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On the explanatory roles of natural selection

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Abstract. Can selection explain why individuals have the traits they do? This question has generated significant controversy. I will argue that the debate encompasses two separable aspects, to detrimental effect: (1) the role of selection in explaining the origin and evolution of biological *traits* and (2) the implications this may have for explaining why *individuals* have the traits they do. (1) can be settled on the basis of evolutionary theory while (2) requires additional, extra-scientific assumptions. By making a distinction between traits affected by a single factor and traits affected by multiple factors I show that selection can, under certain conditions, help explain the origin of traits. Resolving the first aspect enables us to critically assess the various incompatible and independent philosophical commitments made within the second aspect of the debate.

Introduction

Explanations in evolutionary biology make extensive use of natural selection. This much is uncontroversial. The controversy emerges when we look at what selection actually explains, especially with respect to the various traits of individual organisms. Some (Dawkins 1986; Neander, 1988, 1995a, b; Matthen 1999, 2002, 2003) claim that selection plays a "creative" role; it can help explain why individuals have the traits they do. Others (Cummins 1975; Sober 1984, 1995; Walsh 1998; Lewens 2001; Pust 2001) claim that selection plays merely a negative role; it only eliminates variants and so cannot explain why an individual has particular simple or complex properties. The debate over the right explanatory role for selection lacks a resolution.

Distinguishing two aspects of the debate will help provide such a resolution. The two problems, often discussed as one, concern (1) the role of selection in explaining the origin and evolution of biological *traits* and (2) the implications this may have for explaining why *individuals* have the traits they do. I will argue that the confusion over (1) arises only by ignoring a distinction between traits affected by *multiple* factors and traits affected by a *single* factor. *If* several factors affect a trait *and* selection can act on the factors individually *then* selection will help explain how traits originate. In this sense selection has "creative" power. Settling the first aspect will help clarify the issues relevant to the second aspect. I will argue that the resolution to (1) suggests certain implications for (2) but the final conclusion will depend on a variety of philosophical issues quite independent from evolutionary theory.

1. Evolutionary explanations

Sketching the context of the debate will aid the arguments to come. In this section I will describe the basic positions and divide the debate into two entangled but independent aspects: (1) the role of selection in evolutionary explanations of traits and (2) whether selection can help explain why individuals have the traits they do.

Behind the debate lies a deep commitment to a distinction between *developmental* and *variational* explanation (Sober 1984: 147–155). Developmental explanation addresses how individuals change over time and so explains population changes by aggregating the developing individuals. Variational explanation, on the other hand, assumes that the individual remains constant (Sober 1984: 149, 155). On this strategy we can explain population level changes by the differential reproductive success of static variants.

Based on this view, Elliott Sober makes the argument that selection can explain facts about populations but cannot explain facts about the individual in isolation.[1] Selection explains why we all (the human population) have opposable thumbs but not why I have an opposable thumb. We would give a developmental explanation of the latter fact: I inherited the trait from my ancestors and it developed normally. The sieve of selection can act only when there is variation and there must be a population for variation to exist. So selection can explain changes in the population's composition, but to explain why an individual has certain traits we look solely at her genealogy and ontogeny.

Karen Neander does not deny the explanatory distinction but opposes Sober's consequence:

> Even if selection does not explain change in a population by explaining changes in individuals, it can still explain why individuals have the properties they do by explaining changes in populations (Neander 1995b: 71–72).

Past changes in the population will affect what types of traits remain and so selection may help explain why individuals have those traits. On Neander's view, cumulative selection processes help explain why traits originate and so explain why particular individuals have them (1995b). Replies to the "positive" position – that selection is part of the explanation for why *individuals* have the traits they do – usually draw upon the distinction between variational and developmental explanations. Due to certain explanatory or metaphysical assumptions population level properties must receive variational explanations and individual level properties must receive developmental explanations. So while selection, a variational-style mechanism, can explain why there are adaptive traits fixed in a particular population, it cannot explain why particular individuals have those traits. Development plus inheritance explain why an individual has a trait and random mutation, according to this "negative" view, explains how new traits originate; selection plays no part in this explanation.

Part of the issue here is about explaining the origin of *traits*. It is not clear which kind of explanation, variational or developmental, we should use to address why a trait first emerges since it occurs *within* a population but also *in* some particular individual. There are two ways to phrase the question of origin.[2] (i) Why does the frequency of a trait change from 0 to some quantity greater than 0? Or, (ii) Why does some token individual first appear with a trait? Prima facie, a variational explanation only seems appropriate for (i) while the explanation for (ii) would refer to development and new mutations. But we cannot assume this is true at the outset. How to explain the origination of a trait and whether such explanations are relevant to explaining properties of individuals are the issues under debate.

The focus on origin explains why part of the debate concerns the "creative power" of selection. Intuitively, natural selection seems to create novelties and complex adaptations. Without it many of the complicated and fascinating characteristics of organisms would, most likely, never emerge. The creativity of selection seems closely related to the phenomenon of origination of traits. So the idea that natural selection has creative power can be understood as a claim that selection explains the origin of a trait.

The philosophical discussion of this question encompasses two separable aspects.[3] The first concerns whether selection can *ever* explain the origin of *traits*. This part of the debate involves disagreements about the conceptual role of natural selection in evolutionary theory. The second concerns what implications the conceptual role of selection may have for explaining why *individuals* have the traits they do. Both Sober and Neander are interested in taking positions on both issues whereas subsequent debate has begun to focus on the second. For example, Mohan Matthen (2002, 2003) and Joel Pust (2001) argue that taking a position on the second aspect depends on a metaphysical assumption called *origin essentialism*, but they disagree on the viability of such an assumption. The first aspect can be settled on the basis of evolutionary theory and independently of philosophical views about how we explain why individuals are the way they are, or so I will argue.

2. The role of selection

Selection can explain why a trait originates, if it makes that trait more likely to emerge. My supporting argument will use a distinction between traits affected by multiple factors and traits affected by a single factor. In idealized contexts these factors are usually equated with genes. But since selection can act on things other than genes, the argument offered here applies more generally to any case where many factors affect a trait. Abstracting away from genes clarifies this.[4] My approach has two important ties to the literature. First, my distinction is closely related, but not identical, to one used in Neander's arguments (1995a: 584). Second, John Endler (1986), a biologist not in the debate, makes exactly my point using this distinction but addressed it only briefly. Here I will argue in more detail that natural selection can explain the origin of a trait by shaping populations in ways that make well-adapted *combinations* of genes or factors more likely to evolve. Let me explain how this works with a short example.[5]

Consider two loci of a haploid organism, each with two competing alleles. Locus one has the alleles *A* and *a* while locus two has *B* and *b*. Individuals with the *AB* combination do much better than those with *Ab*, *aB*, *ab*. If the *AB* combination emerges then it should quickly dominate the population. Now we ask how the *AB* combination can evolve from a population made up of only *ab* individuals. The role of selection becomes clear when we consider two contrasting cases, one with a selective gradient and one without. In the first case the combinations *Ab* and *aB* do better than *ab* but not *AB*; this represents the selective gradient. In the second, *Ab*, *aB*, *ab* all do equally well. The selective gradient in the first case makes it much more likely for the *AB* combination to emerge. A look at the dynamics makes this clear.

Given that mutations are rare events, the probability that both a mutation $a \rightarrow A$ and $b \rightarrow B$ occur in the same individual and in the same generation is practically zero.[6] So, within an *ab* population, an individual will most likely only come to possess at most one new mutation. Here selection becomes relevant. In the first case, if an $a \rightarrow A$ mutation occurs selection will favor the *Ab* type over the *ab* type. Thus we expect the *Ab* type to increase in frequency and eventually take over the population. In the second case an $a \rightarrow A$ mutation is effectively neutral and will experience random drift. Chances are exceedingly small that it will take over the population. Suppose that sometime later a $b \rightarrow B$ mutation occurs. The probability that this mutation occurs in an *Ab* individual, and thus form the favored *AB* combination, is much higher in the first case than in the second. Because selection can retain the initial mutation of $a \rightarrow A$ in the first case it makes the *AB* combination far more likely to evolve. In the second case there is no mechanism for maintaining the initial mutation; it can only drift randomly and will most likely be lost. So a $b \rightarrow B$ mutations will most likely occur in an *ab* individual, not in an *Ab* individual. Hence natural selection, through the action of a selective gradient, makes accumulating favorable combinations of mutations much more likely.

When traits are affected by a combination of genes or factors we can appeal to the role of selection in forging the combination. Consider again the above example about selective gradients. Suppose we want to know why the well-adapted *AB* combination exists in some population. In the case without a gradient selection explains why the *AB* type proliferates and persists in the population *once it appears* but it does not explain why *AB* appears at all. Only an improbable pattern of mutation and drift explains the origination of the *AB* combination in this case.

In the case with a selective gradient our explanation would be different, for the gradient explains, with reasonable probability, why we see the well-adapted *combination* (*Ab*) appearing at all. Because selection helps explain the origination of *AB* it helps explain why *AB* exists in a population. Mutation and inheritance are no longer sufficient. Selection significantly increases the probability that combinations of favorable mutations will emerge in populations. The point gains force when we extend the case to many loci. With a large, well-adapted combination of genes, each under selection, simple mutation and inheritance cease to explain why the well-adapted combination evolves rather than some other combination. Without selection it becomes *extremely* unlikely that these well-adapted combinations will ever emerge.

So selection can, in part, explain why traits originate. As the example makes clear, this type of explanation requires two premises to succeed. First, there must be combination of factors; the *trait* in question must be a multi-factor trait. Second, there must be positive selection for each factor. If a case meets both premises then selection plays an integral role in explaining why it evolved.

By identifying an origin for a multi-factor trait I make two innocuous simplifications. First, a combination of genes or factors does not have a clear point of origin. Selection must act over time to accumulate well-adapted combinations. This does not present a problem since the ability of selection to combine favorable mutations, and thus explain the origination of combinations, does not depend on having a specific origination event. To simplify the discussion I have referred to the whole process as origination. Second, the process of recombination can break up and shuffle combinations. This introduces an added complication that may work against selection in some cases. Even so, selection would still have the same role in assembling and maintaining combinations. Recombination may work against selection but it does not alter its explanatory role.[7]

The similarity of my distinction between single factor and multi-factor traits and Neander's distinction between single-step and cumulative selection processes should be apparent. But there is one key difference. She claims that a selection process must only be cumulative to help explain the origin of a trait. Like Neander I think a history of cumulative selection is necessary, but unlike her I do not find the condition sufficient. Another fact about the trait besides history is relevant: the trait must be affected by a combination of factors. On Neander's view cumulative selection has a privileged explanatory status because previous trials affect the probability of later outcomes (1995b: 72). But selection must do this *in the right way* by accumulating the multiple beneficial factors that affect a given trait. The difference becomes clear upon closer inspection of one of Neander's key examples (1995b: 77). The problem case concerns situations where the order of mutation seems to matter. Consider three traits, A, B, and C, of increasing adaptive value. Trait A must first change to trait B before the best trait, C, can evolve. Suppose each trait is a single *gene* trait. Then it seems that selection increases the chance of trait C evolving. Here we have a single gene case where selection has an apparent role to play in explaining the origination of trait C.

This necessary order of mutations can, however, occur for different biological reasons. One principled way that the order will matter is if there is a *combination* of factors involved. Otherwise it is not clear why trait A cannot change directly to trait C. If, for example, the gene involved codes for a protein where one structural change ($A \rightarrow B$) must occur before a different change ($B \rightarrow C$) becomes advantageous, then we are dealing with a combination of *two* relevant factors. *Both* must occur before the best trait, C, can emerge. In this case there are *multiple* factors that affect the trait. Abstracting away from *genes* as the sole kind of factor capable of undergoing selection makes this clear. Shifting the framework down treats the functional gene as the relevant trait made up of a combination of aspects: key substitutions that effect adaptive amino acid replacements. One structural change must occur and be preserved by selection for the second to occur. The situation, then, is not a genuine single *factor* case. In this case selection explains the necessary order of mutations phenomenon by playing its same role in explaining the origination of factor combinations.

Suppose instead that the biological explanation is such that there is only a single factor that governs the changes between A, B, and C. Perhaps one mutation at a particular position ($A \rightarrow B$) alters the environment in such a way that then makes the next mutation at the same position ($B \rightarrow C$) advantageous.

Neander claims that selection explains the origin of trait *C* in this case. But, as Sober (1995: 393) recognizes, this is mistaken. If there is a definite single factor governing these changes then the molecular mechanisms of mutation explain the origin of each trait. No combination of factors exists. So selection cannot accumulate these factors and increase the chance that the well-adapted *combination* evolves. The same consideration applies to interactions between different traits. Consider two adaptive traits *P* and *Q* that interact so that *Q* must first evolve before *P* becomes advantageous. Suppose both *P* and *Q* are single factor traits. Selection does not explain the origin of *P* or *Q* because neither are affected by a combination of factors. If we seek to explain the origin of the trait complex *PQ*, then selection can act on the two factors that affect the trait complex. Provided there is a selective gradient for the factors involved selection will help explain the origin of the whole *trait complex*.[8]

As the example with selective gradients demonstrates, selection *can* explain how traits originate provided that the target of explanation counts as a multi-factor trait. This is the crucial point within evolutionary theory and settles the first aspect of the debate.

3. Explanations for individuals

Does selection ever explain why *individuals* have the traits they do? Part of this question concerns the role of selection in explaining the evolution of biological traits. Another involves purely philosophical issues about explanation. With the first aspect settled, I want to examine how the positive view draws an intuitive implication for the second and address how one might resist the implication. This line of inquiry will establish that any view on what explains the properties of particular individuals must involve commitments beyond evolutionary theory. But evolutionary theory makes some commitments look more plausible than others.

Selection has creative power; it can explain why traits originate under certain conditions. This has no immediate logical ties to explaining why *particular individuals* have certain traits. But it does entail that selection can help explain why *some individual or other* has certain traits. This is equivalent to explaining why a trait exists in a population. If a trait occurs at a non-zero frequency then there must be some individuals with that trait. Populations are collections of individuals. So it follows that if selection helps explain the origin of a trait then it helps explain why *some* individuals have that trait. The second aspect of the debate is mainly generated by disagreement over the relevance of this explanation of origin to an explanation of why *particular* individuals have such traits.

The plausibility of the positive view trades on one intuitive way of drawing an implication by adopting an *explanatory continuity* commitment. Within the current framework, the explanation of why a particular individual has a trait involves explaining why the trait emerged in some ancestral individual. So an explanation of the origin of a trait is part of the explanation of why an individual – Bob the bacterium, say – has that trait. On this view the distinction between multi-factor traits and single factor traits becomes relevant to the second aspect as well.

To illustrate this point consider a short example. Suppose we want to explain (i) why a population of bacteria evolved antibiotic resistance and (ii) why Bob the bacterium exhibits antibiotic resistance. Suppose further that antibiotic resistance is a trait affected by a combination of genes and that there is selection for any degree of partial resistance. Our explanation of (i) will then appeal to selection to address both why the trait emerged and why it took over the population. Given the limitation of inheritance, it seems that our explanation of (ii) should address origination as well. If Bob is not the first individual to exhibit the trait then an explanation of why he has antibiotic resistance must address how he got the trait and how the trait came to be around in the first place. In other words, an explanation of why an individual has a particular trait includes a story of how he *inherited* it and how the trait became *inheritable*. In this case selection plays a role in explaining the latter. If Bob is the first individual to exhibit antibiotic resistance then he is the "some individual or other" that first appears with the well-adapted combination of genes. He acquires the last beneficial mutation *and* inherited the relevant genes to complete the well-adapted combination. Selection helps explain the pattern of inheritance and accumulation of mutations that eventually leads to the well-adapted *combination* occurring in Bob (rather than some other combination).[9]

Proponents of the negative view resist this implication by shifting the target of explanation. The origin of the *individual* is what matters for explaining why *individuals* have the traits they do.[10] The success of this maneuver depends on accepting different independent commitments.

The *explanatory preemption* commitment takes the view that developmental explanations of individuals *always* preempt variational explanations of any kind. So a variational explanation of the origin of some trait is never relevant to the explanation of why a particular individual has that trait (Sober 1984, 1995). On this view the developmental explanation for how I came to have an opposable thumb is the sufficient explanation of my trait; it preempts any variational explanation of the trait's evolutionary origin. One clear way of stating the view makes a rigid distinction between trait types and trait tokens. Selection may explain why there are trait types in populations but it never explains why individuals manifest trait tokens (Walsh 1998). As plausible as this commitment may seem, nothing in evolutionary theory entails it. The distinction between variational and developmental explanation distinguishes two different strategies of explaining how populations change. Whether *population* change is relevant to explaining why *individuals* have certain properties is an independent issue. One can consistently accept evolutionary biology and the view that the evolutionary trajectory of a population is relevant to explaining why individuals in that population have the traits they do. So an explanation of why Bob has antibiotic resistance may cite his membership in a particular population with a particular evolutionary history, a history where selection played a prominent role. But, of course, we can consistently deny the relevance of past evolution to this question about Bob as well. The important point is not which explanatory commitment is justified, only that they require *independent* justification.

To support the doctrine of preemption, Sober gives a number of examples to show that, for any given individual, even if selection did *not* act the individual would still have the exact same traits that it does (Sober 1995: 386).[11] If Sober is denying that selection can explain how *traits* originate then his arguments misstep by implicitly assuming that all traits are single factor traits. The clearest expression of this implicit assumption occurs in his reply to Neander. He claims:

> My reply [to Neander's necessary order of mutations example discussed above] is that selection helps explain the gene found in a mutated zygote only if it helps explain the gene found in the parent. However, it does not explain this fact about the parent, though it does explain why the parental generation is 100% G_2 (Sober 1995: 393).

This holds for *traits* only if the trait is affected by a *single factor*. If there is no combination involved Sober is right to deny Neander's claim that selection helps explain how the trait originated. Selection cannot explain why some individual has a particular *factor*, in Sober's case a single gene. The molecular causes of mutation explain the origin of single factor traits. Here the explanatory role of selection is mostly limited to population level properties like persistence.

This argument, however, does not extend to the multi-factor trait case. If we want to explain why some individuals have this kind of trait then we must explain why they have the particular *combination* of factors that affect that trait. If there exists a selective gradient for the separate factors that affect the trait, then selection is part of the explanation of why individuals have the well-adapted combination (rather than some other combination). So, in a sense, selection can act on parts or aspects of a trait by acting on each of the multiple factors that affect the trait. Selection can explain why the parents have the well-adapted combination and so, by Sober's lights, it explains why the individual offspring has it as well. How does this point affect the explanation of why Bob has the polygenic trait of antibiotic resistance? This depends on our extra-scientific commitments. As the quote suggests, Sober endorses the preemption commitment: the developmental explanation of why Bob has the trait preempts any variational explanation of why the trait originated. Sober argues for this conclusion based on the claim that a parent's reproductive success does not influence the traits passed on to offspring (1995: 391). But in the case of multi-factor traits, where the inheritance of combinations is at issue, the reproductive success of parents, grandparents, great-grandparents, etc., *does* influence what *combinations* are passed on to offspring. Sober's conclusion follows for the multi-factor trait case only with the addition of the preemption commitment.

Denis Walsh attempts to defend Sober and argues against the idea that origination matters for the explanation of an individual's traits by making a distinction between trait types and trait tokens (Walsh 1998: 261). According to Walsh, selection may explain the presence and emergence of trait types in a population but it does not explain why individuals manifest trait tokens. But this begs the question against the positive position by denying the continuity commitment in favor of the preemption one. Under the continuity commitment, an explanation of why an individual has some trait token (rather than a token of a different type) includes an explanation of why the trait type occurs in the population. Moreover, for a trait type to emerge in a population there must emerge an individual with the trait token; we cannot have one without the other. On the continuity commitment it follows that an explanation of a particular individual's trait token must cite the fact that the individual belongs to the lineage in which the original token emerged. In the multi-factor case selection can explain why some trait tokens, and thus trait types, initially appear in a population. Therefore selection can explain why some later individual has a token of that trait type. Only by endorsing the preemption commitment can we avail ourselves of the type-token distinction in the way Walsh uses it.

The *essentialist* commitment takes certain facts about an individual to be essential to the identity of that individual. One possible view, called *origin essentialism*, insists that an individual must necessarily have the parents that it in fact did (Pust 2001). Under this commitment the evolutionary trajectory of an individual's lineage is never relevant to explaining why individuals have the traits they do. If the evolutionary trajectory had taken a different course, then different individuals with different traits would have survived. For an individual to have sufficiently different traits, it would have to have different parents.[12] So that individual would not be identical with the individual whose properties we are trying to explain. Selection is irrelevant to explaining why Bob exhibits antibiotic resistance because if selection had not occurred, allowing certain ancestors to survive, then Bob would not exist. Selection may explain why Bob exists, but it does *not* explain why *he* has antibiotic resistance (rather than sensitivity). Again, nothing in evolutionary theory entails such a metaphysical commitment.[13] On some views of identity, it will turn out that we cannot evaluate counterfactuals about Bob that posit a different lineage of ancestors. From the vantage point of evolutionary theory, however, nothing militates against evaluating counterfactual questions about what traits Bob might have had if the evolutionary trajectory of his lineage had been different. In fact, evolutionary theory seems to give us the resources to evaluate these counterfactuals. Using genetics and developmental biology we can ask how an individual might be different had it inherited different genes that neither actual parent possessed.[14] But I do not want to argue about metaphysics here. The key point: if this metaphysical commitment is to decide the second aspect of the debate, it must do so on grounds quite independent from science.

Negative positions on the second aspect of the debate – that the role of selection in evolutionary theory has no implications for explaining why individuals have the traits they do – depend on independent explanatory or metaphysical commitments. The positive position also rests on an independent commitment. The view makes a commitment to explanatory continuity: the explanatory scope of evolutionary theory should not be limited by extra-scientific views on explanation or metaphysics. Since individuals belong to a lineage with an evolutionary history, that history helps explain why individuals have the traits they do. Part of the explanation of why Bob has antibiotic resistance recognizes that Bob is part of a bacterial population with a particular evolutionary trajectory. Evolutionary theory gives us the resources to sensibly answer counterfactual questions about what traits Bob might have had if the evolutionary trajectory of his population had been different. But such a conclusion is possible only if we embrace the *independent* commitment of continuity. From the scientific point of view this commitment seems the most plausible.

To summarize the state of play, the debate over whether selection can explain the properties of individuals involves two aspects. The demonstration that selection can explain the origin of traits under certain conditions settles the first aspect. A full resolution, however, depends on settling the second aspect of the debate. But, as we have seen, the implications of this explanatory role for selection in evolutionary theory depend on independent commitments. The preemption and essentialist commitments conflict with the continuity commitment. So negative positions will accept the preemption or essentialist commitment and oppose the continuity commitment, whereas positive positions opt for continuity over the alternatives.

4. Conclusion

Hence the distinction between single factor traits and multi-factor traits vindicates the spirit of Neander's point with respect to the explanatory role of natural selection. By explaining past changes in the population, selection explains why well-adapted *combinations* tend to emerge and thus why some individual or other has that combination rather than another. Whether this fact about evolutionary theory allows us to explain why a *particular* individual has this trait depends on what independent commitments we are willing to accept.

Dividing the debate into two aspects preserves the insights of Sober. We can still assert, along with Sober, that selection does not explain population changes by explaining changes in individuals. We respect the spirit of the distinction between variational and developmental explanations. Whether we should reify this distinction and insist that explaining population changes *never* explains the properties of particular individuals is an independent issue. This does not change the fact that selection has creative power – it helps explains why complex, multi-factor adaptations originate. Separating this first aspect from the various extra-scientific views we can adopt regarding explanation, metaphysics, and the philosophical priority of science clarifies the debate and allows for critical assessment of these commitments.

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Notes

[1] In the context of a population Sober thinks selection can explain two kinds facts about individuals: why particular organisms survive and why they enjoy a particular degree of reproductive success (Sober 1984: 152). I leave this out because it does not affect the current issue of explaining why individuals have particular traits.

[2] Thanks to Sober (personal communication) for suggesting this way of putting the issue.

[3] Neander identifies the whole issue as the "Creative Question" (Neander 1995b: 63), and does not explicitly separate the theoretical issue from its purported implications for explanation.

[4] Of course a single factor or gene is never *solely* responsible for a phenotypic trait. Proper expression requires that the rest of the organism develops properly. But it is possible that changes in a trait can be effected by changes in only a single factor.

[5] I first came across this example in a lecture by Peter Godfrey-Smith; my explanatory gloss is a departure. Neander presents a similar example with a more restrictive assumption in her (1995b). Although my development differs slightly, it is worth quoting Endler's short proposal in *Natural Selection in the Wild*:

> There is only one way in which an understanding of natural selection might help to explain the origins of new traits or trait values, and that is the case where an evolutionary change requires one or more intermediate steps. For example, a given morphological change may require two genetically different adjustments in the morphogenic "program," or the modification of two different enzymes or regulatory pathways in the developmental genetic network. For brevity, call these two mutations (in the general sense) *A* and *B*. Most mutations are rare events, so the probability that both *A* and *B* occur in the same individual or family could easily be as low as 10^{-10}. If the frequency of the new *A* did not change subsequently, and mutation at both "loci" continued, the probability of forming an individual with both *A* and *B* would remain quite small. On the other hand, if *A* were to occur and increase to a high frequency as a result of natural selection, the probability that *B* appears in at least one *A* individual is greatly increased. Consider a third variant *C* which would work as well with *B* as does *A*, but which is not favored by natural selection unless it is present with *B*. It is clear that the combination *AB* would be more likely or more common than *CB*. The effect would be even greater if *B* were functionally impossible unless *A* or *C* occurred first. Thus natural selection may affect the patterns of the origins of combinations of traits, even though it will not explain the mechanisms of their origins (1986: 246).

[6] To be more precise, if the mutation rate per token allele per generation for both $a \rightarrow A$ and $b \rightarrow B$ is μ then the probability that both mutations occur in each allele of one individual equals μ^2.

[7] This points to an interesting evolutionary consequence. If recombination tends to break up favorable combinations, then the benefits should out weigh this cost. See, for example, Feldman, Otto, and Christiansen (1997) for the theoretical development of these issues.

[8] Thanks to an anonymous referee for helping make this point clear.

[9] Matthen (1999: 146) argues for explanatory continuity based on the premise that in sexually reproducing populations selection affects what mates are available. Tim Lewens (2001) replies that sexual reproduction is not relevant, and so Matthen's arguments are flawed. My view is that selection can explain the origin of traits if it can act on multiple factors that affect the trait. This can occur in either sexually or asexually reproducing populations. Whether this is relevant to explaining why particular individuals have the traits they do requires accepting the separate claim of explanatory continuity. Matthen's later case for continuity seems to support this conclusion (2003: 302–303).

[10] Pust (2001) makes this especially clear.

[11] For the classroom example see (Sober 1984: 148–152) while for more detailed examples see (Sober 1995). Both Walsh (1998) and Pust (2001) give thorough, if not impartial, reviews of examples discussed by Sober and Neander.

[12] In sexual organisms an individual could have the same parents and have different traits so long as the individual inherited a different subset of the parental genes. But why can we not suppose further that an individual's parents had different traits and avoid this limitation? It seems origin essentialism must include the assumption that the parents' traits or genes are

also essential to their identity as well. Sober (2001) makes it clear that origin essentialism is not equivalent to gene (or factor) essentialism.

[13] Matthen (1999, 2002, 2003) argues forcefully for this position.

[14] Matthen (2002, 2003), in his replies to Pust (2001) and Lewens (2001), provides a plausible alternative metaphysical framework conciliate with the explanatory continuity commitment and well equipped to make sense of evolutionary theory without appealing to essences.

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