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. Our synthesis produces six direct links among four selection stages, and from this we define four types of parental effect. 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.

1. 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 [1–3] – see electronic supplementary material for definitions, and comprise tremendous variation in the relative lengths of the component parts [4]. 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., most 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). Across taxa, different start points, complexity, and terminology used to describe life cycles [3] influence the definitions (see supplementary material) of what is an individual, adult, parent and generation. This complicates generalization across cycles, but the main points of our review are applicable to all.

Selection acts on phenotypes [5], which are the product of the genotype and the environmental inputs on development. Natural selection [6] is the differential survival and reproduction of genotypes due to differences in phenotype, while sexual selection [7] is differential reproductive success due to competition with members of the same sex (intra-sexual selection), or choice by members of the opposite sex (inter-sex selection). Both can occur before and after mating (see figure 1). Importantly, gene expression is not necessary in both diploid and haploid phases 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. Selection occurs across four broad stages within biphasic life cycles, but generalizing is challenging because of the inherent variation in terminology used among life cycle types (see Fusco and Minelli [3] for discussion of some of these issues). Our synthesis of general interpretations is given in figure 1a-c and in the text below.

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 diplontic and some haplodiplontic species (e.g., insect pollinated angiosperms), sexual selection can be conceptualized (figure 1a,c; Stage 2) as ‘who gets to mate’ of those capable [8]. As there is no obvious intra-sex competition or inter-sex choice, sexual selection in the diploid phase may not [see 8–11] apply to haplontic taxa (figure 1b), haplodiplontic (figure 1c) bryophytes, and ferns.

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 and 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, but not in seeds plants). 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 [see 12]).

Sexual selection targeting haploid cells (figure 1a-c, Stage 4) is thought to be ancestral to that in the diploid phase [13,14]. It influences 'which functioning gametes fertilize in the presence of gametes from the same sex' and occurs intra-sex in the form of diplontic sperm competition [14,15] and egg competition [see 16], haplodiplontic pollen competition [17] and sperm competition, and haplontic gamete competition [18,19 - refers to gametes not labeled as sperm/egg]. 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 [20]. 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 [21–23]. In yeast, sex pheromones not only help locate mates but can also affect final mate selection by choosing the strongest signallers [24]. In bryophytes, sex-specific chemical secretions attract microarthropods that transport sperm to other individuals [25].

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 review 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 define selection links as being either within-phase, where natural and sexual selection are acting jointly (e.g., antagonistically) on the same 'individuals', or across-phases when experiences of an individual in one phase affects selection in the subsequent phase. This review specifically focuses on highlighting the selection stages and described links, and we illustrate each component with some examples across sexually reproducing lineages.

2. Interactive links (trade-offs) within-phase

2(a) Interaction between natural and sexual selection in the diploid phase (Link A)

Within the diploid phase, the interaction (figure 2, Link A) between natural selection – typically conceptualized as survival (figure 1a-c, Stage 1), and sexual selection – breeding opportunities (figure 1a-c, Stage 2) was even considered by Darwin [6,7], 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 [26]. 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 [27], lizards [28] and birds [29]. In angiosperms, abiotic factors exert selective pressure that can affect the outcome of sex expression in flowers and sex ratios in populations [30,31], 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 [32], and thus who gets to mate. This link does not appear to apply to haplontic and some haplodiplontic taxa, as there is no sexual selection in the diploid phase.

(2b) Interaction between natural and sexual selection in the haploid phase (Link B)

Within the haploid phase, interactions (figure 2, Link B) between natural (figure 1a-c, Stage 3) and sexual (figure 1a-c, Stage 4) selection are more poorly documented, and are rarely framed as a trade-off as is common in the diploid phase. Despite very little work on them, haplontic organisms could provide key insight into this link 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 [19]. 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 [19].

In seed plants, the effects of abiotic factors, such as temperature and humidity, on pollen tube germination and growth are well known [33], although their influence on pollen competition has yet to be determined. 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 [34].

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 a trade-off between sperm quality and quantity [35] could represent a conceptual interaction of Link B (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, Purchase and Moreau [36] found that responses of 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. Likewise, in sea urchins, fertilization success of different males changes in different ways depending on ocean pH [37]. 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 38].

3. One-way bridging links across-phases

The four selection stages (figure 1a-c) are the main drivers of adaptive evolution. For illustration, a male bird that does not survive to adulthood (Stage 1), or survives but does not acquire a mate (Stage 2), contributes no gametes to selection in the next phase, and no direct descendants in the next generation (which is two phases ahead). He also will leave no descendants if he does mate but his sperm are incapable of fertilizing an egg (Stage 3) or winning paternity while under sperm competition (Stage 4). 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. Below, we define four such links that operate from one phase to the next in biphasic cycles. These are conceptually similar to what West-Eberhard [5] refers to as 'bridging phenotypes' (Box 1), and Ritchie and Marshall [39] call 'phenotypic links'. Impacts perpetuating further in time (e.g., parental effects) are considered briefly in Box 2 and are reviewed in more detail elsewhere [e.g., 40].

(3a) Links from the diploid to haploid phase

As we have noted, haplontic species have no diploid mitosis, and we are unaware of any work considering how surviving zygote 'experiences' before meiosis might impact the haploid phase. In diplontic and haplodiplontic cycles, links 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, trade-offs 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., 41].

(3ai) Effect of diploid experiences on natural selection in the haploid phase – Link C

Much of the available information on how diploid adults influence selection during the haploid phase (i.e. the haploid cells they produce) is in the context of natural selection on animal gametes (figure 2, Link C). 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 [42]. 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 [reviewed by 43], 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 [44], contaminants [e.g., 45], and oxidative stress [e.g., 46] 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 [47,48] and temperature [49] 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 [see 12]. These and related topics have been treated in part within other reviews [40,43,50,51].

Similar processes operate in algae and land plants. In brown algae decreased salinity experienced by the diploid adult compromises sperm performance [see ref 52, 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 [53,54]. In grasses the biochemical composition of pollen changes in response to parental temperature and nutrients [55], while increased nutrients results in poorer quality pollen (but higher quantity) in juniper [56]. Squash plants infected with mutualistic mycorrhizae produce larger pollen grains than uninfected plants [57].

(3aii) Effect of diploid experiences on sexual selection in the haploid phase – Link D

Parental experiences in the diploid phase can also have profound consequences for selection occurring at Stage 4 (Link D in 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 [58–62]. Remarkedly, this response can occur quite rapidly [61–64].

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 [65]. Soil fertility may increase pollen size and quality [55,66], which in turn produce higher siring success because larger pollen contains more energy reserves facilitating faster germination and pollen tube growth rates [67,68]. Adverse abiotic conditions experienced by parent plants can reduce pollen competitive ability against heterospecific pollen [69]. 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 [70], and herbivory during the diploid phase can reduce pollen production [71].

(3b) Links from the haploid to diploid phase

How haploid experiences influence the diploid phase of the life cycle is poorly understood. These are conceptually similar (but reversed) to concepts outlined in Section 3a. 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 Link across-phases, from those which simply meet definitions of selection at Stages 3 or 4, the mechanisms not being mutually exclusive [see review by 72]. 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 provide an experimental solution to this problem, as all sperm produced by haploid parents are genetically identical [73].

Some recent literature on haploid selection in animal sperm [74–76] 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 links across-phases. Haploid selection in predominately diploid organisms [74] is given more consideration in Box 3.

(3bi) Effect of haploid experiences on natural selection in the diploid phase – Link E

Haploid experiences may alter characteristics of the subsequent phase in a manner that influences the likelihood of zygote survival (Link E in figure 2). For haplontic cycles, this could be dramatic given the dominant phase is haploid, but it is difficult to identify whether haploid selection has occurred as opposed to phenotypic adjustment (see above). In green algae, UV induced mutations of maturation genes during the haploid phase results in increased zygote mortality due to failure to form a normal cell wall [77]. 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 [33,78]. 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 78], 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 51] such as proteins, might be modified by sperm experience. In an externally spawning marine polychaete, Ritchie and Marshall [39] 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 (e.g., [79] and are covered in wider reviews [40,80]), but clearly distinguishing the mechanism of haploid experiences (figure 2, Link E) from selection (figure 1, Stages 3-4) in these studies is seemingly impossible.

(3bii) Effect of haploid experiences on sexual selection in the diploid phase – Link F

In principle, haploid experiences 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 (figure 2, Link F). The potential certainly exists, if for example, changes brought about under Link E perpetuate into adulthood and influence secondary sexual characteristics. Another possibility is if diploid sex ratios are influenced by haploid conditions [81].

4. 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 [82] provides a useful illustration. For example, in experiments examining the effect of marine oil spills on fish reproduction, Beirão et al. [83] 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 interaction of Link A (figure 2). Other work focuses on effects on reproductive output. Beirão et al. [84] group these studies into two types, the first having “indirect effects”, where the adult is exposed and gametes are examined (in context of our Link C – we are unaware of any work on Link D, 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 [84], but has not been investigated in context of sexual selection at Stage 4 (figure 1a), or Links B, E or F (figure 2). The problem of cascading effects (figure 2, Box 1) caused by exposure to contaminants thus becomes evident.

We argue that considering all stages and all links among stages are of fundamental importance to both understanding evolutionary processes and conducting applied science. Our synthesis produces six possible direct links among four selection stages within a cycle (figure 2). Using these links, we define four types of parental effect (Box 2). It is evident from our literature search that research on selection in general, but the links 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 (Link E) versus selection in the haploid phase (Stages 3, 4) on diploid development, and our review highlights the need for targeted research on this topic. Future studies that incorporate selection in both phases and identify component parts 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 effects (“gametal effects”) to the diploid phase? We have very little understanding of how natural and sexual selection interact in the haploid phase (Link B), or how haploid experiences influence sexual selection in the diploid phase (Link F), or the underlying mechanisms linking haploid experiences to offspring development (Link E).
- What is the potential of haploid selection for human food and health? For instance, to what extent can we use artificial gametophyte selection to 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 [5] 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 [5 - page 92]”. This is depicted as figure I; for most 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) encompassing two generations in most diplontic and haplontic species.

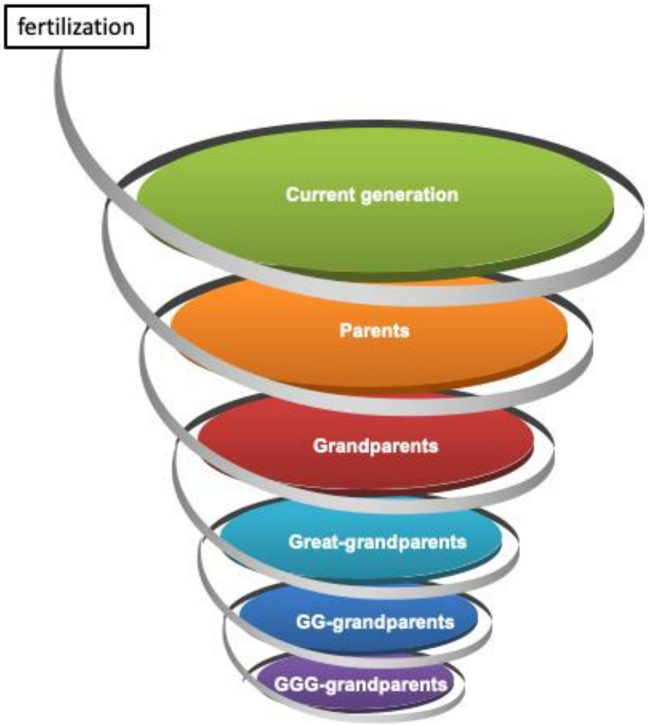

Figure I: Unbroken connections across generations (or groups of generations if >1 generation per cycle). In biphasic life cycles, bridges occur that connect the diploid and haploid phases encompassing one complete circuit. Modified from Fig5.2 in West-Eberhard [5].

The concept becomes important for interpreting our selection links that bridge phases of biphasic life cycles (figure 2). We consider links 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 links 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” [85]. These can be more influential than abiotic variation [86] and may encompass maternal effects [87,88] and paternal effects [40,89]. They are 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-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 [90; their Fig 1].

Parental effect type I (diploid-haploid): How the diploid phase influences the haploid phase of the life cycle. This has been covered in Section 3a on one-way bridging links and encompasses Links C and D in figure 2.

Parental effect type II (diploid-diploid): 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 II) are complementary or antagonistic is poorly understood.

Parental effect type III (haploid-diploid): Although the haploid phase does not typically constitute the idea of ‘parents’ (except haplontic taxa and bryophytes), if haploid ‘experiences’ of one generation (in any cycle) influence the subsequent diploid phase of the next, this may also be considered a parental effect. It has been discussed in Section 3b on one-way bridging links, and forms Links E and F in figure 2. One may conceptualize types III and IV to be ‘gametal effects’ (gamete + gametophyte), as an alternative to parental effects in haplodiplontic and diplontic taxa.

Parental effect type IV (haploid-haploid): 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 III and IV function independently is not known. These types of parental effects are poorly studied, but do exist. For example, Gasparini et al. [91] demonstrated experimentally that the duration of sperm storage in a fish influenced sperm quality of males in the next generation.

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 generation because the phases are under different selection pressures. Restricted gene expression in the haploid phase has the potential to purge deleterious alleles or fix beneficial ones effectively in breeding programs [92].

For instance, artificial selection for stress tolerance in pollen has enabled plant breeders to obtain cold-tolerant chickpeas and tomatoes in the next generation [93,94], and repeated pollen selection for heat tolerance in maize improves tolerance of progenies in up to four generations [95] – 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 [96].

Haploid selection can also apply to animals outside of the context of sperm competition among donor adult males [97]. Sperm swimming longevity [76,98] and thermotaxis [99] 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 [100,101] for agricultural breeding programs, and other aspects related to human fertility treatment [102,103]. 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 [74].

Figures

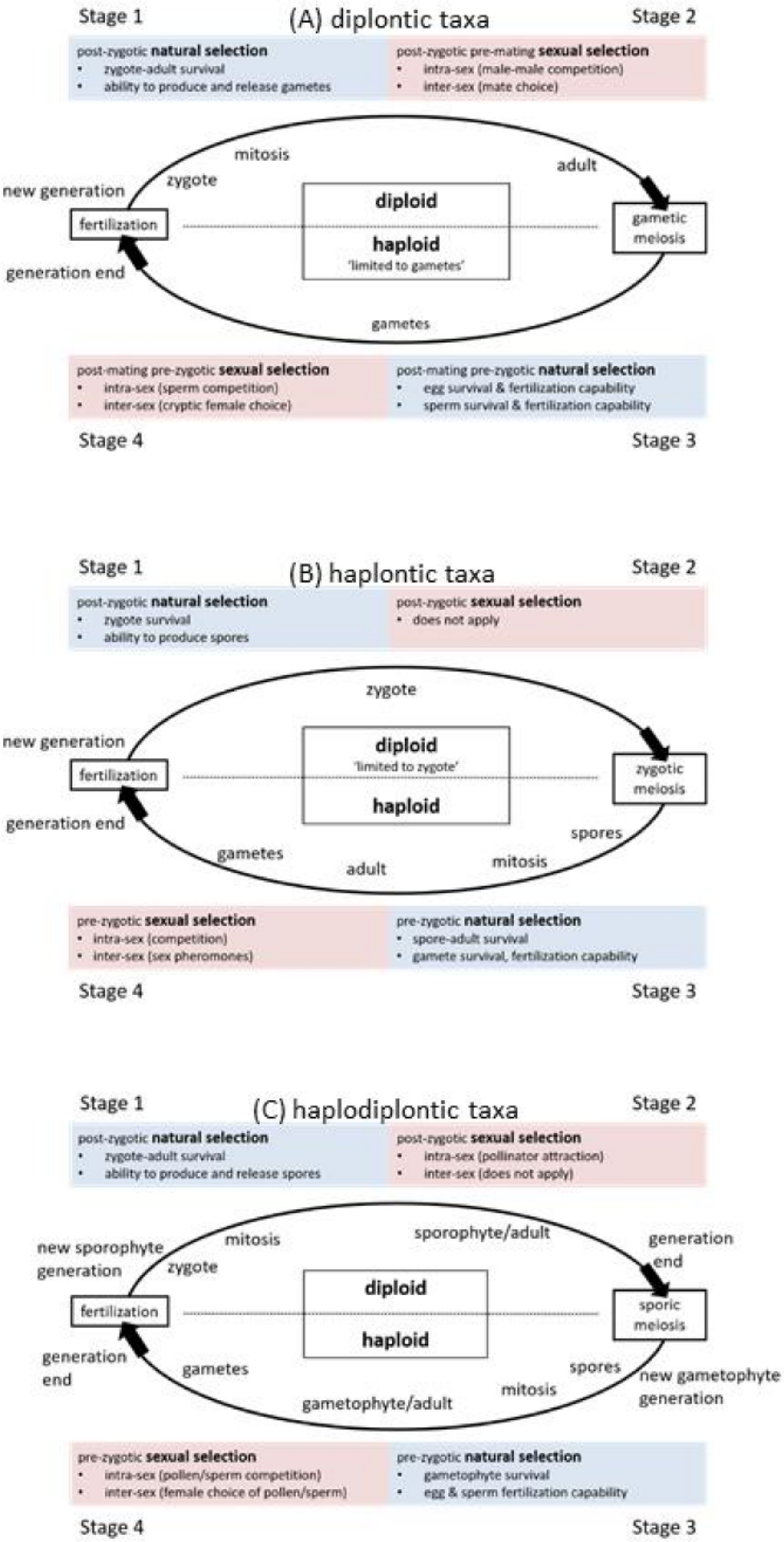
Stage 1
(A) diplontic taxa
Stage 2
post-zygotic natural selection
• zygote-adult survival
• ability to produce and release gametes
post-zygotic pre-mating sexual selection
• intra-sex (male-male competition)
• inter-sex (mate choice)
mitosis
adult
new generation
zygote
fertilization
diploid
haploid
'limited to gametes'
gametic meiosis
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
fertilization
diploid
'limited to zygote'
haploid
zygotic meiosis
generation end
spores
gametes
adult
mitosis
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)
mitosis
sporophyte/adult
generation end
new sporophyte generation
zygote
fertilization
diploid
haploid
sporic meiosis
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

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.

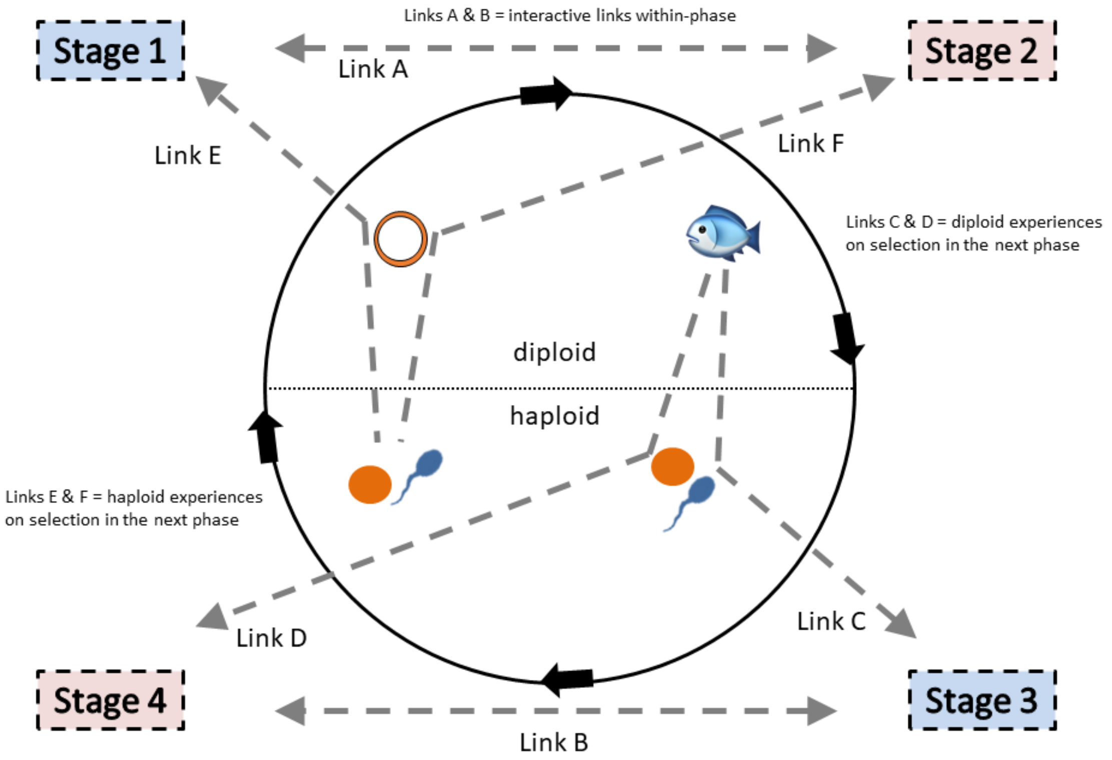

Figure 2

Figure 2: Links (dashed lines) within the biphasic life cycle, showing how selection stages are inter-connected. Illustrated for diplontic cycles but concepts apply to all cycles. Links A & B are trade-offs within-phase. Links C-F are one-way bridges across-phases, where selection in a given phase is tied to experiences in the previous phase - illustrated by the bent arrows. For example, in Link C an adult male fish (diploid) produces sperm (haploid) that can be altered by his experiences, and then those sperm are exposed to selection in the haploid phase. The same would apply when experiences of a diploid plant alter spore-gametophyte-gamete selection in the haploid phase.

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 an 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.