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DEMYSTIFYING DOWNWARD CAUSATION IN BIOLOGY

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Abstract

The concept of downward causation is frequently used in an explanatory capacity in biology to account for certain regularities and processes. Some philosophers, however, argue that downward causation is metaphysically incoherent, providing three main objections. Underlying these objections is the assumption that entities are connected by compositional hierarchies of levels of organization. In this paper, I introduce the notions of weak and strong compositional relations using examples from evolutionary developmental biology. I argue that downward causation becomes unproblematic if we use features of interventionist theories of causation to explain the causal relations between levels. I show that an interventionist account of downward causation successfully responds to the three central objections to downward causation in the philosophical literature and I clarify the explanatory usefulness of the concept in biology. As such, this paper provides an epistemic solution to demystify downward causation in the context of scientific practice. The solution proposed is compatible with how biologists seem to use a concept of downward causation fruitfully in their work.

1. Introduction

Downward causation (DC) comprises a cluster of ideas that describe how upper levels of a system can have a causal influence on the behavior of the system's lower levels. DC is a contentious issue in philosophy, with several philosophers claiming that it is metaphysically incoherent (Kim 1992; Hulswit 2005; Craver and Bechtel 2007). Despite this skepticism, the concept of DC is frequently used in the special sciences that deal with complex systems comprising different levels, where it is deployed in an explanatory capacity to account for certain regularities and processes. DC is particularly relevant in the life sciences because biological entities are complex systems composed of different levels of organization. In these systems, some changes in lower-level conditions seem to be triggered by changes in upper-level conditions. In such cases, causation is said to be downward and causes are described as 'top-down' (a few examples include (Campbell 1974; Uller and Laland 2019; Sultan 2019; Laland et al. 2013; Noble 2012). Biologists use DC rather loosely without necessarily committing to a formal definition. Specific examples described as DC include a wide range of phenomena such as feedback loops and the impact of environmental effects on evolution (Brooks, DiFrisco, and Wimsatt 2021). The ubiquity of DC in some fields of investigation in biology seems to be in tension with philosophical arguments that suggest the concept is incoherent.

In this paper, I propose a solution to the tension between DC's alleged incoherence and its widespread use across various disciplines in the life sciences. While many solutions to DC tend to rely on a deflationary account of levels and composition between upper and lower levels, I argue that compositionality does not pose a significant problem to the coherence of DC. Therefore, by tracing a distinction between *weak* and *strong* compositional relations, I show that under an interventionist view of causality, biologists' claims about DC make sense, that is, their claims can be coherently interpreted in a manner that avoids familiar objections and fits how they test their claims empirically. Additionally, I show that the objections typically raised against DC's coherence can warrant an empirical solution to reevaluate DC in its use in scientific practice. While this approach does not aim to settle metaphysical arguments about causality, it provides a working concept of causality that affords a charitable understanding of biological practice. By looking at specific phenomena that biologists label as DC, I argue that it is possible to 'demystify' DC by looking at the challenge from an epistemic perspective. To do so, I engage work in evolutionary developmental biology (evo-devo), a field that widely relies on the notion of 'top-down' causes by investigating how environmental effects can shape development and evolution (Kaiser 2021; Arthur 2002; Hall 1999).

This paper is structured as follows. In Section 2, I begin by providing an overview of how levels and compositionality are intertwined in discussions of DC in biology. I also describe three common objections raised against DC. In Section 3, I explore how scientists seem to be using DC in explanatory capacity by introducing a distinction between *weak* and *strong* compositionality. In Section 4, I respond to objections against DC in both cases. In Section 5, I discuss the results of this investigation and provide concluding remarks in Section 6.

2. Downward causation, levels, and evolutionary developmental biology

2.1. The fruitfulness of DC in evo-devo:

Within biological research, the concept of causation is essential to a variety of activities, including explanation, theory construction, and the analysis of the dynamics of biological systems. The concept of DC is meant to capture the general claim that upper levels of a system can cause changes in its lower levels. DC can be characterized as a causal relation between *x* and *y* whereby *x* causes *y*, *x* is at an 'upper' level of organization, and *y* is at a 'lower' level. DC can also be conceptualized in terms of boundary conditions or sets of constraints imposed by higher levels on the dynamics occurring at lower levels of a system (Noble et al. 2019). Some prominent examples of putative DC that have been offered by biologists and philosophers of biology include changes in the pigmentation of butterfly wings owing to seasonal changes (Suzuki and Nijhout 2006); models of the sinus node to explain cardiac rhythm (Noble 2012); feedback loops, feedback inhibition, and cellular signaling pathways (Boi 2017) the behavior of ants in colonies (Gregg 1942); top-down developmental control (Coffman 2006) and natural selection as a higher-level life or death switch (Campbell 1974).

DC is especially relevant when describing how upper and lower levels interact in a biological context: a crucial kind of causal relationship in evolutionary developmental biology (henceforth evo-devo), the field interested in investigating how developmental processes shape evolutionary trajectories (Arthur 2002; Hall

1999). One of the distinctive aspects of evo-devo is its reliance on causal-mechanistic explanations to make sense of how development and evolution are intertwined (Kaiser 2021; Baedke 2020; Mc Manus 2012). Since the causal pathways between evolutionary and developmental processes fit the 'top-down' descriptions, DC seems especially pertinent for explanations in evo-devo. Indeed, several biologists have suggested that evo-devo calls for 'top-down' understanding of causes in addition to more traditional 'bottom-up' or gene centric perspective (Uller and Laland 2019). Investigating DC from the perspective of scientific practice is key to make sense of how biologists use this notion in explanations with no apparent metaphysical incoherence. Therefore, defending the usefulness of DC in the specific case of evo-devo can be fruitful to clarify the kinds of causal explanations relevant to the field.

2.2. DC and 'levels'

The notion of 'levels of organization' is widespread in biology. The 'levels' concept is enmeshed with DC since DC is a causal relation running from upper to lower levels. The problem, however, is that its usefulness as well as the metaphysics of levels remain a topic of disagreement. For example, some argue that levels are a problematic way of dividing the world (Potochnik and McGill 2012; Potochnik 2021). Levels have also been characterized as a "metaphor" as there is no literal sense in which one level can be "up" or "down" with respect to another. Such a metaphor may create biases whereby there is a reductionist tendency to represent lower levels as being somehow more concrete (Noble 2012). Levels are also described as having heuristic value and are a useful tool to describe the biological world (Brooks and Eronen 2018; Brooks 2021; 2017). With respect to DC, a common view in the philosophy of biology is to provide a deflationary account of levels in order to make DC coherent (Eronen 2015; Voosholz 2021; Dupré 2021; DiFrisco 2017). For example, Eronen (2015) shows that the notion of levels is not required for analyzing DC and that the coherence of DC becomes apparent when we let go of the notion of levels. Voosholz (2021) argues that it is possible to make sense of DC without relying on the level-picture of nature. DiFrisco (2017) similarly looks for an alternative to the levels concept by proposing the use of time scales and process rates.

Lastly, Dupré (2021) argues that it is fruitful to move from a mechanistic understanding of DC that is tied to levels to exploring the notion as an explanatory feature of how parts and wholes are related.

The present account differs from deflationary accounts of levels of composition by showing that DC can be coherent in compositional systems. Instead, I take levels to be useful when they are seen as 'levels of description'. Here, I do not rely on a strong metaphysical conception of levels that are supposedly ascribed to specific parts of an entity. Instead, by committing to 'levels of description' I wish to capture how practicing biologists seem to be referring to upper and lower levels in empirical settings. I will develop this idea in Section 3 by tracing a distinction between *weak* and *strong* composition which captures different phenomena that biologists label as cases of DC.

2.3. Common objections against DC:

DC has already been scrutinized in many domains in the philosophy of science (for a few examples see Woodward 2021b; 2021a; Ellis 2016; Bitbol 2012; Voosholz 2021; Green and Batterman 2021; Malaterre 2011). To recapitulate the intricacies of the problem lay outside the scope of this paper. Here, I propose instead a summary of objections raised against DC with the goal of showing a common ground for such objections: the fact that they rely on the notion of compositionality. Consequently, typical defenses of DC tend to let go of compositionality to make sense of DC. I outline this background to lay the groundwork for the argument I wish to advance: that compositionality does not pose a major problem to the coherence of DC, if a distinction is made between *weak* and *strong* compositionality (Section 3). While interventionist solutions have already been put forth as solving the problems of DC, they take 'compositionality' in a general manner without tending to the different cases in which biologists seem to be referring to DC. Here, distinguishing between weak and strong compositionality provides a clearer account of how DC is used in explanatory capacity in biology. It highlights how DC can be useful for an area not yet thoroughly covered in the DC literature: evo-devo.

A first objection raised against DC is vicious circularity (i). In the context of mental causation, Kim (1992) argues that one reason why DC is an incoherent notion is that higher levels arise out of lower levels, which, he argues, means that there cannot be any 'top-down' causal efficacy. In sum, without the presence of lower-level conditions, higher-level properties would not arise in the first place. If the presence of higher-level conditions is entirely due to the presence of lower-level conditions, DC cannot be coherent as it is viciously circular (Bedau 2008).

A second (related) objection to DC is causal exclusion (ii), an argument that has received extensive treatment in the DC literature (for examples see Baumgartner 2009; Woodward 2015)[1]. The causal exclusion argument is an objection to DC on the following grounds: if such a thing as DC exists, micro-level causes might explain an event just as well as macro-level causes (Kim 2007). A central premise of the exclusion argument is that all physical events are caused by sufficient lower-level physical causes. In other words, no physical event would arise unless it had a sufficient physical cause attributable to the causal closure of the physical. Consequently, there is usually a more relevant micro-level causes that determines a micro-level effect; including a macro-level cause would lead to the overdetermination of the micro-level effect. In this context, Baumgartner (2009) sees causal exclusion as a challenge to DC on the grounds that micro effects have *sufficient* micro causes, a more plausible scenario. Still under this view, a supervening macro property having a causal downward effect on its supervenience basis would be a highly unlikely case of overdetermination. Specifically, this scenario would be unlikely as overdetermination would be systematic and ubiquitous, and it is therefore more plausible to retain micro or lower-level causes. Once again, the notion of 'levels' is assumed in this objection: causes can be ascribed to distinct levels of reality that vary according to their degree of complexity.

[1] Note that Baumgartner and Woodward discuss a specific form of the argument, namely, the interventionist exclusion argument.

A third objection against DC is the lack of distinctness (iii) between upper and lower levels. For example, Craver and Bechtel (2007) argue that DC is problematic because upper and lower levels are not sufficiently distinct. The relationship between the latter and the former is therefore compositional, rather than causal. As a solution, Craver and Bechtel contend that apparent inter-level causes (both top-down and bottom-up) are, in fact, mechanistically mediated effects.

2.4. Downward causation and the assumption of compositionality

As laid out above, the three objections rely on the notion of upper and lower levels, each respectively ascribed to an entity. It follows, then, that interlevel causation cannot be coherent on the grounds that either (i) it entails a viciously circular relation whereby upper-level properties cannot be causally efficacious since they necessarily arise of their own lower-levels; (ii) micro-level causes are more relevant candidates to determine micro-level effects; or (iii) upper and lower levels are not sufficiently distinct from each other to establish causal efficacy running from upper to lower levels.

An underlying assumption to the objections discussed is that upper and lower levels are arranged in a compositional way. This is especially evident in (iii) and in Craver and Bechtel's (2007) account of top-down causes, but also underlies (i) and (ii). As a result, many attempts to make DC coherent try to let go of compositionality in order to make sense of DC. This solution is, in my view, not entirely satisfactory and a more fruitful approach would be to rescue DC without having to let go of compositionality. This is because, as I argue here, compositionality is not what makes DC mysterious or incoherent if a key distinction is made between cases of weak and strong compositionality. My aim is to provide a new direction for the debate surrounding DC in ways that clarify and demystify its use in scientific contexts. I do so by (i) drawing from scientific practice to flesh out the distinction between weak and strong composition and (ii) applying an interventionist account to the relevant cases in order to make sense of DC in the most problematic cases (i.e., cases of strong compositionality).

3. Weak and strong compositionality in biology

In the life sciences, DC is used to explain a variety of phenomena. The most prominent vindication of DC can be seen in the theory of biological relativity proposed by Noble (Noble 2012; Noble et al. 2019; Noble and Ellis 2022). Under this view, there is no *a priori* privileged level of causation running from lower to upper levels of a system. Upper levels act as constraints and provide boundary conditions under which processes at lower levels operate[2].

The notion of DC captures phenomena in at least two different types of systems. In both cases, it is said that the system's upper levels have a causal influence on the lower levels. An important difference between the systems, I suggest, is how strongly upper and lower levels are connected; while sometimes compositionality is instantiated in the system only weakly, in other cases, systems exhibit a stronger part-whole relationship.

This distinction is key, because compositionality in the broad sense underlies objections raised against DC in the literature. Most available solutions tend to rely on the following logic: compositionality hinders the coherence of DC, therefore, letting go of compositionality is the step needed to make sense of DC. For example, Malaterre (2011) argues that while it is possible to make sense of DC, it does not purport claims of causal efficacy running from upper to lower levels. As such, exclusion arguments would still hinder the pertinence and coherence of DC under this account. What current solutions do not address is whether there are different kinds of compositional relations when phenomena are described as cases of DC in scientific practice. For example, interventionist solutions to DC (such as in Woodward 2021a; 2021b) do not tackle the distinction between different degrees of compositionality. Additionally, the general interventionist

[2] For example, Noble and Hunter (2020) expound the weaknesses of genome sequencing in healthcare for disease associations in cases of non-genetic diseases. According to these authors, this is partly due to a neglect of top-down causal influences running from physiology, through epigenomics and genomics. Such claims are supported by recent findings showing that Polygenic Risk Scores perform poorly in individual risk prediction and population risk stratification (Hingorani et al. 2023).

solution has not yet been put to test in the context of evo-devo, a discipline where DC seems to be particularly fruitful in explanations. Here, I address this gap and take an alternative approach by showing how compositionality, when understood in terms of the weak/strong distinction, does not hinder our understanding of DC. As such, distinguishing between weak and strong compositionality demystifies downward causation as used in explanatory capacity in the life sciences. The present approach therefore tackles causation as a relation between relevant level properties instead of a relation between entities[3]. To do this, I shall abstract a concept of DC from concrete cases of biological explanation and examine the role of compositionality. In the two instances I analyze (parallel evolution of ant castes through environmental changes and soldier-to-worker ratios in ant colonies), compositionality does not hinder the coherence of DC[4].

3.1. Case 1: Weak compositionality

Feedback loops, regulatory systems and environmental effects on evolution are often labelled as cases of 'DC' in biology (Boi 2017; Brooks, DiFrisco, and Wimsatt 2021; Green and Batterman 2021). This can be seen both in the literature but also in the common language description of biological processes. For philosophers, this may seem puzzling. After all, this class of examples does not quite fit the requirements of DC whereby upper levels are *composed* of lower levels. In a strict philosophical sense, such cases point towards spatial externality and spatial containment, rather than 'top-down' causation running from upper to lower levels. This is likely due to different degrees of metaphysical commitments when the term 'DC' is used in philosophy and in biology. While this is perhaps a terminological mismatch, identifying why such

[3] Batterman (2001) rightly points out that emergence can occur in situations without part/whole relations and the account here presented is in line with Batterman's treatment of the nature of compositionality. The goal here is to propose a specific causal analysis of what is usually considered DC, showing that part/whole or compositional assumptions do not hinder the coherence of DC.
[4] Recent work by Ross (2023) explores the notion of causal constraint which is compatible with the current distinction between weak and strong compositionality.

cases are labelled as DC in biology is a first step in demystifying the notion and sheds light onto the pragmatic use of the concept.

For the purposes of this paper, I will focus on an example of importance in evo-devo: how environmental cues are said to act 'downwardly' in ways that modify evolutionary trajectories (Coffman 2006). Such examples are relevant to evo-devo since evolutionary causes are not solely bottom-up factors like genetics, but also understood from a top-down perspective. This example fits what I call here *weak* compositionality. Simply put, *weak* compositionality could refer to cases where a 'top-down' cause fits a description of spatial externality. *Weak* compositionality refers to those cases where the causal relations are between levels related by spatial containment, for example, a cell and the extracellular environment, an organism and its surrounding environment, and so on. Interestingly, several cases of spatial externality are loosely described as cases of DC by biologists. In order to ground my argument, I will use *Pheidole* ants as a model organism since they are key in evo-devo and an interesting case of multi-level causation in colony organization.

Ants are highly complex social insects, and each ant colony is divided into different castes. The *Pheidole* genus of ants comprises around 1,100 species. Recently, it has been shown how a parallel ant caste evolved through environmental induction, which was most likely caused by changing nutrient availability (Metzl, Wheeler, and Abouheif 2018). In *Pheidole*, the queen and her workers in the colony are all female and diploid, whereas the male caste is separate and haploid. The worker caste can be further divided into two subcastes: minor workers that perform most tasks in the nest as well as foraging, and soldiers that defend the nest and process food (Rajakumar et al. 2012). In some species of *Pheidole,* for instance, in *P. rhea* and *P. obtuspinosa,* a third female worker caste called 'supersoldiers' has a disproportionately larger head than the soldiers. The evolutionary reason for the existence of supersoldiers in some *Pheidole* species is probably linked to a selective advantage the disproportionately large head confers in blocking the colony entrance, protecting it from ant raids (Rajakumar et al. 2012; Huang and Wheeler 2011). It is possible to observe supersoldier-like anomalies both in wild species and by environmental induction in the laboratory (for example, Rajakumar et al. 2012 demonstrate parallel evolution of 'supersoldiers' in *P. rhea* and *P. obtuspinosa*).

Environmental induction of supersoldier anomalies, whether in the wild or in the laboratory, is a fruitful study case and a clear example of what biologists label 'top-down' causation. *P. morrisi* (a *Pheidole* species) did not typically exhibit a supersoldier caste but it was possible to induce one environmentally in the laboratory. This novel phenotype was induced in a population of *P. morrisi* through hormone manipulation (such as, for example, changes in the quantities of juvenile hormone), in which the hormone mediates the external environmental cue (nutrition). Both nutrition and hormone manipulation are external factors that trigger the activation of cryptic developmental switches that guide the development of a worker into a supersoldier-like individual rather than ensure that it remains a soldier or minor worker. The ability to experimentally induce supersoldiers in a species that does not contain supersoldiers mimics a mechanism likely instantiated in nature at a much longer timescale.

Examples of environmental conditions that trigger the expression of ancestral phenotypes are commonly described as cases of DC in biology. In Section 5 a discussion of these examples through the lens of interventionism will show that in cases of weak compositionality the objections against DC seem to lose pertinence. Next, I will assess cases of strong compositionality which are the ones that seem to pose major problems to the coherence of DC.

3.2. Case 2: Strong compositionality

At the crux of the objections to DC is the notion of *strong* compositionality. Relations of *strong* compositionality occur when an entity cannot exist without its parts. For example, a colony cannot exist without ants, a population cannot exist without individuals. By definition, an ant colony is an aggregate of ants, a population an aggregate of individuals, and so on. Strong compositionality therefore occurs when an aggregate is constituted by its lowest parts.

The next step in demystifying DC as it is used in biology, then, is to assess whether there are such cases of strong compositionality whereby upper levels cause lower levels to behave differently. With this end in mind, I will ground my argument in a well-known property of ant colonies: caste ratio regulation. In an ant colony, a downward causal relation would be one in which the colony (upper level) is the cause of some change at the level of individuals (lower levels). I take this case to be (i) a case of strong compositionality and (ii) a genuine case of DC and described as such in the biological literature.

Specifically, in *Pheidole,* as discussed above, the worker castes can be divided into two sub-castes: minor workers and soldiers, each performing different roles in the colony by virtue of their morphologies (Gregg 1942). Soldiers are significantly larger than minor workers and have disproportionately larger heads (Lillico-Ouachour et al. 2018). The existing ratio of minor workers to soldiers is known to regulate the development of larvae into soldiers or minor worker castes in an ant colony. Several experiments show this phenomenon which is of interest to evo-devo biologists (Wheeler and Nijhout 1984; Lillico-Ouachour 2017; Gregg 1942; Passera 1974). Specifically, results show that a colony-level property (i.e., the ratio of soldiers to workers) plays a regulatory role in the development of larvae into minor workers or soldiers.

A range of hypotheses have been advanced as to why this may be the case. The main factors contributing to soldier regulation of castes were identified as: the activation of the soldier developmental program through nutrition and the availability of juvenile hormone; the inhibition of the soldier program through pheromones; and external influences such as competition and resource availability (Lillico-Ouachour 2017). While several contributing factors may explain this process, experiments suggest that an important factor is caste ratios, a colony-level property (Gregg 1942; Rajakumar et al. 2018; Wheeler and Nijhout 1984). This property is responsible for maintaining colony equilibrium and adjusting the ratio through the regulation of development. The consensus is that among several other factors, the ratio of existing soldiers to minor workers plays an important role in ant caste regulation, and it may cause other intermediary causes that lead to the inhibition of soldier production.

The regulation of ant castes in a colony fits our description of *strong* compositionality, whereby an upper level of the system, the colony level, is composed of lower levels, individual ants, in a *strong* sense. The ratio of soldiers to minor workers, an upper-level property, depends on individual ants' developmental switches at the larval stage, a lower-level property. Both properties are putative causes of the probability of the next larva developing into either a soldier or a minor worker, a lower-level effect. Thus, we have a situation where an upper level (the colony) is an aggregate of lower levels (individual ants). As a colony-level property influences individual ants' development, we may infer that this is an instance of DC. This means that this example is exposed to the objections raised in section 3, where the assumption of compositionality in the *strong* sense poses problems to the notion of DC. In the following section, I show how we can avoid the incoherence of DC by adopting an interventionist framework.

4. Interventionism in cases of *weak* and *strong* compositionality:

So far, I have argued that objections against DC rely on the assumption that upper and lower levels are organized in a compositional structure. To capture how biologists use this notion in their daily practices, I have introduced a distinction between weak and strong compositionality. This distinction, I argue, is compatible with how biologists refer to phenomena that they label as cases of DC. In this section, I will briefly overview interventionist accounts of causation (such as seen in Woodward 2004) (sub-section 4.1) and show that (i) in cases of weak compositionality, the objections against DC loose pertinence and these cases are unproblematic (sub-section 4.2); (ii) cases of strong compositionality pose a greater threat to the coherence of DC and an interventionist account adequately responds to the most worrisome objections against DC (sub-section 4.3).

4.1. Interventionism and DC:

Part of the conceptual incoherencies of DC stem from the fact that cause and effect are seen as entities or events. An alternative view is to think of cause and effect as properties that can be represented by variables that can take more than one value. For example, an upper-level property (such as worker-to-soldier ratio) is a determinable property that is determined by specific ratios (such as 95:5). Similarly, lower-level properties (such as the number of soldiers) are also determinable properties that are determined by various numbers (determinates). Variables represent determinable properties, and variable values represent those properties' determinates. Multiple combinations of determinate lower-level properties can realize the same determinate upper-level property. For instance, let us suppose that an upper-level ratio is 2:1. Such a ratio can be realized by multiple low-level determinate number pairs, such as <50:25>, <10:5>, and so on, as long as the ratio of 2:1 remains constant. In the case of DC, I argue that what does the causal explanatory work is the relationship between variables that represent relevant properties. Capturing causal relations through variables is a crucial feature of interventionist theories of causation. Variables represent the causally relevant property of an object or an event. As such, variables represent "properties or magnitudes that, as the name implies, are capable of taking more than one value" (Woodward 2004, p. 39). A relevant property here is the property that makes a difference in the occurrence of an event. To be clear, the goal of this paper is not to vindicate the interventionist concept of causality or to argue that interventionism offers the best metaphysics of causality. The more modest goal of using interventionism here is to claim that biologists' claims about DC can be coherently interpreted through an interventionist approach, in such ways as to avoid the familiar objections against DC.

Variables can be binary or assume multiple values. Therefore, when we say that « X causes Y », we are saying that a property of event E_1 can be represented by a variable X (binary or not) and leads to the occurrence of a property of event E_2 also representable by a variable Y (binary or not). When a change occurs at a variable X, a subsequent change will occur at variable Y, which is a necessary (though not sufficient) condition for causation. In this scenario, X and Y are not entities but variables that represent the relevant properties of a given entity or event. In DC, an additional feature is that X and Y are at different levels, X being at an upper level (U) and Y being an effect at a lower level (E).

Interventionist accounts share one basic principle: causal relations can be exploited for manipulation and control. For two variables, X and Y, to be related as cause and effect, a necessary and sufficient condition is that it must be possible to intervene on property X such that the intervention is followed by changes in the value of Y under a range of background conditions (Woodward 2004).

Proper interventions can be made to certain variables while holding other variables fixed. An intervention can be understood as any ideal experimental manipulation of the value of X performed to assess whether the Y value will subsequently change (Woodward 2004, p. 94). In the biological examples being considered here, interventions can be either human interventions or naturally occurring ones. For instance, a human intervention may be a manipulation in a laboratory setting (such as the actual manipulation of ratios within an ant colony). A naturally occurring intervention can also be considered a difference-maker with relevant causal properties[5], such as changes in environmental conditions that trigger the activation of a developmental switch.

I will briefly explain the interventionist solution to cases of weak compositionality before delving into the solution in cases of strong compositionality. The following notation will be applied to the examples discussed. U is a variable representing a property of an entity at an upper level; in the colony example, U represents the caste ratio. *u* is a variable value representing a specific determinate caste ratio. Similarly, L represents a property at the lower level (for instance, the numbers of soldiers and minor workers), and *l* represents the specific numbers (20 and 10, respectively, for instance). Values of U are multiply realizable

[5] Whether this counts as an intervention may depend on the details of how the environmental conditions affect the switch and the resulting effects of the switch. To count as an intervention, have to influence the effects via a route that affects only the switch. Empirically, some experiments have shown this possibility in the development of larvae into different castes depending on changing environmental conditions (Rajakumar et al. 2018).

(i.e., the same value of U may be realized by different values of L). In cases of DC, E is a lower-level effect that can take any value *e,* depending on the interventions being made to the system. One example of E is the probability that the next larva will develop into a soldier.

4.2. DC in cases of weak compositionality

When considering environmental effects on the evolution of novel ant castes, an environmental factor (such as hormone or nutrient availability) can be represented by a variable. When the value of that variable changes, the effect related to that variable also changes and is also representable by another variable (for instance, the switching of a developmental threshold). However, regardless of whether cause and effect are considered entities or properties, the objections simply do not apply in cases of weak compositionality. In both examples discussed, the levels are not strongly compositionally related, so the circularity, exclusion, and distinctness objections vanish because the levels do not stand in part-whole relations. As such, philosophers may raise the point that cases of weak compositionality do not configure the most apparent cases of DC, being only a case of spatial externality or spatial containment. While this may be the case, cases of weak compositionality are loosely described as "top-down" causation and therefore warrant clarification in the present context.

4.3. DC in cases of strong compositionality

In Section 3, I described cases of strong compositionality and suggested that it is in those cases that DC seems most vulnerable to the objections posed. Under an interventionist framework, however, strong compositionality does not pose a significant problem to the coherence of DC, as I shall show through the example of caste determination in *Pheidole* colonies. The upper colony level is strongly composed of its lower levels, the individual ants. There can be no distinctness between the entity "colony" and the entity "ant", which would raise suspicions concerning DC owing to the non-fulfilment of the distinctness requirement. When we represent properties of the system in question by variables, such as an upper-level property being the ratio of soldiers to workers and a lower-level property being the numbers of soldiers and workers, properties do not enter perplexing part-whole relationships, even though the entities they belong to do. The variables representing such properties can take different values, a valuable feature in replying to common objections raised against DC. In terms of variables and properties, U represents the ratio (upper-level property) determined by the value of a variable *u* (U being the ratio of soldiers to minor workers). L represents properties at the lower level, determined by the value of *l.* Unlike U and E, L is represented by a two-valued variable, the number of soldiers and minor workers. The lower-level effect E is the probability *p* that a larva develops into a soldier or a minor worker. In the examples discussed, a downward causal relation would mean that a change in the value of U is a direct cause of a change in the value of E.

To address objections more specifically, I shall first introduce the notion of conditional independence to respond to the causal exclusion objection. I then introduce the condition of independent fixability to assess the distinctness objection. Finally, I provide an account of diachronic analysis of directedness to address the vicious circularity objection. In replying to the objections, I shall closely follow Woodward's recent work on downward causation (Woodward, 2021b; 2021a) and show how interventionist accounts are especially fruitful for explanations in evo-devo.

According to the causal exclusion[6] argument, if an event *e* has a sufficient cause *c* at *t*, no event at *t* distinct from *c* can be a cause of *e* (Kim, 2007, p. 17). Introducing conditional independence of variables is a possible solution to the causal exclusion problem. Conditional independence is a condition that fixes interventions on U such that with U being set, the same value of E will result, regardless of the values of L. Hence, in terms of difference-making, the U-values can capture whatever makes a difference for E. Consequently, we may say that L and E are independent of each other, conditional on the value of U remaining fixed (Woodward, 2020, p. 862).

[6] Nonreductive physicalists have attempted to solve the causal exclusion problem using interventionist accounts of causation. According to Baumgartner, although interventionism is a popular candidate for solving this problem, interventionist causation still "excludes causal dependencies among supervening macro properties and effects of their supervenience basis" (Baumgartner 2009, 162). Although Baumgartner rejects interventionist causation as insufficient to solve the causal exclusion problem, I shall show in section V how variable-thinking, a specific feature of interventionism, is suitable for solving the exclusion problem in empirical situations in the context of evo-devo.

Some additional conditions in this relation require that:

i. U are a coarse-graining of L (L being of higher dimensionality than U);

ii. There is multiple realization of U by L (i.e., different combinations of L can lead to the same U).

The ratio of soldiers to minor workers (U) causes E (the probability *p* that larvae develop into either soldiers or minor workers) while simultaneously, L (the number of soldiers and minor workers in a colony) causes E. I shall now argue that as L and E are conditionally independent, U and L will not overdetermine E, thus avoiding the causal exclusion problem. Condition (i) is fulfilled because U is a coarse-grained variable, meaning there is less information in an upper-level property (a ratio) than in a lower-level property (caste population sizes). Condition (ii) is fulfilled because U is multiply realizable by L, i.e., if U is a ratio of 2:1, several possible combinations of L could realize this ratio. Insofar as U remains constant (e.g., a ratio of 2:1), multiple interventions at L, such as doubling or halving the numbers of both soldiers and minor workers, preserve the value of U. In other words, under different interventions at L, E remains constant insofar as U remains the same because U is a coarse-grained variable representation of the properties represented by L.

Given the fulfilment of conditions (i) and (ii), the numbers in L do not overdetermine the probability that a larva develops into either a soldier or a minor worker. In other words, no intervention on L changes E without changing U; hence, there is no risk of overdetermining E. This is because U are summary representations that are multiply realizable by different possible values of L. U and L are at different levels of description, where U captures a causal pattern that a lower-level description does not. By simply considering L, we miss the fact that there is independence between L and E, precisely because different interventions on L can lead to the same E. Only when we intervene on U can we see the causal pattern.

Conditional independence, however, is not a sufficient condition to respond to the distinctness objection. Recall that cause and effect are not sufficiently distinct in DC according to this objection. The reason is that DC is a relation whereby upper levels have a causal impact on lower levels, and upper levels are, at least in some way, composed of lower levels. It follows that, for DC to be coherent, upper and lower levels must be distinct for there to be any inter-level causal relation. A core tenet of variable thinking is that entities (or events) do not cause each other. In the switch from entity to variable-thinking, variables represent properties of entities or events that take relevant values. Changes in such values explain the difference-making relation between properties. Setting an additional condition of independent fixability of variables can be helpful to ensure that the variables in DC are sufficiently distinct. Under variable-thinking, variables (and the properties they represent) do not enter into part-whole relations. However, one may still object that variables are not sufficiently distinct as they merely represent the same property or two closely dependent properties. Independent fixability (IF) is a criterion that safeguards variables from this kind of problematic dependence. IF stipulates that it must be possible, at least in principle, to set each variable to any value independently of the other variable. Hence, IF allows a distinction between causal and non-causal dependencies (Woodward, 2015). The conditions for IF are expressed as follows:

> (IF): a set of variables V satisfies independent fixability of values if and only if for each value it is possible for a variable to take individually, it is possible (that is, "possible" in terms of their assumed definitional, logical, mathematical, mereological or supervenience relations) to set the variable to that value via an intervention, concurrently with each of the other variables in V also being set to any of its individually possible values by independent interventions (Woodward 2015).

Given that DC is a relation that comprises variables at different levels, such as U and L causing E (a lower-level effect), U and E are sufficiently distinct insofar as it can be shown that they are independently fixable. Let us consider U (ratios of minor workers to soldiers) and E (the probability *p* that a larva develops into a minor worker or a soldier). The variables representing properties of U and E can be fixed independently per the experimental possibility of independent manipulation of those variables. At the upper level, the ratio of minor workers to soldiers can be modified, for instance, by adding or subtracting minor workers of soldiers to a colony. The effect E can be independently manipulated through experimental means. For instance, through nutrition or juvenile hormone stimulation, a larva can develop into either a worker or a soldier in *Pheidole* species that exhibit this polymorphism. Note that the condition of independent fixability of variables is a weaker condition than that of conditional independence. Independent fixability is a suitable solution to the distinctness objection as it guarantees that changing the value at one level (U) does not imply a necessary change in E, even when E is a variable representing a lower-level effect.

In more practical terms, Wheeler and Nijhout's (1984) classic experiment of soldier determination in *Pheidole bicarinata* showed that nutritional history affects the soldier-determining sensitive period. The presence of soldiers in a colony suppresses further development of soldiers by an inhibitory pheromone acting on the larval endocrine system (Wheeler and Nijhout, 1984). From more recent experiments (Abouheif, 2002; Rajakumar et al., 2012), we know that this polymorphism can be triggered by laboratory manipulations of the levels of nutrition and juvenile hormone, indicating that such manipulations allow for the independent fixability of variables *sensu* Woodward. IF is satisfied in these cases owing to the practical possibility of manipulating U and E through different interventions. U and E are sufficiently distinct, so there can be, at least in principle, a downward causal relation between them.

The final objection to be addressed is vicious circularity. Once conditional independence and independent fixability have been clarified, it is easier to establish a condition of directedness in cyclical causal relations. According to the vicious circularity objection, upper-level properties would not exist in the first place if it were not for lower-level properties. Therefore, it is difficult to determine a cause at an upper level, given that upper levels are causally determined in the first place by properties at lower levels. This objection is valid once the system in question is understood in a *strong* compositional sense. For instance, in the ant colony example, the ratio of soldiers to minor workers (U) affects the number of soldiers and minor workers (L), which in turn determines the ratio (U) in an endless cycle.

To respond to this objection, I propose that we assess this example from a diachronic perspective. Woodward, for example, responds to the worry of cyclicity or vicious circularity by suggesting that "underlying" any cyclic graph is "a model with time-indexed variables with temporal lags that is acyclic"

(2021a, p. 12). In other words, what matters is directedness. For instance, we may say that a property at time t_0 causes an effect at time t_1, and that the effect is similarly a property. Development is, by definition, a temporal process whereby individuals change over time. When considering the colony example, the upper-level properties U are at different temporal stages of development (even though U is causally determined by E). In terms of variables that represent properties, we have two different levels represented by properties U and E. Variable values *u* and *e* are values of properties of U and L, respectively. An additional feature is that U and E are instantiated at different times.

The concern over vicious circularity arises because of the mistaken assumption that in DC, U causes the very same lower-level property L that gives rise to U. If that were the case, we would indeed have a viciously circular loop. However, this is not the case once we represent the system through variables whereby E is a lower-level effect. On closer consideration, the lower-level property that is the effect is distinct from the lower-level realization of the upper-level U. Therefore, in the case of a property U at t_0 that causes E at t_1 to happen, the concern over vicious circularity does not apply. There is no vicious circularity insofar as t_0 and t_1 represent different developmental stages of different individuals. U at t_0 represents the upper-level property (ratio of soldiers to minor workers), and E at t_1 represents the probability of larvae developing into either soldiers or minor workers. There is a negative feedback loop whereby the ratio change causes the probability change, thereby causing a number change (and hence, ratio change) and so on.

Under this diachronic perspective, directedness exists even in the occurrence of a cycle, which means that iteration is not problematic or viciously circular. It is possible to intervene in the system such that an intervention on U (for instance, modifying the ratio of soldiers to minor workers) at t_0 leads to a change in E at t_1. Similarly, from the opposite direction, an intervention in L at t_0 will lead to a change in U at t_1. Even in a cyclical relation, the cycle may be iterative without necessarily being viciously circular.

5. A practice-centered epistemology of downward causation in biology:

My argument thus far has been that when biologists label processes as cases of 'top-down' causes, DC need not be doomed to incoherencies and metaphysical doubts if we face the task of demystifying DC as an epistemic project. This required two steps. First, distinguishing between different degrees of commitment to compositionality when biologists use DC in explanatory capacity. Second, following the epistemic nature of the task, deploying an interventionist framework to analyze the more problematic cases of DC (i.e., cases of *strong* compositionality).

My argument has drawn on important recent work by Woodward (Woodward 2021a; 2021b). I have added to the existing framework by specifying that there are at least two kinds of phenomena commonly described as DC in biology: those that are related by *weak* composition and those related by *strong* composition. The distinction between weak and strong compositionality has not yet been explored as an avenue of investigation on DC. Consequently, I have also extended the existing account by applying interventionism to unprecedent study cases that are especially relevant for understanding causation in evo-devo. This article therefore moves beyond current proposals by advancing two main contributions to the literature on DC.

The first epistemic contribution is to diffuse the tension between compositionality and DC in biology. Many solutions to DC in biology rely on a deflation of 'levels' and compositionality in order to make sense of DC (a few examples include Eronen 2013; 2015; DiFrisco 2017). Here I take a different approach: I argue that the compositionality of levels assumption does not hinder the coherence of DC. My argument, therefore, accepts that complex systems such as organisms and biological processes can be conceptualized in terms of levels, while also defending that the degree of compositionality between such levels need not be an obstacle to the construction of a coherent concept of DC. Although I have primarily drawn from Woodward's interventionist accounts of causation, interventionist causation does not explicitly deal with the intricacies of strong compositionality and whether compositionality considerations are generally compatible with DC. In addressing this gap, I have rehabilitated a working concept of DC that is compatible with how it is used to describe biological processes, whether levels are weakly or strongly instantiated. This is in line with the epistemic scope of this paper, which is precisely to understand in which ways DC can be fruitful and coherent in biological practice.

This analysis enables a novel approach to the conceptualization of DC, which leads to a second contribution that is methodological in nature. I have sought philosophical accounts of DC that fit a *pragmatic* analysis of the concept. Methodologically, I proceeded through a practice-centered interdisciplinary analysis, bringing together a philosophical problem to an explanatory one in scientific practice. By starting from a practical investigation into the kinds of processes biologists label as cases of DC, I have shown that there seems to be an entire class of DC that philosophers have neglected and are not present in any of the objections raised against DC. This neglect has unjustifiably tarnished the explanatory credentials of DC. Hence, the second contribution I make to the study of causation in biology is to show the benefits of analyzing concepts by tracing the ways in which practicing biologists use them. Here, the field of philosophy of science in practice (Ankeny et al. 2011; Chang 2011; 2012) has greatly shaped my approach by providing the necessary tools to apply a practice-based methodology for elucidating concepts of causation. As such, this article offered a series of epistemic conditions to identify possible compositional relationships in which DC might occur. The next step would be to trace the epistemic conditions back to metaphysical assumptions and problems. A fruitful avenue of investigation would then be to assess whether interventionism can be interpreted as more ontologically loaded in order to properly solve metaphysical causal puzzles such as DC.

6. Concluding remarks

In this paper, I have proposed an epistemic solution to demystify DC in biology, in ways that avoid the familiar objections against DC in the literature. I have explained the origin of the mismatch between the apparently unproblematic use of DC in biological explanations and the philosophical concerns over the coherence of the concept. I have focused on biological examples to demonstrate how the concept of DC can be coherently applied to complex, evolving systems. I have suggested that we distinguish two cases of DC in biology: weak and strong compositionality. I have shown that in the former, DC raises no major conceptual concerns. It is in the latter, in cases of compositionality in a strong sense, that the conceptual problems arise. By using interventionist theories of causation such as that propounded by James Woodward, I have shown how the concept of DC can be used coherently in fields such as evo-devo. This newfound clarity is partly attributable to a practice-centered methodology, where I worked from examples in the scientific literature to analyze how DC can be coherently reconceptualized. The contention is that when scientists seek to evaluate downward cause and effect relationships, they should assess the difference-making relation between variables that can, in principle, be manipulated and intervened upon. Philosophical and metaphysical accounts of DC need not be in tension with how DC is used in an explanatory capacity, as is the case in biology. On the contrary, these two accounts overlap when the question of DC is demystified from an epistemic perspective such as the one advanced here. Such an approach could be the starting point for fruitful causal models in other complex systems such as in ecology and evolution, as well as in assessments of environmental changes and their impacts on phenotypic novelties. The manipulation of variables is a crucial feature of scientific practice, and the practical use of the concept of DC can be reconciled with its metaphysical analysis.

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