11 Plant Individuality and Multilevel Selection Theory

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Individuality in plants seems as obscure and ambiguous as in animals it appears clear and simple.
—Gray (1849), in White (1979, 113)

Gray's statement may seem an exaggeration to the modern reader. Although philosophers of biology have become accustomed to worrying over whether genes or species are real units of selection, it is generally taken as uncontroversial that organisms, at least, are individuals. Even multilevel selection theorists, who may acknowledge the challenges presented by things such as outlaw genes or eusocial insect colonies, don't tend to include plants among their list of entities that warrant serious philosophical concern. Yet in the nineteenth century such fears were commonplace among biological thinkers. Even before Charles Darwin was discussing the possibility of group selection, his grandfather Erasmus was discussing some of the peculiarities that can prompt confusion over the status of plants. He considered plant buds to be like babies growing on their parent stem. Many writers then subscribed to the view that plants and trees are not individuals at all, but rather metapopulations, or collections of unit parts. The eruption of green shoots and leaves each spring is not mere growth after a dormant period, but the birth of a new generation.

A tree is therefore a family or swarm of individual plants. (Erasmus Darwin 1800, quoted in White 1979, 109)

This chapter explores the motivation behind such views and derives some consequences for multilevel selection theory. The first section explores the problem of individuating plants and the suggestion that individuality should be settled using genetic homogeneity. The second section argues that, in some lineages, high somatic mutation rates might actually be favored, and selection processes acting on these mutations could actually be adaptive for the higher-level individual. The third section concludes that genetic heterogeneity, and the intraorganismal selection it can give rise to, does not always undermine a higher level of selection. Individuals can, given certain conditions, have competition among their parts.

The lesson I draw is that multilevel selection theorists are wrong to assume genetic heterogeneity necessarily results in evolutionary conflict that must be suppressed in order for

higher-level individuals to persist as units of selection. Under particular circumstances (circumstances satisfied by many plants) competition at a lower level can be beneficial for a higher-level individual.

Plants and Individuality

Modularity — The Plant as a Metapopulation

All vascular plants, including ferns, conifers, and flowering plants, grow by the accumulation or iteration of smaller constructional units. When a coconut palm grows, it does so by producing a new leaf at its crown. As every new leaf appears, an older leaf below will die and fall away, leaving its stem to contribute to the trunk. You can clearly see cross-sectional marks all along its trunk where these units have been repeated. Other plants iterate more than one unit at once. An oak tree develops by growing new shoot units in a forked or branching pattern. Clonal plants such as bracken or aspen iterate whole plants, by growing them from the ends of underground runners. All such growth patterns can be called modular. Modular growth is open ended and does not progress toward any fixed adult form, in contrast to development in so-called unitary organisms, which is determinate.

A modular organism grows by the repetition of some unit or module. These modules are self-reproducing, which is part of what prompted Erasmus Darwin and others to say that a modular organism should be viewed as a collection of individuals—reproductive ability is often thought to be the kind of property that only individuals possess. Yet there has to be more to it than that, because even humans are composed of smaller parts that are capable of reproducing themselves—cells. We will see later that it is very important to be clear on what *kind* of reproduction an entity must be capable of, if we are to use that as an indicator of individuality.

A couple of distinctions need to be made. First, clonal growth of the sort described is vegetative. Another type of cloning is parthenogenesis, which occurs even in vertebrate lineages and in which an organism self-fertilizes one of its gametes. For the purposes of this chapter, cloning by parthenogenesis or selfing is less interesting because it involves a single-celled stage, precluding many of the interesting consequences of multicelled propagation that I will be looking at later. Specifically, reproduction by means of a multicellular propagule has the potential to transmit multiple genotypes to the offspring, whereas unicellular propagules will always sample only one genotype from any variance in the parent. All references to "clones" in this chapter should therefore be understood as referring to an organism that has been produced vegetatively rather than parthenogenetically or by selfing.

Second, structural modularity, where an organism is built up out of the repetition of semiautonomous subparts, should be distinguished from developmental modularity. All complex life forms are probably, in part, developmentally modular. Developmental modu-

larity describes the partitioning of ontogenetic or embryonic processes into separate sub-processes, which develop to some degree autonomously of one another. Evolutionary modularity describes yet another separate but related phenomenon, in which parts or sub-processes within a lineage of organisms vary at different rates over evolutionary time (Schlosser and Wagner 2004). For the purposes of this work, whenever I refer to modularity, I am picking out the structural sense of the term, in which parts of the mature organism are iterated vegetatively and operate autonomously (in some respect and to some degree) over the course of the life cycle. Arthropods, for example, with their repeating body segments, are often described as developmentally modular, but I do not include them as being structurally modular.

It is important to define the meanings of some words I will be using:

A *module* is a self-reproducing and semiautonomous unit. In plants, it usually contains one or many meristems in a bud, shoot, or root.

A *meristem* is a special kind of plant cell that can differentiate into both germ and soma.

A *ramet* is a mitotically produced collection of modules that forms a physically coherent structural entity (a tree, or bush, for example.)

A *genet* is the collection of all those modules or ramets that have developed from a single zygote, that is, all the products of a single sexual reproductive event.[1]

When ramets iterate themselves we say the organism is *clonal*.

Clonality and modularity occupy a single spectrum, differentiated primarily by the degree of physical separation between modules. Some organisms, such as grasses, switch between modular and clonal modes according to environmental conditions. (The different modes are described as phalanx and guerrilla strategies, respectively.[2]) Many organisms are clonal as well as modular. For example, bracken ferns, strawberries, and aspen are modular (in fact, all higher plants are) in that their bodies are built by the iteration of root and shoot units. They are *also* clonal because they send out runners that grow into whole new genetic copies of the plant.

Some organisms are more modular than others. The English oak, or *Quercus robur,* has a high degree of differentiation of its parts. The root system differs from the shoot system. The uppermost leaves are dependent on the rest of the tree for water and nutrients. The roots are dependent on the rest of the tree for energy from sunlight. An oak tree is a unitary organism to a large extent. However, it retains a much greater degree of modularity than any metazoan. This is because all plants are developmentally plastic. Cells taken from just about any part of the tree can, given the right conditions, be grown into a whole new and sexually fertile tree. You cannot do this with most metazoans. In metazoans, the cells capable of growing a new organism are usually carefully hidden in the ovaries or testes (this is known as germ-soma separation). In the majority of cases, only sexual fertilization can

start a new life cycle. But plants grow new parts using meristem cells, and these are not sequestered (isolated) as they are in metazoans, but are scattered around the plant body, often remaining dormant. Thus, although the mature oak is differentiated, that specialization can be reversed, so that nearly all parts of the tree retain autonomy and independence, at least potentially, throughout the lifetime of the tree.

One organism we're going to keep coming back to is Quaking aspen, *Populus tremuloides*. Aspen are more modular than oak. Aspen trees look similar to oak trees in that there is a trunk, a root system, and a shoot system. But aspen also send runners underground, and from the ends of these runners grow new trees. There are known aspen genets that are 50,000 ramets strong and estimated to be over 10,000 years old. In fact, all clonal genets are potentially immortal. A forest of aspen trees has the same branching structure as a single aspen tree, except that while the trunk and roots of a tree are visible above ground, those of the forest are hidden under the soil. Of course, an aspen forest isn't perfectly analogous to an enormous and partially buried oak. First, the parts of the forest are less differentiated and more independent of each other than are the parts of an oak. Second, whether or not the aspen trees remain connected to each other is largely a matter of chance, because parts of the connective root structure are known to rot and decay, leaving parts of the network isolated. Land subsidence and burrowing animals likewise threaten the coherence of the structure. This usually fails to impact the health of the isolated trees, whereas severing the branches of an oak from their stem would cause certain death. This suggests that the trees are more autonomous than the shared root connections may suggest, although it may be that younger trees depend more on the network, and its usefulness as a resource declines with age. Aspen ramets certainly exchange water and other nutrients via their shared root system and will frequently graft with roots from other genets (see, e.g., Jelinkova, Tremblay, and De Rochers 2009).

. . . And Other Modular Animals

Higher plants are all modular, but they are not the only modular organisms. Fungi are modular and so are many animals, especially marine invertebrates. Well-known examples include corals—reef-building colonies of tiny coral polyps—and hydroids, such as the Portuguese man-o-war jellyfish, which is really a floating colony of thousands of individual zooids. Therefore, although I will mostly be limiting the discussion here to plants, it is important to realize that the implications reach far beyond that kingdom. All in all, modular organisms are not an insignificant subsection of the living world—in fact they make up well over fifty percent of the earth's biomass. And yet, as we will see, no one can quite agree what exactly these organisms are, or, more pragmatically, how exactly to incorporate them into our current evolutionary theory. An evolutionary theory that covers only a part of the biological diversity that has been generated since life began is not the kind of evolutionary theory we are looking for.

The Units Debate

How can one steer a middle course between indefinite subdivision and indefinite expansion. . . . Which member of the series deserves pre-eminently the title of individual? (Braun, 1853; quoted in White 1979, 134)

In order to test predictions generated using modern evolutionary theory, biologists need to measure fitness. There is a lot of controversy regarding the correct understanding of the fitness concept, but no matter what interpretation of fitness you favor, measuring fitness requires being able to count individuals. Being fit is about contributing to later generations, so measuring fitness requires the ability to differentiate between generations. We need to know what it means for an individual to count as being of a new generation rather than a mere part of its parent, and we need to be able to tell the difference between having a single offspring and having many.

There are three competing characterizations of the individual with respect to aspen (and other modular and clonal organisms.) As we will see, a biologist's preference for one view over the others is affected by their preference for one or another foundational criterion of individuality—sex, heritability, or object-hood. The genet view (Janzen 1977) says that the whole clone or forest is the individual, because an individual is just the developmental product of a zygote. The ramet view (Fagerström 1992; Harper 1977; Pan and Price 2002) holds that the aspen *trees* are individuals, and the module view (Pedersen and Tuomi 1995; Tuomi and Vuorisalo 1989a; Wikberg 1995; Winkler and Fischer 1999) holds that the true individuals are to be found at an even smaller scale—the root and shoot modules or the meristems.

Each of these views has merits as well as serious problems. The genet view allows us to talk about the capacity for clonal (vegetative) growth being an adaptation at the level of the genet. The idea is that the aspen spreads itself out in order to exploit a wider range of environmental resources and distribute its risk of mortality. On the other hand, individuals are commonly presumed to have a life cycle, but genets seem to lack these; it is ramets that reach maturity and senesce (Watkinson and White 1986). Only ramets show specialization of parts. The ramet view is also a fairly intuitive response to the problem, because trees *look like* organisms. Familiar organisms are proper objects or particulars; their parts are physically connected to each other and separated from everything else.[3] While the spatial contiguity of the genet is vague and arbitrary, according to what has or has not decayed in the root structure, ramets have nice clear edges wrapped in bark, ending in leaves at one end and roots at the other. However, although aspen ramets are relatively easy to delineate, because their propagating runners are underground, this apparent obviousness may be just an illusion of scale. If we were able to see underground, the aspen forest would appear not as a collection of discrete trees at all, but as a single stalked mass, topped with branches, something like a head of broccoli (Bouchard 2008). Another attribute thought to belong to
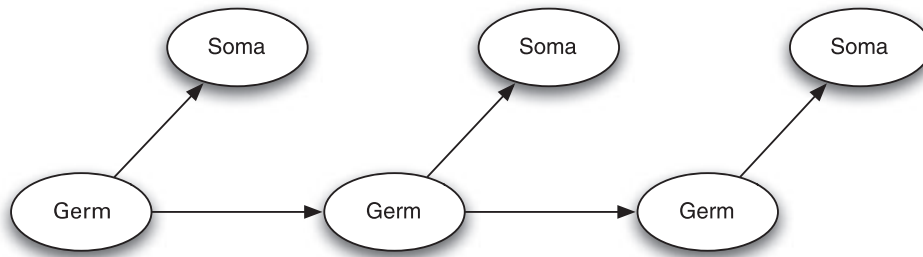
Figure 11.1
Germ-soma separation (reproduced from Buss 1983).

individuals is reproductive autonomy (Santelices 1999). Based on this criterion, modules are the real unit of selection.

With this overview of the different conceptual routes that are available for individuating plants, we are now in a position to summarize the theoretical commitments that determine our path:

1. *Continuity of the germ (heritability).* Weismann's doctrine of the continuity of the germ plasm (Weismann 1893) states that although the germline is continuous, so that traits are inherited from ancestor germlines, and these are passed on to the soma, there is no transmission of traits from soma back to germ. Germ-soma separation is commonly schematized as in figure 11.1.

The arrows in the figure show the direction of heritability, or the transmission of traits. So while both somatic cells and germ cells can be said to reproduce, in that they mitotically divide, Weismann's barrier ensures that only germ, not soma, has the potential for long-term evolution. To count a unitary organism, such as a pig, we use Weismann's barrier to help us decide which pig parts to count. Only the germ pig cells, hidden away in the ovaries or testes, can influence the traits of descendent pigs. Somatic pig cells are evolutionary dead ends, because their traits are not heritable. So when we are thinking about evolution, the genes in the somatic cells can be ignored. Even pig germ cells don't need to be counted separately, because they can only influence the traits of descendents when paired in the right way with complementary germ cells, and as soon as this happens they form part of a new individual. Furthermore, pig germ cells are entirely helpless without the soma. All the different cells and organs and other parts are cooperating in the production of a new piglet, so we don't need to count them all separately. We just count the pig once.

Plants, on the other hand, show somatic embryogenesis. Plant germ cells, meristems, are not sequestered at all, but are distributed around the body of a plant throughout its lifetime. They are usually concentrated at the apices of root and shoot tips, but dormant meristem cells can be found all over the stem, and anyway plant cells are so developmentally plastic that almost all of them can, given the right treatment, be persuaded to be-

come totipotent, start a new developmental cycle, and propagate genetic units to a new generation. Weismann's barrier does not give us reason against counting plant parts separately.

2. *Sexual reproduction*.   We can tell the difference between producing piglets and merely producing new pig cells because piglets are always produced sexually. Piglets always start out as single-celled zygotes, so we can say that everything after this single-celled stage counts as a new individual. Sexual recombination of the genome also guarantees that the new individual will be genetically unique, allowing us recourse to genotypes as a method of distinguishing individuals. But modular organisms like aspen reproduce asexually via runners, as well as sexually. Plant cells can pass on their traits to new plants even in the absence of sex.[4]

3. *Boundaries*.   Last, pigs have edges. We do not need to worry about where one pig ends and another begins because they have reasonably clear boundaries. Aspen lack clear spatial boundaries because whether or not a tree remains physically connected to the rest of the genet is vague and arbitrary.

   In pigs, these three sets of criteria converge to provide a single verdict on pig individuality, but for modular organisms they support separate views. Which view you choose regarding individuality therefore depends largely on which of these three features you see as most important. If you think that sexual reproduction is the most important thing about an individual, then you are likely to opt for the genet view, in which an individual is just the whole product of a sexual reproductive event. If you think that continuity of the germ (heritability) is key, then you will probably be moved to choose a module or meristem view. Finally, if you think that individuality is usually something that can be settled in a straightforward, less theoretically laden way on the basis of boundaries, then some kind of ramet view will most appeal to you.

The Gene's-Eye View

It should be noted that moving from fitness of individuals to fitness of alleles won't help, for how do we know which genes to count? And how often should we count them? The gene's-eye view collapses onto the organism view when you realize that geneticists use generations to define their time intervals. What is more, even with continuous time models, they use Weismann's doctrine of germ-soma separation to decide which genes to count. If a cow eats a lot of grass, it gets bigger because the number of cells in its body increases. Each cell contains a set of genes, so whenever a cow gets fatter, there are more copies of its alleles. Yet we wouldn't say that any of those alleles have raised their fitness. We don't count every single copy of an allele that exists when we count gene frequencies; we only count the ones that matter—that is, those that make it into zygotes. So we count organisms. What about organisms that don't make zygotes? Is the aspen that founds a new aspen grove, stretching to thousands of trees, just like a cow getting fatter? Or should we count

those trees separately because they are new life forms, capable of independent life and re-
production? The gene's-eye view won't tell us.

Clinging to the Genetically Homogenous Individual

The existence of multiple genetic lineages within an organism creates a breeding ground for conflicts
and cheating where lineages pursuing their own interests increase their returns relative to other lin-
eages while decreasing the fitness of the organism. (Pineda-Krch and Lehtilä 2004, 1171)

Many authors prefer the view that a true individual is going to be genetically homoge-
neous—all of its parts will possess one common genotype. The thought is usually that
homogeneity is required in order to prevent outbreaks of conflict among an individual's
parts. The necessity of homogeneity to individuality is frequently taken as a fundamental
underlying assumption in the major transitions literature.

   The claim is that cooperation can be achieved only at higher levels of organization (such
as the level of the multicellular organism) if there is some mechanism or condition that
prevents the lower-level individuals from doing better by cheating (Buss 1983; Frank
1995; Maynard Smith and Szathmáry 1997). Specific policing mechanisms will have to
evolve to prevent those individuals from competing at all (Frank 2003). Alternatively, the
free rider problem is solved automatically whenever the lower-level individuals are ge-
netically identical to one another. Hamilton's explanation of this is in terms of kin selec-
tion: If your genes are identical to mine, then my doing well at your expense is identical, in
terms of allele propagation, to your doing well at my expense. Self-interest and altruism
fail to be separate alternatives.

   Dawkins (1982) defends homogeneity in these terms in his *Extended Phenotype*. He
says that, for something to function as a unit of selection, it must not contain too much
genetic variation. He argues that true individuals must be produced by means of single-
celled bottleneck life stages, partly because single-cell stages ensure that only a single ge-
nome is inherited. Anything that is produced by a multicellular runner, such as a strawberry
plant or an aspen ramet, is not a unit of selection because it will contain too much variation.
He says "a geneticist will not discern a population of plants at all. The whole mass of strag-
gling vegetation will have to be regarded as a population of cells, with cells of any one
genotype being untidily peppered across the different plant." (Dawkins 1982, 260). The
key point is that, in order for individuals to function as units of selection, there must be no
lower-level selection. Genetic homogeneity ensures that there will be no competition
among an individual's parts.

   There is a serious limitation to the argument for using genetic homogeneity as the key
criterion on which to delimit individuals. Homogeneity fails to obtain. All organisms con-
tain genetic variation, because it is produced at a fairly steady rate by mutation during mi-
totic divisions. Replication is not perfect (if it were, of course, we would not be here), and
despite there being lots of evolved mechanisms for minimizing heterogeneity (genetic vari-
ance) within humans (e.g., developmental bottlenecks, apoptosis, and policing systems

such as the immune system and the histocompatibility complex), it is well known that we tend to show a high degree of somatic mutation.[5] Yet we also know that somatic mutation causes a large number of problems, cancer being the most obvious. Cancer can be viewed as a free-rider problem—the lower-level individual (cell) is behaving selfishly and replicating itself at the expense of the higher-level individual. Plants and other modular organisms are known to show much, much higher genetic heterogeneity, because they lack mechanisms for minimizing it. The presumption that seems to follow, in the minds of Dawkins and others, is that plants and other modular organisms must face proportionally more serious free-rider problems. In fact, the problems must be so bad that the higher-level entity gets completely undermined and does not function as an individual at all.

   In the next section, I present a challenge to this assumption, and suggest evidence that genetic heterogeneity may not always be a barrier to successful functioning as a higher-level individual.

Intraorganismal Selection

Evolution has classically been viewed as acting on variation among individuals within a population. Variation within individuals tends to be ignored. In the previous section, we began to see how Weismann's doctrine can explain why somatic mutation has not been treated as significant. Here, I introduce the theoretical idea of intraorganismal selection (IOS) and show how mechanisms that support it might be adaptive. First of all, we need to learn a little about the phenomenon of genetic heterogeneity.

Mutations and Mosaics

The sheer number of cells that must be produced during the development of all but the smallest of organisms ensures that almost every individual is a genetic mosaic. (Otto and Hastings 1998, 509)

Previously we saw how intraorganismal genetic heterogeneity is seen by many to be an aberration, bringing deleterious effects. Maynard Smith and Szathmáry (1997, 244) argue that selection within an individual can be ignored because all the cells within a multicellular organism share a recent common ancestor (the zygote), so there is little or no genetic variation between cells. In fact, genetic heterogeneity is common because of the mutations, crossing over, and gene conversions that can happen during cell mitosis. Organisms can fail to be genetically homogeneous in two main ways: They can be chimeric or they can be mosaic. These states are differentiated in terms of the functional origin of the variation (although some authors use the terms as if they are equivalent). Chimerism is the term for an individual composed by two or more fused genotypes that came from different zygotes. A mosaic individual is composed of two or more genotypes that originated from a single zygote but diverged during mitotic (somatic) growth. In both cases, there is a single structural or functional individual in which different areas carry a different genotype.

Plants can become chimeric when they are grafted together. Seaweeds are known to coalesce (Monro and Poore 2004). Chimerism also commonly occurs in cellular slime molds (Dictyostelium), sponges, corals, and tunicates (and aspen root networks). In other organisms, it is prevented by histocompatibility mechanisms. More frequently, plants are mosaic. Here, we focus exclusively on mosaic heterogeneity because chimerism is not generally heritable.[6] In mosaics, "the branches of an individual tree or parts of a clone represent an archipelago of similar but distinct genetic islands" (Whitham and Slobodchikoff 1981, 287). Many of the plants in cultivation came originally from mosaics; mutations gave us pink grapefruits, seedless grapes, and navel oranges to name just a few (Otto and Hastings 1998). In fact, all the pink grapefruit in existence originate from a single branch of a single tree that was discovered in 1906 (Whitham and Slobodchikoff, 1981).

The level of mutation in mosaics depends on several things; the rate of mutation, the number of cell divisions (dependent on the lifetime of the organism), and the rate of purging. Modular organisms tend to have higher degrees of mosaicism than unitary organisms because of their long lifespan, unsequestered germline, and multicellular propagation. Plants, especially clonal plants, have very long lives; in fact, they do not senesce at all. Genets are, at least potentially, immortal, because they only die if every single one of their ramets dies. They do not always limit heterogeneity during ramet iterations by forcing development through a single-celled bottleneck; in aspen ramet propagation occurs by means of a multicellular runner, and this runner will pass on any heterogeneity that it happens to contain. Modular and clonal organisms are, again, special cases because iteration occurs at several levels and is often multicellular at every level; multicellular modules are iterated *and* ramets are iterated via multicellular runners, too. Furthermore, runners do not spring from a specially sequestered site, protected from mutation. They can arise from all over the root system. Any mutation occurring in any of the dormant meristems found throughout the root system can potentially be passed on to a new ramet, either vegetatively or sexually.

So clonal plants can be expected to show a huge degree of heterogeneity. Many authors have argued that this should be bad for them. Muller's ratchet[7] style explanations for the maintenance of sexual reproduction in an overwhelming majority of organisms center on the idea that sexual recombination purges mutations and thus protects sexual species from "mutational meltdown" (Klekowski 2003). This is the supposed advantage that makes the "twofold cost of sex" worth paying. Without recombination, asexual clonal plants accrue a lethal level of mutations.

In the short term vegetative reproduction can clone genotypes that may be adaptively superior. In the long term, prolonged vegetative reproduction can lead to slow genotypic degradation through the stochastic fixation of deleterious somatic mutations. (Klekowski 2003, 61)

Or so say the theorists. The problem is that botanists and ecologists actually looking at clonal and asexual plants will not agree. Clonal and asexual plants thrive. Dorken and Eckert (2001) have done extensive fertility analyses and found that there is no association

between sexual fertility and plant vigor. Indeed, complex traits like sex are often degraded by mutation when they no longer increase fitness.

Where field biologists associate vegetative vigour with clonality, theoretical biologists view clonality in a different way. (Klekowski 2003, 65)

IOS or Somatic Selection

If somatic mutation of the genome is a frequent feature in modular organisms, natural selection is to be expected within genets and between modules. (Watkinson and White 1986, 47)

I follow convention in calling this "intraorganismal selection" (IOS), although the foregoing discussion should have made it clear that relativizing selection to the organism is not an unproblematic way of singling out the focal level in question. When the organism is clonal and forms physically connected genets, then IOS can be seen as selection between ramets. For nonclonal organisms, IOS will describe selection at a level lower than the ramet, that is, between modules or meristem cells. The basic point of IOS is that evolutionary change can take place within an individual, as well as between successive generations of individuals. The focal level of selection is shifted down so that the individual acts in some ways as a population, and evolutionary change occurs between successive generations of that individual's subparts. Of course, this could be said to be commonplace. After all, an individual wracked with cancer will also show a shift in frequencies of a particular allele over time. The difference has to do with long-term evolutionary consequences. In plants, the intraorganismal evolution is *heritable* because the victors of selective battles can be transmitted via both sexual and asexual routes. A better human analogy may be the immune system; this involves evolution during the lifetime of an individual, but it is also partly heritable—through breast milk, for example—between generations of individuals.

IOS (also called somatic, diplontic, or cell-lineage selection; see Buss 1983, Hughes 1989, Otto and Hastings 1998) occurs when genetic differences between cells or other subunits cause their differential survival or proliferation during an individual's development, and it has been discussed as a theoretical possibility since at least 1965.[8]

Once genetic differences exist between parts of the same plant there is the opportunity for natural selection to modify the gene frequencies within an individual by the process of differential growth. If the parts possessing the mutation grow faster the mutation may spread. If the mutation prevents successful growth then it will be eliminated. (Sutherland and Watkinson 1986, 305)

Mutations within the soma are subjected to immediate selection by the environment as they compete with the wild-type soma. Mutations in sequestered germlines, on the other hand, face only gametic selection, only once per generation. Buss (1983) schematizes the difference between somatic and gametic selection like this:

Somatic selection = mutation → selection → propagation → selection

Gametic mutation = Mutation → propagation → selection

There is one extra round of selection for somatic over gametic mutations. This extra phase of selection potentially increases the capacity for rapid evolutionary change among modular lineages. Buss says that IOS leads to "the disproportionate proliferation of those variants favoured by environmental demands" (Buss 1983, 1390). What is more, when heritable genetic variance exists between cells or other subunits, selection between them can result in within-organism evolution—gene frequency change within a generation.[9] The displacement of the wild type by a mutant in a mitotic cell lineage is evolution.

Somatic selection might be particularly important in the evolution of plants and other modular organisms, because of their high rates of mutation and the way they distribute resources around their parts. Although somatic selection may occur in any multicellular individual, it is especially prevalent in modular organisms because they are composed of a hierarchy of subunits, all of which can undergo selection. Darwinian populations can be found at multiple levels—groups whose members have heritable variation in character, which leads to differences in reproductive output (Godfrey-Smith 2009, 39).[10] In aspen, therefore, the following are all levels at which competition may take place simultaneously: between cells in a meristem stratum (in each stratum), between meristem strata, between modules/buds/shoots, between branches, between trees/ramets, between genets/forests.

Although many authors focus on conflict between levels, it is much more likely that selection at the various levels will act concordantly (Otto and Hastings 1998). In plants, somatic selection is supposed to work as follows: Multicellular transmission, as occurs in propagation by runners and in module iteration, preserves a high prevalence of mutations. Mutated cells are not segregated but can propagate themselves. During development or growth, mutant and wild-type lineages may have different growth rates. This means that different cell lineages can compete. How do they compete? In higher plants, they compete for *apical dominance*. Successful, that is, energy-efficient, modules (leaf-meristem units) produce hormones (auxin and others) that promote cell division while suppressing growth in other modules (Haukioja 1991). This allows plants to direct resources to their most successful parts. Fast-growing mutations can spread throughout the whole ramet or even genet by outcompeting the inferior alleles, that is, by producing sufficient auxin to cause the slower-growing modules or lineages to die. The developing buds of a plant compete for sunlight and nutrients as well as apical dominance. The poorest competitors will lose out and eventually die.

Since a plant is a population of competing buds which grow at different rates and regenerate each year the gene frequency of the plant or clone can change over a period of years and the parent genotype may be completely lost. (Whitham and Slobodchikoff 1981, 289)

Evidence for IOS

Although IOS is not universally accepted as having long-term evolutionary consequences for plants, there is sufficient evidence for its existence and importance that its consequences for evolutionary theory need to be acknowledged.

A well-known example of IOS at work comes from variegated maple (*Acer platanoides drummondii*). The white edging on the leaves arises by somatic mutation and is deliberately preserved by horticulturists for its aesthetic appeal. The white parts contain no chlorophyll and so don't photosynthesize, lessening the leaf's overall efficiency. Often, buds will appear that contain wild-type mutations. Wild-type buds produce normal green leaves with a higher rate of photosynthesis. Left alone, the more efficient wild type will spread throughout the whole ramet (this is known as "reversion"), so horticulturists must continually remove wild-type buds to preserve the plant's variegation. This shows that the gene frequencies of the living plant tissues change over the lifetime of the plant. What is more, because the mutations can end up being propagated to new ramets, either sexually, if they end up in flowering parts, or vegetatively, this change in gene frequencies can have long-term evolutionary consequences.

Munch and Braun argued that the shape of trees provides evidence of interbranch selection, for if the branches were growing entirely independently of one another instead of competing for light and other resources, tree crowns ought all to take the shape of a witch's broom (White 1979). More evidence for IOS can be found in American goldenrods, or *Solidago missouriensis*. In one particular patch, the average age of goldenrod clones is 200 to 400 years, with some being as old as 1,000 years. The clones contain more than 10,000 ramets, each renewed annually, and are well adapted to local conditions as well as to closely related species. Whitham and Slobodchikoff note that a clone like this, according to the theory of diplontic selection, ought to have a high potential for genetic change over the lifespan of a clone. An individual clone certainly lives long enough to span evolutionary time. Somatic mutation during asexual ramet propagation could produce enough heritable variation for the clonal individual to adapt to local conditions. In fact, because there has only been time for eight to twenty-five generations of clones since the last glaciation in the area, sexual reproduction cannot reasonably account for their adaptive plasticity. Adaptive plasticity at the level of an individual clone can be better explained by adaptive evolution among the ramets—the physiological modules—from which the clone is composed (Whitham and Slobodchikoff 1981, 289).

There is more evidence for the evolutionary significance of IOS, and in order to understand it we need to look in closer detail at the structure of plants.

A Closer Look at Meristems

The rate of diplontic selection can be increased by raising the number of initials or the number of generations of cell divisions. Accordingly, the progression from structured apical meristems with few initials to stochastic meristems containing many initials is a general trend both in the ontogeny and phylogeny of higher plants.[11] (Hughes 1989, 257)

Hughes suggests that the pattern of plant evolution shows us that the capacity for IOS (intraorganismal selection) may have been selectively favored. In this section, I introduce some details about plant meristem structure to explain what he means.

The rate of mutational meltdown, Klekowski (2003) explains, depends on the particularities of meristem organization. There are three different kinds of meristem organization in vascular plants.

Phylogenetically most ancient is the monopodial case, where a single apical meristem is the ultimate source of all the cells in the shoot. In these determinate meristems, each initial[12] has a permanent role, so that after mitosis of the cell one daughter cell always remains undifferentiated and functions as the subsequent initial. Thus an effective single-celled bottleneck exists in meristem iteration. This type of meristem is found in *Pteridophytes* (ferns, horsetails, and lycopods). Any mutation occurring in this meristem will be transmitted to all descendent cells. There is no diplontic selection because there is no pool of meristem cells able to compete with one another. Vegetative reproduction is common in pteridophytes, and mutational loads are very high.

A more phylogenetically recent meristem type is found in gymnosperms (e.g., cycads, gingko, and conifers). These stochastic meristems have a population of initial cells from which a few cells are probabilistically assigned to continue as the next generation of initials, whereas the others differentiate. "The apical initials divide mitotically a number of times giving rise to a pool of daughter cells from which subsequent initials are randomly sequestered" (Pineda-Krch and Fagerström 1999, 682). Klekowski points out that, where the shoot lacks permanent initials, diplontic selection will be more common. However, extensive vegetative reproduction is quite rare in this group, possibly because it is too easy for deleterious mutations to spread throughout the meristem.

Last, in angiosperms (flowering plants), meristems are stratified. This is the largest group of vascular plants, and also one in which vegetative or clonal growth is extremely common and has evolved separately multiple times. Many of the most invasive weeds are in this group and are spread vegetatively. Angiosperm meristems are totally different from those of gymnosperms and pteridophytes, and these differences impact on the retention and distribution of mutations in these plants.

Angiosperm meristems are organized into tunica-corpus systems. The outer parts (tunica) consist of one or many discrete layers of cells that divide anticlinally (perpendicular to the plane of the outer surface). Underneath these is the corpus, containing cells that divide in all planes and mostly differentiate into leaves and stem. "A shoot apical meristem consists of relatively isolated subpopulations of meristematic cells" (Klekowski 2003, 62).

Each meristem stratum contains several totipotent initials, so diplontic selection is maximized within the subpopulations. But this structure also allows stable periclinal (i.e., with layers parallel to surface) mosaics to form. A mutant can spread through its whole layer and stay there, so one will often find that each layer has a different mutation fixed within it. This stratification often results in the perpetuation of mosaic ramets containing mutated tissues, as well as the production of mutant gametes. Mutants can persist through many cycles of vegetative growth as periclinal mosaics, because the separation between layers protects them from diplontic selection. Each layer is a mini-Darwinian population, in Godfrey-

Smith's terms. Klekowski and Kazarina-Fukshansky (1984) note that the meristems in higher plants are actually not very adept at losing deleterious mutations, and meristem stratification may even promote the long-term accumulation of mutations. "Thus, paradoxically, angiosperm shoot apical meristems have evolved characteristics that reduce diplontic selection against defective somatic mutants in the short term" (Klekowski 2003, 63).

The layers, however, aren't totally isolated from each other. Anticlinal divisions within the corpus sometimes displace cells, by effectively injecting a cell from one layer into another. Herbivory is especially effective at upsetting the divisions between layers. When this happens, any variation that has been lying dormant is released, prompting diplontic selection between the layers.

Marcotrigiano (2000) hypothesizes that this could be particularly advantageous, allowing the plant to keep some variation up its sleeve and exploit it exactly when it is needed—to adapt to an environmental threat or simply regrow parts that have been eaten. Though Klekowski can offer no explanation for the evolution of stratified meristems (in fact, he says they appear "maladaptive from the viewpoint of buffering against disadvantageous mutations"; Klekowski, Kazarinova-Fukshansky, and Mohr 1985, 1794), Pineda-Krch and Fagerström (1999) provide a quantitative model demonstrating how stratified meristems enable an efficient and rapid elimination of deleterious mutant lineages while resulting in an increased probability of long-lived mosaic states.

Angiosperms, the newest and most successful of all plants, have evolved stratified meristem regions, which make intraorganismal selection maximally effective in three ways: They ensure that deleterious mutations are rapidly purged, they allow high fitness mutations to displace the wild type, and they preserve genetic variance over the long term (Pineda-Krch and Lehtilä 2002). This is what prompted Hughes to infer that the maintenance of IOS has actually been favored in plant evolution by higher-level selection.

Cell lineage selection is most effective in the absence of bottlenecks. Plant module iteration in monopodial plants is via a bottleneck. As you move upwards in the family tree of plant species, you see that meristems first became multicellular, and then stratified to produce several multicellular compartments within the module. Plants had bottlenecks, but they lost them, and then lost them even more. Why? A reasonable answer is that it encouraged cell lineage selection. In the next section, we will see why this might offer benefits.

Benefits of IOS

Differences in the patterns of organization of organisms may lead to different patterns of evolution, genetics and ecology. Plants and animals differ in their fundamental patterns of organization. Plants may be able to take advantage of somatic mutations in ways that are not available to animals. (Whitham and Slobodchikoff 1981, 287)

It might be beneficial to an organism to have competition among its parts. Intraorganismal variation is essential to the functioning of the mammalian immune system, underlying the changes in B cells essential to acquired immunity to disease (French, Laskov, and Scharff,

1989). Cell competition may also play an important part in metazoan development, ensuring only the fittest cells make it into the germline (Khare and Shaulsky 2006). But the biggest advantages of somatic selection can be reaped in modular organisms like plants. IOS has been acknowledged as a way of eliminating deleterious somatic mutations that might otherwise accumulate, especially in clonal plants (Buss 1983; Gill 1986; Klekowski 1988; Otto and Orive 1995; Sutherland and Watkinson 1986; Whitham and Slobodchikoff 1981). So IOS may solve the puzzle of why clonal and asexual plants do not struggle under their mutational load—somatic selection is a mechanism that allows them to purge mutations without sex.

Under the genetic mosaic hypothesis (GMH) (Gill et al. 1995) it is proposed that mosaicism is favored in plants, especially, because it provides the individual with a broader phenotypic repertoire when dealing with pests and herbivores. A single plant may represent a mosaic of genotypes that prevents herbivores from evolving specific metabolic pathways to overcome plant defenses. Mosaicism thereby offers an advantage in the red queen race against pests and parasites. Clonal success deserves a parallel justification to those offered for the success of sexuality, and IOS seems to offer it. The GMH proposes to explain co-evolution between long-lived plants and their short-lived enemies by saying that IOS allows an intragenerational response to herbivore pressure. For every resistant gene in wheat, for example, the Hessian fly must possess a corresponding gene for virulence. Changes at a single locus can thus have a drastic effect on plant-herbivore interactions (Whitham and Slobodchikoff 1981, 290).

IOS also endows modular organisms with phenotypic plasticity on an ecological time scale, allowing them to respond to changing environmental conditions (Monro and Poore 2004). For example, adventitious[13] buds are usually formed after a plant suffers some kind of physical damage. "This suggests that the derivation of these buds from a different meristematic layer may be an adaptive response in that it presents an alternative genotype in a changing environment" (Whitham and Slobodchikoff 1981, 291). Unitary organisms are very conservative in comparison.

Monro and Poore 2009 show that, given intraclonal variation, mitotic cell lineages rather than sexual offspring may act as units of selection. They describe an experiment in which intraclonal genetic variation allowed a red seaweed to evolve adaptively in response to a changing environment, in the absence of sex.

Much Ado about Nothing?

Several authors (Harper 1988; Hutchings and Booth 2004) have expressed skepticism about the evolutionary importance of IOS, arguing that it is a theoretical possibility that has yet to be empirically observed. Although more recent studies have since provided further empirical support (e.g., Khare and Shaulsky 2006; Monro and Poore 2004, 2009), the idea has yet to gain widespread acceptance within biology. Proponents of IOS (Fagerström 1992; Fagerström, Briscoe, and Sunnucks 1998; Pineda-Krch and Lehtilä 2004b; Poore

and Fagerström 2000; Santelices 1999; Tuomi 2004) have speculated that underlying theoretical biases are to blame for this, such as a misplaced allegiance to Weismann's barrier, or a limited focus on the metazoan phyla. To sound an appropriate note of academic caution, I mention that the status of IOS as a mechanism with the potential for long-term evolutionary consequences is still controversial.[14] This chapter should therefore not be viewed as an argument for the existence of IOS. That is an empirical matter. What I do want to argue is that *if* IOS does occur, *then* there are some important adjustments to be made in the way we talk about multilevel selection. But the case discussed here shows that this is not idle speculation. There is serious evidence for IOS, and thus the conflict assumption ought not to be uncritically accepted by multilevel theorists.

IOS and Multilevel Selection Theory

In this section, I look at how multilevel selection theory may need to be revised in light of the possibility of lower-level selection offering higher-level adaptive advantages.

The Contrast Again

One lesson of multi-level theory is that the evolution of cooperative wholes requires suppression of competition among the parts. (Okasha 2006, 150)

Conflicts must be mediated for the new higher-level unit (the multicellular group) to become a true individual. (Michod and Nedelcu 2003, 64)

Group adaptation . . . only obtains if within-group selection is completely abolished. (Gardner and Grafen 2009, 666)

Most people are now happy to accept the possibility of multiple levels of selection, yet many still think that the presence of multiple levels entails some sort of conflict. It is assumed that the direction of fitness at different levels within a multilevel selection model will always be in opposition.[15] Not all authors endorse the claim that genetic homogeneity is required for higher-level entities to act as biological individuals. Homogeneity is rather just *one way* in which the threat of lower-level subversion can be averted. Gardner and Grafen (2009) insist that, in order for something to exhibit group-level individuality, there must *either* be relatedness of one between the group members, *or* some sort of policing mechanisms that totally suppresses selection between them. Policing mechanisms are often accepted as an alternative to genetic homogeneity, so long as they ensure that no within-group competition takes place at all. For example, Frank (2003) discusses the role of fair meiosis in the evolution of chromosomes, and worker policing behavior in insect colonies, while Michod views a complete reproductive division of labor as an adaptation for suppressing within-group competition. Michod (2005) in particular goes so far as to make the suppression of lower-level conflict part of the definition of what it is to be a higher-level individual.

In direct contrast to this, we saw in the earlier section that lower-level selection can, in the right circumstances, offer adaptive benefits at the higher level. We saw that modular plants tend to be genetic mosaics, and that there is plenty of scope for selection between the different parts of the plant, especially between cells found in different meristem compartments. There are no mechanisms in place for eliminating competition between different cell lineages. Nonetheless, angiosperm meristem structure seems to bear all the hallmarks of a higher-level adaptation, evolved for the benefit of the higher-level plant. Plants seem designed at the highest level for the purpose of maximizing their fitness (Gardner and Grafen 2009, 660).

Why Are Plants Different?

It is the modular structure of plants that means IOS can be adaptive for them. Having a modular organization makes something less vulnerable to mutations, because "problems" are contained within the cell lineage within which they arise. Mutations can proliferate by means of cell divisions, but they cannot spread to affect unmutated cell regions. Because modules are by their very essence semiautonomous or independent, they are able to continue carrying out their functions and life processes in the face of considerable deviation in the behavior of the other modules with which they may share a stem, root system, and so on. In a nutshell, problems in one part of a plant will not always impact the health or success of other parts.

Plant parts are more autonomous of one another than are the parts of metazoans and most other nonmodular organisms, largely because they have rigid walls that preclude moving around within the body of the plant. This usually prevents cancer from being fatal in plants (Doonan and Hunt 1996). But there are other features of plant physiology that limit the damage deleterious or free-riding mutations can do. We saw in detail how angiosperm meristems are structurally arranged so that mutations are compartmentalized, limiting their spread by somatic selection. Auxin and other hormones act to regulate the growth of plant modules relative to each other, favoring the fast-growing parts. Stoloniferous plants, in particular, are even able to move their parts around, away from outlaws. As we saw earlier, IOS might allow plants to purge deleterious mutations. Plants can even purge mutations by self-pruning to remove inefficient parts. For example, leaves drop off and die on becoming shaded by higher branches.

In fact, as long as a plant retains a few meristem cells supplied with resources, it can afford the death of all its other parts. Unitary organisms, in contrast, are much more vulnerable to interorganismal conflict. Their parts are very differentiated, so that if one part becomes defective there is overall loss of function and the whole suffers. IOS will often lead to cancers, and bottleneck life cycles mean that even minor developmental disruptions can be fatal. This is probably one reason why metazoans have evolved germ-soma separation and mechanisms that limit mutation. IOS is too risky for metazoans. Plants are a different matter, however. Their uniformity, and the retention of reproductive autonomy by

Table 11.1
Different possible combinations of benefit and cost at two levels

Module	Ramet	Example
+ Beneficial	+ Beneficial	Increased metabolic rate
+ Beneficial	− Deleterious	Flower degradation, cancers
− Deleterious	+ Beneficial	Germline segregation
− Deleterious	− Deleterious	Reduced metabolic rate
Neutral	Neutral	Most mutations

clonal ramets and meristems—their modularity, in effect—allows them to afford within-genet selection. Plants essentially don't need conflict suppression mechanisms because it is just not that easy to free ride in a plant. Plants can capitalize on this by using competition among plant modules to ensure that the fittest modules spread their genes throughout the organism, without risking the overall collapse of the organism.

In any case, not all mutations will be deleterious. We can construct a two-by-two classification scheme (table 11.1) to represent the effects of traits at two levels—the ramet and the module; +/+, +/−, −/+, −/− with the effect of the mutation on the cell given to the left and the effect of the mutation on the ramet given to the right (Otto and Hastings 1998).

The −/− mutations will go extinct in competition with higher fitness modules. The +/+ mutations will sweep through the module population if they are positive enough. Most mutations will be either +/+ or −/−, or have no effect whatsoever. Although there are well-known exceptions, such as cancers, most mutations will have an effect that is concordant between the lower and higher levels. The +/− and −/+ cases tend to be in the minority. Otto and Hastings (1998) explain this in terms of cell function. There are more ways in which function can be lost than ways in which it can be gained, and this tends to be detrimental at both the cellular and the higher level. Mutations that improve the efficiency of metabolic pathways, on the other hand, will be beneficial at both levels. What is good for the cell is good for the higher-level unit in most cases. In fact, angiosperm meristem structure raises the frequencies of all combinations, but then it filters all except the +/+ and +/− kind out. As indicated in these examples, some mutations will be good for the module but bad for the ramet. Flower degradation—loss of sexual fertility—is commonly found in plants with a high degree of clonal vigor, as is to be expected if rates of IOS are high (Dorken and Eckert 2001). Degradation of flowers (or any other mutation that adversely affects the capacity for sexual fertilization) is deleterious at the level of the ramet *only if* it is the case that sexual reproduction forms a necessary component of fitness. Cancers tend to be relatively unproblematic in plants because of the rigidity of cell walls. Still, there will be +/− cases that slip through the net. Fast growth rates may be achieved at the expense of investment in protection against herbivory, for example.

The contention here is that structure within the individual (specifically meristem structure in plants) may be organized in such a way that makes finding +/+ combinations easier. Selection within the individual, then, acts as a sieve, eliminating deleterious mutations and increasing the frequency of beneficial ones. This sets IOS apart from other modifiers of mutation, because they tend to alter the mutation rate in the same way regardless of the effect of the mutation. Altering the strength of IOS will increase the mutation rate for mutations that are beneficial to cell function and decrease it for mutations that are deleterious to cell division or replication. My contention is that IOS can act as a mechanism that increases the chances of finding novel +/+ mutations.

This point needs emphasizing because other authors assume that lower-level selection will come into conflict with higher-level selection for at least some, if not all, traits (Andy Gardner, personal correspondence). In the case of plants, I am not denying that what is best for the module (or cell) will sometimes diverge from what is best for the ramet (or genet), as the third row of table 11.1 indicates. Nonetheless, my argument is that so long as this happens in a minority of cases, and the consequences when it does are never very serious, the mechanism that encourages intraorganismal selection can still benefit the higher-level individual overall.

Homogeneity and Individuality

I have argued that there are some reasons to view plants as individuals at the highest ramet or genet levels, even though their parts may undergo selective processes. I have tried to refute the idea that stoloniferous genets cannot function as units of selection because they contain too much genetic heterogeneity and no conflict suppression mechanisms, and so will be riven by internal conflict and free-riding cell lineages. We saw that, thanks to their modular structure, plants can maintain higher-level functionality in the face of intraorganismal selection. In fact, meristem structure in angiosperms might constitute a higher-level adaptation for the very purpose of enhancing lower-level selection. So genetic heterogeneity and IOS do not provide evidence against higher-level individuality in plants.

The lesson I draw out is that multilevel selection theorists are wrong to use genetic homogeneity and conflict suppression mechanisms as the central criteria of individuality in plants and modular organisms. Michod is wrong to base the definition of individuality on conflict suppression mechanisms; Dawkins is wrong to tie it to genetic homogeneity. We should accept the possibility that biological individuals can have selection among their parts.

One consequence of rejecting genetic homogeneity as a criterion of individuation is that it leaves the way open for us to include as parts of an individual all sorts of genetically distinct entities such as symbiotes, organelles, and perhaps even parasites that have standardly been kept separate. Authors such as Dupre and O'Malley (2007) argue that gut flora and other microbes ought to be reconceptualized as comprising a genuine part of the human organism. My arguments imply that genetic disparity alone does not constitute an argument against such claims.

Where are we left regarding the individuality problem for modular organisms? To what unit—the module, ramet, genet, or perhaps all of the above—should fitness be ascribed? I argued that we ought not to use IOS as a reason against individuating plants at higher levels. The presence of genetic variance within a unit gives us no valid evolutionary reason for ruling out that unit as a level of selection. So at least one argument against individuating aspen at the higher genet level has been eliminated. I do not rule out the possibility of finding other arguments against individuating plants at higher levels. Neither do my claims constitute an argument against endorsing lower-level units of selection in plants, such as modules or meristems. The modular view conflicts with the genet view only if multiple simultaneous levels of selection are ruled out. In most real-life cases it will be reasonable to view multiple units as acting as simultaneous levels of selection. In this case, the best solution is to use something like Pedersen & Tuomi's hierarchical multilevel selection model (1995), which acknowledges and partitions multiple levels of selection.

In this section, I showed why it might be a mistake to think that homogeneity and conflict reduction mechanisms are at the center of our understanding of what it is to be an individual. Once we see that lower-level conflict does not necessarily undermine individuality at a higher level, we can reject arguments from the existence of genetic conflict to individuation at low levels of biological organization. The way is then open to build hierarchical selection models that fully incorporate multiple levels of selection. Plants and other modular organisms are ideal subjects for such models.

Conclusion

In plants and other modular organisms, there may be selection between higher-level units (such as genets and ramets) as well as selection between lower-level units (such as modules and meristem cells) and, *contra the usual assumptions of multilevel selection theory,* these two levels of selection need not be in opposition to each other.

Levels-of-selection theorists are wrong to assume that the central problem in transitions is always that of minimizing within-group competition. Evidence of intralevel conflict does not qualify as evidence against the existence of a higher level of selection.

Finally, plants and other modular organisms such as aspen may be hierarchical individuals, by which I mean that ramets and genets and modules are all simultaneous levels of selection.

Acknowledgments

Notes

1. Other authors mean the term "genet" to imply genetic homogeneity, but I use a developmental definition because, as we will see later, the unit that develops from a zygote rarely stays genetically homogeneous for long.

2. For example, see Ye, Yu, and Dong (2006).

3. De Sousa says individuals are spatiotemporally bounded and continuous (De Sousa 2005).

4. Although, of course, Janzen, who simply defines individuality via sex, would deny that vegetative propagation produces new individuals at all.

5. Furthermore, heterogeneity or variance need not be genetic—selection may also act on nongenetic differences between cells, such as methylation patterns. There is even evidence that such patterns may be heritable (Jablonka 2005).

6. Although see Foster et al. (2002) for discussion of how chimerism seems not to impede individuality in slime mold slugs and insect colonies.

7. Muller's ratchet is the name for a process by which the genome of an asexual population accumulates deleterious mutations over time. Muller suggested this as an explanation for the adaptive value of sex. His argument was that sexual recombination exposed deleterious alleles to selection, allowing them to be purged from the population, and reversing the action of the ratchet.

8. By "as a theoretical possibility" I mean to convey that, while it is universally accepted as a tautological truth, there is no consensus as to whether it acts in such a way that it has long-term evolutionary consequences.

9. Presuming that a mother cell and a mitotically derived daughter cell can be said to belong to different generations. Of course, it should be understood that gene frequencies can change over the course of these generations without any selection taking place, as a consequence of mutation alone. Once variation exists, however, evolution by somatic selection can occur.

10. There is room for further discussion about the extent to which each level constitutes a paradigm rather than marginal Darwinian population, in Godfrey-Smith's terms.

11. There is room for further discussion about the extent to which each level constitutes a paradigm rather than marginal Darwinian population, in Godfrey-Smith's terms.

12. An "initial" is simply a totipotent meristem cell. The word is used to distinguish these from cells in the meristem area that are on their way to becoming differentiated as soma.

13. "Adventitious" buds are those that develop on the roots, leaves, or stem—that is, anywhere other than the tip of a shoot.

14. The *Journal of Evolutionary Biology* devotes the whole of issue 17 to discussing intraorganismal genetic heterogeneity.

15. D. S. Wilson (1980) is an important exception, who has long argued that selection at different levels can act in either opposing or harmonious directions. See also Hadany (2001).

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