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Emergentism in the biological framework: the case of fitness

Vanesa Triviño[1]

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Abstract
In this paper, I aim to explore whether fitness, understood as a causal disposition, can be characterized as an emergent property of organisms, or if it is reducible to the anatomical, physiological, and environmentally relative properties that characterize them. In doing so, I refer to Jessica Wilson's characterization of ontological emergence and examine if fitness meets her criteria for ontological emergent properties (dependence and autonomy); and, if so, to what degree (weak or strong).

Keyword Ontological emergence · Strong ontological emergence · Dispositional account of fitness · Causal autonomy · Metaphysics of biology

Introduction

The problem of fitness is a classic one in philosophy of biology. The explanatory issues created by the equation between fitness and an organism's actual number of offspring (Rosenberg 1985; Millstein 2016), have given rise to a proliferation of definitions that are mainly focused on distinguishing what fitness ontologically is (i.e., ecological fitness), from how it is measured (i.e., predictive fitness) (Matthen and Ariew 2002). The propensity interpretation of fitness is a classic example of this tendency (Mills and Beatty 1979).

In this paper, I will focus on a more recent characterization of fitness that considers it to be a *causal disposition* of organisms (Triviño and Nuño de la Rosa 2016). In this account, besides arguing for the causal dispositional character of fitness, Nuño de la Rosa and I also propose that fitness is *an emergent property* that introduces a new causal power into the world (i.e., making organisms able to survive and reproduce in a particular environment and population). Yet, the arguments to properly justify the emergent character of fitness are not developed. Here, I will cover this gap by appealing to the metaphysical characterization of emergence. I will explore

✉ Vanesa Triviño
vanetriv@ucm.es

[1] Department of Logic and Theoretic Philosophy, Complutense University, Madrid, Spain

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whether the features attributed to emergent properties are met in the case of fitness. In doing so, I will consider Jessica Wilson's recent characterization of ontological emergence (Wilson 2016, 2021).

Although the metaphysical notion of emergence is highly controversial (Kim 2006), it has been widely recognized in different disciplines (Goldstein 1999; Witherington 2011). In philosophy of biology, the notion of emergence is widely used to characterize some biological features, such as the features of biochemical networks (Boogerd et al. 2005), the amount of nectar stored in a hive (Mitchell 2012), or holobionts (Suárez and Triviño 2020). The recourse to the notion of emergence in the particular case of fitness, therefore, can serve to shed light on its ontological status. Appealing to metaphysical theories and notions to clarify the ontological status of the entities to which biological concepts refer is, in fact, one of the forms in which metaphysics of biology can be done. In this sense, this work on fitness can be seen as a case of metaphysics *for* biology (Triviño 2022).

The structure of the paper is as follows: Firstly, I introduce the problem of fitness in philosophy of biology and highlight the main accounts that have been offered to clarify its ontological status, i.e., what fitness is (Sect. "The problem of fitness"). Then, I present Wilson's characterization of weak and strong ontological emergence within the more general framework of emergentism (Sect. "The metaphysical framework: weak and strong ontological emergence"). In Sect. "Dependence relations in fitness", I pay attention to the different forms of dependence that can exist between emergent properties and their bases to explore which one holds in the case of fitness as a causal disposition: modal covariation (Sect. "Modal covariation"), causation (Sect. "Causation"), or non-reductive realization (Sect. "Non-reductive realization"). In Sect. "The causal autonomy of fitness", I focus on the causal autonomy of fitness. In doing so, the potential for fitness to introduce a new causal power into the world (Sect. "Downward causation concerning new causal powers") as well as its impact on constraining the functional dispositions on which it depends (Sect. "Downward causation concerning lower-level constraints") are discussed. Finally, I present some concluding remarks (Section 5).

The problem of fitness

The notion of fitness is used in classic evolutionary biology to explain evolutionary change by means of natural selection. Although its original formulation can be found in Darwin's theory of evolution (Millstein 2016),[1] its characterization was articulated within the framework of the so-called Modern Synthesis (Huxley 1942). Due to the work taking place in population genetics (Fisher 1930; Wright 1931; Haldane 1932), fitness was considered to be a mathematical parameter that refers to an organism's actual number of offspring (Millstein and Skipper 2007).

[1] Darwin, however, did not explicitly use the term 'fitness' but several similar terms such as 'fit', 'fitting', or 'fitted' (Millstein 2016).

This *actualist account* of fitness has been widely criticized for lacking explanatory power and rendering evolutionary explanations based on it circular (Millstein 2016). Due to its conceptual connection with rates of reproduction, if we want to explain *why* the fittest organisms are the reproductively successful ones, the answer will be that the reproductively successful organisms are reproductively successful. To avoid this tautological problem (Brandon 1978; Rosenberg 1985), philosophers of biology developed alternative characterizations of fitness that enable a distinction between what fitness is and how it is measured. The propensity interpretation of fitness exemplifies this tendency (Mills and Beatty 1979).

In the propensity interpretation of fitness (Brandon 1978; Mills and Beatty 1979), fitness refers to an organism's propensity, ability, or disposition[2] to survive and reproduce in a particular environment and population. This ability is expressed in probabilistic terms by considering the reproductive success expected of an organism (expected fitness). Yet, insofar as it is a probability, it can differ from the actual reproductive success of the organism (realized fitness). For Mills and Beatty, evolutionary biologists have difficulties in defining fitness since they confuse "the *post facto* survival and reproductive success of an organism, with the *ability* of an organism to survive and reproduce" (Mills and Beatty 1979: 270). But fitness refers, precisely, to this organism's ability. This propensity, notwithstanding, does not refer to whether the organism would reproduce or not in a given environment, but to the *number* of offspring the organism *might have*. In this sense, it is a quantitative propensity. Furthermore, it is non-deterministic since there is not a unique number of offspring an organism is determined to leave. Rather, there are different propensities for the organism to leave different numbers of offspring (Mills and Beatty 1979: 273).

For Mills and Beatty, the fitness of organisms can be measured in terms of the probabilistic distributions associated with their reproductive propensities, by assigning values to each propensity and calculating the weighted sum of these values. This mathematical result will refer to the 'expected fitness' of organisms (Mills and Beatty 1979: 275). The quantification of the fitness of an organism, therefore, is given through its expected number of offspring, which is an indication of the organism's ability to survive and reproduce in a particular environment and population. The expected fitness of an organism, notwithstanding, might not coincide with the *actual* number of offspring it leaves (realized fitness). Expected fitness is calculated in *ideal conditions*, without considering other factors that might affect the manifestation of the fitness disposition, such as an environmental catastrophe. These kinds of factors, notwithstanding, can occur, and they would explain that the organism with a higher expected fitness is not always the one that survives and reproduces the most.

The dispositional character of fitness can recapture the key properties of the Darwinian conception of fitness: it is an ability of organisms; it is relative to both environment and population; and it encompasses both survival and reproduction

[2] Although philosophical terms such as those of disposition, ability, propensity, or capacity, might have different meanings in different philosophical and metaphysical fields, in the debates concerning the definition of fitness they are used interchangeably.

(Millstein 2016). Furthermore, the characterization of fitness as a disposition also accounts for its *explanatory power*. Thus, fitness explains why a particular organism survives and reproduces in its environment and population in the same way as solubility, a classic example of a dispositional property, explains why a certain substance (e.g., salt) dissolves when introduced in water. The actual survival and reproduction of an organism, just like the dissolution of salt, refers to the manifestation associated with a certain disposition. Thus, it is the possession of the disposition (i.e., fitness) that explains the manifestation it produces (i.e., realized fitness).

Despite all the virtues of the propensity interpretation of fitness (hereafter PIF), some aspects of this approach are considered to need more clarification (Pence and Ramsey 2013), such as (i) the way probability is understood and how the probabilistic quantification of fitness affects the consideration of evolution by natural selection as either a deterministic or an indeterministic process (Rosenberg 1985; Rosenberg and Williams 1986; Hodge 1987); (ii) the time scale that needs to be considered when calculating the expected number of offspring of an organism (Beatty and Finsen 1989); (iii) the role that extrinsic factors, such as population size, play when predicting an organism's expected number of offspring (Sober 2000; Millstein 2016); or (iv) the way fitness as an ability (i.e., ecological fitness) and fitness as the expected number of offspring (i.e., predictive fitness) can be connected.[3]

Ecological fitness is defined in a causal sense insofar as it refers to the physical features of an organism that cause its survival and reproduction. *Predictive fitness*, conversely, refers to the organism's expected number of offspring and is defined in a mathematical form. Although the mathematical formulation of fitness should not be confused with fitness itself, some authors claim that in PIF fitness ends up being identified with the mathematical parameter (Abrams 2007). Due to this identification, there are problems in explaining how ecological fitness is connected to the predictive one since we only seem to have predictive fitness (Millstein 2016: 13).

In a recent paper, Nuño de la Rosa and I have also highlighted the problems of equating fitness to expected fitness (Triviño and Nuño de la Rosa 2016), namely that the explanatory power of fitness cannot be accounted for. In referring to the expected number of offspring, it is not possible to explain how an organism survives and reproduces in a particular environment and population. As we see it, some of the problems that PIF encounters rest on its ontological characterization of fitness as a disposition.

Concerning the ontological status of dispositions, Mills and Beatty are reductionists. They reduce the disposition of fitness to the traits that characterize organisms and that are considered to be the causes of their survival and reproduction when the triggering conditions are given (Mills and Beatty 1979: 271). Yet, for Nuño de la Rosa and me, fitness should be characterized as a dispositional property on its own, such that the capacity of organisms to survive and reproduce can be properly

[3] In this regard, some authors have claimed that these two faces of fitness (Sober 2000) are different but complementary notions (Brandon 1978, 1990; Millstein 2016), whereas others have argued that these two notions of fitness cannot be reconciled since predictive fitness is not strictly speaking derived from ecological fitness (Matthen and Ariew 2002; Walsh 2007).

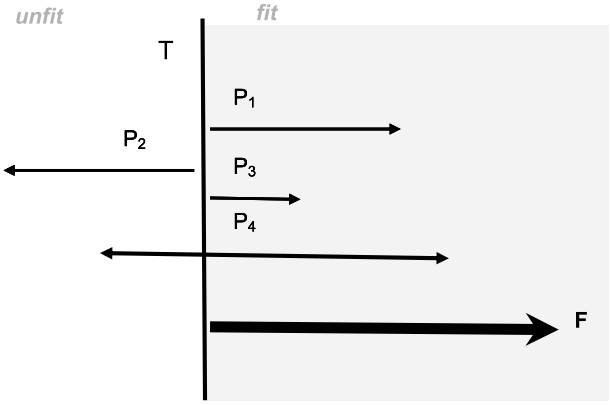

Fig. 1 Fitness as a causal dispositional property. The P_n vectors refer to those dispositional properties whose combination makes an organism fit. Following the DTC, vectors have two properties. First, they have different intensities, as indicated by the different lengths of the arrows. Second, vectors have different directions, indicated by the direction into which the arrowhead is pointing. Functional dispositions are oriented towards (P_1 P_3, P_4) the disposition to survive and reproduce. P_2 is a countervailing factor, that is, a kind of malfunction or trait whose effect is not disposed towards but away from fitness. P_4 reflects a tension in the orientation of that disposition. A sexual trait, for instance, can be oriented towards reproduction (arrow to the right) but be detrimental to the survival of the organism (arrow to the left). Fitness (F) is the resultant of the combination of these dispositions and is manifested once it has exceeded a certain threshold (T). (The figure is in Triviño and Nuño de la Rosa 2016: 4)

explained. Thus, although we recognize the usefulness of the tools and resources offered by PIF regarding the mathematical characterization of fitness (see Triviño and Nuño de la Rosa 2016: §3), we argue that its ontological characterization can be improved if fitness is considered to be a non-reducible disposition of organisms (Triviño and Nuño de la Rosa 2016: 4).

In the causal dispositional account of fitness (hereafter CDAF), fitness is characterized *as a complex and dynamic* disposition of organisms, and it is in virtue of this disposition that they can survive and reproduce in a particular environment and population (Triviño and Nuño de la Rosa 2016: 4. See also Fig. 1). It is a *complex disposition* since it results from the non-linear combination of the functional dispositions (manifested with a particular intensity and direction) that characterize an organism. It is also a *dynamic disposition* since it changes at different stages across organisms' lifetimes. As we argue, the functional dispositions (i.e., the morphological, physiological, and behavioral properties) of an organism are not static but change along its life history (an adult deer, for instance, has features that a young deer does not, such as the antlers). The resultant fitness, therefore, evolves throughout the development of the organism (see also Brandon 1990).[4]

Characterizing fitness as a causal disposition of organisms enables the acknowledgment of both its causal and its explanatory roles. In the propensity account,

[4] In this regard, some authors consider that fitness does not change throughout an individual's life, but remains fixed over its lifetime (Ramsey 2006).

fitness is considered to be a term that plays an explanatory role since, without this term, evolutionary explanations would be impossible due to their unwieldy length (Rosenberg 1983: 459). In Rosenberg's terms: "[fitness] refers to a primitive and undefinable term within the theory of evolution, serving as a convenient shorthand to avoid enumerating all the traits that are connected to an organism's success in survival and reproduction" (Rosenberg 1978: 374). In this account, therefore, fitness is *nothing more than* its component physiological, anatomical, behavioral, and environmentally relative properties (Rosenberg 1978: 374). Every manifestation of fitness can be, in principle, explained and expressed in terms of the different physical and chemical properties of the organism that underlie its viability and fertility levels. In CDAF, notwithstanding, fitness "is *something more than* the properties of an organism" (Triviño and Nuño de la Rosa 2016: 9), in the sense that it has a proper causal power and therefore, plays a causal role in making organisms able to survive and reproduce. Fitness, then, plays both an explanatory and a causal role.

The causal power of fitness has been widely considered in CDAF, where fitness is considered to be an emergent property insofar as it has a causal power that differs from the causal powers of the properties it emerges from. As we claim: "We think the notion of *causal power* is key in understanding the dispositional nature of fitness as well as the causal and explanatory role it plays in evolutionary theory. For us, fitness is an ontological and real property on its own due to the causal power that characterizes it (namely, the ability to survive and reproduce) and that cannot be exercised by any of the properties of the organism" (Triviño and Nuño de la Rosa 2016: 9).

However, in the CDAF we do not develop the arguments to properly justify that the causal power of fitness is, in fact, autonomous, i.e., different from that given at lower-level properties. In this regard, if the causal power of fitness were reducible to the causal power of the different anatomical and physiological properties that characterize an organism, then this account would not differ from the propensity interpretation of fitness. Conversely, if the causal power of fitness were irreducible, then the ontological status of fitness as a causally autonomous property could be argued for. In the following sections, I will address this question and explore whether fitness can be characterized as a causally autonomous property.

The metaphysical framework: weak and strong ontological emergence

The idea of emergence has existed since ancient times (McLaughlin 1992; Kim 2006). Yet, there is still no consensus on a unified account (Kim 2006; Wilson 2016). Generally, it has been claimed that the extant definitions of the concept can be subsumed into two general categories: weak and strong emergence (Chalmers 2006; Clayton 2006). Although weak emergence is usually equated to epistemological emergence (i.e., to those properties that we, humans, characterize as such due to some limitations we have to explain them) and strong emergence tends to be equated to ontological emergence (i.e., to a kind of objective properties given in the world (Bedau 1997; Silberstein and McGeever 1999)), some metaphysicians have argued

that weak and strong emergence just are *degrees* in which both ontological and epistemological emergence can occur (van Gulick 2001; Wilson 2016).

Ontological emergent properties (henceforth OEP) are mainly conceived of on the basis of causal powers. According to the so-called Alexander's dictum, a property is real, i.e., *ontologically* autonomous, when it has causal powers. In this sense, if OEP are real properties in the world, then they must have causal powers. The notion of causal power, notwithstanding, is a problematic one. It can be differently conceived depending on the ontological commitments one might have regarding properties. Here, I will follow Wilson's account of causal powers, according to which a property is causally efficacious if it allows its bearer to enter into causing some effects when the appropriate circumstances are given (Wilson 2002, 2016, 2021). Although this account is neutral regarding whether properties are ontologically categorical or dispositional, I will consider them as dispositions, since it is in terms of dispositions that fitness and its basis are conceived within CDAF.

For a property to be emergent, nonetheless, it is not sufficient for it to have causal power. This causal power must also be *autonomous* from those of the lower-level properties on which the emergent property depends. This is so since causal autonomy implies ontological autonomy, whereas the reverse does not necessarily follow. A property might have a causal power and therefore, be *ontologically autonomous*. Yet, this property might not be *causally autonomous* insofar as its causal power can also be given in the lower-level properties upon which it depends (Kim 2006: 557; Wilson 2016, 2021). In these cases, there is reductionism, but not emergence. The difficult aspect regarding emergence is to properly justify the causal autonomy of these properties. In this regard, Wilson (2016, 2021) offers a taxonomy of two different ways emergent properties might be causally autonomous. These two ways correspond to the two different degrees in which OEP might be given: strong and weak (Wilson 2016):

> *Strong Emergence (SE):* Token higher-level feature *S* is strongly metaphysically emergent from token lower-level feature *P*, on a given occasion, just in case (i) *S* synchronically depends on *P* on that occasion; and (ii) *S has at least one token power not identical with any token power of P on that occasion* (362. Emphasis added. See also Wilson 2021: 53).
> *Weak Emergence (WE):* Token higher-level feature *S* is weakly metaphysically emergent from token lower-level feature *P* on a given occasion just in case (i) *S* synchronically depends on *P* on that occasion; and (ii) *S has a non-empty proper subset of the token powers had by P, on that occasion* (362. Emphasis added. See also Wilson 2021: 72).

As Wilson makes explicit, in both SE and WE, the first condition minimally specifies synchronic dependence, whereas the second one captures the way the emergent properties might be causally, and therefore, ontologically autonomous. For SE, there is causal autonomy insofar as the emergent property incorporates a *new causal power* in the world. In cases of WE, conversely, the emergent property does not incorporate new causal powers, but it has a different *causal power profile* since it only possesses a *proper subset* of the causal powers of the lower-level properties it depends on. Insofar as it has causal power, the property is real (as per Alexander's

dictum). Furthermore, since the causal power profile differs from that of the lower-level properties upon which it depends, the higher-level property is causally autonomous as well (Wilson 2016: 362).

Concerning dependence and causal autonomy as the main features that characterize OEP, Wilson offers a taxonomy of different ways these features can be considered and explores how they match WE and/or SE. In the following sections, I will explain Wilson's schema concerning dependence (Sect. "Dependence relations in fitness") and causal autonomy (Sect. "The causal autonomy of fitness") while applying it to the case of fitness understood as a causal disposition. In doing so, I will consider fitness as a *token* property (unless otherwise specified).[5]

Dependence relations in fitness

Wilson distinguishes four kinds of dependence that can be given between the higher-level property of a system and the lower-level properties of the parts that compose it: *material composition*, *modal covariation*, *causation,* and *non-reductive realization*. I will examine which one is more suitable to capture the relation that is given between individual fitness and its base.[6] In doing so, I will not consider *material composition* since it does not properly refer to a dependence relationship between properties at different levels, but to the requirement according to which nothing immaterial characterizes the bearers of properties. Properties can be emergent or not, but the bearer is always a *physical* entity (Stephan 2002). Material composition, therefore, is compatible with both SE, and WE, and also with the absence of emergent properties (Wilson 2016). Concerning fitness as a causal disposition, the material composition of organisms (i.e., the bearers of fitness) is widely accepted. Fit organisms are fundamentally material entities, and their distinctiveness from non-living entities is based on their properties rather than their composition.

Modal covariation

The relation of modal covariation is associated with that of supervenience. Since its origins in the work of the British Moral Theorists (Kim 1990), the notion refers to a

[5] The distinction between *type* and *token* is important since it refers to the distinction between *properties* and the *instantiation* of properties, respectively. Properties are not able to enter into causal relations, but instantiations of properties are (Kim 2003).

[6] In this regard, it is important to highlight that Wilson put aside some accounts or treatments of emergence, such as Morgan's emergent evolution (1923), since they are not relevant to account for the emergent properties and/or entities that are the target cases of different special sciences (Wilson 2021: fn. 3). Humphreys' (1997) account of emergence in terms of fusion is also put aside since on the one hand, it is irrelevant to give an account or accommodate the existence of higher-level entities (Wilson 2016: fn. 2), and, on the other, Wilson considers that it could be possible to think about cases of fusion or intra-level emergence as simply involving causation (Wilson 2021: fn. 3). As I see it, Humphreys' account is not accurate to explain the kind of dependence given in the case of fitness since the dispositional components that make up the fitness of an organism do not fuse and disappear to create a fit organism. Fitness could not be manifested without these functional dispositions operating.

relation of covariation between two sets of properties, i.e., the lower-level (subvenient) properties and the higher-level (supervenient) ones (Kim 1984, 1990). According to this kind of relation, there cannot be two entities that are alike regarding their subvenient properties but different in the supervenient ones. In other words, an object cannot vary in its supervenient property without a variation in some subvenient property.

The recourse to supervenience to make sense of emergence has been quite common even since the work of the British Emergentists (Beckermann 1992: 103) since supervenience is characterized as a form of dependence that does not imply reduction (O'Connor 1994: 14).[7] In philosophy of biology there is recourse to the notion of supervenience when talking about fitness (Rosenberg 1978; Sober 1984). In this regard, levels of fitness are said to supervene on "those properties, dispositions, and abilities which organisms have in virtue of their anatomical, physiological character, and the interaction of this character with the organism's environment" (Rosenberg 1978: 372). Supervenience allows us to explain both why organisms with the same properties have the same level of fitness, and why organisms with different properties, such as a bird and a squirrel, might have the same level of fitness. The only requirement is that a change cannot be produced regarding the level of fitness of any of these organisms without a change in the lower-level properties that characterize them.

The relation of supervenience, however, does not seem to be the one that is given in CDAF. In this account, fitness is seen as a disposition that results from the non-linear combination of the environmentally relative functional dispositions that characterize an organism. This resultant disposition that is fitness is manifested with a particular *intensity* that corresponds to the higher or lower capacity for the organism to survive and reproduce (in Fig. 1, fitness intensity is represented by the length of the arrow). In CDAF, all organisms are fit, that is, all organisms have the capacity to survive and reproduce in a particular environment and population since all of them possess the fitness property as a result of the non-linear combination of their functional dispositions. Yet, not all organisms manifest this property with the same intensity (Triviño and Nuño de la Rosa 2016: 7).

In CDAF the intensity that characterizes the manifestation of fitness is not static. It can change depending on both the changes and alterations that can affect the functional dispositions that characterize an organism (i.e., the base of fitness), and the environmental and populational factors that interfere with the organism itself (Triviño and Nuño de la Rosa 2016). Concerning the first kind of change, the functional dispositions that characterize an organism manifest themselves with a particular intensity within the proper viable constraints (Triviño and Nuño de la Rosa 2016: 7). An alteration in these intensities, by an organ being damaged due to some

[7] The consideration that supervenience implies dependence without reduction is, in fact, highly controversial. Kim, for instance, has widely argued that a higher-level property of a system cannot *depend on* the lower-level properties of the parts of the system that instantiates it, *without being reduced* to them (Kim 1984, 1989, 1990). For the author, two different notions of supervenience, i.e., weak and strong, need to be at play to capture this idea of dependence without reduction (Kim 1984: 163).

environmental factor, for instance, or due to changes produced as a consequence of the different developmental stages of the organism (sexual traits do not perform their function during the whole life-cycle of the organism with the same intensity), can affect the way fitness is manifested. That is, its intensity.[8]

Regarding the second kind of change, fitness can also vary its intensity insofar as the elements of the environment and population in which the organism is embedded can affect the way it survives and reproduces (without necessarily affecting the functional dispositions that characterize it). The population and environment in which the organism is embedded play a role in the manifestation of fitness itself. It is not only that environmental and populational factors might allow or impede the manifestation of fitness, but also that they influence how fitness is given, i.e., the way the organism is, in fact, able to survive and reproduce. Thus *environmental factors,* such as food supply, the number of predators, or weather conditions, among others, can influence the organism's fitness by increasing or decreasing its intensity. In the same way, *populational factors* can also affect the survival of the organism (for example, in those cases where food resources are scarce and it is necessary to struggle for them) and its reproduction (since population size can change the possibilities for an organism to find a mate to reproduce and its possibility to, in fact, reproduce). In the latest case, the other organisms in a population can affect how fitness is manifested in reproduction since, in sexually reproducing species, the fitness of an organism depends on the *availability*, *fertility*, and *compatibility* of individuals in the breeding group of the organism. In this case, an organism's fitness intensity is modified insofar as its disposition to reproduce is affected by the other organisms in the population. Yet, no changes in the functional dispositions of the organism need to occur.

The possibility for fitness to vary without corresponding changes in its base occurring indicates that the kind of dependence given in this case is not supervenience. In CDAF, fitness intensity can be affected and altered by elements that go beyond its base, and thus, it is not possible to account for an organism's fitness by merely considering the functional dispositions that characterize it. This is precisely due to its dispositional character. Insofar as it is a disposition, the context in which fitness is manifested plays an unavoidable role; organisms are only able to survive and reproduce in a particular environment and population.

In the causal dispositional account, the context-sensitivity of fitness has been explicitly highlighted (Triviño and Nuño de la Rosa 2016: §2.3). This consideration does not only refer to the way environmental and populational factors are relevant when calculating fitness levels, i.e., the expected fitness of an organism or its expected number of offspring (Triviño and Nuño de la Rosa 2016: §3. See also

[8] In this regard, it is important to highlight, as a reviewer suggested, that accounts of supervenience can explain this kind of dynamic changes and variations in intensity. These changes occur due to alterations in the lower-level base. These kinds of changes are introduced here as an illustration of the changes acknowledged in CDAF, but they are not an argument against supervenience. The second kind of changes, i.e. those that refer to changes in the manifestation of fitness without changes in the lower-levels parts of its base are the relevant ones when questioning that the relation between fitness and its base in CDAF is a supervenient one. This is so since in CDAF only the organism's functional dispositions constitute the base of fitness, environmental and populational factors are not included in this base.

Sober 2000; Millstein 2016). But it also refers to the idea that the environment and the population in which the organism is embedded directly affect how it survives and reproduces. That is, the way its fitness is being manifested.

Causation

Another way the dependence relationship between an emergent property and its basis is understood is in terms of causation (O'Connor and Wong 2005; Wilson 2002, 2016); the lower-level properties of the parts of the system *cause* the emergent property to appear (O'Connor and Wong 2005: 664). Concerning fitness as a causal disposition, it seems that the kind of connection that links individual fitness with its basis is a causal one. This is so since CDAF is developed using the metaphysical framework of the dispositional theory of causation (Mumford and Anjum 2011), and thus, the main features attributed to causation in this account (i.e., simultaneity, compositional pluralism, and non-necessitarianism) seem to hold in the case of fitness.

Regarding *simultaneity*, fitness meets this criterion since the functional dispositions that characterize an organism, and that give rise to the manifestation of fitness, are manifesting simultaneously with fitness itself: "a healthy organism, whose heart pumps, or whose legs run when its nose smells a predator, is *simultaneously* a fit organism" (Triviño and Nuño de la Rosa 2016: 5. Emphasis added).

Concerning *compositional pluralism*, in CDAF fitness is seen as a complex disposition that results from the *combination* of the functional dispositions that characterize an organism. These functional dispositions are, furthermore, *non-linearly combined*, which means that the effect they produce, i.e., individual fitness, is more than the mere addition or subtraction of their different effects taken in isolation. It is in their non-linear combination that functional dispositions engage in a process in which fitness, that is, a *fit organism,* appears as the simultaneous effect.[9]

Finally, regarding *non-necessitarianism*, in CDAF there is no necessary connection between individual fitness and its basis since both preventing and interfering factors might intervene and affect the process that gives rise to fitness. When the process is prevented, then fitness stops manifesting with the result of killing the organism. When interfered, the fitness is still given but its manifestation is different from the one that would have occurred without the interfering factor. Thus, the fit organism might differ from the one that would have resulted without the interfering factors since its fitness intensity would be different in each case.

Insofar as fitness meets the features attributed to causation according to the dispositional theory of causation, it is considered to be an emergent property. Effects

[9] In this regard, recall that in CDAF all living organisms, insofar as resulting from the combination of functional dispositions, are fit organisms, that is, all living organisms have the disposition to survive and reproduce in a particular environment and population. Another question refers to the intensity of how this fitness is manifested, and therefore to the particular level of fitness each organism has and that is established in mathematical terms by considering its expected survival and reproduction (Triviño and Nuño de la Rosa 2016).

differ from their causes. In the case of fitness, this difference is due to it introducing a new causal power into the world, i.e., making organisms able to survive and reproduce in a particular environment and population (Triviño and Nuño de la Rosa 2016: 5).

However, although asserting that fitness introduces a new causal power into the world is a way of making sense of its emergent character, additional arguments are needed to justify the claim that fitness constitutes an autonomous causal property due to the novelty of its causal power. I will address this question in the following section (Sect. "Downward causation concerning new causal powers"). Here I will focus on seeing whether fitness is, in fact, wholly distinct from the base that gives rise to it, since it is not clear that the difference between causes and effects holds in this case.

The simultaneous character of fitness and its base serves to illustrate this idea. In the dispositional theory of causation, the simultaneity between causes and effects is one of the key features of causation (Mumford and Anjum 2011: §5). Yet, despite this simultaneity, effects are said to differ from their causes since they can engage in causal processes in which the causes that gave rise to them are not able to participate.

In CDAF, the simultaneity between fitness and its base is a key feature of fitness as a causal disposition. Yet, this simultaneity can be accounted for in terms of a synchronic dependence between fitness and its base, and not in terms of causation as given in Mumford and Anjum's account. This is so since, considered as the effect of a causal process, fitness should be seen as something simultaneous to its causes, i.e., to the functional dispositions that characterize an organism, but different from them. However, in CDAF, fitness is not completely different from its causes. A fit organism is an organism whose heart pumps blood, its nose smells a predator, its lungs produce gas exchange… It is not clear how fitness (as a capacity of organisms to survive and reproduce in a particular environment and population) could be something completely different and novel from the non-linearly combined functional dispositions that give rise to it. This illustrates that causation is not the correct way of capturing this dependence relation.[10]

To claim that fitness is not the result of a causal process does not mean that it cannot be characterized as a causal disposition. As it is shown in CDAF, the characterization of fitness by using the conceptual resources provided in the causal dispositional account, such as threshold, simultaneity, or non-necessitarianism, among others, serves to address and clarify some of the problems that have arisen in the philosophy of biology concerning fitness, while shedding light to its ontological character. Instead, what this analysis illustrates is that a different form of explanation for the dependence relation between fitness and its base needs to be considered.

[10] As a reviewer has pointed out, this consideration regarding fitness not to be *wholly* distinct from its base is important not only for arguing that the relationship between them is not a causal one but also to see that the causal power of fitness cannot be a novel one (unlike Triviño and Nuño de la Rosa consider). I will dwell more on this idea in Sect. "Downward causation concerning new causal powers".

Non-reductive realization

Realization is another form of dependence that can hold between higher and lower-level properties of a system. The core idea of realization is that the function of the higher-level property is performed by the lower-level token properties of the system in which it is instantiated. Some authors have appealed to functional realization to argue against ontological emergent properties (see Kim 1993, 1999, 2006). According to Kim, for instance, functional realization implies functional reduction insofar as it is possible to find, at least in principle, in each particular case, the lower-level realizers that perform the function of a higher-level property (but see Needham 2009). In this sense, functional realization is not compatible with emergentism. Since the higher-level property inherits *all* the causal powers of its lower-level realizers, it is nothing over and above them (Kim 1999: 15). For Kim, therefore, higher-level properties do not have any causal power on their own since the lower-level properties of the parts of the system realize the causal power.

Wilson, notwithstanding, offers an alternative way of conceiving functional realization that is compatible with emergentism (Wilson 2016, 2021). In those cases in which a higher-level property is realized by the lower-level properties of a system without being reducible to them, there is an ontological emergent property. In these cases, the higher-level property of a system *does not inherit all* of the causal powers of its realizers, but a proper subset of them; what Wilson calls the "proper subset of powers condition" (Wilson 2016: 357; 2021: 59). Since the realizing base has more powers than the higher-level realized property, the latter cannot be reduced to the former. In this case, it can be claimed that the higher-level property has a *causal profile* that differs from that of its base, which means that it is both causally and ontologically autonomous.

Is non-reductive realization the kind of dependence that is given in the case of fitness? In other words, does fitness have a *different causal power profile* with respect to its base, i.e., the non-linearly combined functional dispositions that characterize an organism? One initial way of addressing this question is by considering fitness not as a *token* of individual organisms but as a *type*. Characterized in this way, it is possible to see that fitness is a property that can be instantiated in *different types of realizing bases* corresponding to the different non-linear combinations of the different functional dispositions given in different biological species. This variety of realizing bases might differ among them due to the different causal powers they might have. Birds, for instance, have functional dispositions that allow them to fly, whereas fishes have others that allow them to swim, and octopuses have other functional dispositions that allow them to camouflage. Yet, they all can instantiate fitness. Recall that in CDAF all (living) organisms are fit organisms.

The possibility for fitness to be multiple-realized is an indication that it is a non-reductively realized property. In this case, although the different types of realizing bases are similar in the sense that they can instantiate fitness, they differ among them regarding the causal powers they have. In particular, they can have more and different causal powers than those associated with fitness. Fitness, therefore, cannot be reduced to any of the realizing bases that give rise to it, which might indicate that

it only possesses a proper subset of the causal powers given in them, and therefore, a different causal power profile (see Wilson 2016: 369).

The multiple-realizability of fitness can serve as an indication it is an emergent property. In particular, a weak one. Yet, to properly conclude this, something else needs to be said concerning the causal autonomy of fitness.

The causal autonomy of fitness

In this section, I will explore the causal autonomy of fitness in terms of downward causation due to its consideration as a hallmark of emergentism (Kim 2006: 198). There are two different ways in which downward causation can be characterized: i) as involving *new causal powers* that are downwardly exerted by the emergent property of the system; or ii) as the emergent property incorporating *lower-level constraints* to the base it depends on. The first case of downward causation will conform to strong emergence, whereas the second to cases of weak emergence (Wilson 2016). In the following, I will explore both forms of downward causation concerning fitness. In doing so, I will assume Wilson's characterization of causal powers (see Sect. "The metaphysical framework: weak and strong ontological emergence"), such that to claim that fitness has causal power means that it allows its bearer, i.e., the organism, to cause some effects.

Downward causation concerning new causal powers

In CDAF, fitness is an emergent property insofar as it introduces a new causal power into the world. It is in virtue of organisms having fitness that they can behave in a way that is oriented to guarantee their survival and reproduction in a particular environment and population. Insofar as fitness is the effect of a causal process, it differs from the functional dispositions that characterize an organism and introduces a causal power that is new since "it cannot be exercised by any of the properties of the organism" (Triviño and Nuño de la Rosa 2016: 9).

As previously considered (Sect. "Causation"), causation does not seem to be the kind of relation given between fitness and its base. Effects are different from their causes, and it is not clear that this holds in the case of fitness. Besides this consideration, it is not clear either, that fitness introduces a new causal power into the world. In other words, that it meets *the new power condition* according to which "token feature S has, on a given occasion, at least one token power not identical with any token power of the token feature P upon which S contemporary materially depends, on that occasion" (Wilson 2021: 51).

In CDAF, the novelty of the causal power of fitness is argued for on the grounds that any of the functional dispositions that characterize an organism have the property of making it able to survive and reproduce. In some sense, this is true: the heart has the disposition to pump blood, the lungs have the disposition to perform gas exchange… However, the different functional dispositions of the organism taken in isolation are not the base of fitness. It is the non-linear combination of these

functional dispositions that constitute the base of fitness. And it is not completely clear that this base does not possess, in some sense, the causal power that is attributed to fitness. Recall that, due to the simultaneity between fitness and its base, talking about fit organisms means talking about organisms whose functional dispositions are operating. Thus, the effect of fitness, i.e., making the organism able to survive and reproduce in a particular environment and population, is not completely independent of the functional dispositions of organisms.

Another argument that might serve to illustrate this point rests on the idea that if fitness would introduce a new causal power into the world, then it would be difficult for us to establish the connection between the survival and reproduction of the organism and the functional dispositions that characterize it. This is so since effects differ from their causes, and thus, they can participate in new causal processes where the original causes that gave rise to them do not play any role (see Sect. "Causation"). The dissolution of salt in water can serve to illustrate this idea. Saltwater may have the causal power to heal a wound, for instance; however, in this process, neither the salt lump nor freshwater plays any role. The salt lump and the water are the causes that lead to the dissolution of salt into water and, therefore, to the effect of saltwater. However, when saltwater participates in the causal process of healing, neither the salt lump nor freshwater is present. This is not the case with fitness. Considering that fitness introduces a new causal power, means to claim that it would initiate *a new causal process* that consists of making the organism able to survive and reproduce in a particular environment and population. Yet, unlike the case of saltwater, in the causal process of fitness, the functional dispositions that characterize an organism continue playing some role, which means that the capacity of the organism to survive and reproduce is not independent of these functional dispositions, and thus, that fitness cannot be properly considered as introducing a new causal power into the world. Fitness, therefore, is not emergent in the strong sense.

Downward causation concerning lower-level constraints

In exploring the dependence relations between fitness and its base, it seems that non-reductive realization might be the accurate one due to the multiple-realizable character of fitness. Fitness, as a type, can be realized on different bases that widely differ among them (e.g., birds and octopuses), but that have something in common insofar as they all instantiate fitness. This suggestion allows us to claim that fitness has a proper subset of the causal powers that are present in the bases in which it can be given.

Since this consideration applies to the case of fitness as a type, it can also be said to hold in the case of individual, i.e., *token* fitness. As Wilson claims: “In cases of multiple-realizability, however, a functionally realized feature arguably has only a proper subset of the powers of its realizing feature(s), *at both the type and token levels*” (Wilson 2021: 59. Emphasis added). In this sense, the causal power attributed to fitness seems to be synchronically determined by the powers of the different functional dispositions that characterize an organism and that are non-linearly combined. This base, notwithstanding, has more powers than those attributed to fitness

itself. This is so since more effects can be produced by the functional dispositions of the organism besides those corresponding to its survival and reproduction. Fitness, therefore, can be said to have a different causal power profile with respect to its base.

To claim that fitness has a proper causal power profile is what allows us to consider that it is in virtue of it that an organism can behave in ways that are oriented to guarantee its survival and reproduction. That is, the property has causal power insofar as it allows its bearer to behave in a particular form. This causal power, furthermore, seems to be downwardly exerted: to guarantee its survival and reproduction the organism can affect the functional dispositions that characterize it. This idea is captured in CDAF when considering that an organism that runs when smells a predator is a *fit organism*. In some way, therefore, it is in virtue of its fitness that the organism is able to condition, constrain, or affect, the form its functional dispositions behave to guarantee its survival and reproduction. Different biological examples concerning the survival and reproduction of different organisms can serve to illustrate this idea.

Downward causation concerning survival

Regarding the survival dimension of fitness, the way an organism responds to cases of malfunctions can be interpreted as an instantiation of fitness' downward causation. Organisms are said to be the ones responsible for maintaining their existence conditions by creating, constraining, and maintaining, the parts that compose them (Mossio et al. 2009; Moreno and Mossio 2015). In some cases, the components of the organism might be affected such that they do not perform the function they are supposed to do and that might contribute to the existence of the organism itself. In these cases, the organism can produce new constraints over other parts and functions such that the malfunction can be compensated for and survival guaranteed.

The changes involved in phenotypic plasticity, i.e., the capacity of organisms to develop several phenotypic outcomes depending on environmental factors, are a good illustration of this idea. In this regard, consider the case of a goat that was born with a congenital defect that impeded her from walking on its four legs (West-Eberhard 2005). The goat learned to walk on its hind legs, giving rise to a reorganization of the muscles and bones of the limbs, "including a thickened and elongated gluteal tongue and an innovative arrangement of small tendons, a modified shape of the thoracic skeleton, and extensive modifications of the pelvis" (West-Eberhard 2005: 6545). In other words, the goat was able to modify the form and function of its hind limbs such that they played the same role as if she had four limbs.

Cases such as this one can be explained in terms of fitness: it is precisely due to its fitness that the organism can downwardly affect the parts that compose it. The organism's tendency to survive and reproduce, and to do so in better conditions (i.e., to be fitter), makes it able, as a whole, to *constrain* the form and function of its lower-level parts such that it can continue existing. And this constraint exerted by the organism seems to be better explained in terms of downward causation. Thus, it is due to the organism's fitness that it can downwardly affect its lower-level parts to guarantee its survival and reproduction (Witherington 2011: 75).

As previously stated, the causal efficacy of entities lies in their having efficacious properties. In this sense, if the organism were not 'fit' (i.e., if it did not possess the property of fitness), then it would not have the capacity to survive, and no change or constraint on its lower-level parts would be made to guarantee its survival. In this kind of case, it seems plausible to claim that fitness allows the organism to achieve its survival by allowing it to affect the parts that compose it. The causal power of fitness regarding survival, therefore, is manifested in a downward manner by creating, constraining, and maintaining, the functional dispositions that characterize it.

Downward causation concerning reproduction

To illustrate the downward causal power of fitness concerning reproduction, two biological strategies performed in different species are considered: delayed reproduction and tactical deception. Some female organisms have a reproductive strategy called *reproductive delay* that allows them to arrest reproduction until suitable environmental conditions are met (Orr and Zuk 2014). Reproductive delay is common in insects but also in mammals such as bats *(Chiroptera)*, or armadillos *(Dasypodidae)*. It can be manifested in three different ways: *i) delayed fertilization* -females arrest fertilization by delaying the ovulation period or storing the sperm of different males; *ii) delayed implantation* -the blastocyst is not implanted in the uterus but remains unattached in the female reproductive tract; and *iii) delayed development* -the development of the embryo is arrested.

These kinds of reproductive delay are mainly manifest in cases of environmental uncertainty (Koons et al. 2008), where the environmental conditions are not suitable for the organism to leave offspring due to climate conditions, predators, or lack of food resources. Sometimes, reproduction could be arrested for an entire season, or even a year, e.g., the Lander's horseshoe bat *(Rhinolophus landeri)*. In cases of environmental uncertainty, the female delays reproduction until there are more resources, better climate conditions, or fewer predators. Furthermore, the female can also delay reproduction due to populational factors. In this regard, some females can arrest fertilization by storing the sperm of different males until there are no available males in a population. Or, in cases where there has been no opportunity for pre-copulatory mate selection, and the female stores the different sperms to lately choose among them. This is called "cryptic female choice" (Orr and Zuk 2014) and occurs in different species such as fruit flies *(Drosophila melanogaster)* and field crickets *(Gryllus campestris)*.

Reproductive delay, therefore, is a strategy that allows the organism to have more offspring than in those cases where reproduction is not arrested (Koons et al. 2008). Some authors have interpreted this phenomenon as being a mere physiological response of organisms to some environmental conditions such as low temperatures (Hamlett 1935). Yet, this interpretation has been discarded on the basis that many taxa that have reproductive delays live in tropical or warm habitats, e.g., the Jamaican fruit bat *(Artibeus jamaicensis)*, or the long-tongued nectar bat *(Macroglossus minimus)* (Orr and Zuk 2014). As I see it, one way of explaining cases like this is by appealing to fitness. It is precisely due to their fitness that some organisms can

arrest reproduction until the right circumstances are given. If organisms were not fit in this sense, they would reproduce *reactively*. That is, they would reproduce in any circumstance and with negative consequences for their offspring, such as being damaged or even killed. This is not the case, however. Organisms do not merely *react* to the conditions they are embedded in, but they *interact* with their environment and population as ecological agents (Walsh 2023: 256).[11] Thus, it makes sense to claim that it is due to the organism having fitness that it can guarantee its own reproduction by downwardly affecting the mechanism that can arrest reproduction. Fitness, in this sense, is manifesting its causal power in a downward manner, i.e., by activating the mechanisms that allow arresting reproduction.

Tactical deception is another example that can help to illustrate the way fitness downwardly exerts its causal power. In some species of cuttlefishes, such as *Sepia plangon*, males employ different strategies to guarantee their reproduction, such as displaying mate guarding, displacing rivals, or interrupting courtship attempts. Recently, it has been shown that males also use a tactical deception strategy for mating with a female (Brown et al. 2012). Some males mimic a female display towards their rival males on one side of their body while simultaneously displaying typical male courtship patterns towards potential mates on the other side. Thus, the courting male can perform courtship without being interrupted (Brown et al. 2012: 729). This tactical deception is usually performed in those environments where there is only one more male competitor and a female. In other cases, such as those where there are two male competitors and one female, it is more difficult for the courting male to properly orient itself between the female and the other two male competitors.

In explaining tactical deception, one might resort to some kind of signal in the environment (e.g., the fact that there is only one male competitor and one female) that activates this mechanism for a deceptive signal such that courtship in cuttlefishes is possible. However, this interpretation does not seem to be correct. Tactical deception might be costly for the courting male since signals among organisms of the same species are said to be inherently honest (Guilford and Dawkins 1991). Thus, not all courting male cuttlefishes use this strategy to mate with a female despite the circumstances being the accurate ones (Brown et al. 2012: 729).

If it were the environmental factors that activated the lower-level mechanism for deceptive dual display, then the mechanism would be activated in all situations in which the environment was the accurate one. Yet, this is not the case. Just like in delayed reproduction, the disposition to reproduce is not merely triggered by

[11] In philosophy of biology, organisms are conceptualized as having *natural agency*, insofar as they can *interact* with their environment and population (Moreno and Barandiaran 2004). Interaction differs from reaction. The functional dispositions that characterize an organism might *react* to different external or internal stimuli by producing a particular response. The skin, for instance, reacts to sun exposure. Organisms, notwithstanding, are not considered to merely react to the different stimuli they might face, but they interact with their environment and population insofar as they perform certain activities or behave in certain ways that are oriented to ensure their survival (Moreno and Barandiaran 2004: 18), and reproduction. In this sense, the skin reaction to sun exposure does not take place for the sake of survival or the reproduction of the organism. Rather, it is the organism, as a whole, that avoids or looks for sun exposure depending on whether it needs it for its survival or reproduction.

external factors, but internally and contextually regulated. Another objection to this idea might be that this kind of deceptive mechanism is only activated in some courting males but not in others, insofar as not all of them possess this mechanism. Yet, this does not seem to be the way this phenomenon should be interpreted either. The reason is that some males that have already performed deceptive dual displays to mate in previous circumstances might not perform it in other situations in which the environmental conditions also hold. It has been shown that the more the courting male uses this strategy, the more possibilities it has to be discovered by other males, and this might be highly costly for him (Guilford and Dawkins 1991; Brown et al. 2012).

In some sense, therefore, it can be claimed that the fit organism is the one that interacts with its environment and population as an ecological agent and that it either activates or not this deceptive mechanism when the appropriate circumstances are given to reproduce. As in the previous case concerning reproductive delay, it seems that cases of tactical deception such as this one can be explained in terms of fitness. That is, it is due to its fitness that the organism can behave in a way that is oriented to guarantee its reproduction. In particular, the organism can downwardly affect the mechanisms that allow for deception and activate it when necessary.

The previous examples concerning the survival and reproduction of organisms serve to account for the causal autonomy of fitness. In this sense, fitness can be characterized as an ontological emergent property. However, it is not emergent in a strong sense but in a weak one. Fitness, therefore, does not introduce a new causal power into the world. Yet, its emergent character is still maintained insofar as fitness possesses a causal power profile that differs from that of its base, and that allows its bearer (i.e., the organism) to downwardly affect its functional dispositions to guarantee its survival and reproduction.

Conclusions

In this paper, I have focused on clarifying the ontological status of fitness conceived as a causal dispositional property of organisms (Triviño and Nuño de la Rosa 2016). In doing so, I have examined whether fitness satisfies the criteria of dependence and autonomy characteristic of emergent properties and, if so, to what degree: weak or strong (Wilson 2016, 2021). In this regard, contrary to what CDAF considers, fitness is not a strong emergent property as it does not introduce a new causal power into the world. Nevertheless, its emergent character can be maintained insofar as it meets the schema proper for weak emergent properties. Regarding dependence, due to its multiple-realizable nature, fitness appears to be non-reductively realized by the underlying factors on which it depends (i.e., the non-linear combination of functional dispositions characterizing an organism). Concerning autonomy, the causal power of fitness seems autonomous insofar as it possesses a causal power profile that differs from that of its base.

The characterization of fitness as a weak emergent property allows us to make more sense of some of the ideas given in the CDAF. In particular, the simultaneous character between the functional dispositions that characterize an organism and the

effects of fitness regarding its survival and reproduction can be better conceived. Furthermore, insofar as it is characterized as an emergent property, fitness can continue playing both a causal and an explanatory role: the survival and reproduction of organisms in a particular environment and population can be explained in terms of the organism having a property, i.e., fitness, that allows them to do so.

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Conflict of interest The author declares that she has no conflict of interest.

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