Beyond the Darwinian Individual: An Evo-Devo Perspective on the Regulation of Individuality

Recent work on natural selection and evolutionary transitions in hierarchy highlights the central role of Darwinian populations, collections of (Darwinian) individuals with heritable variation and differing reproductive rates (Godfrey-Smith 2009). I expand this framework based on research on the role of individuality in the evolutionary development (evo-devo) of fungi and slime molds. I assess models using four concepts of individuality: history, function, development, and unit of evolution (Wilson 1999), and conclude that a general account of the evo-devo of hierarchy in biology requires not only the treatment of the 'regional' notion of Darwinian individuality but also broader metaphysical notions of individuality.

According to the Darwinian population account, a key process in the evo-devo of a new kind of Darwinian population is the integration of Darwinian individuals into a higher-level individual and the de-Darwinization of those parts through reduction of heritable variation and/or dependence of reproductive fitness on intrinsic characters. For example, in the evolution of animals, increases in developmental complexity (as measured by, e.g., cell type count) are generally accompanied by increased organism-level regulation of cellular differentiation and cell fate. As multicellular animals become more internally integrated and complex, their constituent cells tend to have less independent evolutionary fates and less genetic heterogeneity. This de-Darwinization of the lower-level cells via integration into a higher-level whole stifles the selective tension between cell fitness and organism fitness.

The Darwinian population framework fits the majority of plants and animals but it fails to generalize to groups like the filamentous fungi and the plasmodial slime molds. In the evo-devo of hierarchy these organisms do not integrate individual cells but rather progressively individuate the contents of integrated wholes into separate parts. For example, in the filamentous fungi hierarchical transition occurs in development via septation (compartmentalization) which separates exploratory vegetative or pathogenic states (open networks) with relatively free flow of cytoplasm and organelles from exploitative vegetative or sexual states (gated networks) with finer component control and differentiated structures. Hierarchical transition occurs in evolution via the increasing sophistication of septal (compartment wall) structures and complexity of differentiated structures across the Dikarya (clade containing most visible mushrooms and such). This evo-devo strategy challenges the Darwinian population model because instead of the progressive integration of individuals it involves the progressive individuation of an integrated whole. This evo-devo strategy, which is also seen in plasmodial slime molds, allows the evolution of hierarchy without some of the challenges posed by de-Darwinization and facilitates aspects of saprotrophic and pathogenic lifestyles ubiquitous in the filamentous fungi and plasmodial slime molds.

A key distinction between the Darwinian population account (transition by integration) and the individuation account I develop is that the former models hierarchical transition in terms of the integration into a whole of individual parts whereas the latter models hierarchical transition in terms of the individuation into parts of an integrated whole. This highlights the fact that the Darwinian population takes as a starting point individual cells (when the transition is to a multicellular organism) or individual organisms (when the transition is to a superorganism) whereas the individuation account involves the progressive distinction of lower-level parts. The thesis that life is composed of cells (the cell theory) has a long and controversial history (Reynolds 2010) but its influence on abstract models like the Darwinian population account has engendered in the philosophy of biology a tacit assumption that part individuality in terms of spatial boundaries and internal homeostasis is a given and hierarchical transitions mostly involve shifts in Darwinian individuality – shifts in heritable variation and dependence of reproductive fitness on intrinsic characters, in the status of parts or wholes as units of evolution. Thus the focus is on differing degrees and processes of integration of individuated parts. However, the cases of filamentous fungi and plasmodial slime molds demonstrate that hierarchical transition can involve the dissolution, reorganization and/or reformation of individuals at multiple hierarchical levels in terms not only of variation and fitness but also of more general notions of individuality such as history, function and development. The focus here is on differing degrees of individualization of an integrated whole. In these cases, cell-like parts that come about through development do not have distinct spatiotemporal histories, distinct prior functional identities or functional boundaries, or distinct developmental trajectories as do cells in paradigm cases of transition by integration. Evolutionary transitions and shifts in Darwinian individuality are accompanied by changes in the more general individuality of the contents of the population or whole in question. Of course, this can be understood in Darwinian terms as a strategy for avoiding the problem of inter-level fitness tension to which de-Darwinization is a solution – if growth occurs with integration and without individuated parts, lower-level parts do not exist either in the sense of spatially bounded regions with distinct physiologies or in the sense of Darwinian individuals until the higher-level complex whole is achieved through the individuation of these parts. In other words, an alternative to integrating individuals is regulating the individuality of the contents of the whole from the start.

If hierarchical transitions and the evolution of Darwinian individuals involve not only the integration of Darwinian individuals but the regulation of individuality more generally, the philosophy of biology is in need of a concept of individuality that goes beyond that of heritable variation and dependence of reproductive fitness on intrinsic characters. Insofar as this concept transcends the specifics of the Darwinian individual it is crucial to consult more general accounts of individuality in non-evolutionary biology, philosophy of science and metaphysics. Although this need for a deeper account of individuality arises from the consideration of Darwinian individuality, this account may of necessity be more than biological.

Godfrey-Smith, Peter (2009) Darwinian Populations and Natural Selection. Oxford UP, Oxford.
Reynolds, Andrew (2010) "The redoubtable cell." *Studies in History and Philosophy of Biological and Biomedical Sciences* 41 (194-201).
Wilson, Jack (1999) Biological Individuality. Cambridge UP, Cambridge.