How many kinds of individual are there?

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The concept of the individual links population biology with darwinian selection. In spite of its importance, the concept is used with great ambiguity. Confusions seemingly stem from a limited analysis of the variability found in attributes classically used to characterize individuality. Such characterization involves the simultaneous holding of genetic uniqueness, genetic homogeneity and autonomy, which in turn are considered invariant attributes. Data accumulated over the past 15 years, however, indicate that all three characters can independently be present or absent in different types of multicellular organism. Combining their respective presence or absence leads to recognizing different kinds of individual; a realization that has ecological and evolutionary implications.

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The word individual has a meaning in biology and in the philosophy of biology. Here, I deal with the biological concept. In biology, such a concept links darwinian selection with population biology, and is therefore central to both ecological and evolutionary theories. However, in spite of its importance, current literature shows great ambiguity in the use of the term individual. As Hull[1] remarked, the term individual is sometimes used synonymously with any kind of organism but at other times is used in a more strict sense, to denote a well integrated and localized entity with reasonably well delimited boundaries in space and time. Although efforts have been devoted to define the limits of individuality[1–4], most definitions provided are plagued with exceptions.

Part of the problem seemingly arises from a limited analysis of the attributes traditionally used to characterize individuality. No single study seems to have formally analysed those attributes. A search of the literature indicates that genetic homogeneity[5], genetic uniqueness[5], and physiological unity and autonomy[6] have been considered the key attributes. The concept of an individual has traditionally involved the simultaneous holding of these three attributes. Each attribute was conceived as being invariant and was expected always to be present. Organisms failing to show some of the attributes described were regarded as exceptions.

Relevant biological information accumulated over the past 15 years has documented numerous organisms lacking one or more of the classic attributes of individuality. Thus, exceptions have become too numerous to be regarded only as exceptions. Such an abundance of exceptions suggests that the presently accepted concept of an individual is too restrictive and should be revised.

Classic attributes of individuality

Genetic uniqueness

This was considered one of the attributes of individuality because the possession of a unique genotype should render an individual different from other individuals of the same species[5–7]. The concept was mainly based on unitary individuals. Individuals with non-unique genotypes (e.g. monozygotic twins or vegetatively produced offspring) were regarded as exceptions to this invariable attribute.

Studies of clonal organisms have demonstrated both the limited validity of the above generalization and the existence of variability within this attribute. Clonal organisms grow and propagate through autoreplication of genetically identical units, which can survive and function independently when natural or experimental processes separate them into pieces[8–10]. Thus, clonality enables a given genotype to be simultaneously exposed to various environments, with different probabilities of survival and propagation of that genotype in those environments[10,11]. This type of growth and propagation is common among some invertebrates[2,3], is widely represented among terrestrial plants[10] and also seems to be widespread among multicellular marine algae[12].

The abundant representation of clonal growth in different types of organism questions the invariability of the concept of genetic uniqueness. The genome is unique in individuals of some types of organism (mainly sexually reproducing unitary ones), whereas in others it can have a variable number of replicas through clonal propagation.

Genetic homogeneity

This idea originated in the postulates of Weismann[5] who (in relation to sexually reproducing individuals) distinguished between cells with and without genetically heritable material. Because not all cells contain heritable material and because selection acts at the level of individuals, for selection to act the individuals were assumed to be genetically homogeneous. Research on clonal and unitary organisms has, however, identified many instances of genetic changes during ontogeny, which are not heritable in unitary organisms but can be inherited in clonal organisms[13,14]. Somatic mutations, gene duplications, intragenomic recombinations or changes in ploidy level can occur during the replication of a ramet, modifying one or several of its phenotypic characteristics. These changes have been reported in a variety of clonal invertebrates[2], land plants[3,10,11,15,16] and marine plants[12,17,18]. When these genetic changes occur in the meristematic cells of a seaweed or of a land plant, the cells derived from them will carry the mutation. The mutation can also be expressed in the gametes derived from these cells and in branches and new plants that originate through asexual reproductive mechanisms[15].

Thus, genetic homogeneity is also a variable attribute. Some organisms, especially unitary ones, are closer to being genetically homogeneous or undergo only a small number of genetic changes during ontogeny. However, clones can also be genetically stable or display either small or large genetic variability.

Autonomy and physiological unity

Huxley[6] suggested that autonomy and physiological unity were primary attributes of the individual in the Animal Kingdom. Individuals were recognized as naturally closed and isolated systems, whose morphological and functional heterogeneity only acquire any real significance when considered with respect to the whole. Individuals were considered autonomous whenever they could use the external world for their purposes, among which was the continuity of the whole. The individual should possess independence with respect to the forces of nature and should function in such a way that it and the new individuals that derive from it have the ability to continue functioning in a similar way. In other words, the individual can act independently when responding to the environment in a way that allows it to reproduce.

Social insects that live in colonies are the best examples of organisms that do not fulfill the attributes of unity and

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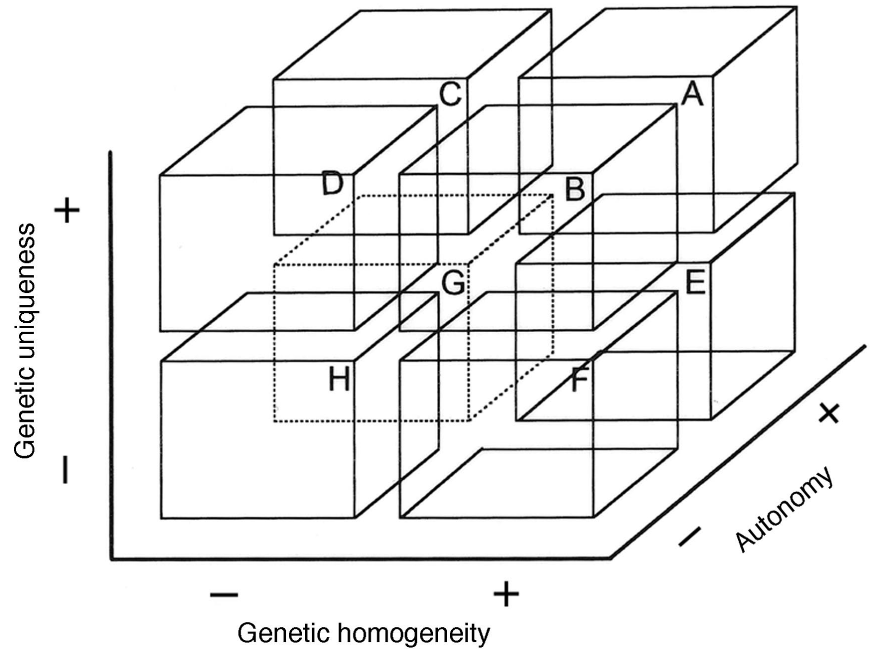
autonomy characterizing individuality[1,3,19]. A colony can be understood as an organized whole, within which its component individuals do not relate to their environment in an isolated manner, but as parts of a whole. Only a few members of the colony transfer their gametes to the next generation. Because of this, authors such as Wilson[20] recognized that the colonies, and not their component individuals, are the units of selection. In such cases, the characteristic of autonomy can no longer be applied to those individuals skipping reproduction. 'Working' individuals of eusocial colonies of insects might be able to act independently with respect to their environment, but they cannot reproduce independently.

In spite of the abundance of social insects, this lifestyle has also been regarded as an exception among the generally autonomous members of the Animal Kingdom, and special efforts have been devoted to understanding its evolutionary processes[21–27].

Recent studies on seaweeds[28] have also reported lack of autonomy among some red algae. During ontogeny, genetically different spores can coalesce and partially fuse, forming what macroscopically looks like a single individual. These genetically polymorphic mosaics of aggregated fronds often have higher growth rates towards the centre of the 'individual'. This results in inequalities in size with a few axes in the centre of the clump being responsible for most of the biomass[29]. These large fronds mature earlier than the peripheral fronds and, in some cases, are the only ones that produce sexual or asexual spores. Peripheral individuals in these aggregations remain sterile.

The ability of red algae to fuse and coalesce ensues from the lack of a cell wall in the early stages of development and from the occurrence of secondary cellular connections during the development of the coalescent masses of spores[28–30]. These characteristics have not been observed in terrestrial plants, which means that similar phenomena involving coalescence and natural formation of chimera might be rare. In fungi, however, the formation of chimeric organisms is common and tends to be achieved through cytoplasmic fusions. Such fusions generally result in increased size. In turn, increases in size result in decreased mortality from competition or predation and in earlier reproduction. Furthermore, the increase in variability derived from the chimeric nature of the fungal mycelia enables them to exploit environmental conditions that would otherwise not allow the separate growth of the two individual components of the chimera[2]. Thus, the applicability of concepts of independence and autonomy to some algae and to many species of fungi is also questionable. Together with the examples from invertebrates and algae already discussed[20–30], the evidence from fungi suggests that autonomy is also an attribute of individuality that can be present or absent in different kinds of organism.

Box 1. Kinds of individual defined by presence (+) or absence (−) of three individuality attributes



The three attributes of individuality (genetic uniqueness, genetic homogeneity and autonomy) are conceived as axes with the minimal possible variability (presence, +; or absence, −). This results in eight possible combinations, each defining a kind of individual. Unit A includes unitary individuals, the only kind fulfilling all three traditional requirements of the concept of individuality. Unit B accommodates organisms lacking autonomy (e.g. workers in social colonies). Units C and D include organisms with genetic uniqueness but with genotypes that change markedly during ontogeny. Given that many kinds of lethal tumor develop as cellular clones from genetic changes in single cells of unitary organisms[31], there might be biological constraints in these character combinations. Quantification of genetic change by means of molecular biology techniques[32–36] during ontogeny of unitary and social organisms should reveal whether organisms in units C and D actually exist. Units E and G include clones, defined as organisms that propagate by self-replication of genetically identical units. The distinction between stable (unit E) and unstable (unit G) clones also awaits research on genome stability. Unit H includes aggregated and chimeric organisms with clonal propagation, genetic instability and lack of autonomy. Some red algae and fungi show this and consequently comprise the most divergent type of individual organization compared with the currently accepted concept of individuality. Unit F includes not only genetically homogeneous individuals lacking autonomy (such as workers of social colonies), but also those lacking genetic uniqueness (as clones do). Such a combination might be potentially viable, but has not been reported for any kind of organism.

(Online: Fig. I)

Introducing variability into parameters of individuality

Given that all the attributes of individuality can be present or absent, they can no longer be thought of as absolute, invariable characters. Combining the respective presence or absence of these attributes yields a $2 \times 2 \times 2$ matrix, which results in eight units, each of which can potentially accommodate a major kind of individual (Box 1). Here, the variability of each axis is considered to be minimal and restricted to the presence or absence of a given attribute. Such a distinction has proved to be useful. Thus, genetic uniqueness sets the limit between unitary and clonal organisms. Presence or absence of genetic homogeneity allows us to distinguish between stable and unstable clones, and the lack of autonomy sets social insects and chimeric organisms apart from all other kinds. Genetic homogeneity and autonomy are discrete characters, but future research might document continuous variability on the axis of genetic homogeneity. Although in such a case the number of combinations would be reduced, there would still be grounds to distinguish between several kinds of individual.

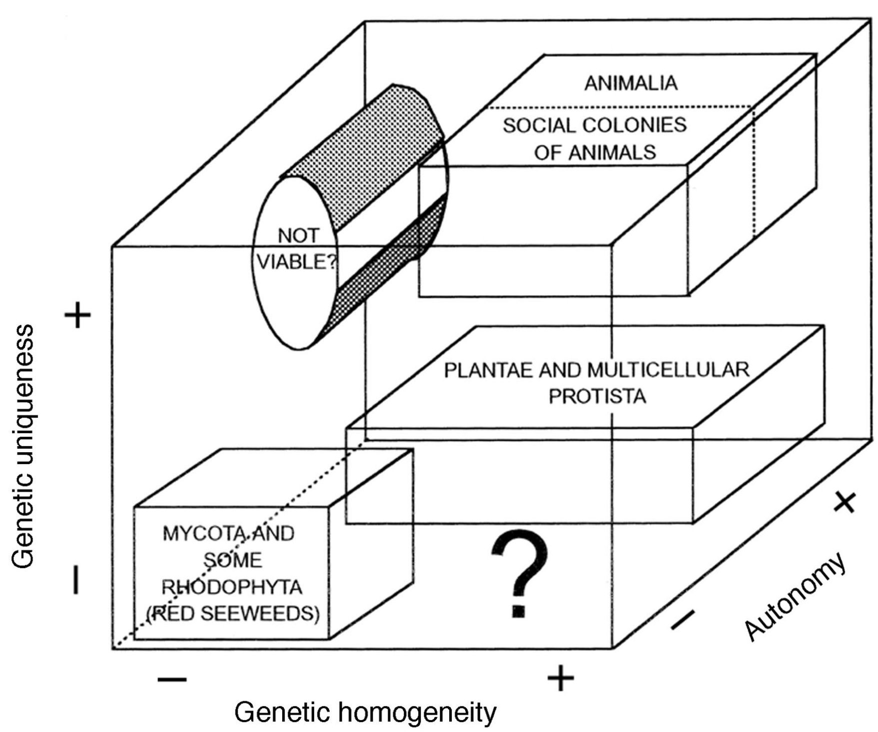


Fig. 1. Distribution of the representative members in the four Kingdoms of multicellular organisms as a function of presence (+) or absence (−) of the three classic attributes of individuality (genetic uniqueness, genetic homogeneity and autonomy). The question mark indicates the theoretical existence of genetically homogeneous individuals lacking autonomy and genetic uniqueness. Such a combination is potentially viable but such a kind of organism is not yet known.

One might wonder if the number of kinds of individual could be increased by the inclusion (Box 1) of additional attributes beyond the three classic dimensions of individuality and, if so, what conditions such attributes should fulfill. If the individual is to be considered as a unit of selection, then such a unit should be characterized by possessing heritable variation in fitness. Any additional attribute significantly affecting this characteristic could be incorporated in a new classification system. Future research should critically evaluate the links between the classic notions of genetic uniqueness, genetic homogeneity and autonomy with heritable variation in fitness. For example, some deleterious mutations in multicellular organisms that lead to loss of cells and tissue function and consequently cause the proliferation of non-cooperating cells might threaten the individual integrity of organisms, decreasing their heritability of fitness[4].

Some biological implications

Types of individual and the Kingdoms of multicellular organisms

Several of the potentially viable kinds of individual predicted from Box 1 are represented in all the Kingdoms of multicellular organisms. Thus, unitary individuals are especially well represented in the Animalia, but unitary individuals also exist in the Plantae, Mycota and among the multicellular Protista (e.g. seaweeds). Stable and unstable clones are abundant among Plantae and multicellular Protista, but this kind of individual also exists among the Mycota and in the Animalia (e.g. Bryozoa and Hydrozoa[2]). Chimeric individuals are common among the Mycota and red seaweeds. However, they have also been found among marine invertebrates (e.g. Tunicates[37–39]). Thus, each of the four Kingdoms of multicellular organisms contains unitary, chimeric and clonal individuals. Therefore, none of these kinds of individual organization should be regarded as an exception. They could be exceptions within a given Kingdom (such as chimeric individuals in the Animalia), but none of them seems an exception when all Kingdoms are considered. This finding suggests a polyphyletic origin of similar kinds of individual organization in the various Kingdoms and indicates that these alternatives of individual organization have existed in each Kingdom independently of the relative abundance displayed by these forms at present. Comparative studies of similar kinds of individual across different Kingdoms should help characterize, in a broader sense, the lifestyle and adaptive traits involved in each kind of individual organization.

Although unitary, clonal and chimeric individuals exist in each Kingdom of multicellular organisms, their relative abundance within each Kingdom are very different. Furthermore, if each Kingdom is placed in the framework of the three attributes according to which kind of individual is most widespread in that Kingdom, then they occupy different portions of the matrix (Fig. 1). This suggests that not all kinds of individual organization are equally suited for the very different roles performed in natural systems by a typical member of the Plantae, the multicellular Protista, the Animalia or the Mycota. Because a typical member of each of the Kingdoms relates differently to the environment compared with members in other Kingdoms[40,41], it should have been anticipated that they would differ in their respective individuality attributes, much as they do in subcellular, cellular and structural organization.

Some evolutionary and ecological consequences

The combined presence or absence of the three classic attributes of individuality, now conceived as axes (Box 1), characterizes each kind of individual as a unit of selection and by its relationship with the environment. On the one hand, although these three attributes are intimately related in any major biological process, it is possible to suggest that genetic uniqueness and genetic homogeneity are the axes principally related to evolutionary processes, including local adaptations, evolutionary rates, speciation and diversity. On the other hand, the autonomy axis is principally related to ecological processes, such as competition, mutualisms and social organization.

Because different kinds of individual occupy different parts of the axes (Box 1), predictions about ecological and evolutionary responses of one kind of individual based on the responses of individuals situated in a different part of each axis would probably be misleading. For example, a growing body of literature[2,10,11,13–15] is correcting predictions about processes of selection in clonal individuals that were previously based on unitary individuals. Similarly, differences in selection and evolutionary rates have been suggested between genetically homogeneous and genetically heterogeneous clones[3,15], and it is likely that similar types of difference would be found when comparing other kinds of individuals or other kinds of processes.

Alternatively, comparative studies on ecological and evolutionary responses of different kinds of individual placed in similar portions of a given axis (Box 1) should help to outline convergent responses.

The study of group selection or the evolution of cooperation could be used as an example. Levels in the biological hierarchy – genes, chromosomes, cells, organisms, kin groups, groups, and so on – possess heritable variation in fitness and consequently function as units of selection[42]. Beginning with Buss[43] and more recently with Maynard Smith and Szathmáry[44,45], attention has focused on understanding transitions between these different levels of individuality. Such a transition from solitary organisms to group-living or societies involves the emergence of cooperation among the lower-level units (i.e. 'workers' in a colony of social insects) to ensure the functioning of the new higher-level unit (i.e. the colony) and the regulation of conflict among the lower-level units[42–45]. Such concepts are applicable to any kind of organismal conglomerate, including chimera and coalescing seaweeds. Up to now, their application has been restricted to the study of social animals only.

Closely related to the evolution of cooperation is the role of positive interactions in ecological systems. In traditional ecological theory, which is heavily influenced by the study of autonomous individuals, positive interactions have often been treated as exceptions in biological systems. Under this new characterization, it is clear that they should be looked at again. In coalescent and chimeric organisms and, more generally, in all those that lack independence and autonomy, the importance and complexity of positive interactions have probably been underestimated.

The distinction between different kinds of individual according to the scheme developed here would help to make more meaningful comparative analyses of ecological and evolutionary processes in different organisms. It would also allow an expansion and re-evaluation of many concepts in population biology and natural selection that, to date, have been based mainly on the study of unitary individuals. There are many different kinds of individual out there and some of them are still waiting to be discovered.

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