



Commentary

Defining clonality and individuals in plant evolution

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Abstract

Aarssen (2014) proposes estimating fitness in clonal and aclonal seed plants by defining an individual as a rooted-unit, which he defines by the root-to-shoot transition in anatomy of the stele. This approach may be helpful for some seed plant taxa, maybe even most seed plants, because of being much more readily operational than most other definitions of individuals. However, the rooted-unit approach seems to falter for many weird plants, such as those with anomalous root and shoot anatomy and plants that can reproduce clonally from leaves or apomictic seeds. Another problem with using rooted-units to circumscribe individuals is the implicit assumption that mitosis constrains genetic variance and meiosis increases genetic variance, when the exact opposite may be true. Although definitions of individuals are arbitrary, there may soon be sufficient data to ascertain which definitions are most useful, i.e. which definitions of individuals help unify evolutionary theory.

Introduction

John Endler (1986) wrote a path-breaking book on how to measure fitness in natural settings. He pointed out that such efforts are fraught with difficulty, but not impossible, at least not for populations in which individuals can be unambiguously identified. Lonnie Aarssen (2014) attempts to extend Endler's work in a fascinating way, by showing that it may be possible to measure fitness of populations in which it has been difficult to identify individuals. Evolutionary biology, in general, and population genetics, in particular, rely on being able to circumscribe individuals, as well as to delineate what actually constitutes a population. Neither

Aarssen nor I are ready to tackle the problem of what constitutes a population versus subpopulation versus metapopulation, but Aarssen contributes a cogent proposal for identifying individuals. The key passage in Aarssen (2014: 80) is:

Accordingly, while selection (differential reproductive success) acts on the phenotypes of RU [rooted-unit] individuals, it is only their resident genes/alleles (and not these individuals) that realize the effects of selection in terms of fitness, defined by their copying and transmission success across multiple generations. This of course cannot be literally measured, practically—but only estimated, commonly by counting offspring, or descendants only in the short term. In other words, the estimated fitness of resident genes/alleles for RU 'X' is greater than that for RU 'Y' if the phenotype of 'X' (with traits informed by the expression of its resident genes/alleles) evokes greater reproductive success for 'X' (i.e. favoured by selection). And importantly, for clonal species, the latter is measured by more than just counting sexual offspring/descendants. The rooted-unit is the minimal operational and circumscribable vehicle in higher plants that can carry gene/allele copies into the future.

Aarssen is saying that fitness is hard to measure and that rooted-units may be a valuable proxy for estimation of fitness of clonal plants. By circumscribing individuals as rooted-units that "can carry gene/allele combinations", he is invoking a genetic homogeneity definition of individuals, albeit without the onerous task of looking directly at the alleles. Alternative classes of definitions

of individuals include physiological autonomy, levels of selection, unicellular bottlenecks, and alternation of generations (Santelices 1999, Gorelick 2012), although with these alternative definitions it is often nigh impossible *in the field* to readily determine what is and isn't an individual.

Even restricting attention to evolutionary biology and ecology, it is still surprisingly difficult to cogently circumscribe or define individuals (Janzen 1977, Clarke 2010, 2012, Gorelick 2012, Minelli 2014). Yet, we truly need to be able to define individuals in order to conduct evolutionary analyses, such as population genetics, quantitative genetics, studies of senescence, demographics, and conservation biology. As Herron et al. (2013: 844) stated:

Biology needs a concept of individuality in order to distinguish organisms from parts of organisms and from groups of organisms, to count individuals and compare traits across taxa, and to distinguish growth from reproduction. Most of the proposed criteria for individuality were designed for 'unitary' or 'paradigm' organisms: contiguous, functionally and physiologically integrated, obligately sexually reproducing multicellular organisms with a germ line sequestered early in development. However, the vast majority of the diversity of life on Earth does not conform to all of these criteria.

Lonnie Aarssen (2014) justifiably highlights how plants, especially clonal seed plants, flummox such attempts at circumscribing individuals, which was already difficult because they lack germ lines, i.e. are not unitary organisms. This problem is even more general because most eukaryotes fall along a continuum of levels of sequestering germ line cells (Buss 1987).

Aarssen (2014) proposes a circumscription of individuals and clonality via so-called 'rooted-units'. By examining stelar transitions between roots and shoots, he suggests that rooted-units may provide a decent proxy for mean fitness of a population of both clonal and aclonal plants, thereby allowing us to operationalize evolutionary theory. The beauty of Aarssen's approach is in how operational it is. With just a knife, it is often easy to see changes in stelar architecture between root and shoot. Contrasts this with some other definitions of individuals in which we are compelled to decide whether two putative individuals have the same DNA, what constitutes physiological autonomy, or whether cryptic meiosis (automixis) has occurred. Aarssen's approach is much more practical.

Aarssen's (2014) definition of clonality and individuals is dependent on identifying rooted-units that are characterized by root-to-shoot transitions in the stele. These are known as stelar transitions because of

the typical loss or diminution of pith in the stele as one descends from shoot to root, especially with secondary growth. Shoots may fragment or roots may fragment to produce new clones, but the telltale stelar transition presumably still exists between shoots and roots. Unfortunately, it is not obvious whether considering rooted-units to be individuals will help because too many seed plants are just plain weird. Below, I show two such problems: (1) that clones can form from things other than rooted-units and (2) it may be impossible to identify root-to-shoot stelar transitions in all seed plants.

Clonal leaves and seeds

A problem with Aarssen's circumscription of clones and individuals as rooted-units is that not all clonal seed plants have clones that originate from roots or shoots. Clones can form from leaf cuttings, such as with many succulent and semi-succulent leaves. Their simple leaves can subsequently form adventitious roots and shoots in many eudicots (e.g. Aizoaceae, Begoniaceae, Crassulaceae, Droseraceae, Gesneriaceae, Linaceae, Scrophulariaceae), monocots (e.g. Dracaenaceae, Liliaceae, Xanthorrhoeaceae), and even a few monilophytes, such as the walking fern *Asplenium rhizophyllum*. Aarssen (2014: 78, emphasis in original) states that "gene/allele copies are transmitted in perpetuity only because parental RUs [rooted-units] (and only *entire* RUs, not their dependent subunits or modules) make offspring RUs that can in turn make 'grand-offspring' RUs". But this cannot be true because the subunits of detachable leaves, which can subsequently become subunits of rooted-units, can transmit alleles to subsequent generations once they grow flowers (or sporangia). Note that while compound leaves are often considered to be highly modified shoots (Arber 1950, Rutishauser and Sattler 1997, Lacroix et al. 2003), the succulent and semi-succulent simple leaves that can form new roots and shoots seem to universally not be considered modified shoots.

Possibly an even bigger problem is that Aarssen (2014) neglected apomictic dandelions (*Taraxacum*), which started the debate on what is an individual, vis-à-vis clonal dandelions and aphids in a classic paper by Dan Janzen (1977). Depending on the individual and time, dandelion seeds can either be produced via mitosis (apomixes, aka agamospermy) or meiosis (automixis). For the purpose of the argument here, it does not matter whether automictic seeds are produced via pre-meiotic doubling, central fusion, or terminal fusion, all of which are self-sexual (Gorelick and Carpinone 2009, Meirmans 2009). For apomictic dandelions and other related plants, such as hawkweeds (*Hieracium*), do separate rooted units really constitute different individuals? Janzen and I would say *no*; Aarssen would say *yes*. Which approach yields better predictions or

better explanations of observed phenomena in these quintessential organisms? There should be sufficient data in the literature on dandelions to provide a horse race between these diametrically opposite perspectives.

Many plants have unrooted stems that can be readily detached and propagated, such as potatoes (*Solanum tuberosum*) and prickly pear cacti (*Opuntia* spp.). In conjunction with apomictic ‘seeds’ in dandelions and several grasses and detachable succulent/semi-succulent leaves, clonal unrooted stems demonstrate that the rooted-unit is not “the minimal operational and circumscribable vehicle in plants that can carry gene/allele copies into the future.”

Aarssen identifies the problem with defining individuals and clones in plants: plants contain latent meristematic tissue (so-called ground tissue) throughout all stems, leaves, roots, and even reproductive parts. There is some truth in ground tissue being a “vascular transition lifeline” because vascular tissue in plant parts is partly composed of parenchyma that can subsequently differentiate into a meristem or cambium (cambia are just specialized forms of meristems). Not only can undifferentiated parenchyma re-differentiate into meristems and cambia, but so can more specialized phloem parenchyma (Alosi and Alfieri 1972). Plants are sufficiently flexible, especially compared with metazoans, that it is harder to define individual plants than individual animals.

Confounding monocots

It is odd that Aarssen (2014) concludes by invoking the Lemnaceae in a paper on rooted-units because it is not altogether obvious whether these floating monocot plants even possess stems. As with the Podostemaceae, it is often difficult to discern stems from leaves from roots in many of the smaller aquatic plants. Furthermore, and this is a very minor point, most contemporary taxonomists consider the Lemnaceae to now be the subfamily Lemnoideae submerged within the Araceae.

Monocots may be problematic for Aarssen’s proposed rooted-unit circumscription of individuals. The other odd lineage in the Araceae includes skunk cabbages in the subfamily Orontioideae. *Symplocarpus foetidus* seems to form massive clonal colonies with enormous contractile roots, although I have not seen clonality definitively tested in this species. Regardless, how does one define a rooted-unit based on root-shoot transitions in stele architecture in such long-lived and large herbaceous monocots? In fact, defining clonality via rooted-units and their stelar transitions may not work for any of the massively clonal monocots, such as Poaceae, Posidonaceae, Typhaceae, and Zosteraceae. *Posidonia oceanica* clones supposedly can be over 15 km across (Arnaud-Haond et al. 2012), so this is an

interesting test case for any framework designed to circumscribe individuals and estimate fitness of clonal organisms.

The problem is not simply that monocots are herbaceous. There are clonal woody monocots with secondary growth or something akin to secondary growth (diffuse thickening), such as in *Nypa* in the Areaceae, *Yucca* in the Asparagaceae, and *Sansevieria* (which will probably soon be subsumed in *Dracaena*) in the Dracaenaceae (Lu and Morden 2014, Walker 2014). Note that *Sansevieria* can be propagated from leaf cuttings (Schubert 1913, Yarbrough 1936), making this taxon doubling confounding for whether rooted-units define individuals and clones. I have not looked at root-shoot stelar transitions in enough monocots to know whether they will confound the definition of individuals as rooted-units, but suspect that monocots may be decent way of gauging Aarssen’s idea.

Clones have higher genetic variance than sexual progeny

I fundamentally disagree with Aarssen (2014) on one major point when he claims that, “Outcrossed sexual (seed) RU offspring are of course genotypically variable, whereas clonal (vegetative) RU offspring (like seed offspring from apomixis or from inbred sexual lines) are normally genotypically identical”. By contrast, Henry Heng and I (Gorelick and Heng 2011) have followed a line of researchers (e.g. Bernstein 1977, Bernstein et al. 1981, Shields 1982, Page and Hawley 2003, Wilkins and Holliday 2009) who instead assert that sex reduces genetic variance, while mitosis increases genetic variance. This fundamental change in perspectives provided the difference in conclusions between Clarke (2012) and Gorelick (2012) in defining individuals, despite starting from the same basic definition. We both asserted that an individual is circumscribed by factors that constrain genetic variance. Clarke (2012) then followed Weismann’s (1891) seemingly incorrect paradigm that mitosis constrains genetic variation, whereas Gorelick and Heng (2011) believed that meiosis constrains (diminishes) genetic, genomic, and epigenetic variance. Because I define ‘genetic’ as ‘heritable’ (Gorelick and Laubichler 2008), epigenetic and genomic variance are therefore merely special cases of genetic variance, all of which seem to be diminished by meiosis. Whether mitosis results in more genetic variation than meiosis is an empirical question, for which data may soon be available, such as recently seen in grapes (Myles et al. 2011) and the apomictic mustard *Boecheira* (Beck et al. 2012). The confounding problem, however, exists that many researchers still consider automixis and autogamy to be forms of asexuality (e.g. Agrawal 2009), precluding easy meta-analysis. In a similar vein, at the start of

Aarssen's (2014) conspectus, there is discussion of recombination during meiosis, but oddly no discussion of mitotic recombination. While mitotic recombination may occur at lower rates than does meiotic recombination, i.e. fewer crossing over events per cell division (Pontecorvo and Käfer 1958), there are a lot more mitotic divisions than meiotic divisions, especially in largely clonal seed plants, rendering mitotic recombination an important source of genetic and genomic variation.

Concluding remarks

For seed plants in which clones form by fragmented roots and/or shoots and in which stelar transitions between roots and shoots are well-defined, Lonnie Aarssen (2014) has provided a nice tool with which to conduct practical "roll your sleeves up" evolutionary analysis of clonal plants.

If Aarssen (2014) is 'correct' that rooted-units are individuals or a decent proxy for individuals, then he has provided an interesting and extremely practical way of measuring fitness of many clonal seed plants. I put 'correct' in quotes because it is philosophically impossible to test definitions, such as of individuals. Definitions are arbitrary. All we can do is gauge whether a definition is useful (Wagner 2010, Gorelick 2011) and maybe only in a specific framework, e.g. evolutionary biology. But this provides possible empirical ways for gauging the utility of definitions. Take my contrary view that fragmented rooted-units that are all products of mitosis, without any intervening meiotic divisions, constitute a single huge disaggregated individual (Gorelick 2012). One huge individual has a much greater rate of mutation simply because it has more DNA (more cells) that are exposed to cosmic rays and other mutagens. One huge individual also means that effective population size is one. Therefore, per my definition of individuals, which is not nearly as operational as Aarssen's, evolution of clonal plants should be dominated by mutation and drift. With Aarssen's (2014) definition of individuals as rooted-units, by contrast, evolution of clonal plants should be much more dominated by selection. Such radically different conceptualizations and instantiations of evolution should be observable, especially with agricultural plants. Sewall Wright and Ronald Fisher developed population genetics for agricultural applications, with the aim of improving yields (farm animals for Wright and crop plants for Fisher, which, in retrospect, makes it seem odd that it was Wright who emphasized drift and Fisher who emphasized selection). Do clonal plants, especially clonal agricultural plants, follow evolutionary trajectories more dominated by selection or by drift/mutation? This may tell us whether it is possible to take a readily operational approach, such

as the one that Lonnie Aarssen has just suggested, or whether we need to take a more cumbersome approach to defining individuals. Those who debate such matters of what constitutes an individual should collegially sit down to talk, with everyone bringing the fermented products of their favourite clonal wine grape. Maybe the debate about who is an individual will drift (or mutate?) away on alcoholic wings of a fine albariño or cabernet franc.

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