A framework for integrating natural and sexual selection within- and across-generations of eukaryotic biphasic life cycles

Running title: Selection in biphasic life cycles

Craig F. Purchase[1,2], Jonathan P. Evans[2] and Julissa Roncal[1]

[1] Department of Biology, Memorial University of Newfoundland. St. John's, Newfoundland & Labrador, A1C 5S7, Canada.

[2] Centre for Evolutionary Biology, School of Biological Sciences, the University of Western Australia. Crawley, Western Australia, 6009, Australia.

Corresponding author: Purchase, C.F. (cfpurchase@mun.ca)

Author contributions:

CFP: conceived the plan for the manuscript, and lead the development of ideas, creation of figures and writing of the text.

JPE: along with CFP created the foundation for Figure 4, developed and refined the selection opportunities and interactions, and wrote and edited text.

JR: expanded the conceptual framework to include haplontic and haplodiplontic taxa, helped refine selection opportunities and interactions, and wrote and edited text.

We have no conflicts of interest to declare.

Acknowledgements

C.F.P. first proposed the concepts presented here to the Ecology and Evolution Discussion Group at Memorial University of Newfoundland, who along with Geoff Parker, provided helpful improvements and encouraged him to publish. Refinements and elaborations of ideas for this manuscript were made during his Visiting Professorship at the University of Western Australia (UWA). This sabbatical opportunity was funded by the Institute of Advanced Studies and the Forrest Research Foundation at UWA, the Natural Sciences and Engineering Research Council of Canada, and Memorial University of Newfoundland. We thank Henry Arenas-Castro, and anonymous reviewers for helpful comments on an earlier version of the manuscript.

A framework for integrating natural and sexual selection within- and across-generations of eukaryotic biphasic life cycles

Abstract

An alternation between diploid and haploid phases is universal among sexual eukaryotes, with three cycle categories distinguished by the presence or absence of mitosis in each phase. Across this biphasic cycle, ‘narrow sense’ natural selection and sexual selection occur in both phases. These opportunities for selection arise from variation in the phenotypes of individuals and influence the evolutionary trajectories of populations. However, selection concepts are not equally understood or applied to different cycles, and the same terms have different meanings for universal processes. 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 biphasic cycle, selection opportunities are modified by within-phase two-way interactions, 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 throughout a wide conceptual context, expanding on the conventional definition of a connection crossing two circuits of the cycle from diploid to diploid. Examples traversing sexual eukaryotes for each interaction and bridge are presented with the aim to highlight knowledge gaps and inspire new research in different taxa.

Keywords: sperm competition, pollen competition, transgenerational effects, cryptic female choice, haploid selection, maternal 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 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 Box 1 for definitions – and comprise tremendous variation in the relative lengths of the component parts (Rescan et al. 2016). In diplontic ('diploid') cycles (e.g., animals) there is no haploid mitosis and the haploid phase is limited to gametes (Figure 1, Box 1), while haplontic ('haploid') organisms (e.g., many green algae) have no diploid mitosis and the diploid phase occurs only as a zygote (Figure 2, Box 1). In haplodiplontic ('haploid-diploid') species (e.g., land plants and red algae) mitosis occurs in both phases (Figure 3, Box 1).

Selection arises from variation in 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 in the 'broad sense' (Endler 1986) includes all fitness components, including sexual selection. Nonetheless, it is customary and useful to distinguish natural and sexual selection when exploring interactions between traits (Shuker and Kvarnemo 2021). We thus adopt 'narrow sense' natural selection (Endler 1986), which encompasses 'viability selection' and 'fecundity selection', but excludes sexual selection. Since first considered (Darwin 1859, 1871) sexual selection has been defined in many ways. We employ that proposed by Shuker and Kvarnemo (2021), "sexual selection is any selection that arises from fitness differences associated with nonrandom success in the competition for access to gametes for fertilization". All sexual selection is based on intra-sex competition, and is agnostic to sexual identity. Our framework is generally robust to different characterizations, including the broader definition offered by Janicke (2024) where sexual selection is “competition for access to reproductive resources provided by potential mating partners”, however it would influence whether certain interactions between natural and sexual selection exist or not (see below).

Both natural and sexual selection can occur before and after mating, during the diploid and haploid phases. 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 Box 1) of what is an individual, adult, parent and generation. This complicates generalization among different cycle categories, thus our synthesis is an attempt to place components of natural and selection throughout the biphasic life cycles of sexually reproducing eukaryotes (Figures 1-3). As pointed out by Endler (1986, p.xii) the “same terms mean different things to different people”. Forty years ago he held “no hope of convincing those who are used to a particular meaning of a word to conform to the suggested standardization”, and in that time silos remain, which may have hindered integration. This is particularly problematic in comparing (1) animals and plants, where literature often defaults to different nuances of definitions for the same process (e.g., sperm competition in animal literature defaults to among-males, whereas in plants it often considers within-males as well), along with (2) algae and land plants, when they do not follow the same “rules” (Haig 2010). Within one complete circuit of a biphasic life cycle, we present the different opportunities for selection starting at the formation of a zygote (Figures 1-3). Interactions among selection opportunities are provided in the next Section.

Natural selection in the diploid phase (nD) - In the diploid phase of diplontic (Figure 1) and haplodiplontic (Figure 3) taxa, 'narrow sense' natural selection can be interpreted as zygote-adult survival, or 'who lives to mate' (viability selection), and the ability to produce and release gametes or spores (fecundity selection). The combination of the two determines who enters the fertilization game (how well one performs in the fertilization game depends on sexual selection in the diploid and haploid phases). For haplontic cycles (Figure 2) there is no diploid mitosis, but natural selection still applies to zygote survival before meiosis and the ability to produce spores.

Sexual selection in the diploid phase (sD) - In many diplontic species (e.g., highly mobile animals) sexual selection in the diploid phase can be relatively easily conceptualized (Figure 1) as 'who gets to mate' of those capable (Andersson 1994; Shuker and Kvarnemo 2021) – and forms the basis of 'Darwinian sexual selection' (Simmons and Wedell 2020). It is based on intra-sex competition, but some mechanisms require inter-sex mediation (mate choice). Sexual selection in the diploid phase of plant life cycles is less obvious or accepted (Andersson 1994; Willson 1994; Moore and Pannell 2011; Tonnabel et al. 2021; Ritchie and Pannell 2025). In non-seed plants with no pollen and no diploid male-female structures, such as haplontic taxa (Figure 2) and haplodiplontic bryophytes and ferns (Figure 3), there is no intra-sex competition for access to gametes in the diploid phase, and sexual selection in the diploid phase does not apply (it does in the haploid phase) in these groups (Zavada and Taylor 1986; Andersson 1994; Willson 1994; Moore and Pannell 2011). However, sexual selection will target traits that increase the number of mates acquired in seed plants (Figure 3). This can be achieved by improving pollen dispersal and phenological adaptations that beat other males (similar to scramble competition) in competition to access gametes. The clearest examples are in haplodiplontic angiosperms with intra-sex competition for limited insect pollinators (Paterno et al. 2020; Kwok and Dorken 2022; Barbot et al. 2023), but morphological traits that improve wind dispersal of pollen could also be under sexual selection (Tonnabel et al. 2019).

Natural selection in the haploid phase (nH) - In the haploid phase, 'narrow sense' natural selection can be conceptualized readily in haplontic (Figure 2) and haplodiplontic (Figure 3) taxa, where it involves the survival of the haplont or gametophyte. It is harder to separate natural and sexual selection on gametes as they may align, and 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 to be naturally selected (Shuker and Kvarnemo 2021). In diplontic cycles (Figure 1) 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 fish sperm to function under different water chemistries (Beirão et al. 2018)).

Sexual selection in the haploid phase (sH) - Sexual selection targeting haploid cells (Figures 1-3) is ancestral to that in the diploid phase (Parker 2014, 2020) and represents 'Parkerian sexual selection' (see Simmons and Wedell 2020). It influences 'whose 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 (Lavaut et al. 2023), 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. Sexual selection in the haploid phase also involves inter-sex mediation through 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 female organs contribute to differential success of plant 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), and a similar argument has been made for female choice within the trichogyne structure of red macroalgae (Lavaut et al. 2023). In yeasts, 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 opportunities for selection (nD, sD, nH, sH) determine the phenotypes of individuals and influence the evolutionary trajectories of populations. Despite the clear interrelationships among them, they are seldom studied together. To promote a more holistic understanding of how selection targets phenotypes across phases and generations, we use this article 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 4. We use the term ‘within-phase two-way interactions’ where ‘narrow sense’ natural and sexual selection are acting on the same ‘individuals’ (Box 1), and ‘across-phase one-way bridges’ when experiences of an individual in one phase affects selection in the subsequent phase (not the same individual). This article specifically focuses on highlighting the selection opportunities and their interactions and bridges, which we illustrate with examples covering sexually reproducing lineages. Detailed literature reviews of each interaction and bridge are beyond our scope. Some have already been reviewed many times while others need scrutiny, especially in certain taxa (Table 1).

Within-phase two-way interactions (alignments and compromises)

In the diploid phase (Figure 4 nD↔sD)

Within the diploid phase, ‘narrow sense’ natural selection can be viewed as an interaction between viability selection and fecundity selection acting on the same individual, where they may be aligned (e.g., if large females are better at surviving and produce more eggs) or misaligned and create a compromise (e.g., if antipredation behaviour reduces energy investment into eggs). Similarly, the interplay (Figure 4 nD↔sD) between ‘narrow sense’ natural selection and sexual selection in the diploid phase is widely recognized as a central evolutionary process. Natural and sexual selection commonly align if for example males in better condition have improved survival probability and are better at attracting mates. In such instances sexual selection will increase nonsexual fitness (Rowe and Rundle 2021).

The interaction between natural and sexual selection was famously considered by Darwin (1859, 1871), who referred to the ‘inconvenience’ of elaborate tail feathers in many male birds. In animals, individuals with elaborated secondary sexual characteristics associated with mate choice (e.g., songs, colours, or structures), are often more prone to predation (Moore and Martin 2018; Amdekar and Thaker 2019; 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 interactions (Figure 4 nD↔sD) do not apply to haplontic and some haplodiplontic taxa (Table 1), as there is no sexual selection in the diploid phase (Figures 2-3).

In the haploid phase (Figure 4 sH↔nH)

Within the haploid phase, the interactions (Figure 4 sH↔nH) between natural and sexual selection are more poorly documented but have higher taxonomic diversity than in the diploid phase (due to all cycles having sexual selection in the haploid phase). Despite very little work on them, haplontic organisms and haplodiplontic species with free living gametophytes, could provide key insight. 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, the same sperm characteristics (Simmons and Parker 2021) could be exposed to natural selection (if under sperm limitation) and sexual selection (if under sperm competition), which may align (Rowe and Rundle 2021). However, if for example sperm quantity is primarily targeted by sexual selection - whose functioning gametes fertilize in presence of gametes from the same sex, while sperm quality is primarily important for natural selection - 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. Similarly, a trade-off would also exist if an adult animal 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 performed. The topic is ripe for targeted experimentation (Table 1), and should incorporate various environmental stressors, one being temperature (García-Roa et al. 2020; Kustra et al. 2026).

Across-phase one-way bridges (‘broad scope’ parental effects)

The four selection opportunities nD, sD, nH, sH (Figures 1-3) are the main drivers of adaptive evolution. However, selection that targets phenotypes expressed during the diploid and haploid phases do not operate in isolation (Albecker et al. 2021), and the ‘experiences’ (e.g., diet, perceived predation risk, stress) of the specific individuals that contribute to the subsequent phase may impact selection in it (Figure 4). 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. These are different than the within-phase two-way interactions in the previous Section as they do not operate on the same individuals. The concepts are the same for animals and plants, but unfortunately literature often defaults to different nuances for definitions of each process. Below, we define two such ‘bridges’. These are conceptually similar to what West-Eberhard (2003) refers to as ‘bridging phenotypes’ (see Box 2), and Ritchie and Marshall (2013) call ‘phenotypic links’. They bridge one phase to the next in biphasic cycles, and could be interpreted as ‘broad scope’ parental effects (Box 3). In literature focused on diplontic animals, the term parental effect is more restrictive (‘narrow scope’, Box 3) as it usually implies impacts perpetuating further in time, across more than one circuit of the biphasic life cyclc (e.g., animal maternal effects on embryo development, which is diploid to diploid). These are considered briefly in Box 3 and are reviewed in more detail elsewhere (e.g., Evans et al. 2019).

Bridges from the diploid to the 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 (e.g, resting stomatocysts) might impact the haploid phase (Table 1). 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 (priming hypothesis). 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). The extent to which adaptations that improve performance in one phase trade-off against those in the other is largely unknown (see Albecker et al. 2021). This has been termed ploidally antagonistic selection (Immler et al. 2012) and can be considered a form of intragenomic conflict (Gardner and Úbeda 2017).

On natural selection in the haploid phase (Figure 4 D→nH, Box 3)

Much of the available information on how diploid (D) adults (Figure 4) influence selection during the haploid phase (i.e., the haploid cells they produce) is in the context of natural selection on animal gametes (nH). 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. 2018) – a natural selection context. 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 some 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 (Figure 4 D→sH, Box 3)

Parental experiences in the diploid phase can also have profound consequences for sexual selection occurring in the haploid phase (Figure 4). 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) – a sexual selection context.

Sexual selection in the haploid phase 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 sexual selection in the haploid phase. 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

How haploid experiences influence the diploid phase of the life cycle is poorly understood (Table 1). These are conceptually similar (but inversed) to concepts outlined in the previous Section. They can occur if free-living haplonts or gametophytes alter energy allocation to specific gametes that influences zygotes (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 (Figure 4), from those which simply meet definitions of selection in the haploid phase (Figures 1-3, nH and sH), the mechanisms not being mutually exclusive (see review by Marshall 2015). One cannot easily isolate effects caused by which sperm fertilized from those caused by what experiences that sperm had. 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 (Figures 1-3, nH and sH) or what happened to the fertilizing sperm (Figure 4, H→D bridge). 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 using the term haploid selection (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). This phenomenon, along with among-ejaculate sperm competition, falls under selection in the haploid phase (Figures 1-3) and does not constitute a bridge across-phases. Haploid gene expression in predominately diploid organisms (Immler 2019) is given more consideration in Box 4.

On natural selection in the diploid phase (Figure 4 H→nD, Box 3)

Haploid experiences may alter characteristics of the subsequent phase in a manner that influences the likelihood of zygote survival (Figure 4). 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 selection in the haploid phase (Figure 3, e.g., within-donor pollen competition) or phenotypic adjustment attributable to haploid experiences (Figure 4) are not clearly discernible (reviewed in Baskin and Baskin 2015), and needs future work (Table 1).

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 4, H→D = what happened to the sperm) from selection within-phase (Figure 1, nH and sH = which sperm) in these studies is seemingly impossible.

On sexual selection in the diploid phase (Figure 4 H→sD, Box 3)

In principle, haploid to diploid bridges (Figure 4) may also alter diploid development in a way that influences pre-mating sexual selection (Figures 1, 3 - sD), although we are unaware of any study addressing this question (Table 1). The potential certainly exists, if for example, H→nD perpetuate into adulthood and influence secondary sexual characteristics (such experiments would take longer). Another possibility is if diploid sex ratios are influenced by haploid conditions (Eppley et al. 2018).

Conclusion and future directions

The complex and often intertwined opportunities for selection within the biphasic life cycle create challenges for researchers attempting to understand key ecological and evolutionary problems in sexual eukaryotes. This is complicated when terminology and default nuances are different for the same process in different taxa. As a step forward, our synthesis produces a standardized approach, with two within-phase two-way interactions between ‘narrow sense’ natural selection and sexual selection, and two across-phase one-way bridges where selection in one phase is tethered to experiences in the previous phase (one circuit of biphasic life cycle). These bridges can be considered a type of ‘broad scope’ parental effect, which expands the traditional ‘narrow scope’ concept of a connection across animal generations (two circuits of biphasic life cycle) from diploid to diploid (Box 3). It is evident (Table 1) that research on selection in general, but the within-phase interactions 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 (Figure 4, H→D) versus selection in the haploid phase (Figures 1-3, nH and sH) on diploid development, and our article 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.

References

Agarwal, A., M. Rana, E. Qiu, H. AlBunni, A. D. Bui, and R. Henkel. 2018. Role of oxidative stress, infection and inflammation in male infertility. Andrologia 50:e13126.

Alavioon, G., C. Hotzy, K. Nakhro, S. Rudolf, D. G. Scofield, S. Zajitschek, A. A. Maklakov, and S. Immler. 2017. Haploid selection within a single ejaculate increases offspring fitness. Proc. Natl. Acad. Sci. U. S. A. 114:8053–8058.

Albecker, M. A., L. G. E. Wilkins, S. A. Krueger-Hadfield, S. M. Bashevkin, M. W. Hahn, M. P. Hare, H. K. Kindsvater, M. A. Sewell, K. E. Lotterhos, and A. M. Reitzel. 2021. Does a complex life cycle affect adaptation to environmental change? Genome-informed insights for characterizing selection across complex life cycle. Proc. R. Soc. B Biol. Sci. 288:20212122.

Amdekar, M. S., and M. Thaker. 2019. Risk of social colours in an agamid lizard: implications for the evolution of dynamic signals. Biol. Lett. 15:20190207.

Andersson, M. B. 1994. Sexual selection. Princeton University Press.

Badyaev, A. V., and T. Uller. 2009. Parental effects in ecology and evolution: mechanisms, processes and implications. Philos. Trans. R. Soc. B Biol. Sci. 364:1169–1177.

Barbot, E., M. Dufaÿ, and I. De Cauwer. 2023. Sex-specific selection patterns in a dioecious insect-pollinated plant. Evolution 77:1578–1590.

Bartlett, M. J., T. E. Steeves, N. J. Gemmell, and P. C. Rosengrave. 2017. Sperm competition risk drives rapid ejaculate adjustments mediated by seminal fluid. eLife 6:e28811.

Baskin, J. M., and C. C. Baskin. 2015. Pollen (microgametophyte) competition: an assessment of its significance in the evolution of flowering plant diversity, with particular reference to seed germination. Seed Sci. Res. 25:1–11.

Beekman, M., B. Nieuwenhuis, D. Ortiz-Barrientos, and J. P. Evans. 2016. Sexual selection in hermaphrodites, sperm and broadcast spawners, plants and fungi. Philos. Trans. R. Soc. B-Biol. Sci. 371:20150541.

Begcy, K., and T. Dresselhaus. 2018. Epigenetic responses to abiotic stresses during reproductive development in cereals. Plant Reprod. 31:343–355.

Beirão, J., J. A. Lewis, B. F. Wringe, and C. F. Purchase. 2018. A novel sperm adaptation to evolutionary constraints on reproduction: pre-ejaculatory sperm activation in the beach spawning capelin (Osmeridae). Ecol. Evol., doi: 10.1002/ece3.3783.

Bell, A. M., and J. K. Hellmann. 2019. An integrative framework for understanding the mechanisms and multigenerational consequences of transgenerational plasticity. Annu. Rev. Ecol. Evol. Syst. 50:97–118.

Bhutani, K., K. Stansifer, S. Ticau, L. Bojic, C. Villani, J. Slisz, C. Cremers, C. Roy, J. Donovan, B. Fiske, and R. Friedman. 2019. Widespread haploid-biased gene expression in mammalian spermatogenesis associated with frequent selective sweeps and evolutionary conflict. biorxiv, doi: 10.1101/846253.

Celaya, I. N., G. Arceo-Gómez, C. Alonso, and V. Parra-Tabla. 2015. Negative effects of heterospecific pollen receipt vary with abiotic conditions: ecological and evolutionary implications. Ann. Bot. 116:789–795.

Clarke, H. J., T. N. Khan, and K. H. M. Siddique. 2004. Pollen selection for chilling tolerance at hybridisation leads to improved chickpea cultivars. Euphytica 139:65–74.

Crean, A. J., and R. Bonduriansky. 2014. What is a paternal effect? Trends Ecol. Evol. 29:554–559.

Crean, A. J., J. M. Dwyer, and D. J. Marshall. 2012. Fertilization Is not a new beginning: the relationship between sperm longevity and offspring performance. PLOS ONE 7:e49167. Public Library of Science.

Crean, A. J., and D. J. Marshall. 2008. Gamete plasticity in a broadcast spawning marine invertebrate. Proc. Natl. Acad. Sci. 105:13508–13513.

da Silva, J., and V. L. Drysdale. 2018. Isogamy in large and complex volvocine algae is consistent with the gamete competition theory of the evolution of anisogamy. Proc. R. Soc. B Biol. Sci. 285:20181954.

Darwin, C. 1859. On the origin of species by means of natural selection. Murray, London.

Darwin, C. 1871. The descent of man, and selection in relation to sex. Murray, London.

Delph, L. F., M. H. Johannsson, and A. G. Stephenson. 1997. How environmental factors affect pollen performance: ecological and evolutionary perspectives. Ecology 78:1632–1639.

Domínguez, E., J. Cuartero, and R. Fernández-Muñoz. 2005. Breeding tomato for pollen tolerance to low temperatures by gametophytic selection. Euphytica 142:253–263.

Donohue, K. 2009. Completing the cycle: maternal effects as the missing link in plant life histories. Philos. Trans. R. Soc. B Biol. Sci. 364:1059–1074.

Egunyomi, A. 1978. Studies on polysety in the Nigerian moss flora with special reference to *Octoblepharum albidum* and *Calymperes subdecolorans*. The Bryologist 81:94.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton.

Eppley, S. M., T. N. Rosenstiel, M. W. Chmielewski, S. C. Woll, Z. M. Shaw, and E. E. Shortlidge. 2018. Rapid population sex-ratio changes in the moss *Ceratodon purpureus*. Am. J. Bot. 105:1232–1238.

Evans, J. P., and R. A. Lymbery. 2020. Sexual selection after gamete release in broadcast spawning invertebrates. Philos. Trans. R. Soc. B-Biol. Sci. 375:20200069.

Evans, J. P., A. J. Wilson, A. Pilastro, and F. Garcia-Gonzalez. 2019. Ejaculate-mediated paternal effects: evidence, mechanisms and evolutionary implications. Reproduction 157:R109–R126.

Fan, Y., and Q. Zhang. 2018. Genetic and molecular characterization of photoperiod and thermo-sensitive male sterility in rice. Plant Reprod. 31:3–14.

Firman, R. C., C. Gasparini, M. K. Manier, and T. Pizzari. 2017. Postmating female control: 20 years of cryptic female choice. Trends Ecol. Evol. 32:368–382.

Fisher, H. S., K. A. Hook, W. D. Weber, and H. E. Hoekstra. 2018. Sibling rivalry: males with more brothers develop larger testes. Ecol. Evol. 8:8197–8203.

Fitzpatrick, J. L., and S. Lüpold. 2014. Sexual selection and the evolution of sperm quality. MHR Basic Sci. Reprod. Med. 20:1180–1189.

Frenkel, J., W. Vyverman, and G. Pohnert. 2014. Pheromone signaling during sexual reproduction in algae. Plant J. 79:632–644.

Fusco, G., and A. Minelli. 2019. The biology of reproduction. Cambridge Univerity Press.

García-Roa, R., F. Garcia-Gonzalez, D. W. A. Noble, and P. Carazo. 2020. Temperature as a modulator of sexual selection. Biol. Rev. 95:1607–1629.

Gardner, A., and F. Úbeda. 2017. The meaning of intragenomic conflict. Nat. Ecol. Evol. 1:1807–1815.

Gasparini, C., R. Dosselli, and J. P. Evans. 2017. Sperm storage by males causes changes in sperm phenotype and influences the reproductive fitness of males and their sons. Evol. Lett. 1:16–25.

Haig, D. 2010. What do we know about charophyte (Streptophyta) life cycles? J. Phycol. 46:860–867.

Harth, J. E., J. A. Winsor, D. R. Weakland, K. J. Nowak, M. J. Ferrari, and A. G. Stephenson. 2016. Effects of virus infection on pollen production and pollen performance: implications for the spread of resistance alleles. Am. J. Bot. 103:577–583.

Immler, S. 2019. Haploid selection in “diploid” organisms. Annu. Rev. Ecol. Evol. Syst. 50:219–236.

Immler, S. 2018. The sperm factor: paternal impact beyond genes. Heredity 121:239–247.

Immler, S., G. Arnqvist, and S. P. Otto. 2012. Ploidally antagonistic selection maintains stable genetic polymorphism. Evolution 66:55–65.

Immler, S., and S. P. Otto. 2018. The evolutionary consequences of selection at the haploid gametic stage. Am. Nat. 192:241–249.

Janicke, T. 2024. Sexual selection: competition for resources provided by mating partners. Behav. Ecol. 35:arae016.

Jensen, N., R. M. Allen, and D. J. Marshall. 2014. Adaptive maternal and paternal effects: gamete plasticity in response to parental stress. Funct. Ecol. 28:724–733.

Ji, H., M. Miao, H. Liang, H. Shi, D. Ruan, Y. Li, J. Wang, and W. Yuan. 2018. Exposure of environmental Bisphenol A in relation to routine sperm parameters and sperm movement characteristics among fertile men. Sci. Rep. 8:17548.

Johnson, M. G., and A. J. Shaw. 2016. The effects of quantitative fecundity in the haploid stage on reproductive success and diploid fitness in the aquatic peat moss *Sphagnum macrophyllum*. Heredity 116:523–530.

Kappeler, L., and M. J. Meaney. 2010. Epigenetics and parental effects. BioEssays 32:818–827.

Kekäläinen, J., P. Oskoei, M. Janhunen, H. Koskinen, R. Kortet, and H. Huuskonen. 2018. Sperm pre-fertilization thermal environment shapes offspring phenotype and performance. J. Exp. Biol. 221:jeb181412.

Kustra, M. C., L. M. Alissa, M. M. Rogers, M. M. Molinari, K. A. Stiver, S. Marsh-Rollo, J. K. Hellmann, and S. H. Alonzo. 2026. Warm waters undermine cryptic female choice. Funct. Ecol.

Kwok, A., and M. E. Dorken. 2022. Sexual selection on male but not female function in monoecious and dioecious populations of broadleaf arrowhead (*Sagittaria latifolia*). Proc. R. Soc. B Biol. Sci. 289:20220919.

Lankinen, Å., and S. Hydbom. 2017. Effects of soil resources on expression of a sexual conflict over timing of stigma receptivity in a mixed-mating plant. Oikos 126:692–702.

Lankinen, Å., and K. Karlsson Green. 2015. Using theories of sexual selection and sexual conflict to improve our understanding of plant ecology and evolution. AoB PLANTS 7.

Lau, T.-C., X. Lu, R. T. Koide, and A. G. Stephenson. 1995. Effects of soil fertility and mycorrhizal infection on pollen production and pollen grain size of *Cucurbita pepo* (Cucurbitaceae). Plant Cell Environ. 18:169–177.

Lavaut, E., M. Valero, S. Mauger, M. L. Guillemin, C. Destombe, and M. Dufay. 2023. Sexual selection in seaweed? Testing Bateman's principles in the red alga *Gracilaria gracilis*. Proc. R. Soc. B Biol. Sci. 290:20231668.

Mable, B. K., and S. P. Otto. 1998. The evolution of life cycles with haploid and diploid phases. Bioessays 20:453–462.

Marshall, D. J. 2015. Environmentally induced (co)variance in sperm and offspring phenotypes as a source of epigenetic effects. J. Exp. Biol. 218:107–113.

Mazer, S. J., A. A. Hove, B. S. Miller, and M. Barbet-Massin. 2010. The joint evolution of mating system and pollen performance: predictions regarding male gametophytic evolution in selfers vs. outcrossers. Perspect. Plant Ecol. Evol. Syst. 12:31–41.

McAndry, C., A. J. Wilson, P. A. Cotton, and M. Truebano. 2025. Transgenerational plasticity research: challenges and opportunities. Funct. Ecol. 39:3083–3104.

McCallum, B., and S.-M. Chang. 2016. Pollen competition in style: effects of pollen size on siring success in the hermaphroditic common morning glory, *Ipomoea purpurea*. Am. J. Bot. 103:460–470.

McQueen, A., B. Kempenaers, J. Dale, M. Valcu, Z. T. Emery, C. J. Dey, A. Peters, and K. Delhey. 2019. Evolutionary drivers of seasonal plumage colours: colour change by moult correlates with sexual selection, predation risk and seasonality across passerines. Ecol. Lett. 22:1838–1849.

Moore, J. C., and J. R. Pannell. 2011. Sexual selection in plants. Curr. Biol. 21:R176–R182.

Moore, M. P., and R. A. Martin. 2018. Trade-offs between larval survival and adult ornament development depend on predator regime in a territorial dragonfly. Oecologia 188:97–106.

Mulcahy, D. L. 1979. The rise of the angiosperms: a genecological factor. Science 206:20–23.

Nätt, D., U. Kugelberg, E. Casas, E. Nedstrand, S. Zalavary, P. Henriksson, C. Nijm, J. Jäderquist, J. Sandborg, E. Flinke, R. Ramesh, L. Örkenby, F. Appelkvist, T. Lingg, N. Guzzi, C. Bellodi, M. Löf, T. Vavouri, and A. Öst. 2019. Human sperm displays rapid responses to diet. PLOS Biol. 17:e3000559.

Navarro-Costa, P. A., A. Molaro, C. S. Misra, C. D. Meiklejohn, and P. J. Ellis. 2020. Sex and suicide: The curious case of Toll-like receptors. PLOS Biol. 18:e3000663.

Oseguera-Lopez, I., S. Ruiz-Diaz, P. Ramos-Ibeas, and S. Perez-Cerezales. 2019. Novel techniques of sperm selection for improving IVF and ICSI outcomes. Front. Cell Dev. Biol. 7:298.

Parker, G. A. 2020. Conceptual developments in sperm competition: a very brief synopsis. Philos. Trans. R. Soc. B-Biol. Sci. 375:20200061.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45:525–567.

Parker, G. A. 1998. Sperm competition and the evolution of ejaculates: towards a theory base. Pp. 3–54 *in* T. R. Birkhead and A. P. Møller, eds. Sperm competition and sexual selection. Academic Press, San Diego.

Parker, G. A. 2014. The sexual cascade and the rise of pre-ejaculatory (Darwinian) sexual selection, sex roles, and sexual conflict. Cold Spring Harb. Perspect. Biol. 6:a017509–a017509.

Parker, G. A., and T. Pizzari. 2010. Sperm competition and ejaculate economics. Biol. Rev. no-no.

Paterno, G. B., C. L. Silveira, J. Kollmann, M. Westoby, and C. R. Fonseca. 2020. The maleness of larger angiosperm flowers. Proc. Natl. Acad. Sci. 117:10921–10926.

Penney, H. D., J. Beirão, and C. F. Purchase. 2018. Phenotypic plasticity during external embryonic development is affected more by maternal effects than multiple abiotic factors in brook trout. Evol. Ecol. Res. 19:171–194.

Pérez-Cerezales, S., R. Laguna-Barraza, A. C. de Castro, M. J. Sánchez-Calabuig, E. Cano-Oliva, F. J. de Castro-Pita, L. Montoro-Buils, E. Pericuesta, R. Fernández-González, and A. Gutiérrez-Adán. 2018. Sperm selection by thermotaxis improves ICSI outcome in mice. Sci. Rep. 8:2902.

Perry, J. C., L. Sirot, and S. Wigby. 2013. The seminal symphony: how to compose an ejaculate. Trends Ecol. Evol. 28:414–422.

Pers-Kamczyc, E., Ż. Tyrała-Wierucka, M. Rabska, D. Wrońska-Pilarek, and J. Kamczyc. 2020. The higher availability of nutrients increases the production but decreases the quality of pollen grains in *Juniperus communis* L. J. Plant Physiol. 248:153156.

Pitnick, S., M. F. Wolfner, and S. Dorus. 2020. Post-ejaculatory modifications to sperm (PEMS). Biol. Rev. 95:365–392.

Prieu, C., A. Matamoro-Vidal, C. Raquin, A. Dobritsa, R. Mercier, P.-H. Gouyon, and B. Albert. 2016. Aperture number influences pollen survival in *Arabidopsis* mutants. Am. J. Bot. 103:452–459.

Purchase, C. F., and D. T. R. Moreau. 2012. Stressful environments induce novel phenotypic variation: hierarchical reaction norms for sperm performance of a pervasive invader. Ecol. Evol. 2:2567–2576.

Rescan, M., T. Lenormand, and D. Roze. 2016. Interactions between genetic and ecological effects on the evolution of life cycles. Am. Nat. 187:19–34.

Retuerto, R., J. Sánchez Vilas, and S. Varga. 2018. Sexual dimorphism in response to stress. Environ. Exp. Bot. 146:1–4.

Ritchie, H., and D. J. Marshall. 2013. Fertilisation is not a new beginning: sperm environment affects offspring developmental success. J. Exp. Biol. 216:3104–3109.

Ritchie, M. G., and J. R. Pannell. 2025. Speciation: sexual selection also plays a role in plants. Curr. Biol. 35:R393–R395.

Rogers, D. W., and D. Greig. 2009. Experimental evolution of a sexually selected display in yeast. Proc. R. Soc. B Biol. Sci. 276:543–549.

Rosengren, F., and N. Cronberg. 2014. The adaptive background of nannandry: dwarf male distribution and fertilization in the moss *Homalothecium lutescens*: Dwarf male distribution and fertilization in a moss. Biol. J. Linn. Soc. 113:74–84.

Rosenstiel, T. N. 2012. Sex-specific volatile compounds influence microarthropod-mediated fertilization of moss. Nature 489:431–433.

Rothäusler, E., C. Uebermuth, F. Haavisto, and V. Jormalainen. 2019. Living on the edge: gamete release and subsequent fertilisation in *Fucus vesiculosus* (Phaeophyceae) are weakened by climate change–forced hyposaline conditions. Phycologia 58:111–114.

Rowe, L., and H. D. Rundle. 2021. The alignment of natural and sexual selection. Annu. Rev. Ecol. Evol. Syst. 52:499–517.

Rusman, Q., E. H. Poelman, F. Nowrin, G. Polder, and D. Lucas-Barbosa. 2019. Floral plasticity: herbivore-species-specific-induced changes in flower traits with contrasting effects on pollinator visitation. Plant Cell Environ. 42:1882–1896.

Schmid, M. W., A. Schmidt, and U. Grossniklaus. 2015. The female gametophyte: an emerging model for cell type-specific systems biology in plant development. Front. Plant Sci. 6:907.

Scott, C., F. F. de Souza, V. H. V. Aristizabal, L. Hethrington, C. Krisp, M. Molloy, M. A. Baker, and J. A. Dell'Aqua. 2018. Proteomic profile of sex-sorted bull sperm evaluated by SWATH-MS analysis. Anim. Reprod. Sci. 198:121–128.

Shuker, D. M., and C. Kvarnemo. 2021. The definition of sexual selection. Behav. Ecol. 32:781–794.

Silva, W., P. Saez-Espinosa, S. Torijo-Boix, A. Romero, C. Devaux, M. Durieux, M. J. Gomez-Torres, and S. Immler. 2019. The effects of male social environment on sperm phenotype and genome integrity. J. Evol. Biol. 32:535–544.

Simmons, L. W., and M. Lovegrove. 2017. Socially cued seminal fluid gene expression mediates responses in ejaculate quality to sperm competition risk. Proc. R. Soc. B Biol. Sci. 284:20171486.

Simmons, L. W., and G. A. Parker. 2021. The devil is in the details: a comment on Shuker and Kvarnemo. Behav. Ecol. 32:798–799.

Simmons, L. W., and N. Wedell. 2020. Fifty years of sperm competition: the structure of a scientific revolution. Philos. Trans. R. Soc. B Biol. Sci. 375:20200060.

Singh, A., S. H. Antre, R. L. Ravikumar, P. H. Kuchanur, and H. C. Lohithaswa. 2020. Genetic evidence of pollen selection mediated phenotypic changes in maize conferring transgenerational heat-stress tolerance. Crop Sci. csc2.20179.

Smith, K. E., M. Byrne, D. Deaker, C. M. Hird, C. Nielson, A. Wilson-McNeal, and C. Lewis. 2019. Sea urchin reproductive performance in a changing ocean: poor males improve while good males worsen in response to ocean acidification. Proc. R. Soc. B-Biol. Sci. 286.

Snook, R. 2005. Sperm in competition: not playing by the numbers. Trends Ecol. Evol. 20:46–53.

Sutter, A., and S. Immler. 2020. Within-ejaculate sperm competition. Philos. Trans. R. Soc. B-Biol. Sci. 375:20200066.

Taugbol, A., A. B. Mazzarella, E. R. A. Cramer, and T. Laskemoen. 2017. Salinity-induced phenotypic plasticity in threespine stickleback sperm activation. Biol. Lett. 13:201705016.

Thompson, K. A., and M. T. J. Johnson. 2016. Antiherbivore defenses alter natural selection on plant reproductive traits. Evolution 70:796–810.

Tonnabel, J., P. David, T. Janicke, A. Lehner, J.-C. Mollet, J. R. Pannell, and M. Dufay. 2021. The scope for postmating sexual selection in plants. Trends Ecol. Evol. 36:556–567.

Tonnabel, J., P. David, and J. R. Pannell. 2019. Do metrics of sexual selection conform to Bateman's principles in a wind-pollinated plant? Proc. R. Soc. B Biol. Sci. 286:20190532.

Umehara, T., N. Tsujita, and M. Shimada. 2019. Activation of Toll-like receptor 7/8 encoded by the X chromosome alters sperm motility and provides a novel simple technology for sexing sperm. PLOS Biol. 17:e3000398.

Umen, J., and S. Coelho. 2019. Algal sex determination and the evolution of anisogamy. Annu. Rev. Microbiol. 73:267–291.

Varga, S., and C. D. Soulsbury. 2020. Environmental stressors affect sex ratios in sexually dimorphic plant sexual systems. Plant Biol. plb.13125.

Vasudeva, R., A. Sutter, K. Sales, M. E. Dickinson, A. J. Lumley, and M. J. G. Gage. 2019. Adaptive thermal plasticity enhances sperm and egg performance in a model insect. Elife 8:e49452.

West-Eberhard, M. J. 2003. Developmental plasticity and evolution. Oxford University Press, New York.

Williams, J. H., and S. J. Mazer. 2016. Pollen - tiny and ephemeral but not forgotten: new ideas on their ecology and evolution. Am. J. Bot. 103:365–374.

Willson, M. F. 1994. Sexual selection in plants: perspective and overview. Am. Nat. 144:S13–S39.

Wolf, J. B., and M. J. Wade. 2009. What are maternal effects (and what are they not)? Philos. Trans. R. Soc. B Biol. Sci. 364:1107–1115.

Zavada, M. S., and T. N. Taylor. 1986. The role of self-incompatibility and sexual selection in the gymnosperm-angiosperm transition: a hypothesis. Am. Nat. 128:538–550.

Zimmermann, B., M. Bağcıoğlu, V. Tafinstseva, A. Kohler, M. Ohlson, and S. Fjellheim. 2017. A high-throughput FTIR spectroscopy approach to assess adaptive variation in the chemical composition of pollen. Ecol. Evol. 7:10839–10849.

Figure legends

Figure 1: Selection across biphasic life cycles in sexually reproducing eukaryotes, illustrated and defined for diplontic cycles (e.g., animals), which lack mitosis in the haploid phase. Labels nD and sD are natural and sexual selection in the diploid phase (nH and sH similar for haploid phase) and match those of Figure 4. Circuits of cycles perpetuate unbroken across generations (Box 2).

Figure 2: Selection across biphasic life cycles in sexually reproducing eukaryotes, illustrated and defined for haplontic cycles (e.g., green microalgae), which lack mitosis in the diploid phase. Labels nD and sD are natural and sexual selection in the diploid phase (nH and sH similar for

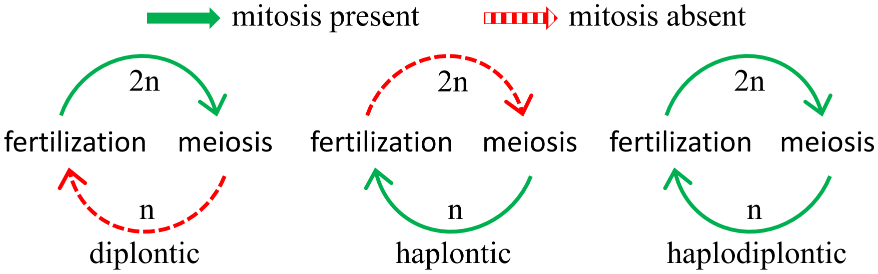
haploid phase) and match those of Figure 4. Circuits of cycles perpetuate unbroken across generations (Box 2).

Figure 3: Selection across biphasic life cycles in sexually reproducing eukaryotes, illustrated and defined for haplodiplontic cycles (e.g., land plants), which have mitosis in both diploid and haploid phases. Labels nD and sD are natural and sexual selection in the diploid phase (nH and sH similar for haploid phase) and match those of Figure 4. Circuits of cycles perpetuate unbroken across generations (Box 2). Diversity of taxa challenges interpretation, for example in angiosperms there is sexual selection in the diploid phase, but they have no flagellated (swimming) sperm in the haploid phase, while the opposite occurs in bryophytes and ferns.

Figure 4: Within-phase interactions and across-phase bridges (dashed lines) within the biphasic life cycle, showing how selection opportunities are inter-connected. Illustrated for diplontic cycles but concepts apply to all cycles. nD↔sD are within-phase two-way interactions where natural and sexual selection act on the same individual in the diploid phase, while sH↔nH illustrate similar concepts in the haploid phase. H⟶nD and H⟶sD are across-phase one-way bridges (different 'individuals') 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. These connections among selection opportunities perpetuate unbroken across generations, and can be visualized as a stack of Figure 4 cycles in Box 2.

Box 1. Glossary 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 (diploid): Life cycle where 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 (haploid): Life cycle where 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 (haploid-diploid): 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 University 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.

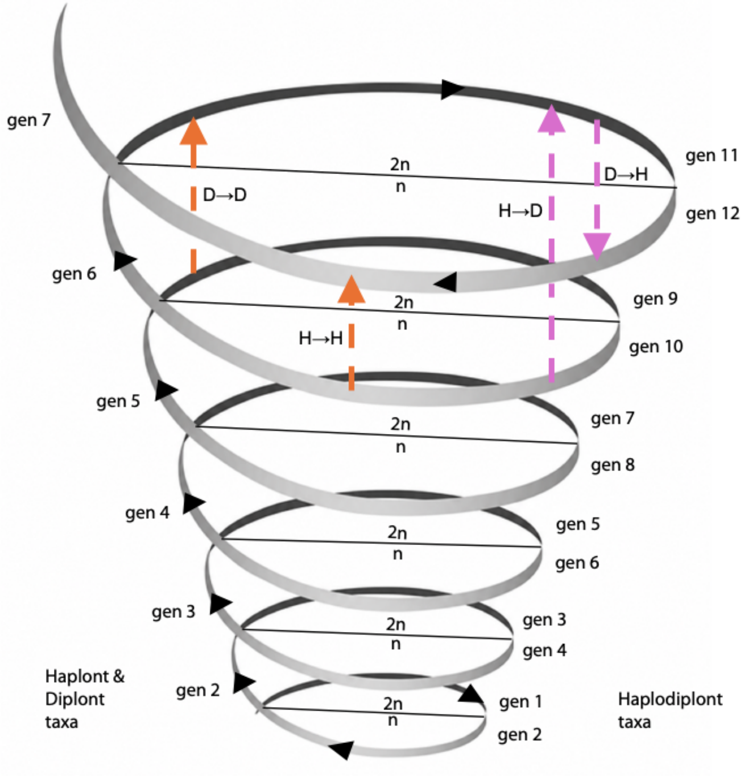
Adult: For diplontic taxa an adult is considered the mature diploid individual that is capable of producing haploid gametes. Similarly, in most haplodiplontic plants the adult is the diploid sporophyte. However, in bryophytes, the haploid gametophyte that produces sex cells is considered the adult, as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

Box 2. ‘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 Box 2-Figure A; for most diplontic and haplontic species one complete loop around this circuit represents a life cycle and generation in Figures 1-3. Three sequential phases (diploid-haploid-diploid or haploid-diploid-haploid) encompass two generations in diplontic and haplontic species, but three generations in haplodiplontic species (Box 1).

The concept becomes important for interpreting our across-phase bridges of biphasic life cycles (Figure 4). 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 are considered briefly in Box 3 on parental effects (e.g., diploid-diploid).



Box 2-Figure A: Modified and expanded from Fig 5.2 in West-Eberhard (2003), showing unbroken connections across generations of biphasic life cycles. Arrows in pink (D⟶H and H⟶D) are parental effects (Box 3) that bridge sequential diploid and haploid phases within a circuit, and match patterns in Figure 4. Arrows in orange (D⟶D and H⟶H) show parental effects (Box 3) that connect two circuits of the biphasic life cycle.

Box 3. ‘Parental effects’: a melting pot of connections 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) 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 restrictive as it does not work for different cycles. Under a ‘broad scope’, we consider here four types of parental effect, of which the above diploid-diploid definition encompasses only one (‘narrow scope’). Our types match some of the ‘paths’ presented by Badyaev & Uller (2009; their Fig 1).

<u>Parental effect D→H (diploid→haploid; selection tethered to **one** phase previous):</u> 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 4. 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 H→D, which is framed as a parental effect for plants and animals (see Evans et al. 2019).

<u>Parental effect H→D (haploid→diploid; selection tethered to **one** phase previous):</u> 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 4.

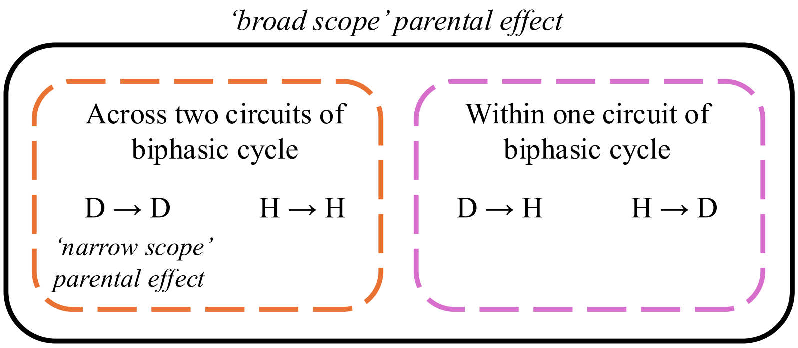
<u>Parental effect D→D (diploid→diploid; selection tethered to **two** phases previous):</u> The traditional definition of a ‘narrow scope’ paternal or maternal effect (e.g., amount of egg yolk). In this context a parental effect on offspring could be caused by intrinsic or extrinsic experiences of the diploid adult, whereas the term transgenerational plasticity (Bell and Hellmann 2019;

McAndry et al. 2025) is restricted to extrinsic sources. Whether parental (diploid) influences on the haploid phase (D→H) or subsequent diploid phase (offspring, D→D) are complementary or antagonistic is poorly understood.

Parental effect H→H (haploid→haploid; selection tethered to **two** phases previous):

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 H→D and H→H function independently is not known. These types of parental effects are difficult to study. 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, but whether this is due to genetic (Figure 1, nH and sH) or other mechanisms (D→H + H→D, or H→H) is obscure. One may conceptualize H→D and H→H to be 'gametal effects' (gamete + gametophyte) in haplodiplontic and diplontic taxa.

Schematic showing relationships among definitions of types of Parental effect:



Box 4. 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 selection opportunities provided by biphasic life cycles (Figures 1-3), but has traditionally focused on changing diploid phenotypes by using breeding programs that bypass sexual selection in the diploid phase (e.g., dog, horse, pigeon, chicken breeding). This also bypasses sexual selection in the haploid phase, 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 the life cycle due to different tissues or functions operating in the two phases. Expressed genes in the haploid phase have 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). 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; Sutter and Immler 2020).

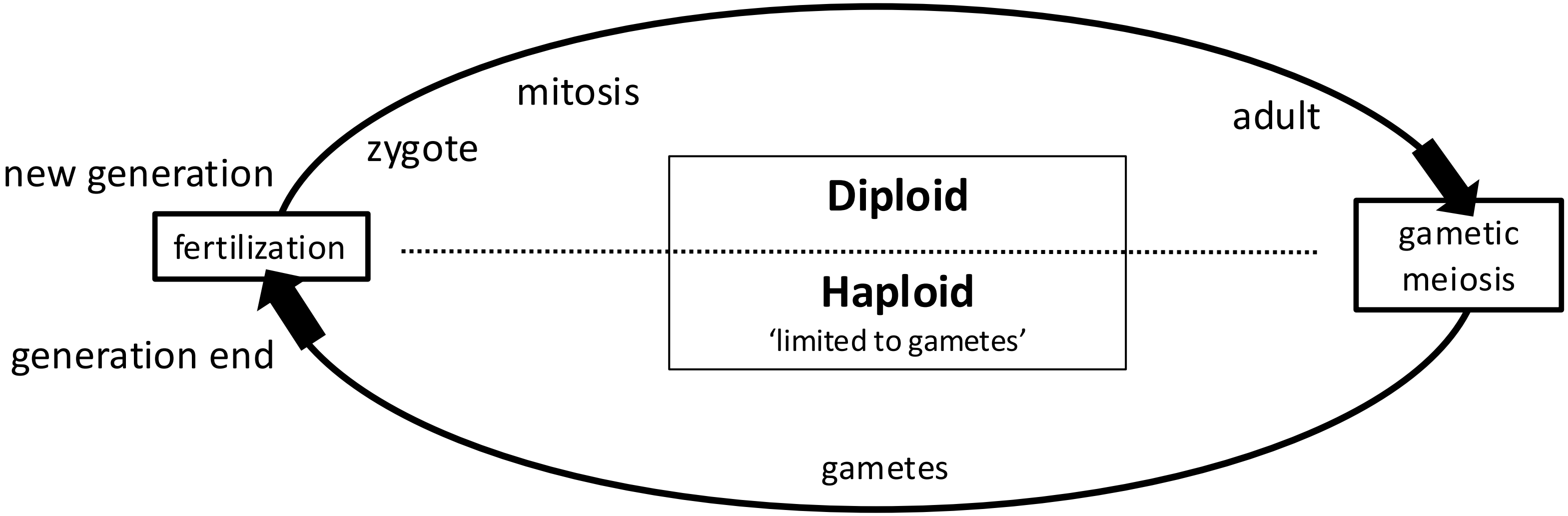
Diplontic life cycles

nD

post-zygotic 'narrow sense' **natural selection**
- zygote-adult survival
- ability to produce and release gametes

sD

post-zygotic pre-mating **sexual selection** (intra-sex)
- intra-sex competition (scramble competition, endurance rivalry, contest competition)
- inter-sex mediation (mate choice)



post-mating pre-zygotic **sexual selection** (intra-sex)
- intra-sex competition (sperm competition, egg competition)
- inter-sex mediation (cryptic female choice)

sH

post-mating pre-zygotic 'narrow sense' **natural selection**
- sperm survival & fertilization capability
- egg survival & fertilization capability

nH

Figure 1

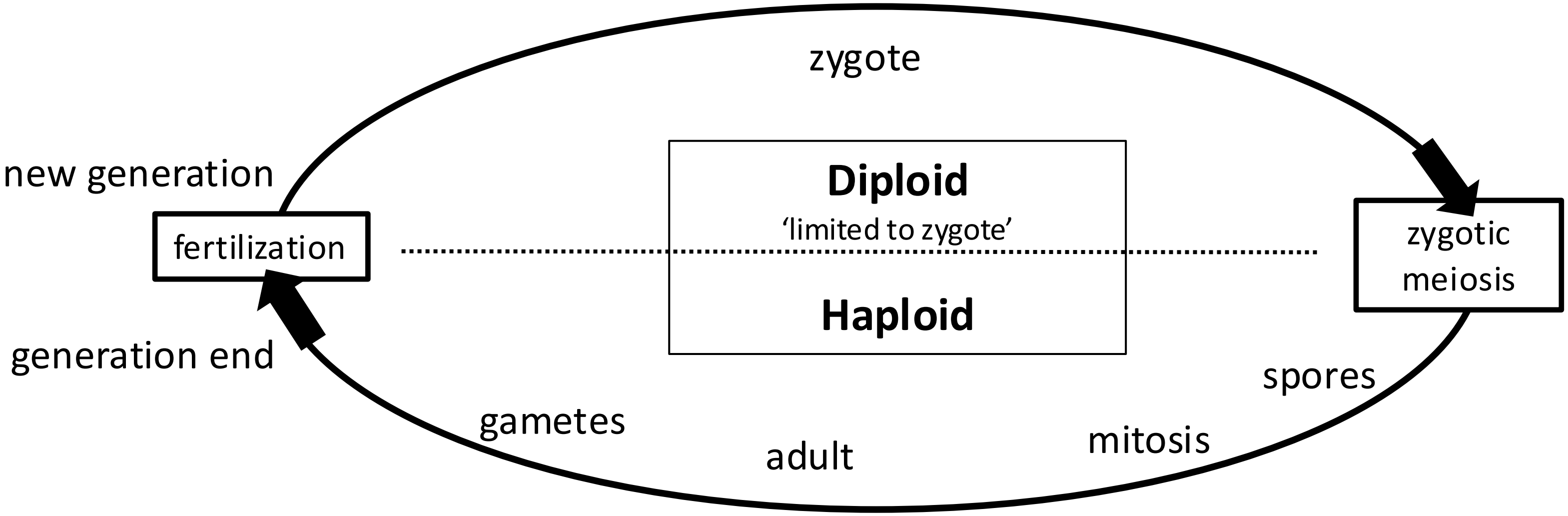
Haplontic life cycles

nD

sD

post-zygotic ‘narrow sense’ **natural selection**
- zygote survival
- ability to produce spores

post-zygotic **sexual selection** (intra-sex)
- 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)
- intra-sex gamete competition
- inter-sex mediation (sex pheromones)

pre-zygotic ‘narrow sense’ **natural selection**
- spore-adult survival
- gamete survival, fertilization capability

sH

nH

Figure 2

Haplodiplontic life cycles

nD

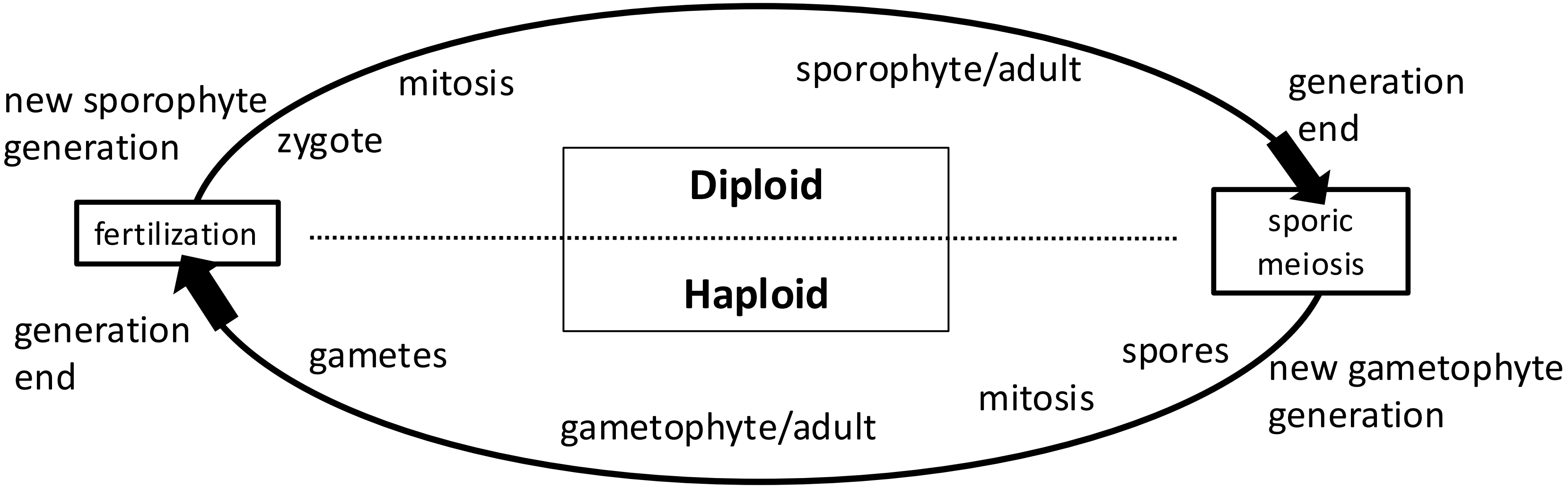
sD

post-zygotic ‘narrow sense’ **natural selection**

- zygote-adult survival
- ability to produce and release spores

post-zygotic **sexual selection** (intra-sex)

- intra-sex competition (pollinator attraction, wind dispersal)
- inter-sex mediation (does not apply)



pre-zygotic **sexual selection** (intra-sex)

- intra-sex competition (pollen/sperm)
- inter-sex mediation (female choice of pollen/sperm)

pre-zygotic ‘narrow sense’ **natural selection**

- gametophyte survival
- sperm & egg fertilization capability

sH

nH

Figure 3

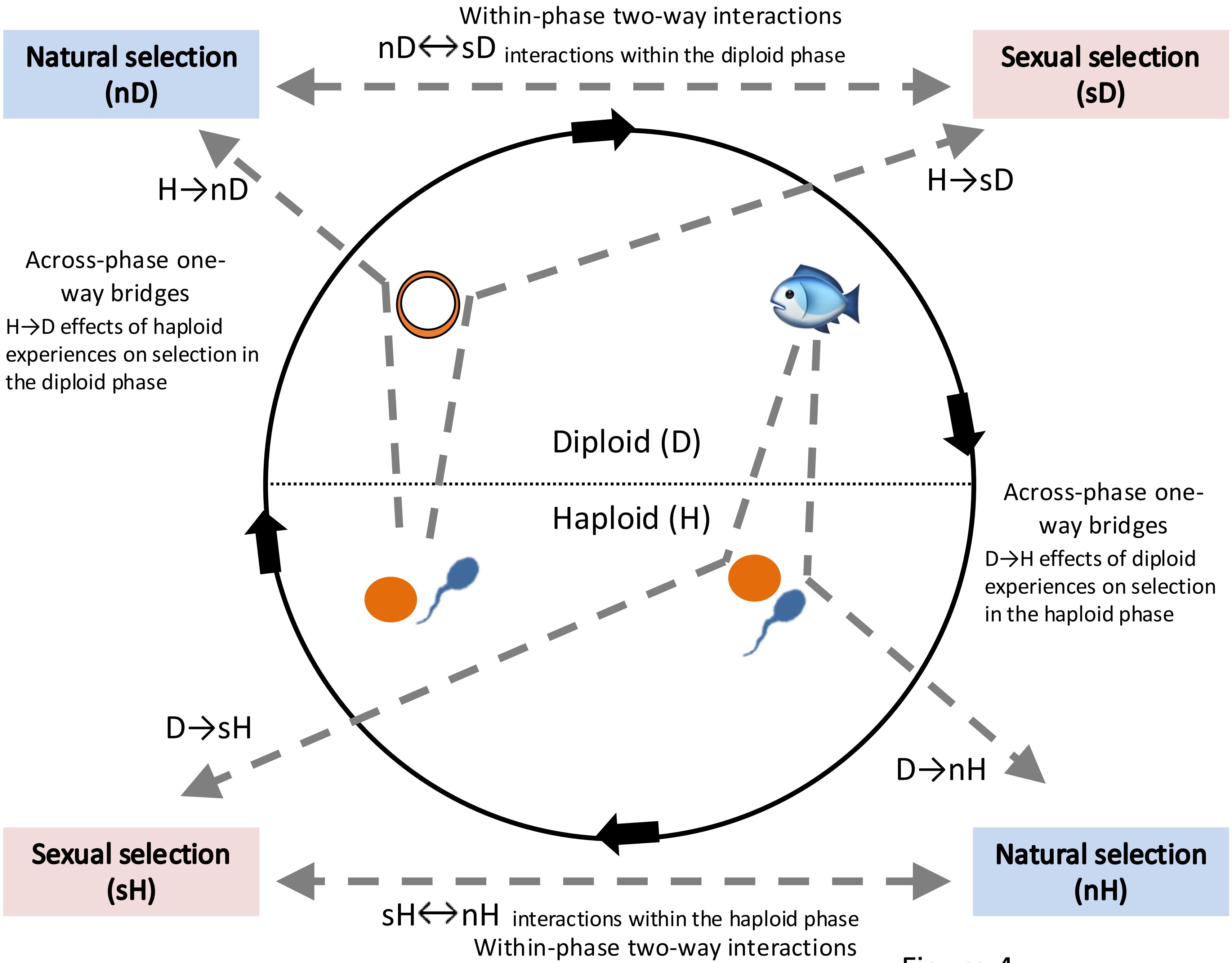

Within-phase two-way interactions
nD↔sD interactions within the diploid phase
Natural selection (nD)
Sexual selection (sD)
H→nD
H→sD
Across-phase one-way bridges
H→D effects of haploid experiences on selection in the diploid phase
Diploid (D)
Haploid (H)
Across-phase one-way bridges
D→H effects of diploid experiences on selection in the haploid phase
D→sH
D→nH
Sexual selection (sH)
Natural selection (nH)
sH↔nH interactions within the haploid phase
Within-phase two-way interactions

Figure 4

Table 1: Opportunities for selection within and across the biphasic life cycle of sexual eukaryotes are listed in rows as described in Figures 1-4, and Box 3. For each life cycle type, opportunities for selection are categorized as X or ✓, and the clarity of evidence as either *extensive*, *moderate*, *limited or not applicable*; with further elaboration.

	Life cycle type		
Selection opportunities	Diplontic (diploid) e.g., animals	Haplontic (haploid) e.g., green microalgae	Haplodiplontic (haploid-diploid) e.g., ferns
Within one circuit of biphasic life cycle			
Figs 1-3 - natural selection in diploid phase (nD)	✓, extensive Darwinian natural selection	✓, limited Only applies to the zygote	✓, extensive Darwinian natural selection
Figs 1-3 - sexual selection in diploid phase (sD)	✓, extensive Darwinian sexual selection	X, not applicable No male / female structures, no diploid mates	✓, limited Only in seed plants, can be confused with sH
Figs 1-3 - natural selection in haploid phase (nH)	✓, moderate Gamete quality rarely framed this way	✓, moderate Haplont survival, gamete function	✓, moderate Gametophyte survival, gamete function
Figs 1-3 - sexual selection in haploid phase (sH)	✓, extensive Parkerian sexual selection, sperm competition	✓, limited Gamete competition	✓, moderate Pollen tube growth race, sperm competition
Fig 4 - nD↔sD interaction in diploid phase	✓, extensive Classic examples from Darwin	X, not applicable	✓, moderate Only in seed plants
Fig 4 - sH↔nH interaction in haploid phase	✓, limited Rarely framed this way, ripe for targeted experimentation	✓, limited Haplonts provide potential for insight	✓, limited Free living gametophytes provide potential for insight

Fig 4 - D→nH bridge, Box 3 - Parental effect D→H	✓, extensive Rarely framed this way	✓, limited Conceptually inverse of H→nD in diplontic species	✓, moderate Rarely framed to isolate selection in nH vs sH
Fig 4 - D→sH bridge, Box 3 - Parental effect D→H	✓, extensive Rarely framed this way	✓, limited Inverse of H→sD in diplontic animals	✓, moderate Rarely framed to isolate selection in nH vs sH
Fig 4 - H→nD bridge, Box 3 - Parental effect H→D	✓, limited Hard to isolate from nH and sH	✓, limited Inverse of D→nH in diplontic animals	✓, limited Free living gametophytes provide potential for insight
Fig 4 - H→sD bridge, Box 3 - Parental effect H→D	✓, limited Experimentally harder to isolate than H→nD	X, not applicable	✓, limited Experimentally harder to isolate than H→nD
Across two circuits of biphasic life cycle			
Box 3 - Parental effect D→D	✓, extensive Classic ‘narrow scope’ parental effect	X or Y, limited No mitosis in diploid phase eliminates or limits scope	✓, moderate ‘Narrow scope’ parental effect
Box 3 - Parental effect H→H	✓, limited Poorly studied	✓, limited Similar to D→D in diplontic animals	✓, limited Gametophyte to gametophyte