Integrating natural and sexual selection across the biphasic life cycle

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Abstract

An alternation between diploid and haploid phases is universal among sexual eukaryotes. Across this biphasic cycle, natural selection and sexual selection occur in both phases.

Together, these four stages of selection act on the phenotypes of individuals and influence the evolutionary trajectories of populations, but are rarely studied holistically. Here, we provide a conceptual framework that transcends taxonomic groups, and unifies the entire selection landscape within and across the diploid and haploid phases. Within a single cycle, our synthesis produces within-phase trade-offs, and across-phase one-way bridges where selection in one phase is tethered to a given genotype's phenotypic experience in the previous phase. From this, we define four types of parental effect across a wide conceptual context, expanding on the conventional definition of a connection across cycles from diploid to diploid. Examples across sexual eukaryotes for each trade-off and bridge are presented with the aim to highlight knowledge gaps and inspire new experimentation in different taxa. We argue that knowledge of the complex and intertwined opportunities for selection within biphasic life cycles will offer clearer insights into key ecological and evolutionary processes, with benefits to applied science.

Keywords

sperm competition, pollen competition, transgenerational effects, cryptic female choice, haploid selection, parental effect

Selection in the biphasic life cycle

Sexual eukaryotes share the common feature of a biphasic life cycle, which includes both diploid and haploid phases that are separated by meiosis (diploid to haploid), and fertilization, syngamy and the formation of a zygote (haploid to diploid). Three categories of biphasic life cycle (Figure 1A-C) are distinguished by the presence or absence of mitosis in each phase (Mable and Otto 1998; Fusco and Minelli 2019; Umen and Coelho 2019) – see electronic supplementary material for definitions – and comprise tremendous variation in the relative lengths of the component parts (Rescan et al. 2016). In diplontic cycles (e.g., animals) there is no haploid mitosis and the haploid phase is limited to gametes (Figure 1A), while haplontic organisms (e.g., many green algae) have no diploid mitosis and the diploid phase occurs only as a zygote (Figure 1B). In haplodiplontic species (e.g., land plants) mitosis occurs in both phases (Figure 1C).

Selection acts on phenotypes (West-Eberhard 2003), which are the product of the genotype and the environmental inputs on development. Natural selection (Darwin 1859) is the differential survival and reproduction of genotypes due to differences in phenotype, and encompasses the terms ‘viability selection’ and ‘fecundity selection’. Sexual selection (Darwin 1871) is defined as differential reproductive success due to competition with members of the same sex (intra-sex selection), or choice by members of the opposite sex (inter-sex selection). Arguments exist about whether sexual selection is a component of natural selection, instead of a different process (Lyon and Montgomerie 2012; Roughgarden 2012; Alonzo and Servedio 2019), as there are often ‘grey’ zones where categorizing becomes problematic. Nonetheless, it can be helpful to distinguish the two when exploring trade-offs between traits and fitness, since the patterns can differ depending on the fitness component under study.

Both natural and sexual selection can occur before and after mating (Figure 1). Selection thus occurs across four broad stages within biphasic life cycles. Importantly, gene expression is not necessary from both diploid and haploid genomes for selection to occur in both phases, as cells under selection in one phase may have been produced by the genome of the other phase. Across taxa, different start points, complexity, and terminology used to describe life cycles (Fusco and Minelli 2019) influence the definitions (see supplementary material) of what is an individual, adult, parent and generation. This complicates generalization across cycles, which may have hindered integration, but the main points of our perspective are applicable to all cycles. Our synthesis of general interpretations is given in Figure 1A-C and in the text below, and is an attempt to categorize definitions of selection across eukaryotes. We label the selection stages as 1-4 in the sequence they occur from the formation of a zygote (Figure 1).

In the diploid phase of diplontic and haplodiplontic taxa, natural selection can be interpreted (Figure 1A,C; **Stage 1**) as zygote-adult survival, or ‘who lives to mate’, and the ability to produce and release gametes or spores. For haplontic cycles (Figure 1B) there is no diploid mitosis, but zygote survival before meiosis still applies, as does the ability to produce spores. In some diplontic species (i.e. ‘higher animals’) sexual selection can be conceptualized (Figure 1A,C; **Stage 2**) as ‘who gets to mate’ of those capable (Andersson 1994) – and forms the basis of ‘Darwinian sexual selection’ (Simmons and Wedell 2020). As there is no obvious intra-sex competition or inter-sex choice in haplontic taxa (Figure 1B) or haplodiplontic bryophytes and ferns (Figure 1C), sexual selection in the diploid phase may not apply in these groups (Zavada and Taylor 1986; see Andersson 1994; Willson 1994; Moore and Pannell 2011). It may in angiosperms (haplodiplontic), under the context of intra-sex competition for limited insect pollinators – but that is debated (Moore and Pannell 2011).

In the haploid phase, natural selection can be conceptualized readily in haplontic and haplodiplontic taxa (Figure 1B-C, **Stage 3**), where it involves the survival of the haplont or gametophyte. It is harder to separate natural and sexual selection on gametes as some traits seem to be adaptive for both processes. We consider traits that determine the success of gametes outside of the context of competition from gametes of the same sex (e.g., sperm swimming ability in algae, bryophytes, ferns) to be naturally selected. In diplontic cycles (Figure 1A, Stage 3) there is no mitosis, and little or no gene expression, in the haploid phase, but natural selection will still target gamete phenotypes (even if coded by the diploid genome) that affect their functional capacity to fertilize opposite sex gametes independent of competition from gametes of the same sex (e.g., the capacity of sperm to function under different abiotic conditions (Beirão et al. 2018a)).

Sexual selection targeting haploid cells (Figure 1A-C, **Stage 4**) is thought to be ancestral to that in the diploid phase (Parker 2014, 2020) and represents 'Parkerian sexual selection' (see Simmons and Wedell 2020). It influences 'which functioning gametes fertilize in the presence of gametes from the same sex' and occurs intra-sex in the form of haplodiplontic pollen competition (Mulcahy 1979) and sperm competition, diplontic animal egg competition (see Evans and Lymbery 2020) and sperm competition (Parker 1970, 2020), and gamete competition in non-animal diplontic cycles as well as haplontic species (Frenkel et al. 2014; da Silva and Drysdale 2018) – where the terms sperm and egg do not apply. It also occurs inter-sex with cryptic female choice, a process described mostly for animals whereby females bias the outcome of male-male sperm competition via a range of morphological, physiological and behavioral mechanisms (Firman et al. 2017). The extent of a similar process in other taxa is less clear, but examples where plant female organs contribute to differential success of pollen (e.g., via pistil length, or selective ovule abortion) are known (Lankinen and Karlsson Green 2015; Beekman et al.

2016; Tonnabel et al. 2021). In yeast, sex pheromones not only help locate mates but can also affect final mate selection by choosing the strongest signallers (Rogers and Greig 2009). In bryophytes, sex-specific chemical secretions attract microarthropods that transport sperm to other individuals (Rosenstiel 2012), but whether this would bias sperm competition is unclear.

Together, these four stages of selection act on and determine the phenotypes of individuals, and influence the evolutionary trajectories of populations. Despite the clear interrelationships among these stages, they are seldom studied together. In order to promote a more holistic understanding of how selection targets phenotypes across these stages, we use this perspective to synthesize contemporary research that reveals the interplay between natural and sexual selection across the biphasic life cycle of sexual eukaryotes, which is supported by the framework outlined in Figure 2. We use the term "within-phase trade-offs" where natural and sexual selection are acting (e.g., antagonistically) on the same 'individuals', and "across-phase one-way bridges" when experiences of an individual in one phase affects selection in the subsequent phase. This perspective specifically focuses on highlighting the selection stages and their trade-offs and bridges, which we illustrate with some examples across sexually reproducing lineages.

Within-phase trade-offs

In the diploid phase (nD↔sD)

Within the diploid phase, the trade-off (Figure 2) between natural selection – typically conceptualized as survival (Figure 1A-C, Stage 1), and sexual selection –

breeding opportunities (Figure 1A-C, Stage 2) was famously considered by Darwin (1859, 1871), who referred to the ‘inconvenience’ of elaborate tail feathers in many male birds, and how their full development must be checked by natural selection. When viewed exclusively through the lens of natural selection, such traits are almost impossible to explain, but sexual selection illuminates a balance between the opposing forces (Endler 1980). The interplay between natural and sexual selection in the diploid phase is now widely recognized as a central evolutionary process. In animals, for example, individuals with elaborated secondary sexual characteristics associated with mate choice (e.g. songs, colours, or structures), are often more prone to predation, as seen in dragonflies (Moore and Martin 2018), lizards (Amdekar and Thaker 2019) and birds (McQueen et al. 2019). In angiosperms, abiotic factors exert selective pressure that can affect the outcome of sex expression in flowers and sex ratios in populations (Retuerto et al. 2018; Varga and Soulsbury 2020), imposing trade-offs with other plant functions like growth and defense. Investment in antiherbivore defenses can alter selection on plant reproductive traits, such as petal morphology and inflorescence structure, which are known to attract pollinators (Thompson and Johnson 2016), and thus who gets to mate. These trade-offs do not appear to apply to haplontic and some haplodiplontic taxa, as there is no sexual selection in the diploid phase.

In the haploid phase (sH↔nH)

Within the haploid phase, the trade-off (Figure 2) between natural (Figure 1a-c, Stage 3) and sexual (Figure 1A-C, Stage 4) selection is more poorly documented. Despite very little work on them, haplontic organisms could provide key insight by revealing many of the same trade-offs as in diplontic species. For example, when subject to nitrogen starvation, green algae induce gamete production, and who reproduces depends on the liberation of female gamete pheromones that attract male gametes (Frenkel et al. 2014). Heat shock or drought can also trigger the production of sex pheromones in algae, which can be species- or even strain-specific, avoiding interspecific hybridization (Frenkel et al. 2014). In some mosses females chemically induce the development of dwarf males (influencing sexual selection), but the process is mediated by natural selection on the habitat of the female (Rosengren and Cronberg 2014).

In seed plants, the effects of abiotic factors, such as temperature and humidity, on pollen tube germination and growth are well known (Williams and Mazer 2016), although their influence on paternity is unclear. The presence of apertures in pollen provides a selective advantage as they facilitate water and gas exchange. However, a trade-off between pollen survival and germination has been proposed, where more pollen apertures is expected to accelerate pollen germination on the stigma (higher competitive ability), but has a negative impact on pollen survival since pollen mortality increases with increased aperture number (Prieu et al. 2016).

In animals, if sperm quantity is primarily targeted by selection at Stage 4 (which functioning gametes fertilize) while sperm quality is also important for Stage 3 (gamete performance outside of the context of competition from gametes of the same sex), then sperm quality vs quantity (Parker and Pizzari 2010) could represent a conceptual within-phase trade-off (Figure 2). Similarly, a trade-off would also exist if an adult adjusted its gametes to perform better under acclimated abiotic conditions (see next Section) but this had implications for sexual selection in the form of sperm competition or cryptic female choice. We are unaware of studies the have explicitly tested for such patterns, although some provide hints. For example, sperm swimming performance to changing river pH varies among male trout, such that predictions of winners of sperm competition are altered by the abiotic environment (Purchase and Moreau 2012). Likewise, in sea urchins, fertilization success of different males changes in different ways depending on ocean pH (Smith et al. 2019). In neither study, however, were sperm competitions actually performed. The topic is ripe for targeted experimentation, and should incorporate various environmental stressors, such as temperature (see García-Roa et al. 2020).

Across-phase one-way bridges

The four selection stages (Figure 1A-C) are the main drivers of adaptive evolution. However, selection stages that target phenotypes expressed during the diploid and haploid phases do not operate in isolation, and the 'experiences' (e.g., diet, perceived predation risk, stress, etc.) of the specific individuals that contribute to the subsequent phase may impact selection in it. In other words, within one circuit of a biphasic life cycle, selection in one phase is tethered to a given genotype's phenotypic experience in the previous phase. Below, we define two such 'bridges'. These are conceptually similar to what West-Eberhard (2003) refers to as 'bridging phenotypes' (Box 1), and Ritchie and Marshall (2013) call 'phenotypic links'. They bridge one phase to the next in biphasic cycles and could be interpreted as parental effects (see Types I and II in Box 2). Impacts perpetuating further in time (e.g., parental effects across more than one circuit of the biphasic life cycle, like diploid to diploid) are considered briefly in Box 2 (Types III and IV) and are reviewed in more detail elsewhere (e.g., Evans et al. 2019).

Bridges from the diploid to the haploid phase (D→H, Box 2 Type I)

As we have noted, haplontic species have no diploid mitosis, and we are unaware of any work considering how surviving zygote 'experiences' before meiosis (e.g, resting stomatocysts) might impact the haploid phase. In diplontic and haplodiplontic cycles, effects from the diploid to haploid phase may cause adaptive or maladaptive influences on selection in the haploid phase. Adaptive responses include the ability to alter the phenotypic expression of the haploid phase to ensure optimal performance under the environmental conditions that are likely to be encountered. However, antagonism between phases are relevant in this context, because if an individual invests more energy into survival or acquiring mates in the diploid phase (amount of relative energy expenditure being an 'experience') there would be less energy available to contribute to gametes or spores in the next phase (e.g., Parker 1998).

<u>On natural selection in the haploid phase (D→nH)</u>

Much of the available information on how diploid adults (Figure 2) influence selection during the haploid phase (i.e. the haploid cells they produce) is in the context of natural selection on animal gametes. For example, in ascidians, females have the capacity to adjust egg size according to variation in spawning densities, which can have important implications for the development of zygotes due to the prevalence of lethal polyspermy at high sperm concentrations (Crean and Marshall 2008). Larger eggs may allow for an increase in sperm-egg collision rates under sperm limitation, while smaller eggs reduce the probability of polyspermy at high sperm concentrations.

In animals it is difficult to separate egg functionality from that of embryos, but sperm performance can be measured with relative ease. Sperm quality parameters take many forms (Snook 2005), such as swimming ability, and a considerable body of research shows that environmental conditions experienced by adult males can influence the quality of their sperm. In humans, factors such as high sugar diets (Nätt et al. 2019), contaminants (Ji et al. 2018), and oxidative stress (Agarwal et al. 2018) reduce the quality of sperm. However, many studies have demonstrated that adjustments to sperm can be adaptive. For example, in external fertilizers, adult male acclimation to salinity (Jensen et al. 2014; Taugbol et al. 2017) and temperature (Vasudeva et al. 2019) fine tunes sperm performance to subsequent spawning conditions. This is important because abiotic factors influence sperm performance, and sperm cells only swim optimally under certain conditions (Beirão et al. 2018a). These and related topics have been treated in part within several reviews (Snook 2005; Fitzpatrick and Lüpold 2014; Immler 2018; Evans et al. 2019).

Similar processes operate in algae and land plants. In brown algae decreased salinity experienced by the diploid adult compromises sperm performance (see Rothäusler et al. 2019, where the term dysfunction is used), drastically reducing fertilization success. Development and function of plant gametophytes (most notably in males) are influenced by environmental conditions of the adult sporophyte. Examples in cereals include an interrupted germline development (lack of functional pollen) in response to drought, or alterations in photoperiod and temperature (Begcy and

Dresselhaus 2018; Fan and Zhang 2018). In grasses the biochemical composition of pollen changes in response to parental temperature and nutrients (Zimmermann et al. 2017), while increased nutrients results in poorer quality pollen (but higher quantity) in juniper (Pers-Kamczyc et al. 2020). Squash plants infected with mutualistic mycorrhizae produce larger pollen grains than uninfected plants (Lau et al. 1995).

On sexual selection in the haploid phase (D→sH)

Parental experiences in the diploid phase can also have profound consequences for selection occurring at Stage 4 (Figure 2). For instance, studies spanning numerous animal species have manipulated the social environment experienced by breeding adults and shown that males can facultatively adjust ejaculate characteristics according to the level of sperm competition predicted under the new conditions (Perry et al. 2013; Bartlett et al. 2017; Simmons and Lovegrove 2017; Fisher et al. 2018; Silva et al. 2019).

Sexual selection at Stage 4 is also clearly influenced by environmental conditions experienced by flowering plants in the diploid phase. Low soil quality can generate variability in the ability of female recipients to sort among pollen from competing donors (Lankinen and Hydbom 2017). Soil fertility may increase pollen size and quality (Delph et al. 1997; Zimmermann et al. 2017), which in turn produce higher siring success because larger pollen contains more energy reserves facilitating faster germination and pollen tube growth rates (Mazer et al. 2010; McCallum and Chang 2016). Adverse abiotic conditions experienced by parent plants can reduce pollen competitive ability against heterospecific pollen (Celaya et al. 2015). Other species interacting with plants in the diploid phase may also impact selection at Stage 4. For example, pollen from virus-infected squash are less likely to achieve fertilization than pollen from resistant plants when both pollen types compete within a style (Harth et al. 2016), and herbivory during the diploid phase can reduce pollen production (Rusman et al. 2019).

Bridges from the haploid to the diploid phase (H→D, Box 2 Type II)

How haploid experiences influence the diploid phase of the life cycle is poorly understood. These are conceptually similar (but reversed) to concepts outlined in the previous Section. They can occur if free-living haplonts or gametophytes alter energy allocation to specific gametes (animal alteration of egg size is diploid experience, not haploid), or in species with any type of life cycle if there are epigenetic changes to fertilizing gametes that affect subsequent embryos. Many experimental studies show changes in embryo development as a result of alterations in the haploid phase. However, it is very difficult to separate mechanisms into what constitutes a bridge across phases, from those which simply meet definitions of selection at Stages 3 or 4, the mechanisms not being mutually exclusive (see review by Marshall 2015). In animals and most plants, each sperm produced by diploid parents carries unique genetic information. Thus, even if there is only a single male donor, offspring effects could result from either which sperm fertilized or what happened to the fertilizing sperm. Mosses, lycopods and ferns provide an experimental solution to this problem, as all sperm produced by haploid parents are genetically identical (Johnson and Shaw 2016).

Some recent literature on haploid selection in animal sperm (Alavioon et al. 2017; Immler 2019; Sutter and Immler 2020) is focused on within-ejaculate selection (i.e.

selection that favours sperm phenotypes that are attributable to variation encoded by the haploid genome), although this phenomenon, along with among-ejaculate sperm competition, falls under selection in the haploid phase (Figure 1A-C, Stages 3-4) and does not constitute a bridge across-phases. Haploid selection in predominately diploid organisms (Immler 2019) is given more consideration in Box 3.

On natural selection in the diploid phase (H→nD)

Haploid experiences may alter characteristics of the subsequent phase in a manner that influences the likelihood of zygote survival (Figure 2). For haplontic cycles, this could be dramatic given the dominant phase is haploid. In bryophytes the diploid phase is physically attached to the maternal haploid phase throughout its development. What controls the number of sporophytes for each haploid female (polysety) is unclear, but this number can influence spore production in the diploid phase (Egunyomi 1978).

As a result of haploid mitosis in haplodiplontic cycles, including pollen tube and ovule development in angiosperms, we can expect that gametophyte experiences will affect plant sporophytes (Baskin and Baskin 2015; Williams and Mazer 2016). Such experiences could include environmental maternal gametophyte effects, pollen-pistil interactions, and non-random seed abortion, among others. Changes to the diploid phase include modification of seed size, germination success and seedling vigour, but whether mechanisms can be attributed to either haploid selection (e.g., within-donor pollen competition) or phenotypic adjustment attributable to haploid experiences are not clearly discernible (reviewed in Baskin and Baskin 2015), and needs future work.

Although animals are thought to have no or limited haploid gene expression, haploid experiences can still alter selection in the diploid phase. Sperm transmit more than just genetic material to eggs, and 'sperm factors' (see Immler 2018) such as proteins, might be modified by sperm experience. In an externally spawning marine polychaete, Ritchie and Marshall (2013) used a split-ejaculate and split-brood design to manipulate the salinity that sperm were exposed to prior to fertilization, and the conditions of subsequent incubation. They found that larval survival was highest when developmental conditions matched that of the sperm treatment, and suggest epigenetic factors as the most likely cause. Other examples of haploid conditions influencing embryo development in animals are readily available (Kekäläinen et al. 2018) and are covered in several reviews (Evans et al. 2019; Pitnick et al. 2020), but clearly distinguishing the mechanism of bridges across-phases (Figure 2, H→D) from selection within-phase (Figure 1, Stages 3-4) in these studies is seemingly impossible.

On sexual selection in the diploid phase (H→sD)

In principle, haploid to diploid bridges (Figure 2) may also alter diploid development in a way that influences pre-mating sexual selection (Stage 2), although we are unaware of any study addressing this question. The potential certainly exists, if for example, H→nD perpetuate into adulthood and influence secondary sexual characteristics. Another possibility is if diploid sex ratios are influenced by haploid conditions (Eppley et al. 2018).

Concluding remarks and future directions

The complex and often intertwined opportunities for selection within the biphasic life cycle create major challenges for researchers attempting to understand key ecological and evolutionary problems in sexual eukaryotes. Toxicological research (Aulsebrook et al. 2020) provides a useful illustration. For example, in experiments examining the effect of marine oil spills on fish reproduction, Beirão et al. (2019) exposed fish embryos directly to contaminants. Such work, and that using juvenile/adult exposure to such contaminants, commonly examines resulting changes on traits related to natural selection on the diploid phase (Figure 1A, Stage 1), but rarely if ever considers sexual selection at Stage 2, or the trade-offs (nD↔sD) within the diploid phase (Figure 2). Other work focuses on effects on reproductive output. Beirão et al. (2018b) group these studies into two types, the first having “indirect effects”, where the adult is exposed and gametes are examined (in context of our D→nH; we are unaware of any work on D→sH, Figure 2). Other situations have “direct effects” where in external fertilizers the gametes themselves are exposed to contaminants, which can then be used to examine natural selection at Stage 3 (Beirão et al. 2018b), but has not been investigated in context of sexual selection at Stage 4 (Figure 1A), or trade-offs within the haploid phase (sH↔nH), or the H→D across-phase bridges (Figure 2). The problem of cascading effects (Figure 2, Box 1) caused by exposure to contaminants thus becomes evident.

We argue that considering all four selection stages within a cycle, along with their within-phase trade-offs and across-phase bridges, are of fundamental importance to both understanding evolutionary processes and conducting applied science. Our synthesis produces two within-phase trade-offs between natural and sexual selection, and two across-phase one-way bridges where selection in one phase is tethered to experiences in the previous phase. These bridges can be considered a type of parental effect, which expands the traditional scope of a connection across generations from diploid to diploid (Box 2). It is evident from our literature search that research on selection in general, but the within-phase trade-offs and across-phase bridges in particular, is available mostly for animals and seed plants, and to a much lesser extent for bryophytes, algae, and fungi (or at minimum such publications are not framed in the same context and are thus harder to find). What more, for example, could be learned from studies focusing on haplontic species? There is also a clear dearth of studies that tease apart mechanisms of haploid experience (H→D) versus selection in the haploid phase (Stages 3, 4) on diploid development, and our perspective highlights the need for targeted research on this topic. Future studies that incorporate selection in both phases and identify fitness components may provide significant advancement on many fronts. Some key outstanding questions are:

- What are the consequences of drawing conclusions about selection from isolated snap-shots of processes that are fundamentally intertwined? To help address this, can studies be practically undertaken that measure cascading impacts across all stages of selection?
- Trade-offs are a tenet of life history theory but what are the scope and consequences of antagonistic selection between the phases? Fined tuned adaptation is hindered by trade-offs between natural and sexual selection within a phase. Nevertheless, the extent to which adaptations that improve performance in one phase trade-off against those in the other is largely unknown. Similarly, for diploid dominant species, how does gene expression in the haploid phase influence the diploid phase?

- How important are haploid parental effects ("gametal effects") to the diploid phase? We have very little understanding of how natural and sexual selection interact in the haploid phase, or how haploid experiences influence sexual selection in the diploid phase, or the underlying mechanisms linking haploid experiences to offspring development.
- What is the potential of haploid selection for human food and health? For instance, to what extent can we use artificial gametophyte selection to further improve crop production? Female gametophyte selection needs further exploration in particular, because of its significant contribution to the tissue nurturing the embryo. What is the true level of haploid gene expression in animals and can this be exploited, for instance in assisted fertilization programs in livestock and humans?

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Box 1. ‘The bridging phenotype’ and biphasic life cycles across generations

West-Eberhard (2003) emphasizes phenotypic continuity among generations, which is enabled by what she calls ‘bridging phenotypes’. An egg being a bridge across generations/cycles; its influence on subsequent development is a combination of the genetic material it contains along with phenotypic adjustments that have occurred due to experiences of the adult that created it. Life cycles are “just one loop in a continuous string of ontogenies linked by these gametic bridges between generations (West-Eberhard 2003 - page 92)”. This is depicted as Figure I; for most diplontic and haplontic species one complete loop around this circuit represents a life cycle and generation in Figure 1. Three sequential phases (diploid-haploid-diploid or haploid-diploid-haploid) encompass two generations in most diplontic and haplontic species, but three generations in haplodiplontic species.

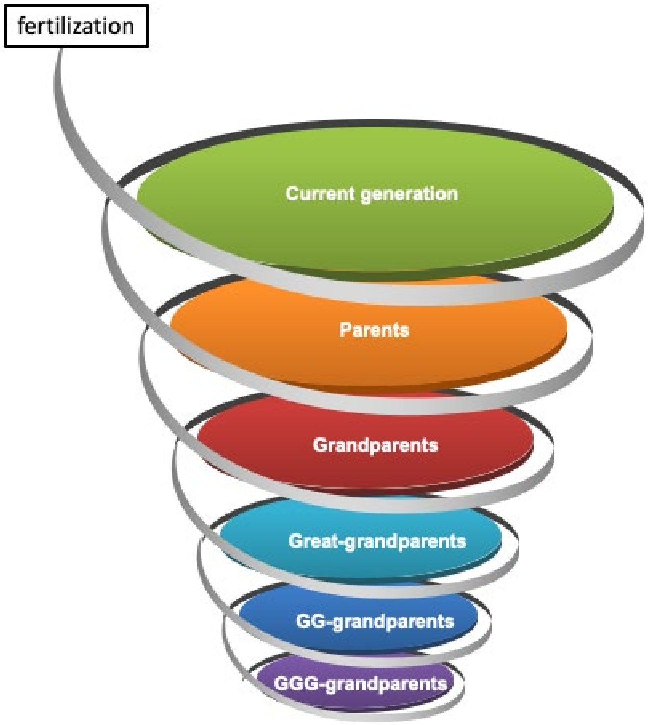

Figure I: Unbroken connections across generations (or groups of generations if >1 generation per cycle). In biphasic life cycles, bridges occur that connect the diploid and haploid phases encompassing one complete circuit. Modified from Fig5.2 in West-Eberhard (2003).

The concept becomes important for interpreting our across-phase bridges of biphasic life cycles (Figure 2). We consider a bridge to be from one phase to the next immediate one (either diploid-haploid or haploid-diploid). It becomes easy, however, to see how effects can propagate further in time, which we consider briefly in Box 2 on parental effects (e.g., diploid-diploid).

Box 2. 'Parental effects': a melting pot of bridges across the biphasic life cycle

Parental effects are ".. sustained influences on any component of the phenotype of the offspring that derives from a parent, apart from nuclear genes" (Kappeler and Meaney

2010). These can be more influential than abiotic variation (Penney et al. 2018) and may encompass maternal effects (Donohue 2009; Wolf and Wade 2009) and paternal effects (Crean and Bonduriansky 2014; Evans et al. 2019). They are usually framed as influences of diplontic parents (adult form of diploid phase, Figure 1) on their offspring. By definition, a parental effect is thus a connection across generations from diploid to diploid, but in most situations (parental care is an exception), this is bridged directly through the haploid phase. The traditional definition of a parental effect is thus too narrow. We consider here four types of parental effect, of which the above definition encompasses only one. Our 'types' match some of the 'paths' presented by Badyaev & Uller (2009; their Fig 1).

Parental effect type I (diploid⟶haploid; selection tethered to **one** phase previous): How the diploid phase influences the haploid phase of the life cycle. This has been covered in the Section on across-phase bridges from the diploid to the haploid phase and encompasses D⟶nH and D⟶sH in Figure 2. Conventionally, it has not been framed as a parental effect in diplontic centred literature, but under a wider taxonomic context, it is conceptually similar to type II – which is framed as a parental effect for plants, and animals (see Evans et al. 2019).

Parental effect type II (haploid⟶diploid; selection tethered to **one** phase previous): Although the haploid phase does not typically constitute the idea of 'parents' (except haplontic taxa and bryophytes), if haploid 'experiences' (in any cycle) influence the subsequent diploid phase, this may also be considered a parental effect (see Evans et al. 2019). This has been covered in the Section on across-phase bridges from the haploid to the diploid phase, and encompasses H⟶nD and H⟶sD in Figure 2.

<u>Parental effect type III (diploid→diploid; selection tethered to **two** phases previous):</u> The traditional definition of a paternal or maternal effect (e.g., embryo yolk, nutrient transfer across a placenta). Whether parental (diploid) influences on the haploid phase (type I), and subsequent diploid phase (offspring, type III) are complementary or antagonistic is poorly understood.

<u>Parental effect type IV (haploid→haploid; selection tethered to **two** phases previous):</u> These occur if haploid experiences in one generation, influence performance in the haploid phase of the subsequent generation. Such information must bridge via the diploid phase, but whether types II and IV function independently is not known. These types of parental effects are poorly studied, but do exist. For example, Gasparini et al. (2017) demonstrated experimentally that the duration of sperm storage in a fish influenced sperm quality of males in the next generation. One may conceptualize types II and IV to be 'gametal effects' (gamete + gametophyte), as an alternative to parental effects in haplodiplontic and diplontic taxa.

Box 3. Haploid selection in predominately diploid organisms and its potential applications

Artificial selection is human-induced change in the selection environment, and is often purposely done. It could target any of the four stages (Figure 1A-C), but has traditionally focused on changing diploid phenotypes by using breeding programs that bypass Stage 2 (e.g., dog, horse, pigeon, chicken breeding). This also bypasses Stage 4, with unknown long-term consequences. For diploid dominant organisms such as humans and most of their agricultural food, haploid selection provides tremendous opportunity. Genes are known to be differentially expressed during the two phases of a given life cycle due to different tissues or functions operating in the two phases. Expressed genes in the haploid phase has the potential to purge deleterious alleles or fix beneficial ones effectively in breeding programs (Immler and Otto 2018).

For instance, artificial selection for stress tolerance in pollen has enabled plant breeders to obtain cold-tolerant chickpeas and tomatoes in the next generation (Clarke et al. 2004; Domínguez et al. 2005), and repeated pollen selection for heat tolerance in maize can hasten the incorporation of heat tolerance alleles in a short time (Singh et al. 2020) – see Boxes 1 & 2. Gametophytic selection is an attractive tool in plant breeding programs because the large population size of male gametophyte (the germinated pollen) allows an exhaustive screening of economically important traits (in a process not constrained by greenhouse size). Female gametophyte selection needs further exploration in crop improvement programs because of its significant contribution to the tissue nurturing the embryo (Schmid et al. 2015).

Haploid selection can also apply to animals outside of the context of sperm competition among donor adult males (Bhutani et al. 2021). Sperm swimming longevity (Crean et al. 2012; Alavioon et al. 2017) and thermotaxis (Pérez-Cerezales et al. 2018) appear to filter sperm within-ejaculates in such a way that influences which are available for fertilization. This has applied implications, for example with *in vitro* fertilization including sperm sexing (Scott et al. 2018; Umehara et al. 2019) for agricultural breeding programs, and other aspects related to human fertility treatment (Oseguera-Lopez et al. 2019; Navarro-Rubio and Guell 2020). More thorough research on the complete suite of haploid-expressed genes is needed in animals, followed by empirical testing of artificial selection on those genes. Emerging molecular technologies should provide new opportunities to investigate haploid selection in diploid animals (Immler 2019).

Figure legends

Figure 1: Four stages of selection across biphasic life cycles in sexually reproducing eukaryotes, illustrated and defined for diplontic (A), haplontic (B), and haplodiplontic (C) cycles, which vary depending on the presence or absence of mitosis in each phase. Diversity of taxa within some cycles challenges interpretation, for example in haplodiplontic angiosperms there is sexual selection at Stage 2, but no flagellated (swimming) sperm at Stage 3, while the opposite occurs in bryophytes and ferns.

Figure 2: Within-phase trade-offs and across-phase bridges (dashed lines) within the biphasic life cycle, showing how selection stages are inter-connected. Illustrated for diplontic cycles but concepts apply to all cycles. H⟶nD and H⟶sD are one-way bridges from the haploid to the diploid phase, where natural and sexual selection in the diploid phase are tethered to experiences in the previous haploid phase - illustrated by the bent arrows. Likewise, D⟶nH and D⟶sH are one-way bridges from the diploid to the haploid phase, where natural and sexual selection in the haploid phase are tethered to experiences in the diploid phase.

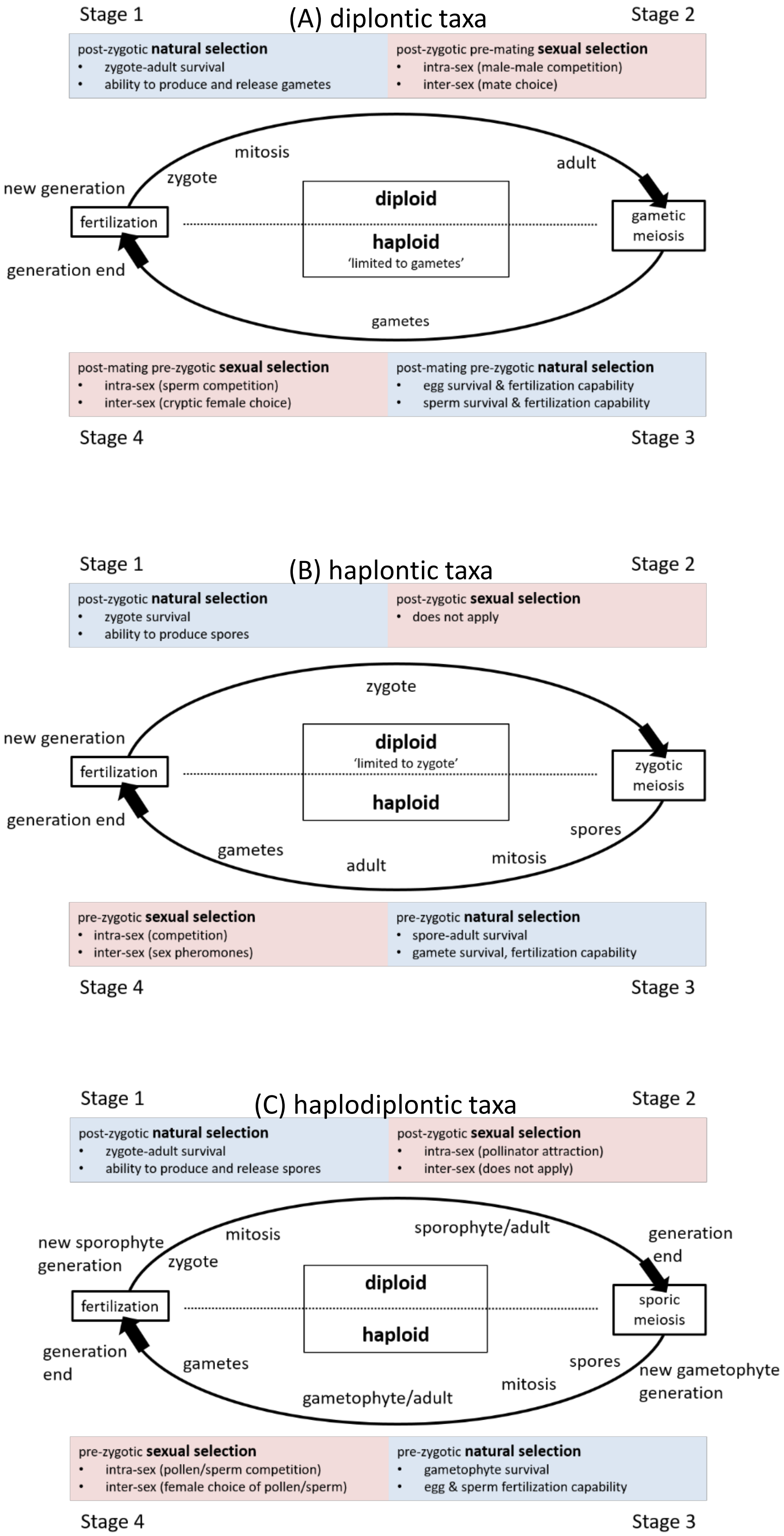
Stage 1
(A) diplontic taxa
Stage 2
post-zygotic natural selection
• zygote-adult survival
• ability to produce and release gametes
post-zygotic pre-mating sexual selection
• intra-sex (male-male competition)
• inter-sex (mate choice)
mitosis
adult
new generation
zygote
diploid
fertilization
gametic meiosis
haploid
'limited to gametes'
generation end
gametes
post-mating pre-zygotic sexual selection
• intra-sex (sperm competition)
• inter-sex (cryptic female choice)
post-mating pre-zygotic natural selection
• egg survival & fertilization capability
• sperm survival & fertilization capability
Stage 4
Stage 3
Stage 1
(B) haplontic taxa
Stage 2
post-zygotic natural selection
• zygote survival
• ability to produce spores
post-zygotic sexual selection
• does not apply
zygote
new generation
diploid
'limited to zygote'
fertilization
zygotic meiosis
haploid
generation end
spores
gametes
mitosis
adult
pre-zygotic sexual selection
• intra-sex (competition)
• inter-sex (sex pheromones)
pre-zygotic natural selection
• spore-adult survival
• gamete survival, fertilization capability
Stage 4
Stage 3
Stage 1
(C) haplodiplontic taxa
Stage 2
post-zygotic natural selection
• zygote-adult survival
• ability to produce and release spores
post-zygotic sexual selection
• intra-sex (pollinator attraction)
• inter-sex (does not apply)
sporophyte/adult
mitosis
generation end
new sporophyte generation
zygote
diploid
fertilization
sporic meiosis
haploid
generation end
gametes
spores
new gametophyte generation
mitosis
gametophyte/adult
pre-zygotic sexual selection
• intra-sex (pollen/sperm competition)
• inter-sex (female choice of pollen/sperm)
pre-zygotic natural selection
• gametophyte survival
• egg & sperm fertilization capability
Stage 4
Stage 3

Figure 1

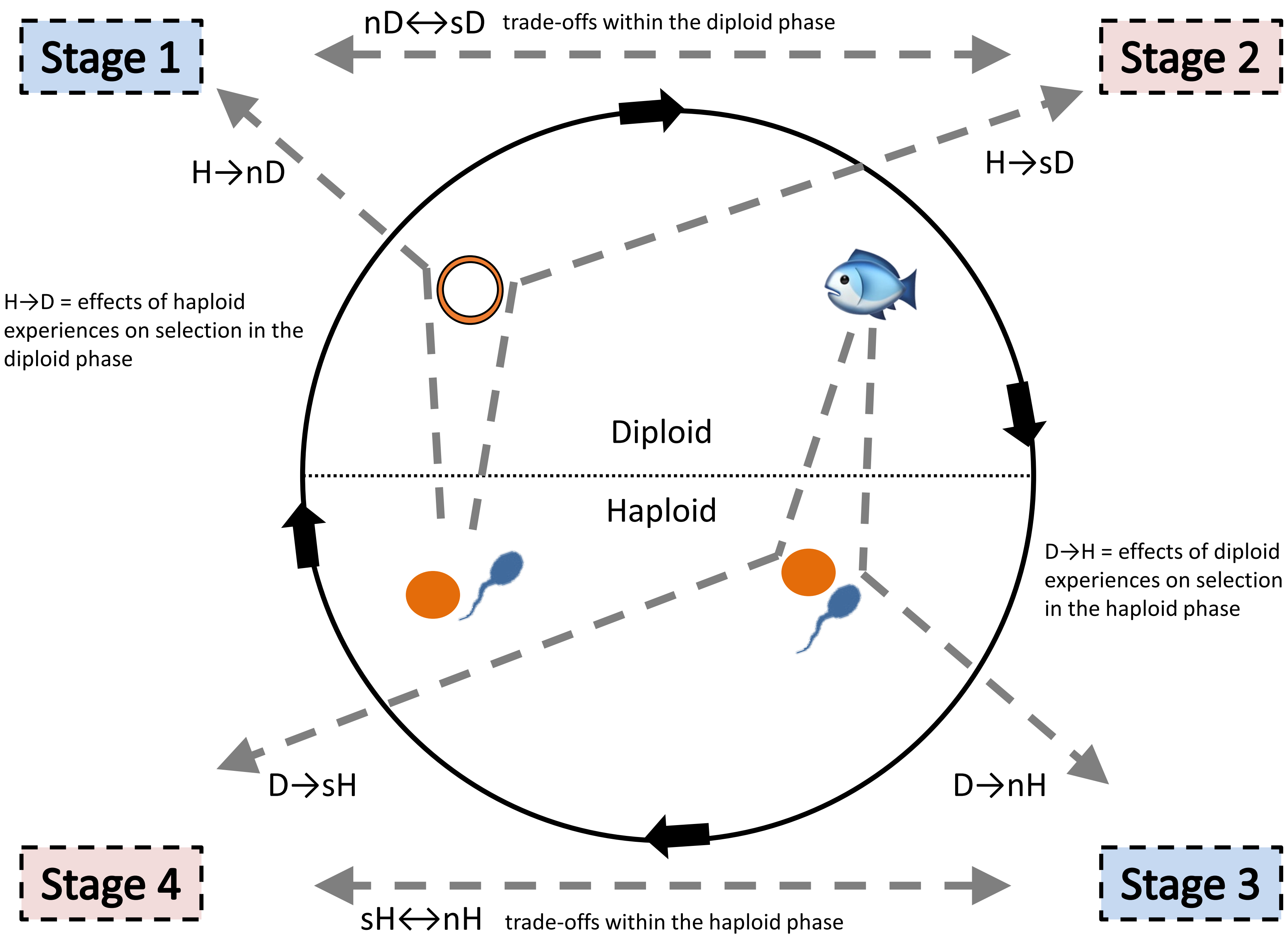
Stage 1
nD↔sD trade-offs within the diploid phase
Stage 2
H→nD
H→sD
H→D = effects of haploid experiences on selection in the diploid phase
Diploid
Haploid
D→H = effects of diploid experiences on selection in the haploid phase
D→sH
D→nH
Stage 4
Stage 3
sH↔nH trade-offs within the haploid phase

Figure 2

Supplementary material

Key terms distinguishing diplontic/haplontic/haplodiplontic biphasic life cycles

Biphasic life cycle: Alternation between diploid and haploid phases through one or more generations; both phases do not have to be free living. Cycles can be monogenerational (one generation per cycle) or multigenerational.

Diplontic: Life cycle where meiosis occurs at the end of the dominant, diploid phase of the cycle giving rise to gametes. Mitosis (of unicellular organisms or as part of the developmental process in multicellular organisms) occurs only in the diploid phase. In sexual reproduction meiotic recombination precedes syngamy.

Diplont: An organism that is diploid for most of its life cycle, except for the gamete phase. It has a diplontic life cycle. Includes all animals, most protists (e.g., diatoms), some brown algae (e.g., *Fucus*), and some fungi.

Haplontic: Life cycle where meiosis occurs at the beginning of the dominant, haploid phase of the cycle. Mitosis (of unicellular organisms or as part of the developmental process in multicellular organisms) occurs only in the haploid phase. In sexual reproduction syngamy precedes meiotic recombination.

Haplont: An organism that is haploid for most of its life cycle, except for the zygote phase. It has a haplontic life cycle. Includes most green algae, charophytes, sac and club fungi.

Haplodiplontic: Life cycle where mitosis (of unicellular organisms or as part of the developmental process in multicellular organisms) occurs in both the haploid and diploid phases. The process of sexual reproduction occurs in both phases: syngamy of gametes produced in the haploid phase, while the production of spores with meiotic recombination is carried in the diploid phase. Haplodiplontic taxa include land plants, red algae, most brown algae, some green algae, some fungi.

Sporophyte: The multicellular diploid individual of species with haplodiplontic life cycles.

Gametophyte: The multicellular haploid individual of species with haplodiplontic life cycles.

Generation: A complete circuit around the biphasic life cycle can encompass one or more generations. The genealogical definition being focused on the individual. In monogenerational life cycles the same developmental phase is achieved through one cycle in one generation, while multigenerational life cycles have individuals in different generations representing different developmental forms.

Alternation of generations: During reproductive phases offspring may be of a different organizational form than their parents so that more than one generation is needed to close the life cycle, which is synonymous with multigenerational life cycles. In haplodiplontic life cycles, the alternation of phases coincides with the generations (haploid=gametophyte, diploid=sporophyte).

Individual: Can be interpreted in a number of ways. Following [Fusco, G. and Minelli, A. (2019) *The biology of reproduction*, Cambridge Univerity Press.] an undivided functioning entity, able to respond to the environment and reproduce. In biphasic life cycles, selection targets cells in both phases, regardless of whether they are considered individuals or not.

Adult: For diplontic taxa an adult is considered the mature diploid individual that is capable of producing haploid gametes. Similarly, in most haplodiplontic plants the adult is the diploid sporophyte. However, in bryophytes, the haploid gametophyte that produces sex cells is considered the adult, as is the case in haplontic taxa.

Parent: In diplontic and haplontic taxa, parents are diploid or haploid individuals, respectively, that produce gametes that give rise to a zygote in the next generation. In haplodiplontic taxa, a parent is the sporophyte (diploid) that produces spores or the gametophyte (haploid) that produces gametes.