case, the explanandum is the model that represents the Moon's spatio-temporal trajectory around the Earth actually measured, and the explanans is the mechanical model that includes masses and forces and is defined by certain mechanical laws. We explain the Moon's trajectory when we embed it in the mechanical system, i.e., roughly, when we "obtain" the measured kinematic trajectory "from" the mechanical model. In the simplest case, leaving idealizations aside, this means that we find the data model to be part (a sub-model) of the theoretical model. In our genetic case, the explanandum is the data model that describes certain transmission of phenotypes – which is diagrammatically depicted by Fig. 1 – and the explanans is the theoretical model that includes genes and is defined by certain genetic laws. We explain the transmission of traits if we succeed in embedding the data model

[8] The embedding would take place *ideally*, in an exact way, but as many have emphasized this is in general unrealistic for there always are *idealizations* and *approximations* involved. We will not enter into this complication here. For a structuralist treatment of these features, see Balzer, Moulines & Sneed, 1987, Ch. VII.

into the theoretical one, that is, if we obtain the observed phenotype sequence from the genetic model.

This is the basic idea of explanation as nomological embedding. As is apparent, it preserves (a weakened version of) the Hempelian condition of nomic expectability: obtaining *DM* from *TM* is a way of achieving "expectability"; and it is nomological, non-accidental expectability in that *TM* is defined using non-accidental generalizations. Note, first, that the sense of 'nomological' here is very weak: just the presence of non-accidental regularities in the definition of the explanatory models, no matter how local, relational, context dependent or domain restricted they are, thus making room for nomological explanations in fields such as some parts of biology or economics in which it is argued that there are no universal or robust laws. Second, expectability is no longer committed to logical inferences in a literal sense, thus making room for probabilistic explanations with low probabilities if needed.

For the embedding not to be explanatorily trivial, it is essential that the determination/measurement of *DM* does not depend on *TM*, that is, that the identification of the relevant values in the explanandum is independent of the explanatory machinery we use in the explanans. Explanations are (at least) certain kinds of predictions, but construed in such a way that they are not a priori successful: they may fail. This is guaranteed by the fact that the model operating as the explanandum is defined using **T**-non-theoretical terms: terms whose extension is determined/measured without presupposing the validity of the laws through which theoretical models are defined.

All this sounds pretty much like neo-Hempelianism in model-theoretic jargon. But, one may complain, among philosophers of science it is common knowledge that Hempel's account patently failed, and not only due to eventual problems it may have encountered in fields such as biology, but for general reasons that have to do with the well-known counterexamples to the sufficiency of Hempel's conditions: symmetries (e.g. the pole and the shadow), forks (e.g. the barometer and the storm), irrelevances (e.g. anti-pregnancy pills) and time order (e.g. eclipses) all bear witness to the fact that we have pairs of nomological expectabilities that are indistinguishable according to Hempel's conditions but such that one of them intuitively qualifies as a possible explanation whereas the other obviously does not (Salmon, 1989). To the extent that this model-theoretic version preserves the sufficiency of nomic expectability, the objection goes, it falls prey to the same problems. Here is where Díez's (2014) **ASE** account enters into play. It departs from this neo-Hempelian model-theoretic nomological expectability but introduces additional constraints, precisely to resolve the traditional counterexamples and to distinguish merely phenomenological, non-explanatory embeddings (e.g. Galilean kinematics, Keplerian astronomy, etc.) from explanatory ones (e.g. Newtonian mechanics).

Not every model-theoretic embedding is (potentially) explanatory. In order to be so, the embedding must satisfy two additional conditions. First, the embedding must be *ampliative*: the explanans system must introduce new (conceptual or, if we prefer, ontological) machinery with respect the one already present in the explanandum system. The difference between e.g. Keplerian non-explanatory embeddings/predictions and Newtonian explanatory ones is that the former predict spatiotemporal phenomena (trajectories of planets) from spatiotemporal regularities (Kepler's Laws) and initial spatiotemporal conditions, while the latter predict spatiotemporal trajectories through introducing into the theoretical model dynamic parameters, i.e. masses and forces, that

are not part of the explanandum. In a standard, well-developed theoretical explanation by a theory **T**, the **T**-data models are build up from **T**-non-theoretical terms (which are used by **T** but whose determination/measurement does not require the use of **T**-laws), while the **T**-theoretical models introduce **T**-theoretical entities that do the explanatory work: **T** explains **T**-data, data consisting of the values of certain properties/functions determined **T**-independently, by postulating the existence of additional **T**-theoretical entities that interact with the **T**-non-theoretical ones in the way specified by **T**-laws.

However, being ampliative does not suffice. In order to exclude ad hoc, purely formal, not-really-empirical embeddings a second condition is needed. We have seen that guiding principles have a peculiar confirmational status: without their specialization laws they are very easy to satisfy. For instance, if the only constraint on embedding in **CM** were Newton's Second Law ($\sum f = m \cdot a$), then with just some mathematical skill we would be able to embed *any* trajectory, no matter how crazy, devising a series of functions, no matter how strange, whose vector addition would embed the trajectory in **CM**. The same is true in the case of Ptolemaic astronomy, whose guiding principle is that any apparent orbit is a combination of a series of epicycles on a deferent (Carman, 2015): if (contrary to what was actually the case in Ptolemy's work) this were the only constraint, then again it would be possible to embed any (closed, periodical, continuous) orbit just through mathematical skill (see Carman, 2010, for funny examples). Of course, these embeddings are not "really" empirical but just purely mathematical exercises. In order to have genuinely empirical embedding, some specific specialization of the guiding principle must be used. These specializations are what introduce the specific empirical constraints. In other words, scientists establish the specific empirical hypothesis/constraints/laws through postulating specializations of the guiding principle. Thus, for instance in mechanics, in order to have a really empirical explanatory embedding, a specific specialization of Newton's Second Law must be used: not just any (crazy) mathematical function is permitted. Which specializations are permitted is something that theorists "establish" (often only implicitly); there is nothing formally specifiable a priori, scientists specify this in their scientific practice when developing the theory/paradigm, the theory-net, which determines the limits of acceptability. This is an irreducible pragmatic component of scientific practice.

With these two additional conditions to hand, we can face down traditional objections to nomic expectability accounts of explanation (Díez, 2014), and obtain a minimalist analysis that works for all varieties of explanatory practices, some of which will, in addition, be causal, or mechanistically causal, or unifying, or functional, etc. For instance, according the **ASE** account, we explain, e.g., the spatio-temporal trajectory of the Earth and its acceleration effectively measured around the Sun (represented by a structure/data model of the type $\langle P, T, s\rangle$ (where $P = \{p_E, p_S\}$, with p_E being the Earth and p_S the Sun, and time T and space s having specific trajectory values), by embedding it into some branch of the **CM** theory-net, i.e., into some of its (theoretical) models of the type $\langle P, T, s, m, F\rangle$ that introduce new dynamical functions (masses and gravitational force) that are related to the kinematical functions in the way some specialization law establishes, in this case the law of gravitation. The data model is (approximately) embedded into the theoretical model in the sense that by the latter introducing additional parameters that, together with the previous ones, behave in the way the special laws say, one can (approximately) obtain the actually measured data model of the trajectory. Likewise, we

explain the color of the seed albumen in peas (represented by a structure/data model of type $\langle J, P, APP, MAT, DIST\rangle$) by embedding it into some branch of the **CG** theory-net, i.e., into some of its models, represented by a structure/theoretical model of the type $\langle J, P, G, APP, MAT, DIST, DET, COMB\rangle$.

Let us consider the case of *Pea Seed Color* in more detail. The system under consideration consists of a set, *J*, of individuals (plants or animals in general, peas in this case, parents and offspring), which form the objects involved in this intended application: $J = \{i_1,..., i_n\}$. The characteristic considered is only the color of the seed. Thus, $P = \{c_1, c_2\}$, where c_1 symbolizes yellow and c_2 green. These are the only characteristics possessed by the individuals: $APP(i_i) = c_1$, $APP(i_i) = c_2$. If we represent the crossing of the parental individuals that gives rise to the first filial generation (or F_1) by *MAT*, we have: $MAT(i_1, i_2) = \langle i_1,..., i_m\rangle$; the same applies to the second filial generation (or F_2): $MAT(i_1, i_2) = \langle i_1,..., i_m\rangle$. If we represent the distribution of parental characteristics in the offspring by *DIST*, we have: $DIST(c_1, c_2) = 1c_1$ in F_1, and: $DIST(c_1, c_1) = \langle 0{,}7505c_1, 0{,}2495c_2\rangle$ in F_2. We can now represent the *data model* for the case of a monohybrid cross – for the color of the seeds – in peas by $\langle J, P, APP, MAT, DIST\rangle$, which expresses what we want to explain, i.e., the relative frequency $0{,}7505c_1$, $0{,}2495c_2$ of yellow and green seed coats, respectively, or (approximately) ¾ of offspring have a yellow seed coat and ¼ have a green seed coat or a proportion of 3:1, as follows: $\langle\{i_1,..., i_n\}, \{c_1, c_2\}, \{\langle i_1, c_1\rangle, \langle i_2, c_1\rangle\}, \{\langle i_1, i_2, i_1,..., i_m\rangle\}, \{\langle c_1, c_1, 0{,}7505c_1, 0{,}2495c_2\rangle\}\rangle$, in F_2. So, let us call such a structure "the **CG** *data model* of *Pea Seed Color*", or $DM_{CG}(PSC)$ for short.

Recall that, in order to account for this data model, it is now postulated hypothetically that:

(i) there is only one pair of factors or genes involved (that we can symbolize by $\langle f_1, f_2\rangle$),

(ii) the factors or genes combinations are equally probable, the parental factors or genes are distributed in the offspring with the same probability; such a function can be in general represented in the following manner: $COMB(\langle a_1, b_1\rangle, \langle c_1, d_1\rangle) = (¼\ a_1c_1 + ¼\ a_1d_1 + ¼\ b_1c_1 + ¼\ b_1d_1)$, where a_1, b_1, c_1, d_1 symbolize any factor or gene, and, in a specific manner, for the crossing carried out (F_2) with one pair of factors or genes involved (symbolized by $\langle f_1, f_2\rangle$): $COMB(\langle f_1, f_2\rangle, \langle f_1, f_2\rangle) = (¼\ f_1f_1 + ¼\ f_1f_2 + ¼\ f_2f_1 + ¼\ f_2f_2)$, and

(iii) one of the factors (f_1), which is "responsible" for the yellow color of the seed albumen, is *dominant* over the other (f_2), *recessive* one, which is "responsible" for the green color of the seeds; the determining function can be represented as follows:

a) $DET(f_2, f_2) = c_2$

b) $\left.\begin{array}{l} DET(f_1, f_1) \\ DET(f_2, f_1) \\ DET(f_1, f_2) \end{array}\right\} = c_1$

All three assumptions are represented in the theory-net of **CG** by the terminal specialization **OC** (Fig. 5). If we put all this information together with the antecedent conditions (initial conditions plus other empirical assumptions) and the theoretical predictions for the "empirical", i.e. **CG**-non-theoretical, values for the distribution of characteristics (*DIST*) in F_2, we obtain the following type of structure: $x = \langle J, P, G, APP,$

MAT, *DIST*, *DET*, *COMB*⟩: ⟨{i_1,..., i_n}, {c_1, c_2}, {⟨f_1, f_2⟩, ⟨f_1, f_2⟩}, {⟨i_1, c_1⟩, ⟨i_2, c_1⟩}, {⟨i_1, i_2, i_1,..., i_m⟩}, {⟨c_1, c_1, 0,75c_1, 0,25c_2⟩}, {⟨f_1, f_1 , c_1⟩, ⟨f_2, f_1 , c_1⟩, ⟨f_1, f_2 , c_1⟩, ⟨f_2, f_2 , c_2⟩}, (¼ f_1f_1 + ¼ f_1f_2 + ¼ f_2f_1 + ¼ f_2f_2)⟩. Let us call it "the **CG** *theoretical model* of *Pea Seed Color*", or TM_{CG}(*PSC*) for short.

Now, it can be seen that the **CG** data model of *Pea Seed Color* (DM_{CG}(*PSC*)) is explained by embedding it into the **CG** theoretical model of *Pea Seed Color* (TM_{CG}(*PSC*)):

> ⟨{i_1,..., i_n}, {c_1, c_2}, {⟨i_1, c_1⟩, ⟨i_2, c_1⟩}, {⟨i_1, i_2, i_1,..., i_m⟩}, {⟨c_1, c_1, 0,7505c_1, 0,2494c_2⟩}⟩ is (approximately) embedded into ⟨c_1, c_1, 0,75c_1, 0,25c_2⟩}, {⟨f_1, f_1 , c_1⟩, ⟨f_2, f_1 , c_1⟩, ⟨f_1, f_2 , c_1⟩, ⟨f_2, f_2 , c_2⟩}, (¼ f_1f_1 + ¼ f_1f_2 + ¼ f_2f_1 + ¼ f_2f_2)⟩,

In brief: DM_{CG}(*PSC*) is (approximately) embedded into TM_{CG}(*PSC*). For such an embedding to be possible, it is clear that any given TM_{CG} must have at least as many components as the specific DM_{CG} in question. This is the $m \geq n$ condition that we mention in the previous section.

As we have said, sometimes, but not necessarily always, the ampliative machinery, the new **T**-theoretical concepts/entities, may be interpreted in a causalist way. For instance, in Classical Mechanics (**CM**), forces may be interpreted in a causalist way. But in Relativistic Mechanics, where what is introduced and carries the explanatory weight is the geometry of space-time, the causal nature of the explanation is far from clear (see Hoefer, 2009, for a discussion). In the theory of interest here, **CG**, part of the ampliative machinery introduced, genes (*G*), and the determination relation *DET* between genes/genotypes and characteristics/phenotype, may be interpreted in a causalist manner (plausibly in the difference-making sense), but other elements that are introduced and are also essential for the explanatory import of the theoretical model, such as the distribution of parental genes/genotypes in the offspring (given by the function *COMB*) are not so clearly interpretable in causal terms. Thus, even if **CG** explanations include some causal components, not every component that is explanatorily relevant in the explanans has a clear causal nature. So, causation does not exhaust the explanatory dimension of **CG**, which is better explicated by the ampliative, specialized model-theoretic embedding account, to which one may add a causalist interpretation (mechanistic, manipulativist, or some other) of *part* of the ampliative machinery.

Before concluding, it is worth emphasizing the novel aspects of our account compared to other approaches in the literature that may look similar in some regards. Besides its structuralist ancestors, already mentioned, the account in the literature that may have similarities with **ASE** is Leuridan's (2014) causal structural account. Leuridan combines ideas from Sneedian structuralism, Kitcher's unificationism, Woodward's interventionism and Bayesian causal nets to elaborate his causal structural account in terms of casual nets, and applies it as a case study precisely to Classical Genetics. Leuridan's account is probably the richest and most complex, and we think the most promising, version of a causal theory of explanation, but space limitations do not allow us to enter into its details here. What matters to our present concerns is that, despite the use Leuridan makes of some structuralist ideas (mainly the different theory-elements within the same theory, the notion of **T**-theoreticity and the general idea of explaining by embedding – which actually as we have said is just the model-theoretic version of

expectability), there are essential differences between his account and **ASE**. To begin with, Leuridan does not impose as conceptual conditions that the explanans must be ampliative and specialized, at least not explicitly as clauses in the analysans of his analysis. It is true that in his application to **CG** he makes use of the new, **CG**-theoretical concepts, and also of special genetic laws, but these two **ASE** conditions are not explicitly demanded in his analysis as conceptually necessary for every explanation. Yet, the most important difference is that Leuridan's account is explicitly causal; actually, he explicitly takes the lack of causal conditions in previous accounts as defective, while **ASE** is explicitly non-causal.

According to Leuridan, it is causal information (structured in some specific manner) that constitutes explanatoriness, while according to **ASE** causation is not conceptually necessary for explanatoriness, just ampliative and specialized embedding is. **ASE** defends as one of its virtues that the account does not conceptually require causation, which allows **ASE** to explicate cases of non-causal explanations with the same analytical framework, while Leuridan's takes causation as conceptually necessary for his explication (whether because he takes that every explanation is causal or because he confines his analysis only to causal explanations, is not clear to us). We agree that in the case of **CG** the **T**-theoretical entities (mainly genes) have a causal role, but according to Leuridan, this causal nature is what constitutes the explanatory import of these explanations, while for us it is not, it is the (not necessarily causal) specialized ampliative embedding what carries explanatory import, in this case, and in all other cases. According to **ASE**, all explanations are conceptually ampliative specialized embeddings and this is why they are explanatory. Some explanations have additional features, that is, some explanations are *in addition* causal, or causal-mechanist, or unifying, or etc., but according to **ASE** this is not what makes them explanatory, but what makes them specific (causal, mechanist, unifying,…) sub-types of explanations. Be **ASE** correct or not in not making causation a conceptually necessary condition for explanation, in any event this is an essential difference with respect Leuridan causal structural account.

6. Concluding remarks

By analogy with a paradigmatic unified explanatory theory (Classical Mechanics), we have applied the model-theoretic account of explanation as ampliative, specialized embedding (**ASE**) to the case of Classical Genetics. Other accounts of explanation do not suit the case of **CG** well. The main account applied nowadays in biology, the mechanistic account, does not square with **CG**, since the *classical* relation between genes/factors and phenotypes is not mechanistic in any non-ad hoc way. Other causalist accounts, such as manipulativism, may fit *some* aspects of **CG** explanations well, but remain silent concerning other aspects/components. Unificationism may explicate the unifying power of **CG**, but does not specify the unifying, guiding principle-driven structure of the theory, and does not draw any distinction between ampliative/explanatory and non-ampliative/non-explanatory unifications. Functional and teleological accounts do no better. It is our claim that **ASE** fares better than its competitors, and well enough to explicate the general aspects of **CG** explanations, both those that are causal and those that are not. **ASE** also explicates the unifying structure of **CG** *in detail*, as a guiding principle-driven theory, in this case via a guiding principle not explicitly formulated in the theory's

literature. **ASE** identifies the key explanatory elements of **CG** as the new ampliative elements that are introduced and their specialized lawful connection with the components already present in the explanandum. This also sheds light on the sense in which **CG** explanations are *nomological*: a sense that is weak yet strong enough to allow us to understand the counterfactual-supporting dimension of **CG** explanations. We claim that all these aspects, as explicated by **ASE**, dispel the alleged oddities of **CG** and clarify the unifying, nomological, and partially non-causal explanations in Classical Genetics.

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