**Bivalent Selection and Graded Darwinian Individuality**

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ABSTRACT

Philosophers are approaching a consensus that biological individuality, including evolutionary individuality, comes in degrees. Graded evolutionary individuality presents a puzzle when juxtaposed with another widely embraced view: that evolutionary individuality follows from being a selectable member of a Darwinian population. Population membership is, on the orthodox view, a bivalent condition, so how can members of Darwinian populations vary in their degree of individuality? This article offers a solution to the puzzle, by locating difference in degree of evolutionary individuality at the level of population lineages, some of which are more Darwinian than others. In doing so, it sheds light on graded individuality in overlapping and nested population lineages, such as those that arise in multilevel selection and symbiotic collectives.

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**1 Introduction**

Two trends shaping contemporary philosophy of biological individuality are the embrace of pluralism, which recognizes multiple kinds of biological individuals, and graded individuality, the idea that individuals come in degrees (Pradeu [2016], Haber [2016]). Both trends are exemplified in Peter Godfrey-Smith’s ([2009]) distinction between organisms and Darwinian individuals, the former being units of physiological integration and the latter being units of selection according to evolutionary theory, both of which admit of degrees. It’s easy to see how one thing can be more tightly integrated physiologically than another. A nucleus, for example, is physiologically integrated and hence individuated to a certain degree, though to a lesser degree than the cell of which it is a functional part (Booth [2014]). It’s harder to see how evolutionary individuality can come in degrees, as whether an entity such as a nucleus is the targetor objectof natural selection (Mayr [1997]) seems to be a yes or no kind of question. The status of being one thing that might be selected appears to come in a single degree, and this generates a puzzle when juxtaposed with graded evolutionary individuality; I seek here to resolve that puzzle.

The puzzle arises from a widely held background assumption that population membership, like set membership, is a bivalent condition. Bivalent population membership is assumed in the equations of population genetics, and, as I argue below, is a metaphysical consequence of David Hull’s ([1976]) individuality thesis. While graded population membership could be posited as a mechanism of graded evolutionary individuality, and while there might be good reasons to countenance graded membership in some evolutionary contexts, the view that each Darwinian population is constituted by some whole number of members at any given time is an important theoretical assumption, so it is worth considering whether graded Darwinian individuality forces a revision of this widely held view[[1]](#footnote-1). I show that bivalent selection need not be abandoned in order to accommodate varying degrees of evolutionary individuality, as it remains a background assumption in Godfrey-Smith’s account of graded Darwinian individuality.

The account of Darwinian populations offered here I take to be the received view, so readers familiar with Godfrey-Smith’s population concept should find my solution to this puzzle unsurprising. Those immersed in recent literature that emphasizes the effects of causal interactions on population identity and degree of Darwinian character (Matthewson [2015]), however, might be drawn to think of graded membership as a way to account for varying degrees of Darwinian individuality. In section four, I examine two population structures that might be modeled in terms of graded membership, and I explain why those structures are not the kind of populations whose membership determines degree of Darwinian individuality. This paper seeks to show, using a standard Darwinian population model, how natural selection operating simultaneously at different levels impacts evolution to varying degrees.

Key to my argument is that while being a unit of selection is a bivalent condition, it is also a relative condition, in that each Darwinian individual is a unit of selection only in relation to the evolving Darwinian population lineage of which it is a part. Because selection happens at multiple levels, Darwinian population lineages can be nested and overlapping, both within species, as in the case of multilevel selection, and across species, as in the case of symbiotic collectives which function as evolutionary individuals. The account of bivalent selection and graded evolutionary individuality articulated here provides a metaphysical framework for understanding differences in the evolutionary significance and hence individuality of nested and overlapping population lineages, while preserving the widespread assumption of bivalent selection.

**2 The Puzzle of Graded Evolutionary Individuality**

Richard Lewontin ([1970]) identifies units of selection as reproducing members of evolving populations, a view adopted by David Hull ([1976]) when he conceives of biological individuality in terms of evolutionary role. Hull distinguishes between two kinds of evolutionary individuals: units of selectionare individuals which are selected, while units of evolutionare individuals that evolve. Following Lewontin and Hull[[2]](#footnote-2), Godfrey-Smith ([2009]) argues that units of selection are Darwinian individuals(members of evolving Darwinian populations), but Godfrey-Smith’s formulation differs from his predecessors’ in that it conceives of Darwinian individuality as a graded condition. If being a unit of selection/Darwinian individual turns on being a reproducer, and if the capacity to reproduce comes in degrees, as Godfrey-Smith argues, then it follows that Darwinian individuality must also come in degrees.

Graded Darwinian individuality presents a puzzle, however, if membership in a Darwinian population is taken to be a bivalent condition. Selection pressure will of course favor some members of a population more than others, but the most and least fit members of a population are nonetheless units of selection to the same degree, insofar as they are equally constituents that could be selected for multiplication in or elimination from their population. Graded membership might play a role in more complex population models, such as Jacob Stegenga’s ([2014]) massively multi-dimensional population pluralism, or John Mathewson’s ([2015]) exchangability population model, both of which represent the effects of graded ecological interactions on population identity and evolutionary significance. Bivalent membership is assumed, however, in Darwinian populations, whose members are necessarily linked by reproductive interactions, which come in a single degree.[[3]](#footnote-3)

The inclusion of ecological parameters in a population model does not force one to countenance graded population membership. Millstein’s CIPC grounds population identity in both reproductive and ecological interactions, but explicitly denies graded or partial population membership ([2015], p.8). Godfrey-Smith ([2009]) notes a link between ecological interactions and reproductive competition, such that varying degrees of ecological interaction can be reflected in the degree to which a population is Darwinian, but he does not claim that varying degrees of ecological interaction result in populations with graded membership. The population concepts articulated in Stegenga ([2014]) and Mathewson ([2015]), on the other hand, might allow for populations with graded membership (personal communication with both authors), though no explicit claim of graded population membership appears in these articles.

The assumption of bivalent population membership is reflected in the equations of population genetics, which represent trait frequencies as a ratio of individuals having a trait to the total number of individuals in the population; whenever total population is counted or calculated, bivalent population membership is assumed. Bivalent population membership also follows as a metaphysical consequence of the part-whole relation between units of selection and units of evolution articulated in Hull’s ([1976]) individuality thesis, as on the ‘orthodox view’ (Haber [2015]), the parthood relation is bivalent (more on this below). If we want to acknowledge graded evolutionary individuality without modifying the equations of population genetics or abandoning the view that evolutionary lineages are individuals composed of selectable parts, then we will have to resolve the following puzzle.

*Evolutionary individuality follows from being a member of a Darwinian population, and membership in a Darwinian population is an all or nothing proposition. How can evolutionary individuality come in degrees?*

**3 The Solution**

This paper offers a solution to the puzzle which embraces pluralism, and, I think, represents the correct interpretation of Godfrey-Smith’s graded evolutionary individuality. If differences in magnitude of evolutionary individuality are understood to arise at the level of populations, rather than at the level of individual reproducers, then membership in a Darwinian population, and hence status as a unit of selection, can be understood as a bivalent condition, even while members of some populations attain a higher degree of evolutionary individuality than members of other populations. Godfrey-Smith describes a spectrum of Darwinian populations, from paradigm to marginal, and argues that selection from paradigm populations has a greater impact on overall evolution than selection from populations that are only marginally Darwinian. While members of all populations on the Darwinian spectrum function equally as units of selection, the degree of individuality attained by each unit of selection grades up or down with the degree to which its population is Darwinian.

To say, as Godfrey-Smith does, that a particular buffalo is a Darwinian individual to a greater degree than a buffalo herd is not to assert that the former is a unit of selection to a greater degree than the latter, but rather acknowledges a state of affairs in which selection due to differential fitness between particular buffalo has a greater effect on buffalo evolution than selection due to differential fitness between herds. A particular buffalo and a buffalo herd are both selectable members of Darwinian populations, so both are equally units of selection in the sense of being one thing that might be selected, but because selection from the former population has a greater impact on overall evolution than selection from the latter, members of the former population attain a greater degree of individuality.

**4 Graded Population Membership and Univalent Darwinian Individuality**

A metaphysical error this paper seeks to forestall could arise in contexts where we have good reasons to model graded population membership. Recent work on populations has focused on regions of the genealogical nexus where population lineages of a single species bifurcate, anastomose, and grade into one another due to migration between populations, a phenomenon I will call lateral population blurriness[[4]](#footnote-4). One way to model lateral blurriness would be to say that some organisms belong to multiple populations. Consider for example the case of an organism who migrates back and forth between otherwise isolated populations. Millstein ([2015]) argues that such a wanderer changes its population membership each time it migrates, belonging at t1 to population A, at t2 to population B, and at t3 to population A again. Millstein suggests that this and similar ‘degenerate’ cases expose the limits of her population concept, which is presented as a defeasible model, not a set of necessary and sufficient conditions for population identity. In the maximally degenerate case of a wanderer who migrates very frequently and splits its interactions evenly between two populations, the wanderer’s impact on the evolutionary processes of each population might be best rendered as divided between the two. Using metrics such as time spent in the home territory of each population, resources consumed, or number of offspring parented, we might assign to a wanderer some percentage of membership in population A and some complementary percentage of membership in population B.

By countenancing split and graded population membership, we could precisely model the impact over time of the wanderer’s causal interactions on the evolutionary fates of organisms in both populations. It would be a mistake, however, upon modeling split population membership, to continue thinking of population membership as the ground of evolutionary individuality. We would not want to say the wanderer is partially a Darwinian individual relative to population A and partially a Darwinian individual relative to population B. Indeed, in dividing its membership between these populations, we assume the wanderer is one evolutionary individual, whose impact can be dispersed. If we want to model graded population membership, while continuing to hold that evolutionary individuality derives from being a selectable part of an evolving population lineage, as Hull and Godfrey-Smith claim, then we must recognize that Darwinian individuality derives from membership in a population broad enough to subsume lateral blurriness. The wanderer is not a Darwinian individual because it belongs to either population A or B, but rather because it belongs to a higher order unit of evolution of which A and B are both parts.

Degenerate wanderers are rare in nature, but other population structures that might be described in terms of graded membership are quite common, such as when population density grades along a natural cline to produce a population with diffuse and fuzzy outer boundaries. Consider for example a colony of sulfur metabolizing bacteria surrounding a hydrothermal vent. Population density is greatest at the center, where nutrients from the vent are plentiful, and becomes progressively less dense further away from the vent. Bacteria at the center of the population engage in causal interactions more frequently and with greater numbers of other population members than bacteria dispersed on the outskirts. If populations are understood to be groups of individuals whose causal interactions mutually impact each other’s evolutionary fates, and if individuals at the center of population density have a greater impact in this regard than those on the edges, then it might make sense to model the difference in magnitude of causal interaction as a difference in degree of population membership.

Modeling degree of causal interaction as degree of population membership would enable a more fine-grained resolution of evolutionary dynamics than is possible with models that abstract these differences away. It would be a mistake, however, to link degree of evolutionary individuality with degree of population membership in such a model. We would not want to say a bacterium at the center of a population is a Darwinian individual to a greater degree than one on the edge. As with models that resolve lateral blurriness by positing split population membership, models that posit graded membership to represent population fuzziness should not be mistaken as positing populations whose members vary in their degree of Darwinian individuality. If we choose to include graded population membership in a model, we must recognize that the model represents finer-grained population structures than those which determine an organism’s degree of Darwinian individuality.

**5 Relative and Bivalent Parthood**

Key to this paper’s formulation of bivalent selection and graded evolutionary individuality is the parthood relation between units of selection and units of evolution (Hull [1976]). A population is Darwinian only insofar as it is one in a sequence which forms a lineage that persists and evolves through time. To be a member of a Darwinian population is thus to be a part of an evolving population lineage, which Hull calls a unit of evolution. Hull’s unit of evolution is a spatiotemporally extended physical object, a ‘chunk of the genealogical nexus’ (Hull [1976], p. 174), composed of spatiotemporally extended physical parts. Some of those parts play functional roles as units of selection, making them functional as well as spatiotemporal parts of their unit of evolution. Something can function as a part only relative to some whole, so there is no such thing as a standalone unit of selection or Darwinian individual in its own right; each unit of selection has its role as such only relative to the unit of evolution of which it is a selectable part.

On the ‘orthodox view’ (Smith [2005], Haber [2015]), the logic of parts and wholes includes an axiom of categorical composition, the idea that parthood does not admit of degrees. Graded parthood might make sense for functional parts. It would be reasonable to think a thumb is a functional part of a hand to a greater degree than a hangnail is, for example, but a thumb and its hangnail are spatiotemporal parts of a hand to the same degree, as vague or graded spatiotemporal composition is inconsistent with the rules of geometry - something either is or is not within the geometric bounds of a chunk of the space-time continuum occupied by an extended object such as a hand or a unit of evolution. The claim here is not that organisms or other units of selection must have non-vague boundaries; I think their boundaries are indeed vague. Material overlap between parent and offspring (Griesemer [2001]), which ensures spatiotemporal continuity between generations in a unit of evolution (Hull [1976]), makes for vague boundaries between subsequent generations of reproducers, while processes such as respiration and nutrition make for vague boundaries between units of selection and their environments, as material parts are constantly passing into and out of most biological individuals. The point here is that units of selection emerge organically from previous generations of their unit of evolution, in the same way a leaf emerges organically from a branch of a tree. A unit of selection cannot be vaguely a part of its unit of evolution any more than a leaf can be vaguely a part of its tree. If we embrace Hull’s view that units of selection are spatiotemporal parts of spatiotemporally continuous units of evolution, then we must also accept that being a unit of selection is a bivalent as well as a relative condition.

**6 Nested and Overlapping Population Lineages**

Selection relative to particular units of evolution can impart varying degrees of individuality at different levels of organization. Stegenga ([2014]) notes that populations can overlap, such that a single biological entity might simultaneously function as a selectable part of more than one evolving population. A gene, for example, might be selected as part of an organism in a population of conspecific organisms, while simultaneously functioning as a distinct unit of selection in a population of genes that transcends multiple species (Sterelny [2009], in Stegenga [2014], p. 8). In such a case, the population lineage of conspecific organisms functions as one unit of evolution, while the population lineage of genes functions as a second overlapping unit of evolution. While selection from both populations affects evolutionary outcomes, its effects need not be equal in magnitude.

Units of evolution are often nested one inside another within a species. While Hull considers species to be the primary units of evolution and organisms the primary units of selection, both he and Lewontin acknowledge selection and evolution at other levels of organization.

As Lewontin (1970) has argued, selection occurs at an even wider range of levels of organization, from macromolecules to kinship groups, probably at the level of populations, possibly even at the level of species. There is no doubt that entities such as genes, gametes, organisms, and certain kinship groups possess the degree and kind of organization necessary to function as units of selection… Organisms possess the degree and kind of organization necessary to compete with other organisms and be selected… Like mutation and selection, evolution occurs at more than one level of organization. At the very least, populations and species evolve (Hull [1976], p. 182).

Within a given species, which is itself a unit of evolution for Hull, there are multiple nested units of evolution, each composed of different units of selection. Organisms are Darwinian individuals insofar as they are members of Darwinian populations of organisms, genes are Darwinian individuals insofar as they are members of Darwinian populations of genes, family groups are Darwinian individuals insofar as they are members of Darwinian populations of family groups, etc. Each of these nested populations forms its own evolving lineage, but the interwoven units of evolution which result from nested Darwinian populations are not equal in the amount of evolutionary work they accomplish. At each of these levels, individual members of populations function as units of selection, but being a unit of selection in one population, the population of organisms for example, might entail greater individuality than membership in, for example, a population of family groups, as selection from a population of organisms has a greater overall effect on evolution within a species than selection from a population of family groups.

Recognizing bivalent selection from population lineages with varying degrees of evolutionary impact can help to locate and grade evolutionary individuals in a multiply decomposable species (Wimsatt [2007], Haber [2012]) and in a cluster of overlapping plural populations (Stegenga [2014]). I suggest here that it might also help illuminate evolutionary individuality in symbiotic collectives. Godfrey-Smith ([2012]) notes that when symbionts are vertically transmitted, such as in the case of aphids and their obligate *Buchnera* bacteria, the symbiotic collective functions as a Darwinian individual in a population of other symbiotic collectives. Pea aphids (*Acyrthosiphon pisum*) bundle their obligate *Buchnera aphidicola* bacteria into gametes when they reproduce, and thus generate composite parent-offspring lineages between subsequent generations of aphid-buchnera collectives. These composite reproductive lineages enable transmission and multiplication of symbiotically constructed adaptive traits, and thus make aphid-buchnera collectives Darwinian individuals according to Godfrey-Smith’s Darwinian populations model[[5]](#footnote-5).

The Darwinian individuality of a reproducing symbiotic collective does not, however, preclude its component symbionts from functioning as Darwinian individuals in their own right, as the symbionts remain selectable parts of their respective species and local monospecific populations. The insect part of an aphid-buchnera reproductive lineage encapsulates the bacterial part, analogous to the way a plastic insulator encapsulates a copper wire. The bacterial part of the composite lineage is not, however, composed of a single strand, but instead consists of many replicating *B. aphidicola* individuals, each of which generates its own reproductive lineage. The composite parent-offspring lineage is therefore more like a shielded cable than an insulated wire, in that it consists of many bacterial lineages encapsulated by a single insect lineage, which both confines the bacteria and isolates them from other members of *B. aphidicola*. Because they are confined together, each bacterium in the composite lineage competes for resources with other encapsulated bacteria, such that mutations and environmental pressures could lead to differential replication, and hence to evolution in the encapsulated *Buchnera* population. It follows that the bacteria contained in a composite aphid-buchnera reproductive lineage function as selectable members of a Darwinian population of bacteria, even though the entire bacterial population is part of a symbiotic collective which itself functions as a unit of selection in a population of symbiotic collectives.

Each bacterium also remains an eliminable or multipliable part of its species, as do the insect parts of each collective, so individual bacteria and aphid macrobes function as units of selection relative to their species, as well as relative to their local populations, while simultaneously undergoing selection as parts of symbiotic collectives. The result is a ‘thickened’ region of the genealogical nexus, in which evolving symbiotic population lineages overlap and include as parts the monospecific units of evolution of both symbionts. Whether a contained bacterium or a monospecific aphid attains a greater or lesser degree of Darwinian individuality than the symbiotic collective composed of both depends on the relative impact selection from each population has on overall transformation or stasis in the region of the genealogical nexus occupied by the overlapping lineages.

Empirical evidence suggests that it is indeed the symbiotic collective which plays a more impactful role in aphid and *Buchnera* evolution. Anderson ([2000]) notes that *Buchnera* bacteria have lost many of the genes their ancestors relied upon for survival before they took up residence inside the coddled environment of an insect’s bacteriocyte. The loss of these genes makes *Buchnera* propagation wholly dependent upon the host insect’s survival and reproduction. It follows that any *Buchnera* trait which evolves from selection in local bacterial populations, but which hampers insect propagation, will be eliminated by selection at the level of the symbiotic collective, before it has a chance to multiply or become fixed in the larger *Buchnera* population. Selection on symbiotic collectives likewise limits evolutionary innovations that might arise in monospecific aphid populations, as any change to an aphid’s genome which makes the insect inhospitable to *Buchnera* will be eliminated by selection on the containing symbiotic collective, as aphids have evolved dependence on their bacterial partners. Selective pressure at the level of the symbiotic collective thus washes out evolutionary innovations which might arise from selection on symbionts, except for those which are adaptive at the level of the collective. Selection from the population of aphid-buchnera collectives, therefore, has a greater evolutionary impact than selection from either of its overlapping monospecific units of evolution, so aphid-buchnera collectives attain a higher degree of Darwinian individuality than either the insects or bacteria that compose them.

The nested and overlapping units of evolution generated when symbiotic collectives reproduce are similar to those generated when selection operates at multiple levels within a species. Just as particular buffalo and buffalo herds are equally units of selection, despite the former being Darwinian individuals to a greater degree than the latter, an aphid-buchnera collective and its component symbionts are equally units of selection, but because selection from the population of aphid-buchnera collectives has a greater overall effect on evolution than selection from populations of the component symbionts, an aphid-buchnera collective is a Darwinian individual to a greater degree than a monospecific aphid or a *Buchnera* bacterium.

**7 Conclusion**

On an idealized model of evolution by natural selection, in which species are thought to be the only units of evolution and organisms the only units of selection, it’s natural to think of each evolving species as having equal evolutionary significance, and the units of selection which compose them as exhibiting evolutionary individuality to the same degree. When we expand the model and recognize all the nested and overlapping Darwinian population lineages which function as units of evolution, pan-equal Darwinian individuality becomes implausible, as differences in evolutionary significance of populations become manifest. That units of selection exhibit varying degrees of evolutionary individuality might at first appear puzzling, as population membership both entails individuality and comes in a single degree, but if gradations in evolutionary individuality are understood to arise at the level of population lineages, the units of evolution, then the puzzle dissolves. Membership in a Darwinian population is an all or nothing proposition on the orthodox view, so being a unit of selection is a bivalent condition, but Darwinian individuality nonetheless comes in degrees, because the units of evolution constituted by Darwinian individuals themselves grade up or down in their degree of individuality, according to their degree of evolutionary impact.

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1. The most influential contemporary population concept, Roberta Millstein’s ([2009], [2010], [2015]) Causal Interactionist Population Concept (CIPC), is grounded in Hull’s individuality thesis and includes an assumption of bivalent population membership. [↑](#footnote-ref-1)
2. Godfrey Smith’s ([2009]) identification of Darwinian individuals as units of selection is contrary to Hull’s ([1980]) replicator/interactor model of natural selection, but it follows organically from Hull’s earlier ([1976]) view that units of selection are parts of units of evolution. [↑](#footnote-ref-2)
3. I refer here specifically to Godfrey-Smith’s ([2009]) “Darwinian Populations and Natural Selection”, which I take to be an organic extension of the population concepts advanced by Darwin, Lewontin, and Hull ([1976]). [↑](#footnote-ref-3)
4. Lateral blurriness is distinct from vertical population overlap, which arises when populations at different levels of organization occupy the same region of spacetime, as in Godfrey-Smith’s example of buffalo and buffalo herds. [↑](#footnote-ref-4)
5. Other evolutionary theoretic models ground the individuality of symbiotic collectives in their interactions with the environment (Hull [1980], Sterelny [2011]), or in the symbionts’ persistent functional integration and shared fate (Bouchard [2013]). On these alternate views, a mutualistic symbiotic collective might function as an evolutionary individual, even in case its symbionts reproduce independently. While environmental interaction, persistent functional integration, and shared fate, no doubt contribute to, and in part constitute, reproduction in symbiotic collectives, it is the reproduction itself, or the potential to reproduce, which grounds evolutionary individuality in Darwinian populations, so I focus here exclusively on symbiotic associations which collectively reproduce. [↑](#footnote-ref-5)