Philosophy of Science (2024), **91**, 869–886
doi:10.1017/psa.2024.5

PSA PHILOSOPHY OF SCIENCE ASSOCIATION
PHILOSOPHY OF SCIENCE

ARTICLE

Developmental Channeling and Evolutionary Dappling

Grant Ramsey[1] and Cristina Villegas[2]

[1]Institute of Philosophy, KU Leuven, Leuven, Belgium and [2]Centro de Filosofia das Ciências, Departamento de História e Filosofia das Ciências, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal
Corresponding author: Grant Ramsey; Email: grant.ramsey@kuleuven.be

(Received 19 July 2023; revised 20 January 2024; accepted 12 February 2024; first published online 22 March 2024)

Abstract

The developmental properties of organisms play important roles in the generation of variation necessary for evolutionary change. But how can individual development steer the course of evolution? To answer this question, we introduce *developmental channeling* as a disposition of individual organisms that shapes their possible developmental trajectories and *evolutionary dappling* as an evolutionary outcome in which the space of possible organismic forms is dappled—it is only partially filled. We then trace out the implications of the channeling-dappling framework for contemporary debates in the philosophy of evolution, including evolvability, reciprocal causation, and the extended evolutionary synthesis.

1. Introduction

The evolutionary-developmental research program (evo-devo), broadly considered, includes both the study of how developmental systems evolve, and the study of how development affects the course of evolution. The latter is the focus of this article. The evolutionary impact of development has been a point of controversy within the evolutionary sciences and the philosophy of biology, for it is sometimes perceived as undermining the causal and explanatory role of selection in shaping evolution (Huneman 2017). Much of the disagreement about the significance of development relates to how we understand evolutionary causation and what place development has in the evolutionary causal nexus (Moczek 2019). In this article, we provide a framework for understanding how development—particularly in the sense of *developmental channeling* that we introduce here—acts as an evolutionary cause. We show that developmental channeling can be a cause of the evolutionary outcome that we term *dappling*. We further show how this framework contributes to clarifying some of the current disputes over causation and explanation in evolution.

The key role that development plays in evolution has often been conceptualized in terms of limitations on the possible phenotypic variants that serve as the raw

material for evolution. That is, *developmental constraints* limit evolutionary possibilities and thus weaken the power of natural selection to move populations through the space of possible phenotypes (e.g., Gould and Lewontin 1979; Maynard Smith et al. 1985). Because selection can act only on extant variation, constraints on the generation of variation limit what selection can act upon.

More recent works move beyond the purely constraining side of development and point to the positive role that development plays in generating variation. In so doing, terms such as *developmental drive* (Arthur 2001) or *developmental bias* (Brigandt 2015) have been proposed. Development is therefore considered not just limiting or constraining, but as a process that can push or drive evolution in particular directions, affecting which variants are possible as well as which are more or less probable (Lewens 2009; Nuño de la Rosa and Villegas 2022).

Constraints are negative and drives are positive. Is there a term that includes both? One contender, which is gaining weight for conceptualizing the evolutionary effects of development, is *evolvability* (Brigandt 2015). As we will argue later (section 4.1), however, evolvability cannot serve as a complete replacement for the concepts of developmental constraint and drive. One reason is that a developmental constraint/drive is best understood as a feature of individual development, while evolvability concerns higher levels (populations or beyond)—see Brigandt et al. (2023) for discussion. Thus, while developmental constraints/drives play important roles in evolvability, we must not conflate them.

We thus need a label that has both the limiting connotation of *constraint* and the constructive one of *drive* but can be applied to individual development. The neutral term we will use to bridge this gap is *developmental channeling*. Developmental channeling plays a guiding role in evolution and, depending on the nature of the developmental system, this role can be large or small and it can operate with, against, or independently of the direction of selection. The key effect of channeling is *dappling*—where dappling refers to the uneven filling of the space of possible phenotypes. That is, the space of possible phenotypes is incompletely and unevenly filled. Thus, if we overlay actual phenotypes on possible phenotypes, the result is dappled.

The channeling-dappling distinction serves not only to clarify the role that individual development plays in evolution but also to integrate evo-devo ideas on developmental constraints and biases within a general framework of evolutionary causation in which individual-level dispositions are responsible for evolutionary changes (Ramsey 2016). The channeling-dappling framework links proximate (developmental) causes with ultimate (evolutionary) effects, connecting our project with debates over how the proximate-ultimate cause distinction can and should be drawn—if, indeed, it is a coherent distinction (Bateson and Laland 2013). This bears on larger questions about how we should think about causes in evolutionary biology, questions that have moved to the foreground in discussions of whether evolutionary biology should be reconceptualized in terms of an extended evolutionary synthesis (EES; Pigliucci and Müller 2010) and whether "reciprocal causation" means that there is no clean proximate-ultimate distinction.

We first describe in detail how we understand the concepts of channeling and dappling, as well as how the former causes the latter, before we turn to exploring the connections of this framework to evolvability, the ultimate-proximate distinction, and the EES.

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

2. The nature of developmental channeling and evolutionary dappling

Developmental channeling includes the drives and constraints that limit and propel organismic development. Evolutionary dappling, however, refers to the irregular occupation of organismic morphospace. To make our argument that developmental channeling is a cause of evolutionary dappling, we will flesh out both concepts in this section.

2.1. Varieties of developmental channeling

Let's suppose you are accomplished at the standing long jump and have a record of 3.3m. The sport was part of the Olympics from 1900 to 1912 and the record was then set by Ray Ewry at 3.47m. You might think to yourself, "If only I were a bit taller, I could easily defeat the Olympic record." Now here is the interesting question: If we just scaled you up, made you bigger but exactly proportional to your previous you, what would this do to your standing jump? To answer this, let's make a few reasonable assumptions: Your strength is proportional to the cross-sectional area of your muscles and thus increases proportional to the square of your height. Your weight, however, is proportional to the cube of your height.

Now we can see what happens if we increase your height. To make it as clear as possible, let's say we double your height. How long a jump can you now make? (Let's assume that doubling does not impair organs like your brain or heart, so the relevant factors are only how your strength and mass increase.) Your height is doubled, which means your mass increases eightfold, while your strength increases fourfold. Thus, the double-sized you is half as strong relative to your mass and could therefore jump only half as far relative to your height. But you are twice as tall, so jumping half as far relative to your (double) size means that double you jumps exactly as far as normal you. The same with a version of you half as tall. A grasshopper that jumps two meters no longer seems all that impressive. Shrink yourself to grasshopper size and you could do the same.[1]

What explain the constancy of jump length are basic physical truths, truths about natural laws and the geometry of spacetime. Such features of the world channel organismic forms: Phenotypes develop and change according to what is physically possible (i.e., they reflect *physical* constraints on development). Physical laws and properties prevent organisms from developing in (possibly adaptive) divergent ways, such as the scaling laws standing in the way of your Olympic record. This is the constraining side of this form of channeling, though the very same laws allow for incredible feats in very small organisms. A flea can typically jump more than fifty times its length (Krasnov et al. 2003), not unlike a two-meter-tall human jumping 100 meters, the length of a football field. This is the constructive side of channeling: The same properties that constrain the emergence of some phenotypes enable the appearance of others. Importantly, facts about the scaling possibilities of phenotypic changes are independent from the potential fitness value of the changes, such as jumping larger distances. The nature of scaling implies that insects can have the luxury of walking about on gossamer appendages, whereas elephants require blunt, stumpy limbs.

[1] One of us (Ramsey) thanks Jack Longino for long ago introducing him to the wonders of scaling and the profound effect scaling has in the world of insects.

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

There are other kinds of physical features that channel organismic form in similar ways. The nature of chemical bonds, the rates at which molecules diffuse through liquids, and the oxygen level of air are all examples of physical features that channel organismic forms at the molecular level. These forms of channeling apply to all organisms and are what Maynard Smith et al. (1985) label *universal constraints*. This universal channeling can be based on physical laws, but it can also rest on universal features of life on Earth. Life on Earth is based on cells and thus the physical properties of cell growth and differentiation are mechanical properties of evolved systems that determine the available pathways leading to possible adult forms (Newman et al. 2006).

Another feature of life on Earth is that each developing organism has a fixed set of genes and can draw only on these genes in its development.[2] The availability of genes therefore channels the development of the organism: If it needs a particular protein, it cannot synthesize a segment of DNA for use in coding this protein. Furthermore, the roles that a gene can play in development are determined by elements such as its genomic and epigenetic context. The resulting phenotype is thus the effect of the generative rules of development guiding the interaction and expression of genes (Müller 2007). These genes do not merely code for specific proteins, but they have a mechanistic function in particular developmental pathways (Gilbert 2000). Such pathways channel phenotypic results using the interaction of coding and regulatory regions of DNA with other molecular, cellular, and tissue aspects of the embryo. The complexity of these interactions in turn channels the functions that particular genes can play in the development of specific traits.

While some channeling is universal, other kinds differ greatly across taxa, due to their different forms and evolutionary histories. There is thus taxon- and trait-specific channeling. Such channeling is local instead of universal (and was labeled *local constraints* by Maynard Smith et al. 1985). For example, *Carrier's constraint*, proposed by Carrier (1987), holds that two-lunged vertebrates that laterally flex their bodies while they locomote will have difficulty breathing while moving, due to the compression that such movement imposes on their lungs. Lizards are one such taxon. This is a constraint that has to do with the physics of breathing and of locomotion, and their combination in a particular quadrupedal form of movement. No vertebrate can have two lungs, laterally flex while walking or running, and have its breathing unaffected by this locomotory movement. Similarly, no vertebrate limbs have evolved into wheels, not because they would not be useful, but because—among other things—you can't have blood vessels flowing into revolving structures.

Development is path-dependent, with later stages depending on earlier ones. One form of dependency leads to what Wimsatt (1986, 2015) labels *generative entrenchment*, which means that early stages of development tend to be more conserved because changes in them typically alter later ones as well. Development is thus *canalized*, in the sense that the process of development is like the flowing of a branching river (Waddington 1942)—once the system commits itself to one branch, this can have permanent consequences for subsequent developmental possibilities.

[2] This is not to deny that mutations and horizontal gene transfer occur, but they generally play a minor role in the course of each organism's development, especially in the case of multicellular organisms, which are the focus of developmental biology.

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

Some of the restrictions of generative entrenchment can be offset by *modularity*, in which development can operate in parallel modules. That is, the development of one body part can be a relatively autonomous process within the entire development of the organism (Schlosser and Wagner 2004). But modules are only partially isolated from other modules, and both integration and generative entrenchment typically remain *within* modules, even if modularity partially frees the development of some modules from that of others. In addition, some developmental processes are highly *robust* with respect to environmental or genetic perturbations, channeling the organism or the developmental module toward a particular target phenotype under a wide range of conditions (De Visser et al. 2003). By contrast, other developmental processes show high levels of *plasticity*, meaning that the phenotypic outcomes are strongly environment specific (Pigliucci 2001).

Individual development extends into the production of gametes, and the channeling of this production is based on limitations on available developmental resources. A human female, for instance, is born with all the eggs she will ever use to make offspring. Each egg is unique, but they all result from the same meiosis process in which the formation of gametes involves the reduction of genes from diploid (two copies of each gene) to haploid (one copy). These haploid combinations are restricted to the possibilities created by the diploid cell and are thus channeled by both its genetic material and the meiosis process.

These various forms of channeling can have evolutionary implications, which we will explore in section 3. But before we do so, we first need to jump from the organism-level phenomenon of developmental channeling to the ensemble-level outcome of evolutionary dappling.

2.2. The dappling of organismic forms

All vertebrates have four or fewer limbs. Terrestrial vertebrates can be traced back to the evolution of tetrapods from bony fish in the Devonian, around four hundred million years ago (Clack 2012). An early tetrapod was *Tiktaalik*, which bore features of fish (scales and gills) but had a flattened head like that of a reptile or amphibian (Daeschler et al. 2006). *Tiktaalik* had limbs capable of carrying it out of its submerged state and into shallow water or even dry land. From the first tetrapods descended all reptiles, amphibians, and mammals. There are tens of thousands of tetrapod species and the overwhelming majority retain four limbs. Some have two limbs: Whales evolved from terrestrial tetrapods, and in so doing lost their rear limbs and had their forelimbs transformed into flippers. And there are tetrapods that lost all four limbs, such as snakes, caecilians (limbless amphibians), and pygopodids (legless lizards).

Thus, while limb number for vertebrates could in principle be 0, 1, 2, 3, 4, 5, and so on, we find only 0, 2, and 4 represented by extant or ancestral taxa. Instead of the possibility space being uniformly filled, it is only partially filled—it is what we, here, label *dappled*. Some limb numbers would be unlikely to be adaptive were they to evolve. For example, it is difficult to imagine forms with an odd number of limbs having fitness advantages. But we should be careful not to attempt to explain the lack of particular limb numbers based on the imagined fitness cost of the limbs. Before fitness costs play a role, the traits must arise, and the development of limbs plays a key role in which possibilities are present.

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

What evolution can do—and has done—is to transform and repurpose limbs, or to eliminate them altogether. The forelimbs of tetrapods have evolved into adaptations for flight three different times (Rayner 1988). The pterosaurs evolved long, strong fifth fingers (pinkies), which formed the basis of their wings. (Pterodactylus means winged finger.) Birds fly with extended arms, whereas bats have elongated splayed fingers with connecting skin like a pitcher's mitt. This shows some degree of underlying anatomical flexibility in supporting adaptive functions. But this flexibility—this multiple realizability of wings—when examined closely, shows strong conservatism. While evolution seems to be able to stretch and shrink and fuse bones, and sometimes even to multiply homologous structures, it is much more difficult for it to generate novel structures, that is, structures not homologous to those of other vertebrate species.

The irregularly occupied morphospace represented by vertebrate limb number is a widespread phenomenon. Extant phenotypic traits are in general irregularly distributed across what could be seen as an ideal space of all possible phenotypes (Oster and Alberch 1982). Evolutionary dappling refers to this irregular distribution, what Alberch (1982, 317) described as "the empty spaces and the ordered pattern in morphology-space." This is distinct from *morphologic disparity*, which is defined as "the amount of difference between related phyla, classes, species, individuals, proteins, genes etc." (Runnegar 1987, 40; see also Gould 1989). While disparity is about the degree to which taxa vary in their features, dappling has a broader scope and considers the entirety of morphospace and how it is populated.

While we may imagine that evolution can bring about any nomologically possible organismic form, the result of billions of years of evolution clearly shows the conservation of a relatively small number of forms around which most species are clustered. Explaining this clustering requires resources not found in traditional population-genetic approaches to evolution, which are mostly focused on genetic and fitness differences within inbreeding populations. Indeed, the higher-level biases encountered in morphospace have typically been approached from the comparative branches of biology, such as comparative morphology and embryology, and are currently under the scope of evo-devo (Hall 2012; Love and Raff 2003).

Because the concept of morphospace is foundational to the concept of dappling, we should pause here for a moment to consider the former in more depth. Take the game of chess, with its 64 squares and 32 pieces. If we are allowed to freely place the pieces on the board, there is a vast number of arrangements we can create. Let's call the full set of such arrangements the *chess piece arrangement space*. Now we can ask of this space which regions can be reached through the course of legal chess play. Because of the fixed starting arrangement of chess pieces combined with the strictures of the legal moves for each piece, only a subset of this space can be reached through legal chess play. The chess piece arrangement space is thus dappled by legal play.

Consider just the first move. There are twenty legal chess openings. How many illegal (though physically possible) openings are there? This is unanswerable without giving at least some constraints. If we begin with the normal setup and hold that white starts (as it does in legal chess), and that any white piece can move to any unoccupied space on the board, then the number of possible openings is 512, resulting in about 25 illegal moves for every legal move. The combination of the legal moves and a fixed starting position results in a vast space of impossible (as well as highly improbable)

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

chess arrangements. Because of this, chess play is nonergodic. An ergodic system is one in which all regions of the state space will (in the long run) be occupied with equal frequency. This is clearly not a feature of chess play, where not all pieces can visit every point in the chess piece arrangement space, let alone with the same frequency.

When it comes to phenotypes, an evolving system would be ergodic if given enough time it would visit all regions of morphospace. However, evolving systems are nonergodic. Just as there is an initial arrangement and set of rules for chess play, so is there an initial arrangement of organisms and a set of developmental rules. These rules are not as perspicuous as are chess rules, but they have the same effect of dappling the possibility space. Further, just as the rules are clearer in chess than in biology, so is the space more easily defined. A chessboard is a closed space with discrete positions. There is either a white pawn at c2 or there is not. For organisms, many traits—height, for example—vary continuously and are unbounded, resulting in a much more complex, highly dimensional morphospace.

What is important to see is that the space of possible chess arrangements is larger than the arrangements reachable through legal chess play. Analogously, the space of possible organismic forms is larger than is reachable through evolution. Our argument in this article is that just as chess rules make the exploration of chess piece arrangement space nonergodic, channeling makes the evolutionary exploration of morphospace nonergodic. Many piece arrangements are not reachable because of how each individual piece can move at any given time. Similarly, many regions of morphospace are unreachable (or unlikely to be reached) using the evolutionary process due to the developmental possibilities of organisms—that is, to developmental channeling.

While channeling concerns the individual-level developmental process, dappling is a higher-level product. Channeling concerns the constraints and drives controlling the course of development, whereas dappling concerns the way the space of possible forms is occupied. Dappling does not concern one particular level but can be observed at a variety of levels. For instance, we can inquire into the dappling within the scarabs, within the beetles, within the insects, or within the arthropods. In the following section, we will explore how developmental channeling can be a cause of evolutionary dappling.

3. Developmental channeling as a cause of evolutionary dappling

Development is a process that occurs in individual organisms. Dappling is an evolutionary outcome represented by how populations or species—or even higher taxa—are distributed across morphospace. The task now is to link the two, to show how developmental channeling can result in evolutionary dappling. To do so, let's begin by further considering the question of limb number.

Why are there no six-limbed vertebrates? It could be that naked mole-rats would benefit from having six limbs, allowing them to better navigate their subterranean lair. If this is so, the reason they lack six legs is not because such a form would have a low fitness and be selected against. Instead, the reason seems to be that six-limbed vertebrates have never originated at all, most likely due to the rules governing vertebrate development. It may simply be developmentally unworkable (and thus

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

impossible or at least highly unlikely) to build an extra pair of limbs while keeping the rest of the creature in working shape.

In other words, creating whole new limbs beyond the four of the basal tetrapod may exceed the developmental resources of tetrapods. Developmental biologists have worked on the question of why the general paired limbs-gut architecture is so well conserved in the tetrapods. One theory focuses on how tissue is used during development, the argument being that limbs can be established only in front of or behind the gut, but not on the gut (Nuño de la Rosa et al. 2014). If this is right, the very structure of the developmental processes of tetrapods rules out six-legged naked mole-rats—or other six-legged tetrapods—resulting in a dappling of morphospace.

Let's now generalize and connect these ideas with how other individual-level dispositions have been thought to cause evolutionary outcomes. According to the propensity interpretation of fitness, fitness is an individual-level propensity to survive and reproduce (Brandon 1978; Mills and Beatty 1979). We should note that there has been much debate about how to quantify the fitness propensity (see Pence and Ramsey 2013) and how the propensity can cause evolutionary outcomes (Ramsey 2013a, 2013c; Otsuka 2016). We will sidestep those debates and simply ask: If fitness is an individual-level propensity, what does it cause and how does it do so? We can then discern whether channeling can be a cause in the same way.

What kind of outcome does fitness produce and how does it do so? The key outcome of fitness is *adaptation*. Fitness leads to adaptation through what we label a *population-level bridge*. The population-level bridge is needed because the individual level of fitness must be connected to higher levels because evolution is a higher-level phenomenon. For fitness to lead to adaptation, there must be a population of individuals that vary in fitness due to differences in their heritable traits. Thus, our picture of how fitness causes adaptation has three parts. First, there is the individual-level cause, then the population-level[3] bridge, then, finally, the evolutionary response. These parts correspond to the three columns of Table 1.

To have a clear understanding of the distinction between fitness and channeling, it is useful to follow Ramsey (2006, 2016) in considering how these propensities relate to life histories. As organisms live their lives they realize a life history, but this life history is only one among an array of possible life histories. The heritable material an organism possesses, in combination with the environmental arena in which it develops, generates a set of possible life histories that vary in their phenotypic and reproductive outcomes. Imagine an organism that has only two possible life history reproductive outcomes, either one or two offspring (with equal probability). The fitness for this organism is the average over its possible life histories, 1.5.[4]

Before turning to channeling, let's consider one more individual-level propensity, one that leads to drift. Fitness differences are based on average reproductive outcomes over possible lives. But what of drift? Ramsey (2013b) offered the concept of

[3] By "population-level" we do not assume that the population-level structure is the only structure that matters to evolution. Smaller group structures or larger metapopulation structures, for instance, can affect evolutionary dynamics. Instead, we focus on the population because Darwinian populations (in the sense discussed by Godfrey-Smith 2009) are required for evolution by natural selection.

[4] We are using the simple arithmetic mean as a proxy for fitness and ignoring the debates about how best to quantify fitness.

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

Table 1. Three foundational evolutionary causes (fitness, driftability, and channeling) and their associated evolutionary effects. The effects arise only in the context of a population, its structure, and the nature of its constituents

Individual-Level Disposition	Population-Level Bridge	Evolutionary Response
Fitness (expected number of descendants)	**Fitness variation** (heritable fitness differences among individuals in a population)	**Adaptation** (evolutionary response to heritable differences in fitness resulting in adaptive change or stasis)
Driftability (variance in possible sets of descendants)	**Population size** (number of individuals of particular types in a population)	**Drift** (evolutionary response to variance in possible sets of descendants in a population)
Channeling (possible organismic developmental trajectories and their associated probabilities)	**Channeling distribution** (the nature, distribution, and inheritance of the channeled forms across the population)	**Dappling** (evolutionary response to the nature, distribution, and inheritance of the channeled forms)

driftability for the individual-level cause of drift. Just as an organism has an expected number of offspring (in this case 1.5), it also has variance in its possible reproductive outcomes. In the absence of this variance, a population cannot drift: A population of organisms each with a probability of one of producing two offspring, for instance, cannot drift, no matter the population size. All other things being equal, as the variance in possible life history outcomes increases, the amount of drift in the population is expected to rise. Driftability is thus an individual-level disposition that causes drift at the population (or higher) level. Driftability, like fitness, needs a population-level bridge to lead to its evolutionary outcome, in this case drift. The key part of the bridge is the number of individuals of a particular type in a population (or more specifically, the effective population size). See the second row in Table 1.

Channeling, like fitness and driftability, is an individual-level disposition that has evolutionary effects achieved through a population-level bridge. (See the third row of Table 1.) Fitness and driftability concern offspring *number*—expected number in the case of fitness and variance in possible numbers in the case of driftability. Channeling, however, is not about offspring number, it is about phenotypic *form*. Channeling concerns how life histories unfold, what morphological direction they take, and why. Why don't some naked mole-rats have six legs instead of four? Because they are channeled toward the outcome four by the basic developmental architecture of tetrapods. Insects, by contrast, have a different set of developmental resources that channel development toward the outcome of six limbs and not any other number.

In comparing fitness, driftability, and channeling, it is important to see that they refer to different aspects of the same ideal space of the possible lives. To understand the differences among them, let us return to the chess piece arrangement space. While legal play can lead to a vast number of possible chess games, the set of possible moves at each turn is highly constrained by the rules and the previous moves (and the consequences they have for how the board is filled). Similarly, as an organism plays its game of life

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

(develops), its possible developmental moves are constrained by the previous moves (the previous sequence of developmental outcomes) and the "legal" (i.e., developmentally possible) moves. Just as we can imagine impossible chess moves (a king moving two spaces instead of one, e.g.) and the consequences (a knight captured that would have been safe), so we can imagine impossible developmental sequences leading to unrealized consequences (such as the six-legged mole-rat). Such a creature is in a region of unoccupied morphospace just as the capturing of the knight would take place in an unoccupied region in chess piece arrangement space. The dappling of these spaces is thus a consequence of the channeling of the processes that fill them.

To further develop the chess example in relation to channeling, fitness, and driftability, consider that we can establish the propensity of a particular game to bring about a specific arrangement of pieces (analogous to a specific phenotype). And we can see how certain move sequences are linked with particular results (like black wins, white wins, or stalemate). Thus, we can establish the propensity of, say, a particular opening (like the Catalan Opening) ending in a win. We can also consider which openings result in a highly variable set of possible games. Analogously, we can see that an organism has a propensity to develop its phenotype in certain ways (channeling), a propensity to leave a specific average number of offspring (fitness), and variance in the possible numbers of offspring it can leave (driftability). Importantly, there is no one-to-one mapping between these propensities. Just like many different piece arrangements in a chess game can lead to the same result (e.g., black wins), many different phenotypes can produce, for instance, the same number of offspring.

By claiming that channeling can be a cause of dappling, we are not claiming that it is the only cause. When you play chess, you generally do not move at random from among the set of legal moves. Instead, you play to win. Thus, there is an additional narrowing of possibility space beyond the constraints of legal possibilities. Making "bad moves" will be unlikely, especially for skilled players. And if a bad move was attempted on a previous game, it is unlikely to be repeated. The drive to win leads to selection against it. In a similar way, some evolutionary outcomes will be selected for over others, and those selected against may thereby be eliminated from the species—and, more generally, from morphospace. And just as we can make errors when playing chess, thereby moving into improbable areas of chess piece arrangement space, improbable areas of morphospace can become occupied—or fail to be occupied—through drift. Thus, we are not arguing that channeling is the one and only cause of dappling, but, like legal moves in chess, it serves as a foundational cause of it.

The picture is thus this: Channeling is a causal disposition of individual organisms. This disposition causes evolutionary outcomes. At the most basic level, it is a foundational cause of the dappling of populations over the course of a single generation. But while channeling, like other evolutionary causes, has an effect over a single generation, it is only over many generations that its full significance can be observed. Over many generations, fitness differences can help to produce exquisite complex adaptations like the vertebrate eye. Similarly, channeling has within-generation effects: The drives and limitations of developmental trajectories are immediately apparent in individual growth. But like fitness, it is over generations that channeling has its greatest effects. It is unremarkable if a generation of wolves gives rise to four-legged young. It is much more striking to see that the basic four-limbed architecture realized by the wolf has persisted for hundreds of millions of years.

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

The effects of channeling go far beyond the population—or even species—level. The four-limbed architecture that has persisted in wolves has done so for most vertebrate species. Common descent explains the origin of such commonality, but what explains the *persistence* across such a wide variety of species—including humans, wolves, turtles, and robins—appears to be that their developmental systems are all channeled toward the same area of morphospace. While differences in selective pressures and contingent factors have produced a differentiation of limb forms, the number of limbs has remained the same in different environments because of the basic developmental architecture of vertebrates. In other words, while changes in the reproductive material and conditions of vertebrate species may have produced specific changes in the morphology of their limbs, these changes have mostly been channeled toward the preservation of limb number and structure. As a result, we observe that only a small fraction of possible forms are present in living beings, and that this small number of forms is represented by a huge range of taxa. This is how the individual channeling of organisms plays a fundamental role in the dappling of morphospace over evolutionary time.

4. The evolutionary significance of channeling and dappling

The preceding discussion shows how channeling can cause evolutionary dappling. It therefore shows how developmental biases and constraints fit into a general evolutionary causal framework. In this section, we argue that this framework has interesting consequences for two major current topics in the philosophy of evolution: evolvability and the extended evolutionary synthesis.

4.1. Distinguishing evolvability from channeling and dappling

As discussed previously, one might think that evolvability could play the role of channeling or dappling, which would undermine our arguments for the usefulness of these concepts. Let's now consider how evolvability relates to the channeling-dappling framework. One difficulty with juxtaposing our framework with evolvability is that evolvability is not univocal (Lynch 2007; Villegas et al. 2023) and has been the subject of discussion within different branches of evolutionary biology (e.g., Wagner and Altenberg 1996; Hansen and Houle 2008; Pavličev et al. 2011; Payne and Wagner 2019) as well as the philosophy of biology (Love 2003; Brown 2014; Brigandt 2015; Nuño de la Rosa and Villegas 2022). Some have argued that rather than being a single notion, evolvability refers to "a family of related concepts" (Pigliucci 2008, 75).

What is agreed upon is that evolvability refers to a capacity or disposition, but what this capacity is *of* and *for* is not always clear (Brigandt et al. 2023). Bearers of evolvability can range from traits (Hansen and Houle 2008) to lineages (Kirschner and Gerhart 1998), while what evolvability is the capacity *for* is often conceptualized differently depending on the explanatory context. For instance, it can be the capacity to respond to selection (Hansen and Houle 2008) or the ability to produce improved phenotypic variation (Wagner and Altenberg 1996). Under some conceptions, evolvability is linked with selection, while others hold that it is a capacity involving only internal features of the population, not their selective consequences. If one considers populations as bearers of evolvability, a central internal feature affecting this disposition is the developmental channeling of the organisms composing the

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

population. But in addition, some views of evolvability may include other populational components affecting the ability to evolve. In a well-known account of evolvability, Brown (2014, 550) takes this latter approach:

> [Evolvability is] used to explain the evolutionary trajectory of populations by capturing the influence that the internal features of populations can have on the outcomes of evolution . . . . [Its] physical basis is the many non-selection-based features of populations (such as mutation rate, developmental constraint, and population structure) that can influence the parts of phenotypic space populations are able to access over evolutionary time.

Under Brown's framework, channeling is certainly a part of evolvability, but evolvability involves more. To take just one example, population structure is one of the listed features of evolvability. Population structure is clearly a property of populations, not individuals. Nor is it a simple additive result of individual properties (in the way that the mass of a population is simply the additive result of individual masses). Thus, whether or not one takes fitness values to bear on evolvability, evolvability is clearly not identical with channeling or with dappling.

To get a clearer sense of evolvability's relationship with dappling and channeling, let's take a simplified species with only two traits: height and weight. We can place every member of the species on a simple two-dimensional plane in which one trait (height) is on one axis and the other (weight) is on the second axis. Now add fitness as the third dimension, forming valleys of low fitness and peaks of high fitness. Each organism will occupy a particular point on the landscape and a population will be a cloud of points.

Now we can ask what the capacity is for a population to evolve from the place it currently occupies to another place on the landscape. One reply to this question would be that it is both the fitness gradients across the landscape, as well as internal features of the population, that constitute this capacity. But one could instead follow Brown (2014) and others in separating the tendencies afforded by fitness from evolvability. If one does so and considers populations as bearers of evolvability, developmental channeling will play a role in it. But in addition, other higher-level components affecting the ability to evolve, such as population structure, will be included within evolvability. Evolvability is thus a higher-level disposition resting on the foundation of (organism-level) channeling as well as population-level properties.

Now take the simplified landscape mentioned in the preceding text and add more and more traits. And instead of a single population, or even a single species, let's populate the landscape with all the species from a particular higher taxon. We can frame channeling, evolvability, and dappling with respect to this landscape. If we zoom into individual organisms, we can ask about their possible life history trajectories, how they are constrained and driven in specific ways. This is channeling.

Now we can zoom out to populations and ask about their capacity to evolve from one place in the landscape to another. Setting aside fitness and the challenges of crossing adaptive valleys, we are asking here only about the capacity that the population has to go from occupying one place in the landscape to another. This is evolvability.

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

Finally, we can ask about the phenotypic patterns exhibited over this landscape and observe how the space is filled by the various populations over the range of species. Instead of being evenly distributed, the landscape will be patchy at all taxonomic scales, with rich clumps of species, genera, families, and so on separated by broad deserts. The landscape is thus dappled.

Evolvability therefore plays different roles than channeling or dappling. The channeling-dappling framework links individual-level dispositions with evolutionary outcomes. Evolvability, however, points to a disposition not of organisms, but of evolvable units such as populations or species. The evolvability of a population can be changed, for instance, merely by changing the size of the population. It is an important question how population size has evolutionary consequences, but this is a distinct question from asking how individual development has evolutionary consequences. Both are important questions, highlighting the importance of both evolvability and channeling.

4.2. The extended evolutionary synthesis and reciprocal causation

There is an ongoing debate about the nature and explanatory resources of evolutionary theory. This debate is often framed in terms of "standard evolutionary theory" (SET) versus the EES (Pigliucci and Müller 2010). EES proponents view their account as needed to overcome the limitations of SET. The first thing to note is that it is misleading to hold that there is a univocal SET. Instead, evolutionary theory developed and changed over time and is not understood in the same way by all SET advocates (Stoltzfus 2017). Setting these complications aside, what EES defenders argue is that the evolutionary causes acknowledged by SET are overly restrictive. One case they point to is the traditional assortment of causes into two categories, *proximate* and *ultimate* (Mayr 1961). To take the classic example of bird migratory behavior, proximate causes include things like a change in day length that triggers the behavior in particular birds (Pokrovsky et al. 2021), whereas ultimate causes include the fitness benefits gained from spending part of the year in one region, part in another (such as spending summers in temperate zones with a seasonal abundance of food and reduced predators, and winters in tropical regions with warmer temperatures), which explain why the trait evolved (and is maintained).

Within SET, proximate and ultimate causes are traditionally conceptualized as distinct and nonoverlapping. EES proponents, instead, argue that the causes are intertwined, that proximate causes can be evolutionary causes. One way this argument is made is by asserting that there can be "reciprocal causation," in which the actions of organisms modify the selection pressures acting on those very organisms (Laland et al. 2015), making some proximate causes also ultimate causes. Niche construction is a key example of this (Aaby and Ramsey 2022). Earthworms change the characteristics of the soil, which then exert selection pressures on the behavior of the worms (Ramsey and Aaby 2022). Does the channeling-dappling framework have implications for this debate as well?

To get at this question, let's revisit the tripartite structure introduced in Table 1. This structure highlights organism-level dispositions that play key roles in evolution. We identified three: fitness, driftability, and channeling. These dispositions become evolutionarily important only through the population-level bridge. This is where

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

reciprocal causation—and thus the conflation of proximate and ultimate causes—can be identified. Let's thus examine this bridge in more detail, beginning with fitness and driftabiliity before turning to channeling.

In the case of fitness, it is clear that organismic activities can have evolutionary consequences. Behaviors are not merely the passive result of selection, but they can actively shape selection pressures. The case of the earthworms just mentioned is an interesting example since, as Ramsey and Aaby (2022) discuss, an important activity they perform is to lower the soil matric potential, which is the amount of energy required to extract moisture from soil. Without performing this activity, the worms wouldn't just be less well off, but they wouldn't even be able to live where they do. Importantly, these fitness-affecting activities have evolutionary effects in virtue of variation in fitness values within a population. Thus, the population-level bridge needed for organismic fitness to produce adaptation, as we saw in Table 1.

With driftability, organismic activities can also have effects on evolution. Driftability concerns variance in possible offspring number and organisms can change driftability values from one generation to the next by changing the variability of life histories (by, e.g., altering environmental heterogeneity). Organisms can also have an effect on population structure, and in so doing, can change effective population size. This can occur in the absence of driftability changes, but because it is driftability in conjunction with effective population size that determines drift probabilities (Ramsey 2013b), these changes have evolutionary effects.

With channeling, we can examine the proximate causes that lead to particular organismic forms (and not others). But, as we have seen, channeling also has evolutionary effects. Think again of the set of possible life histories and the range of phenotypic forms they represent. Changes to this possibility space that change the phenotypic forms or their probabilities of occurring can take place through changes in the heritable material or the environmental arena. For example, sexual reproduction generates new organisms with new sets of possible life histories. The recombination of alleles involved in such a process will help determine the possibility space for the offspring.

In section 2.1, we outlined some of the developmental properties that channel organismic form. Take, for example, the modularity of forelimbs and hindlimbs in bats. This relative autonomy of limb development is similar to that of humans but unlike most other mammals (Young and Hallgrímsson 2005). When bats reproduce, the modular development of their limbs allows new allelic combinations to produce small wing changes that don't affect hindlimbs, and vice versa. Thus, the properties that channel individual forms (in this case forelimb and hindlimb modularity) help to determine evolutionary trajectories, implying that channeling is a proximate cause with ultimate effects. To see this, notice that the developmental properties that determine possible organismic forms, like modularity, are also considered to be crucial components of the *evolvability* of populations (Pavličev and Wagner 2012).

It is thus clear that proximate causes have evolutionary effects. Does this also imply that the reason for this is reciprocal causation? The answer to this question requires thinking carefully about the relata in reciprocal causation. As Hazelwood (2023) points out, EES proponents often frame the reciprocal relationship as obtaining between *processes* (like the process of niche construction and the process of natural selection) instead of *entities* (such as organisms and their environment). If the

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

reciprocity is between processes, there is a puzzle: How can a process like niche construction simultaneously be an evolutionary process yet undergo reciprocal causation with the very same evolutionary process? As Hazelwood argues, it is better to simply view niche construction as a part of the evolutionary processes without positing another process with which it is reciprocally interacting. In other words, niche construction is not a process interacting with evolution in a reciprocal way, but a part of evolution. Similarly, the channeling of individuals can be seen as part of the evolutionary process rather than as a separate process causally interacting with population-level ones.

Regardless of how one conceptualizes reciprocal causation, it is clear that proximate and ultimate causes are imbricated. However, this need not imply that the proximate-ultimate distinction is incoherent. Some have argued that one can understand the distinction in terms of overlapping causes (Ramsey and Aaby 2022) or in terms of explanatory abstractions (Scholl and Pigliucci 2015). Our framework is compatible with these possibilities.

5. Conclusion

In this article, we provided a framework for understanding how developmental causes can have evolutionary effects. In doing so, we identified *channeling* as a developmental disposition that leads to the evolutionary outcome of *dappling*. Channeling concerns the drives and constraints in individual development, whereas dappling concerns the uneven filling of morphospace.

In connecting dappling with channeling, we outlined a tripartite structure capable of linking individual-level dispositions with evolutionary outcomes using a population-level bridge. This structure highlights the links between fitness and adaptation as well as driftability and drift. We argue that this structure can also link channeling with dappling. The structure's population-level bridge involves a complex causal nexus, implying (among other things) that the proximate-ultimate cause distinction cannot be a distinction among mutually exclusive sets of causes.

We have also shown how channeling and dappling are related to evolvability. We argued that while channeling is an organism-level disposition, evolvability is a higher-level disposition. They are, however, connected: Channeling is an important part of evolvability. It is just that evolvability includes more than token organismic properties. For example, populational features—such as standing genetic variation—can play roles in evolvability but not channeling. In sum, identifying the individual-level disposition of channeling helps to show how development can have evolutionary effects and how it can play roles in evolutionary explanations.

Acknowledgments. The authors wish to thank James DiFrisco, Brian McLoone, and two anonymous reviewers for their thoughtful comments on previous versions of this paper. We also thank the audiences at the 2019 European Philosophy of Science Association conference and the 2019 meeting of the International Society for the History, Philosophy, and Social Studies of Biology, as well as the members of the KU Leuven Philosophy of Biology reading group, for helpful discussions of this work. GR's work was funded by the Research Foundation—Flanders (FWO) (Grant No. G070122N). CV's work was funded by national funds through FCT—Fundação para a Ciência e a Tecnologia, I.P., in the R+D Center for Philosophy of Sciences of the University of Lisbon (CFCUL), strategic project FCT I.P. UIDB/00678/2020, and through the contract with reference 2021.03186.CEECIND/CP1654/CT0008.

References

Aaby, Bendik and Grant Ramsey. 2022. "Three Kinds of Niche Construction." *The British Journal for the Philosophy of Science* 73 (2):351–72. https://doi.org/10.1093/bjps/axz054

Alberch, Pere. 1982. "Developmental Constrains in Evolutionary Processes." In *Evolution and Development*, edited by John Bonner, 313–32. Heidelberg: Springer. https://doi.org/10.1007/978-3-642-45532-2_15

Arthur, Wallace. 2001. "Developmental Drive: An Important Determinant of the Direction of Phenotypic Evolution." *Evolution and Development* 3 (4):271–78. https://doi.org/10.1046/j.1525-142x.2001.003004271.x

Bateson, Patrick, and Kevin Laland. 2013. "Tinbergen's Four Questions: An Appreciation and an Update." *Trends in Ecology & Evolution* 28 (12):712–18. https://doi.org/10.1016/j.tree.2013.09.013

Brandon, Robert. 1978. "Adaptation and Evolutionary Theory." *Studies in History and Philosophy of Science* 9 (3):181–206. https://doi.org/10.1016/0039-3681(78)90005-5

Brigandt, Ingo. 2015. "From Developmental Constraint to Evolvability: How Concepts Figure in Explanation and Disciplinary Identity." In *Conceptual Change in Biology*, edited by Alan Love, 305–25. Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9412-1_14

Brigandt, Ingo, Cristina Villegas, Alan Love, and Laura Nuño de la Rosa. 2023. "Evolvability as a Disposition: Philosophical Distinctions, Scientific Implications." In *Evolvability, a Unifying Concept in Evolutionary Biology?*, edited by Thomas Hansen, David Houle, Mihaela Pavličev, and Christophe Pélabon, 55–72. Cambridge, MA: MIT Press. https://doi.org/10.7551/mitpress/14126.003.0006

Brown, Rachel. 2014. "What Evolvability Really Is." *The British Journal for the Philosophy of Science* 65 (3):549–72. https://doi.org/10.1093/bjps/axt014

Carrier, David. 1987. "The Evolution of Locomotor Stamina in Tetrapods: Circumventing a Mechanical Constraint." *Paleobiology* 13 (3):326–41. https://doi.org/10.1017/S0094837300008903

Clack, Jennifer. 2012. *Gaining Ground: The Origin and Evolution of Tetrapods*. Bloomington: Indiana University Press. https://www.jstor.org/stable/j.ctt16gz91r

Daeschler, Edward, Neil Shubin, and Farish Jenkins, Jr. 2006. "A Devonian Tetrapod-Like Fish and the Evolution of the Tetrapod Body Plan." *Nature* 440 (7085):757–63. https://doi.org/10.1038/nature04639

De Visser, Argan, Joachim Hermisson, Günter Wagner, Lauren Ancel Meyers, Homayoun Bagheri-Chaichian, Jeffrey Blanchard, Lin Chao, James Cheverud, Santiago Elena, Walter Fontana, Greg Gibson, Thomas Hansen, David Krakauer, Richard Lewontin, Charles Ofria, Sean Rice, George von Dassow, Andreas Wagner, and Michael Whitlock. 2003. "Perspective: Evolution and Detection of Genetic Robustness." *Evolution* 57 (9):1959–72. https://doi.org/10.1111/j.0014-3820.2003.tb00377.x

Gilbert, Scott. 2000. "Genes Classical and Genes Developmental." In *The Concept of the Gene in Development and Evolution*, edited by Peter Beurton, Raphael Falk, and Hans-Jörg Rheinberger, 178–91. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511527296.010

Godfrey-Smith, Peter. 2009. *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199552047.001.0001

Gould, Stephen Jay. 1989. *Wonderful Life: The Burgess Shale and the Nature of History*. W. W. Norton & Co.

Gould, Stephen Jay, and Richard Lewontin. 1979. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." *Proceedings of the Royal Society of London. Series B. Biological Sciences* 205 (1161):581–98. https://doi.org/10.1098/rspb.1979.0086

Hall, Brian. 2012. *Evolutionary Developmental Biology*. Dordrecht: Springer Science & Business Media. https://doi.org/10.1007/978-94-011-3961-8

Hansen, Thomas, and David Houle. 2008. "Measuring and Comparing Evolvability and Constraint in Multivariate Characters." *Journal of Evolutionary Biology* 21 (5):1201–9. https://doi.org/10.1111/j.1420-9101.2008.01573.x

Hazelwood, Caleb. 2023. "An Emerging Dilemma for Reciprocal Causation." *Philosophy of Science*: 1–43. https://doi.org/10.1017/psa.2023.124

Huneman, Philippe. 2017. "Why Would We Call for a New Evolutionary Synthesis? The Variation Issue and the Explanatory Alternatives." In *Challenging the Modern Synthesis: Adaptation, Development, and Inheritance*, edited by Philippe Huneman and Denis Walsh, 68–110. Oxford: Oxford University Press. https://doi.org/10.1093/oso/9780199377176.003.0002

Kirschner, Marc, and John Gerhart. 1998. "Evolvability." *Proceedings of the National Academy of Sciences of the United States of America* 95 (15):8420–27. https://doi.org/10.1073/pnas.95.15.8420

Krasnov, Boris, Sergey Burdelov, Irina Khokhlova, and Nadezhda Burdelova. 2003. "Sexual Size Dimorphism, Morphological Traits and Jump Performance in Seven Species of Desert Fleas (Siphonaptera)." *Journal of Zoology* 261 (2):181–89. https://doi.org/10.1017/S0952836903004096

Laland, Kevin N., Tobias Uller, Marcus W. Feldman, Kim Sterelny, Gerd B. Müller, Armin Moczek, Eva Jablonka, & John Odling-Smee. 2015. "The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions." *Proceedings of the Royal Society B: Biological Sciences* 282 (1813):20151019. https://doi.org/10.1098/rspb.2015.1019

Lewens, Tim. 2009. "What Is Wrong with Typological Thinking?" *Philosophy of Science* 76 (3):355–71. https://doi.org/10.1086/649810

Love, Alan. 2003. "Evolvability, dispositions, and intrinsicality." *Philosophy of Science* 70 (5):1015–27. https://doi.org/10.1086/377385

Love, Alan, and Rudolf Raff. 2003. "Knowing Your Ancestors: Themes in the History of Evo-Devo." *Evolution & Development* 5 (4):327–30. https://doi.org/10.1046/j.1525-142X.2003.03040.x

Lynch, Michael. 2007. "The Frailty of Adaptive Hypotheses for the Origins of Organismal Complexity." *Proceedings of the National Academy of Sciences* 104 (1):8597–8604. https://doi.org/10.1073/pnas.0702207104

Maynard Smith, John, Richard Burian, Stuart Kauffman, Pere Alberch, John Campbell, Brian Goodwin, Russell Lande, David Raup, and Lewis Wolpert. 1985. "Developmental Constraints and Evolution: A Perspective from the Mountain Lake Conference on Development and Evolution." *The Quarterly Review of Biology* 60 (3):265–87. https://doi.org/10.1086/414425

Mayr, Ernst. 1961. "Cause and Effect in Biology: Kinds of Causes, Predictability, and Teleology Are Viewed by a Practicing Biologist." *Science* 134 (3489):1501–6. https://doi.org/10.1126/science.134.3489.1501

Mills, Susan, and John Beatty. 1979. "The Propensity Interpretation of Fitness." *Philosophy of Science* 46 (2):263–86. https://doi.org/10.1086/288865

Moczek, Armin. 2019. "The Shape of Things to Come: Evo Devo Perspectives on Causes and Consequences in Evolution." In *Evolutionary Causation*, edited by Kevin Lala and Tobias Uller, 63–80. Cambridge, MA: MIT Press.

Müller, Gerd. 2007. "Six Memos for Evo-Devo." In *From Embryology to EvoDevo: A History of Developmental Evolution*, edited by Manfred Laubichler and Jand Maienschein, 499–524. Cambridge, MA: MIT Press.

Newman, Stuart, Gabor Forgacs, and Gerd Müller. 2006. "Before Programs: The Physical Origination of Multicellular Forms." *International Journal of Developmental Biology* 50 (2–3):289–99. https://doi.org/10.1387/ijdb.052049sn

Nuño de la Rosa, Laura, and Cristina Villegas. 2022. "Chances and Propensities in Evo-Devo." *The British Journal for the Philosophy of Science* 73 (2):509–33. https://doi.org/10.1093/bjps/axz048

Nuño de la Rosa, Laura, Gerd Müller, Brian Metscher. 2014. "The Lateral Mesodermal Divide: An Epigenetic Model of the Origin of Paired Fins." *Evolution & Development* 16 (1):38–48. https://doi.org/10.1111/ede.12061

Oster, George, and Pere Alberch. 1982. "Evolution and Bifurcation of Developmental Programs." *Evolution* 36 (3):444–59. https://doi.org/10.2307/2408093

Otsuka, Jun. 2016. "A Critical Review of the Statisticalist Debate." *Biology & Philosophy* 31 (4):459–82. https://doi.org/10.1007/s10539-016-9528-0

Pavličev, Mihaela, and Günter Wagner. 2012. "Coming to Grips with Evolvability." *Evolution: Education and Outreach* 5 (2):231–44. https://doi.org/10.1007/s12052-012-0430-1

Pavličev, Mihaela, Jim Cheverud, and Günter Wagner. 2011. "Evolution of Adaptive Phenotypic Variation Patterns by Direct Selection for Evolvability." *Proceedings of the Royal Society B: Biological Sciences* 278 (1713):1903–12. https://doi.org/10.1098/rspb.2010.2113

Payne, Joshua, and Andreas Wagner. 2019. "The Causes of Evolvability and Their Evolution." *Nature Reviews Genetics* 20 (1):24–38. https://doi.org/10.1038/s41576-018-0069-z

Pence, Charles, and Grant Ramsey. 2013. "A New Foundation for the Propensity Interpretation of Fitness." *The British Journal for the Philosophy of Science* 64 (4):851–81. https://doi.org/10.1093/bjps/axs037

Pigliucci, Massimo. 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore: Johns Hopkins University Press.

Pigliucci, Massimo. 2008. "Is Evolvability Evolvable?" *Nature Reviews Genetics* 9 (1):75–82. https://doi.org/10.1038/nrg2278

https://doi.org/10.1017/psa.2024.5 Published online by Cambridge University Press

Pigliucci, Massimo, and Gerd Müller. 2010. *Evolution: The Extended Synthesis*. Cambridge, MA: MIT Press. https://doi.org/10.7551/mitpress/9780262513678.001.0001

Pokrovsky, Ivan, Andrea Kölzsch, Sherub Sherub, Wolfgang Fiedler, Peter Glazov, Olga Kulikova, Martin Wikelski, and Andrea Flack. 2021. "Longer Days Enable Higher Diurnal Activity for Migratory Birds." *Journal of Animal Ecology* 90 (9):2161–71. https://doi.org/10.1111/1365-2656.13484

Ramsey, Grant. 2006. "Block Fitness." *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 37 (3):484–98. https://doi.org/10.1016/j.shpsc.2006.06.009

Ramsey, Grant. 2013a. "Can Fitness Differences Be a Cause of Evolution?" *Philosophy & Theory in Biology* 5: e401. http://dx.doi.org/10.3998/ptb.6959004.0005.001

Ramsey, Grant. 2013b. "Driftability." *Synthese* 190:3909–28. https://doi.org/10.1007/s11229-012-0232-6

Ramsey, Grant. 2013c. "Organisms, Traits, and Population Subdivisions: Two Arguments against the Causal Conception of Fitness?" *The British Journal for the Philosophy of Science* 64 (3):589–608. https://doi.org/10.1093/bjps/axs010

Ramsey, Grant. 2016. "The Causal Structure of Evolutionary Theory." *Australasian Journal of Philosophy* 94 (3):421–34. https://doi.org/10.1080/00048402.2015.1111398

Ramsey, Grant, and Bendik Aaby. 2022. "The Proximate-Ultimate Distinction and the Active Role of the Organism in Evolution." *Biology & Philosophy* 37 (4):31. https://doi.org/10.1007/s10539-022-09863-0

Rayner, Jeremy. 1988. "The Evolution of Vertebrate Flight." *Biological Journal of the Linnean Society* 34 (3):269–87. https://doi.org/10.1111/j.1095-8312.1988.tb01963.x

Runnegar, Bruce. 1987. "Rates and Modes of Evolution in the Mollusca." In *Rates of Evolution*, edited by K. S. W. Campbell and M. F. Day, 39–60. London: Allen and Unwin. https://doi.org/10.4324/9780429293849

Schlosser, Gerhard, and Günter Wagner. 2004. *Modularity in Development and Evolution*. Chicago: University of Chicago Press.

Scholl, Raphael, and Massimo Pigliucci. 2015. "The Proximate–Ultimate Distinction and Evolutionary Developmental Biology: Causal Irrelevance Versus Explanatory Abstraction." *Biology & Philosophy* 30:653–70. https://doi.org/10.1007/s10539-014-9427-1

Stoltzfus, Arlin. 2017. "Why We Don't Want Another 'Synthesis.'" *Biology Direct* 12 (1):1–12. https://doi.org/10.1186/s13062-017-0194-1

Villegas, Cristina, Alan Love, Laura Nuño de la Rosa, Ingo Brigandt, and Günter Wagner. 2023. "The Conceptual Roles of Evolvability across Evolutionary Biology: Between Diversity and Unification." In *Evolvability. A Unifying Concept in Evolutionary Biology?*, edited by Thomas Hansen, David Houle, Mihaela Pavličev, and Christophe Pélabon, 35–54. Cambridge, MA: MIT Press. https://doi.org/10.7551/mitpress/14126.003.0005

Waddington, Conrad. 1942. "Canalization of Development and the Inheritance of Acquired Characters." *Nature* 150 (3811):563–65. https://doi.org/10.1038/150563a0

Wagner, Günter, and Lee Altenberg. 1996. "Perspective: Complex Adaptations and the Evolution of Evolvability." *Evolution* 50 (3):967–76. https://doi.org/10.1111/j.1558-5646.1996.tb02339.x

Wimsatt, William. 1986. "Developmental Constraints, Generative Entrenchment, and the Innate-Acquired Distinction." In *Integrating Scientific Disciplines*, edited by William Bechtel, 185–208. Dordrecht: Springer. https://doi.org/10.1007/978-94-010-9435-1_11

Wimsatt, William. 2015. "Entrenchment as a Theoretical Tool in Evolutionary Developmental Biology." In *Conceptual Change in Biology*, edited by Alan Love, 365–402. Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9412-1_17

Young, Nathan, and Benedikt Hallgrímsson. 2005. "Serial Homology and the Evolution of Mammalian Limb Covariation Structure." *Evolution* 59 (12):2691–2704. https://doi.org/10.1111/j.0014-3820.2005.tb00980.x

Cite this article: Ramsey, Grant and Cristina Villegas. 2024. "Developmental Channeling and Evolutionary Dappling." *Philosophy of Science* 91 (4):869–886. https://doi.org/10.1017/psa.2024.5