Sperm-dependent asexual species matter in ecology and evolution

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Abstract

In a world of metazoans, where sexual reproduction vastly predominates, asexual organisms are nonetheless very important. The aim of this review is to show that asexuals can have general effects on other species, ecosystems and biological networks via mechanisms that deserve more attention. These include 1) impact on the genepool of coexisting sexual species by either restricting their population sizes or by providing bridges for interspecific gene-flow whose type and consequences substantially differ from gene flow mechanisms expected under sexual reproduction; 2) impact on diversification rate, either direct by serving as stepping-stones in speciation or indirect by promoting the formation of pre- and postzygotic reproduction barriers among nascent species; and 3) impact on spatial effects, via direct or indirect (apparent) types of competition and Allee effects. We specifically point to these important mechanisms, provide empirical examples how asexuals impact the evolution of sexual species and ecosystems, and, finally, show that these broad effects may last beyond the tenure of the individual asexual lineages causing them. We also propose new research directions to incorporate the aforementioned impacts of asexual organisms which will ultimately enhance the understanding of evolution of genomes and ecosystems in general.

Keywords: speciation, hybridization, meiosis, population dynamics, apparent competition

Introduction

Reproduction, or the ability to transmit genomes from one generation to another, is a fundamental property of all living organisms. In the world of metazoans, this is mostly realized by meiotic sex with recombination, which probably has a single origin very early in eukaryotic evolution (Bernstein and Bernstein 2010), but there is considerable variability on this theme as many organisms transmit their genomes partly or entirely clonally, commonly being referred to as asexuals. In fact, many sexual species – including our own – pass on parts of their genome, such as mitochondria and sex chromosomes, essentially in an asexual mode with no or very limited recombination. Thus, while ***sex*** and ***asexuality*** (Glossary) are usually presented as a dichotomy, in reality, there is a continuum between full meiosis and ***mixis*** (Glossary) on the one hand, and vegetative reproduction and ameiotic formation of gametes on the other hand. The term asexuality is thus used very broadly to capture a large diversity of reproductive mechanisms that differ in some aspect from full blown sexual reproduction with meiosis and recombination in every generation (Neiman et al. 2014). Leaving aside cases such as budding, life cycles with sexual and asexual phases, alternating gametic and sporophytic phases (like in some parasites) or polyembryony (the production of multiple clonal embryos from a single fertilized egg (Prodöhl et al. 1996)), forms of asexual reproduction based on production of at least partly clonal gametes have evolved many times independently in plants and most major taxa of animals (Suomalainen et al. 1987). Although obligate asexuality evolved relatively infrequently, a survey of the literature indicates that parthenogenetic taxa with clonal gametes evolved in at least 15 out of 31 metazoan phyla (Supplementary Material, Figure S1 and references there), suggesting this trait has high relevance for evolution.

In this review, we do not intend to provide an exhaustive overview of all asexual taxa, which would be a book-length endeavor, nor to summarize all research on asexual organisms, which recently attracted new critical thinking and synthesis (e.g., (Laskowski et al. 2019; Fujita et al. 2020)) and contributed significantly to understanding the disadvantages and advantages of meiotic sex. Indeed, because of their atypical meiosis and non-Mendelian propagation of genomes, asexuals serve as excellent natural models for understanding fundamental questions in evolution, ecology and cell biology (Bengtsson 2009; Meirmans 2009), such as, for example, the ***Red Queen Hypothesis*** (Glossary; (Van Valen 1973; Brockhurst et al. 2014; Lively and Morran 2014)), homology search and recombination, mutational load or sperm-egg interactions during fertilization (recently reviewed by e.g. (Laskowski et al. 2019; Dalziel et al. 2020)). Instead, we present new hypotheses and emphasize specific mechanisms how the very existence of asexuals and the complexity of their reproductive modes directly and indirectly shapes the evolution of interacting sexual taxa and ecosystems they occur in by exerting specific types of evolutionary interactions, which are unparalleled in sexually reproducing lineages.

The so-called asexual organisms employ a wide spectrum of independently arisen cytological mechanisms for gamete production, which range from completely ameiotic processes (apomixis) to those involving more or less distorted meiotic divisions (automixis) (Stenberg and Saura 2009, 2013). Consequently, some organisms transmit their genomes in a strictly ***clonal*** way (Glossary) while others, like hybridogens, transmit clonally only parts of their genomes while the rest undergoes recombination or even mixis (Figure 1). The distinction between sexual and asexual reproductive modes is particularly difficult in plants, where various intermediates exist and several types of apomixis may emerge from one type of sexuality (Hojsgaard and Hörandl 2015). Variability also exists with respect to the process of fertilization since true parthenogens (Figure 1A) are completely independent of gamete fusion, while other types of asexuals are referred to as ***sperm-dependent parthenogens***, pseudogams or sexual parasites (Glossary) as they rely on sperm, which is usually, but not always, provided by closely related sexual species, e.g. (Choleva et al. 2008). The sperm-dependent parthenogens may need the sperm just for egg activation with its genome rejected after fertilization (***gynogenesis***; Glossary and Figure 1B), but the sperm may also contribute genetically to the progeny either by subgenomic components, such as microchromosomes (Figure 1C) (Schartl et al. 1995) or its entire genome may be incorporated into progeny which would either utilize it for ploidy increase (genome addition; Figure 1F) or eliminate it after one generation in the next round of gamete production (***hybridogenesis***; Glossary and Figure 1E). However, the situation often is more complex than such textbook examples, as e.g., in the case of *Ambystoma* salamanders from the northeastern USA, where, over evolutionary time, genomes have been added or replaced in the original hybrid lineages (the mode of reproduction known as kleptogenesis) (Bi et al. 2008; Bogart 2019).

To be precise, in the present review, we point out that ongoing research on the aforementioned traditional questions relating to asexuality often lacks careful consideration of the effects – both negative and positive – that asexuals have on the sexually reproducing species they occur with. This is especially the case of sperm-dependent parthenogens, traditionally viewed as combining disadvantages of both reproductive modes, asexuality and sexuality because they are deprived of regular recombination and segregation of their genetic material, while on the other hand they cannot take full advantages of asexual reproduction, being dependent on mating with sexual counterparts (rev. in (Beukeboom and Vrijenhoek 1998)). Therefore, we compile evidence for wide-ranging effects that sperm-dependent asexuals have on interacting sexual species and ecosystems they occur in. In particular, we suggest that even if individual asexual lineages may be short-lived, their impact on ecosystems where they occurred (and eventually perished) is substantial and probably quite higher than currently assumed.

Although asexual taxa are not as widespread as sexual taxa, we contend that overlooking or ignoring them may lead to an incomplete understanding of ecological and evolutionary dynamics and can be perilous as historically illustrated by Johann Gregor Mendel's example. Like any good scientist Mendel wanted to "verify" the results he obtained with peas (*Pisum)* in 1866 (Bicknell et al. 2016) but he inadvertently made a mistake that delayed the recognition of his findings by many years: He picked a popular model system of the time, *Hieracium* and largely failed to replicate his original findings, as reported in his second paper in 1869. The reason, however, was not that his ideas were incorrect, but rather that *Hieracium* is a facultative asexual plant which Mendel could not know in his time (Krahulcová et al. 1999). Nonetheless, this cast doubt on the generality of Mendel's discovery and delayed the general acceptance of genetics for decades, thus changing history (Bicknell et al. 2016). Had Mendel been able to take the asexual reproduction of his model organism into account, the history of evolutionary biology might have been very different.

We argue here that although individual asexual lineages eventually go extinct - just like any other species - the particularities of asexual reproduction likely have characteristic effects on coexisting species extending well beyond the lifespan of such clones. In particular, we focus on sperm-dependent parthenogens and show what important impacts they have on the biological networks they occur in. For example, by playing a role as sexual parasites that "steal" gametes of sexual species for their own reproduction (Hubbs 1964; Avise 2008; Lehtonen et al. 2013), they indirectly affect the effective population size of their sexual counterparts, thereby modifying their gene pool. Based on recent advances we show that the very existence of asexuals in general implies several effects on the ecosystems they are embedded in and very important properties of coexisting sexual species in terms of their 1) genetic architecture, 2) diversification and speciation, and 3) spatial distribution.

1. Impact on the gene pool of sexual species

1.1 Direct impact on a sexual species' gene pool via asexual to sexual gene flow

Asexual species are typically assumed to produce clonal progeny, but clonality is seldom perfect and many asexuals can produce gamete types that enable their genes to flow back into sexual populations (Figure 1C, F). In plants, for instance, phylogenetic reconstruction of angiosperm evolution indicated that reversals from apomixis to sexuality occurred (Hörandl and

Hojsgaard 2012). Backcrossing to sexual relatives has been directly reported from several apomictic species, e.g., in *Hieracium*, *Ranunculus* and *Taraxacum* (Hörandl and Paun 2007), which supposedly helps to generate new cytotypes (Sailer et al. 2020) and local reversal to sex (Majeský et al. 2012), thereby contradicting Darlington's „dead end of evolution" hypothesis (Darlington 1939). The geneflow from asexual to sexual populations has also been demonstrated in various asexual animals ranging from flatworms to vertebrates (Hotz et al. 1992; Goddard and Schultz 1993; Vorburger 2001; Sousa-Santos et al. 2006; D'Souza and Michiels 2009; Scali 2009; Angers et al. 2018).

It may take various forms: For example, let us assume a hybridogenetic female hybrid between two species A and B which pre-meiotically eliminate A-type chromosomes, thus clonally transmitting only the B genome into her eggs. Normally, these eggs are fertilized by A - sperm restoring the hybrid state of AB. However, fertilization with B – sperm would lead to formation of sexually reproducing BB diploids, where now half of their nuclear genome has an asexual history and the other half has not (Figure 1G and other mechanisms of mtDNA replacement in Figure 1H, I) (Mikulíček et al. 2014; Denton et al. 2018; Kwan et al. 2019; Suzuki et al. 2019). Furthermore, some asexual organisms do not pass on their genomes only via females, but also produce males (e.g., *Daphnia* water fleas (Paland et al. 2005), *Pelophylax* frogs (Graf and Polls-Pelaz 1989; Mikulíček et al. 2015)) or sperm in case of hermaphrodites like *Schmidtea* flatworms (D'Souza and Michiels 2010), or *Corbicula* clams (Hedtke et al. 2008; Hedtke and Hillis 2011) which fertilize related sexual females, thereby further facilitating the introgression of asexual genomes back into sexual gene pools.

Clearly, such gene flow from an asexual to a sexual genepool fundamentally differs from any classical mechanisms of gene exchange between sexual species because asexuals transmit their genetic material *en bloc*, and in a non-Mendelian fashion (Glémin et al. 2019). Since many asexuals are of hybrid origin and reproductively interact with their two parental species, they thus can serve surprisingly often as a hub between sexual species. However, owing to the specific nature of asexual transmission of genomes, the effect on the recipient genomes would be different from other types of introgression found in 'classical' sexual hybrids.

For example, if the aforementioned hybridogenetic hybrid originated from hybridization between a female from species A and a male from the species B, its eggs would possess A-type mtDNA but B-type nucleus (Figure 1G). If fertilized by B – sperm, such gametes would thus create cyto-nuclear mosaics (also known as ***cybrids***; Glossary) and hence facilitate the transfer of cytoplasmatic and/or complete nuclear genomes at rates superseding many unidirectional backcrosses via meiotic hybrids. Such massive unidirectional mtDNA flow mediated by sperm-dependent parthenogens without any substantial nuclear admixis has been reported for example in water frogs *Pelophylax ridibundus* (Hotz et al. 1992; Plötner et al. 2008; Mikulíček et al. 2014), several species of the *Bacillus* insect (Scali 2009), asexual *Corbicula* clams (Hedtke et al. 2008; Hedtke and Hillis 2011) as well as various fishes including loaches of the family Cobitidae (Kwan et al. 2019) and cyprinids of the genera *Squalius* (Alves et al. 2001, 2002; Sousa-Santos et al. 2006) and *Chrosomus* (Binet and Angers 2005; Angers et al. 2018). Angers et al. (2018) documented that such a type of mtDNA introgression might have had considerable adaptive value during the postglacial range expansion in *Chrosomus*. In an extreme case, the gene flow from asexuals might have even caused complete replacement of the original mtDNA by an allospecific mitochondrial genome as suggested by cytonuclear mosaicism of *Cobitis tanaitica* spined loaches (Choleva et al. 2014). Sperm-dependent asexuals may also mediate interspecific gene flow between nuclear gene pools of related sexual species, as found in the European complex of water frogs where hybridogenetic hybrids *P. esculentus* mediate introgression between parental species *P. ridibundus* and *P. lessonae* (Uzzell et al. 1976; Schmeller et al. 2005; Mikulíček et al. 2014).

In addition, when considering the effects of asexual to sexual introgression, we have to emphasize that asexual' genomic elements that introgress into a sexual genepool have evolved many generations in a (quasi)clonal way and passed through very different selection regimes than homologous sequences in a sexual species' genepool. First, asexual genomes are assumed to evolve under relaxed purifying selection due to whole-genome linkage, suggesting that a recipient sexual species may acquire genetic material with high numbers of deleterious mutations, depending on the duration of clonal evolution and the speed of mutation accumulation processes, like ***Muller's ratchet*** (Glossary). Moreover, asexual species may benefit from complete loss or loss of function of many genes coding traits that are not needed or even maladaptive for asexual reproduction, such as genes related to meiosis or mating behavior (Schartl et al. 1991; Schlupp et al. 1992; Kooi and Schwander 2014; Parker et al. 2019). Introgression of asexual genomes may therefore deteriorate the genepool of the sexual recipient species even more than simple mutation accumulation. It should be noted, though, that predicting the negative impact of gene flow from asexuals into sexual genepools is difficult as models for mutation accumulation in asexuals are far from clear. For example, mutation rates seem to be generally male-biased, which might counteract Muller's ratchet (Redfield 1994) and partly explain why accumulation of deleterious mutations appears to be surprisingly slow in many investigated asexual all-female species (Janko et al. 2011; Pellino et al. 2013; Warren et al. 2018; Kočí et al. 2020). Furthermore, in Amazon mollies (*Poecilia formosa*), a gynogenetic fish species from Southern Texas and Northeastern Mexico, loss of sex-related traits was not found (Warren et al. 2018). By contrast, in fully asexual organisms such as the snail *Potamopyrgus antipodarum,* loss of male function has been reported (Jalinsky et al. 2020).

On the other hand, introgression from asexuals may also be beneficial since restriction of recombination may have many positive aspects for genome evolution, because it favors the spread of advantageous combinations of alleles in regions where recombinants are expected to have lower fitness (Neiman and Linksvayer 2006). Selection for restricted recombination has indeed been documented between loci contributing to adaptation (Thompson and Jiggins 2014), speciation (Ortiz-Barrientos et al. 2016), or *de novo* evolution of separate sexes (Charlesworth and Charlesworth 1978). Asexual genepools, for their whole-genome linkage, may therefore represent unprecedented testing fields where selection acts on various allelic combinations with much greater efficiency than could ever be observed in any sexual species, and multiply, due to clonal reproduction, the fittest multilocus genotypes (Barbuti et al. 2012). Therefore, when asexual to sexual gene flow is possible, it is likely to introduce whole chromosomes that evolved for a long time without recombination into particularly suitable combinations of alleles. Positive effects of such a gene exchange with asexual hybrids have already been documented, for example, by Schmeller et al. (2005) who showed that bi-directional introgression between sexual water frog species *P. ridibundus* and *P. perezi* mediated by the hybridogenetic hybrids *P. grafi* increased the probability of local adaptation to hypoxic conditions and range expansion of the sexual species.

In summary, when asexual to sexual geneflow is possible, the potential effects on the sexual species' fitness, either positive or negative, may last longer than the existence of individual clones from which the introgression originated.

1.2. *Indirect impact on a sexual species gene pool via modification of effective population size*

Yet, even if a sexual species is not directly affected by gene flow from an asexual species, its genepool would still be modified indirectly by interactions with coexisting sperm-dependent parthenogenetic asexuals, because the very presence of sperm-dependent asexuals likely affects selective pressures operating in sexual populations and their demographic parameters. To understand the underlying reasons, it must be kept in mind that although asexual taxa often diverged ecologically from their sexual counterparts (see e.g. (Ross et al. 2012; Van der Kooi et al. 2017), many asexual species, especially the sperm-dependent parthenogens, are ecologically relatively similar to their sexual ancestors, with which they often coexist (Beukeboom and Vrijenhoek 1998; Vrijenhoek and Parker 2009). Consequently, part of the environmental carrying capacity potentially available for sexual population is taken up by asexuals when these are present.

In general, sperm-dependent competitors may affect the ***effective population size (N_e)*** (Glossary) of related sexuals via several mechanisms. These include stochastic effects increasing the strength of genetic drift, such as (a) modifying extinction/recolonization dynamics of sexual metapopulation, and (b) increasing the variance in reproductive success of the sexual species, and (c) modifying selective pressures resulting from biased operational sex ratio (OSR) in mixed sexual-asexual populations. Let us consider these mechanisms in the following paragraphs.

(a) Sperm-dependent parthenogenesis depends on access to males of a sexual species and consequently the asexuals may not outcompete their sexual host, lest they lose a vital resource, leading to the collapse of the whole sexual-asexual complex (Schlupp and Riesch 2011). Kokko et al. (2008) published a mathematical model proposing that coexistence with sexuals is possible provided that outcompeting the sexual species by the asexuals occurs locally and asynchronously in discrete populations. Sexuals immigrating from nearby populations may re-colonize the areas of extinction until being invaded by another wave of asexuals in a multi-species metapopulation dynamic. For the sexual species, however, Kokko et al.'s model implies one additional consequence which stems from classical population genetic theory: if the sexual metapopulation is forced to pass through such extinction-recolonization cycles induced by sperm-dependent parthenogens, it follows that its effective population size will be diminished. Additionally, it also follows that at each moment, some parts of range potentially suited for the sexual species will be temporarily unavailable.

(b) Coexistence with sperm-dependent parthenogens also likely increases the variance in reproductive success in a host sexual species because sexual individuals may spend a considerable portion of their reproductive potential on mating with sperm-dependent parthenogens rather than conspecific individuals (Schlupp 2010). Consequently, in each generation the sexual gene pool would be re-constituted from fewer fathers than it would normally have in absence of sperm-dependent parthenogens. It follows from classical population genetic theory that such an increased variance in reproductive success would subsequently further reduce the effective population size of the sexuals (Figure 2).

(c) Another consequence of the presence of sperm-dependent parthenogenetic females is that male mate choice as well as female competition (Makowicz and Schlupp 2015) can occur because the operational sex ratio is female biased (Schlupp 2009). Under some conditions, the OSR, the ratio of reproductively active males and females, may be altered, which has consequences for which sex is choosier (Amundsen 2018; Schlupp 2021). Simply put, if males become the rare sex, they may switch from competing for females to being choosy. Such a mechanism has, for example, been documented in some sexual fishes such as two-spotted goby, *Gobiusculus flavescens* (Forsgren et al. 2004). In this mating system males become rare late in the season, and consequently become choosier than females showing how important ecological conditions can be in modifying sexual selection (Amundsen 2018). The presence of excessive number of asexual females may have drastic effect on sex allocation and ratio in interacting sexual species. This occurs e.g., in sexual brine shrimp *Artemia franciscana*, which adaptively adjust their sex ratio under natural conditions. However, when co-occurring with the related obligate asexual all-female species *A. parthenogenetica* in recently invaded parts of its distribution range *A. franciscana* maladaptively produces extremely male-biased sex ratio (Lievens et al. 2016). The presence of sperm-dependent females in sexual/asexual mating systems may have even a stronger effect and alter the OSR in such a way that female choice is diminished, and male choice prevails (Figure 2). A skewed OSR and increased variance in reproductive success of a sexual species thus further reduces its effective population size, especially in those mixed populations where the proportion of sperm-dependent parthenogenetic females is high. Such high proportions of sperm-dependent parthenogens have been documented in several asexual-sexual complexes, often reaching over 70%, for example in frogs (*Pelophylax*, (Graf and Polls-Pelaz 1989; Mikulíček et al. 2015)), salamanders (*Ambystoma*, (Bogart et al. 2009)), and fishes (*Squalius*, (Cunha et al. 2008); *Cobitis* (Janko et al. 2007) and *Poecilia* (Heubel and Schlupp 2008).

All those mechanisms reducing effective population size have important implications for the gene-pool of the sexual species, which can be predicted from population genetic theory. For example, populations with diminished effective size have higher likelihood of inbreeding depression and extinction (Byers and Waller 1999). Selection becomes less effective while the effect of genetic drift increases, allowing more frequent fixation of deleterious alleles due to chance. Additionally, the faster fixation of positively selected alleles leads to a greater loss of genetic diversity in small populations (e.g. (Lande 1976; Lacy 1987)). Population size reduction further increases the ***Allee effect*** (Glossary) in sexual populations and directly impacts metapopulation connectivity by reducing the effective number of migrants (Lowe and Allendorf 2010). Consequently, lower efficiency of homogenizing geneflow speeds up local fixation of alternative alleles in small, isolated populations (Cosentino et al. 2012), which may also contribute to faster adaptation to local environments, potentially limiting the plasticity of population-wide responses to stochastic events.

Despite clear predictions, the detection of such indirect effects on sexual gene pools is a challenging task. Nevertheless, long-term studies of sperm-dependent asexual complexes may provide suitable model systems to test this hypothesis. For instance, we can assume that in a hybridogenetic complex of water frogs, the parental species *P. lessonae* is more affected by hybridogenetic hybrids *P. esculentus* because in most populations it serves as a gamete donor for them. Hybridogenetic hybrids thus could decrease the effective population size of *P. lessonae*. One of the consequences of reduced population size and the higher rate of genetic drift could be the higher genetic differentiation of *P. lessonae* populations, as we observe in nature, compared to another parental species *P. ridibundus* that does not coexist frequently with hybrids and has lower levels of population differentiation (Pruvost et al. (2015)). Another example of such indirect effects comes from spined loaches, the *Cobitis* hybrid complex, where gametogenic performance of males of the sexual species changed in response to a female-biased sex ratio a in mixed sexual-asexual population (Juchno and Boroń 2006; Jablonska et al. 2020). Specifically, unlike their counterparts from purely sexual populations, sexual males serving as sperm donors in mixed populations had to meet the reproductive challenge of a high proportion of sperm-dependent parthenogenetic females, which lead continual year-round sperm-production, higher production of spermatogonia during and after spawning and lower rates of apoptosis in their testes.

2. Impact on speciation

In this section we discuss how asexual organisms, and sperm-dependent asexuals in particular, contribute to the existing biodiversity either indirectly by facilitating the speciation in coexisting sexual species or directly by forming new species themselves.

2.1. Indirect impact on speciation: promotion of reproductive isolation barriers

We first present several ways, how sperm-dependent parthenogens, by their very presence, may considerably affect population divergence as well as establishment of both prezygotic and postzygotic reproductive isolation barriers (RIB) between populations of related sexuals. Such mechanisms are rather cryptic and were appreciated only recently.

Postzygotic RIB: As already mentioned, the presence of asexuals, especially sperm-dependent parthenogens, has a negative effect on effective population sizes and connectivity among demes of interacting sexual species. This ultimately increases local drift, which in turn increases inter-population differentiation (Figure 2). Moreover, if there is introgression from clones, local sexual populations may diverge from each other even more rapidly because introgression patterns mediated by asexuals substantially differ from those mediated by sexual hybrids (see section 1). Sexual species coexisting with clones may thus become genetically more fragmented than similar species without asexual counterparts.

Moreover, asexual hybrids can themselves play a role as primary postzygotic barrier promoting speciation between diverging taxa. Indeed, postzygotic reproductive incompatibilities are known to accumulate with genetic divergence between emerging species (Seehausen et al. 2014) and although such ‘speciation clocks’ do not tick at an universal rate for all taxa (Edmands 2002; Russell 2003; Bolnick and Near 2005; Matute et al. 2010), the initial stages are generally characterized by decreased fertility or sterility of hybrids, while hybrid viability tends to be compromised only at later stages with substantial genetic divergence. Interestingly, Ernst (1918) noted already a century ago that the likelihood of asexual reproduction in hybrids also correlates with divergence between its parental species, following a continuum from sexually reproducing hybrids between closely related parents to obligate asexual hybrids between distant parental species. Several later publications implied that distortion of hybrid’s gametogenesis towards production of clonal gametes is possible in a particular ‘window of genetic divergence’ before complete hybrid sterility emerges (Wetherington et al. 1987; Moritz et al. 1989; Carman 1997; De Storme and Mason 2014). Some forms of asexual reproduction, both in animals and plants, may even rescue the sterility of interspecific hybrids by allowing them to produce clonal gametes, which further contributes to reproductive isolation of genepools of sexual parents (Carman et al. 2019; Dedukh et al. 2020). Finally, as recent analysis of spined loaches demonstrated, formation of hybrid asexuality is not only correlated with divergence of parental species, but it also has common cytogenetic background with hybrid sterility (Janko et al. 2018; Dedukh et al. 2020).

Thus, a century after seminal works by Bateson (1909) and Ernst (1918), it is becoming clear that the formation of hybrid asexuality has many analogies with Bateson-Dobzhansky-Muller speciation models. Moreover, since asexually reproducing hybrids restrict the gene flow between parental species to much higher extent than fertile sexual hybrids, hybrid asexuality may be viewed as a special type of postzygotic incompatibility, which arises at earlier stages of speciation than other barriers like complete hybrid sterility or inviability (Janko et al. 2018) (Figure 3). Empirical examples do support the view of a link between the ‘classical speciation continuum’ and hybrid asexuality (Lampert et al. 2007; Janko et al. 2018), which has recently been called ‘***extended speciation continuum***’ (Stöck et al. 2021). Among vertebrates, for instance, on one end, there are dynamically hybridizing species pairs that produce diverse assemblages of asexual hybrids such as *Cobitis* (Choleva et al. 2012), *Pelophylax* (Hotz et al. 1985; Hoffmann et al. 2015), and

Poeciliopsis (Schultz 1973). On the other end there are single clonal hybrid taxa stemming from one or a few ancient events whereas attempts to cross their contemporary sexual relatives fail to produce clones, such as *Poecilia* (Lampert and Schartl 2008; Stöck et al. 2010). Cases like the fish *Chrosomus* (the former *Phoxinus*) may represent an intermediate condition, where historical hybridizations produced a highly diverse asexual assemblage, but new clones can no longer be produced by contemporary diverged parental species (Angers and Schlosser 2007). Similarly, some species pairs appear unable to produce sexual hybrids and their hybridization gives rise to asexuals only (e.g., *Cobitis elongatoides-taenia*) while clonal and sexual hybrid females co-occur, and fertile hybrid males may exist in other hybridizing pairs. This is found in fishes such as *Fundulus* (Hernández Chávez and Turgeon 2007), and *Rutilus rutilus* x *Abramis bramma* (Slyn'ko 2000).

Such a view of the link between speciation and asexuality (Janko et al. 2018; Stöck et al. 2021) has important implications for the perception of the role of asexuality in evolutionary biology. Given that asexual lineages are often assumed to have a short evolutionary life span, e.g. (Butlin et al. 1999), and that the phase when diverging species can produce asexual hybrids is transient, it is possible that many extant "good" sexual species might have historically produced asexual hybrids as part of the speciation process, with the transitory forms gone extinct.

Prezygotic barriers: The presence of sperm-dependent parthenogens also affects the premating isolation mechanisms, e.g., by exerting selection pressure on mate-recognition systems in co-occurring sexuals. While such asexuals rely on sperm, from the point of view of a sexual host mating with them represents a costly behavior and hence it has been postulated that the stability of sexual- sperm-dependent parthenogen complexes relies on the ability of sexual males to discriminate hybrid and conspecific females (Schlupp and Plath 2005; Mee and Otto 2010; Morgado-Santos et al. 2015); Figure 2. This process is somewhat similar to reinforcement where the evolution of mate choice is often selected for in zones where ranges of hybridizing species overlap (Marshall et al. 2002) and character displacement is predicted (Gabor and Ryan 2001). However, contrary to classical cases, the distribution of sperm-dependent parthenogenetic hybrids represents something like a hybrid zone extended in time and space because such hybrids often expand over large parts of parental ranges, sometimes well beyond their area of origin (Janko et al. 2019). Hence, contrary to a classical reinforcement scenario which takes place in narrow zones of sympatry, sperm-dependent parthenogens exert selective pressures over vast areas deep in allopatry and may therefore considerably speed-up the establishment of prezygotic isolation.

While only a few studies examined geographical variation in male mate choice against asexuals, some empirical support for such hypothesis exists. For instance, Gabor and Ryan (Gabor and Ryan 2001) and Gabor et al. (Gabor et al. 2005) found that males of the sexual sailfin molly

(*P. latipinna*) living sympatrically with gynogenetic Amazon mollies (*P. formosa*) showed a significantly stronger mating preference for conspecific females than males from populations that were allopatric with Amazon mollies. Another study by Gabor et al. (Gabor et al. 2013), however, showed that male mate choice varied geographically and may be associated with variation among populations in the length of sympatry with the gynogenetic Amazon molly (*P. formosa*). Furthermore, metapopulation dynamics may depend also on a conflict between species and mate quality recognition cues (visual, chemical, and tactile). Asexual – sexual mating systems in mollies represent complex networks where, moreover, not just male mate choice should evolve, but also interspecific female competition (Makowicz and Schlupp 2015).

In addition, given that at least some sexual and asexual species pairs substantially differ ecologically (Vrijenhoek 1994; Pantel et al. 2011; Ross et al. 2012; Van der Kooi et al. 2017), it may also be hypothesized that asexuals could drive character displacement in sexual species also in its ecological characters. In such a case, the presence of asexuals may ultimately generate ecological divergence between allopatric sexual populations and those in sympatry with asexuals, perhaps even providing a first step in ecological speciation.

2.2. Direct impact on speciation: Species formation by asexuals

Finally, there is a more direct way how asexuals may contribute to biodiversity; they may form new species themselves. The question whether speciation can occur without sex is longstanding (Coyne and Orr 2004; Shcherbakov 2010; Dubois 2011; Hausdorf 2011) but recent theoretical studies show that species-level taxa may be formed also in asexuals (e.g. (Cohan 2001, 2002; Franklin 2007; Birky and Barraclough 2009)). This has been empirically indicated in some ancient asexual organisms like bdeloid rotifers, oribatid mites, ostracodes, as well as in plants like *Boechera*, where genetically, morphologically, and ecologically distinct species-like clusters occur within asexual clades (Domes et al. 2007; Fontaneto et al. 2007; Schön et al. 2012; Carman et al. 2019). Interestingly, the rates of cladogenesis in asexual taxa can achieve similar or even higher values than in comparable sexual lineages (Fontaneto et al. 2012). The potential of diversification in asexuals is thus becoming increasingly appreciated.

What may be even more interesting for general biology is that at least in some groups, the asexuals could play a role as stepping-stones in the evolution of new sexual species. The idea that asexuals may somehow revert to sex and thereby give rise to new sexual species attracted considerable attention particularly in the botanical literature and has been used as a possible explanation for the origin of hybrid and polyploid species (Figure 1D). Namely, because the emergence of a novel hybrid/polyploid form is supposedly a rare phenomenon and its establishment is thus threatened by a frequency-dependent disadvantage (i.e., the minority cytotype exclusion principle, e.g. (Husband 2000)), the establishment of novel strains could be facilitated by asexual reproduction, which offers immediate reproductive isolation and clonal multiplication of genotypes (Rieseberg and Willis 2007; Choleva and Janko 2013; Hojsgaard and Hörandl 2015). Asexuality can thus represent the first stages towards hybrid speciation. For example, clonally reproducing triploids were suggested to serve as ‘triploid bridge’ towards tetraploid species with re-assumed sexual reproduction (Cunha et al. 2008; Choleva and Janko 2013; Hojsgaard and Hörandl 2015; Dubey et al. 2019). This mechanism is particularly appealing in sperm-dependent asexuals since they rely on sperm source and hence seem particularly prone to fertilization with ploidy increase. However, recent data offer controversial support for this hypothesis since most known tetraploids derived from extant triploids are rather sterile or have a fitness disadvantage (reviewed in (Choleva and Janko 2013)). Still, there exists empirical evidence that established obligatory asexuals may revert to sex, as found for example in fish, *Squalius* (Cunha et al. 2008), Oribatid mites (Domes et al. 2007) and some plant taxa, like *Hieracium pilosella* (Fehrer et al. 2005).

The apparent paucity of asexual to sexual transitions may result from the fact that established asexuals may be selected for the loss of sexual traits, which are disadvantageous or unnecessary for clonal reproduction (Kooi and Schwander 2014), thereby preventing the re-evolution of sex. However, this should not be the case in sperm-dependent parthenogens, which have to maintain the full genetic machinery allowing them to mate with sexuals (Schlupp et al. 1998; Warren et al. 2018). Scarcity of asexual to sexual transitions may thus be only apparent, because the identification of sexually reproducing species which passed through a phase of clonality is extremely difficult, and probably easily overlooked.

There is indeed sound evidence for the ability of some sperm-dependent parthenogens to form populations independent of sexual sperm-donors, which might be a first step towards either true parthenogenesis or sexuality. Such cases have been recently documented in gynogenetic lineages of a nematode (Grosmaire et al. 2019) and sexual speciation in *statu nascenti* occurs in hybridogenetic water frogs, where a transition occurred from hemiclonal to sexual hybrids, which are reproductively independent from the parental species and form pure-hybrid populations with a high proportion of triploids. Triploid hybrids form gametes with the genome of each of the parental species and thus substitute parental individuals in pure-hybrid populations (Berger 1983; Christiansen et al. 2005; Christiansen and Reyer 2009) (Figure 1F).

What makes such a case extremely interesting is the discovery by Stöck et al. (2002) who described an all-triploid bisexual frog species, *Bufotes baturae*. This species combines two genomes (two copies of the so-called NOR$^+$ genome and one copy of NOR$^-$ genome), whose transmission to gametes sharply differs between males and females. While males eliminate the NOR$^-$ genome and recombine and segregate NOR$^+$ genomes in order to produce haploid sperm, females produce diploid gametes containing clonally transmitted NOR$^-$ genomes and recombined NOR$^+$ genomes. Fusion of such gametes restores triploidy in every generation. Given the similarity to the *P. esculentus* system, there is an intriguing possibility that bisexual *B. baturae* evolved through an asexual stage and that other systems, like *P. esculentus* may be on a similar evolutionary pathway just at a different stage.

These cases indicate that a transition from asexual to sexual is at least a plausible scenario for how asexuals can directly contribute to formation of the regular sexual species.

3. Impact on spatial distribution of sexual species

On a large spatial scale, asexuals are known to occupy more disturbed or weedy habitats, displacing sexual species from these areas. This ***geographical parthenogenesis*** (Glossary) seems to be widespread and is probably the most prominent pattern of asexuality (Peck et al. 1998; Kearney 2005; Hörandl 2009; Tilquin and Kokko 2016). Due to tight link between asexuality (apomixis) and polyploidy and hybridization, there is an ongoing debate as to what extent the patterns of geographical parthenogenesis relate to asexuality *per se* and to what extent they reflect these confounding effects (Kearney 2005; Lundmark 2006), such as for example the niche shifts related to ploidy (Coughlan et al. 2017; Kirchheimer et al. 2018) or higher competitiveness of polyploids in peripheral areas (Karunarathne et al. 2018). Whatever the underlying reason, the patterns of geographical parthenogenesis imply that parthenogens outcompete related sexual species in marginal, resource-poor environments because sexual populations cannot efficiently adapt to local adverse conditions due to dispersal and admixis with individuals from denser-populated more favorable regions.

This means, however, that even after the demise of the asexual (e.g., due to the accumulation of deleterious mutations, or other processes), the sexual species will be less successful in colonizing any open ecological niche because they did not have an opportunity to adapt to the conditions. Instead, they are adapted only to the more favorable habitats to which they were restricted. Hence, the effect of asexuality would persist beyond the extinction of an asexual species. This can turn into a cyclical process, if another asexual clone colonizes a niche before the sexual species can adapt to it.

As we have discussed in section 1, the presence of sperm-dependent parthenogens also has considerable demographic consequences for its sexual host whose population sizes and density are reduced by direct competition for males and other resources. For instance, Janko & Eisner (2009) used a mathematical model to demonstrate that a sexual population "infected" with sperm-dependent parthenogens should have a limited potential of spatial expansion and colonization of new habitats compared to a situation where no sperm-dependent parthenogens affect it (Figure 4). Such a reduction in population expansion speed stems from reduced density along the expanding wave and therefore a decreased chance to find a mating partner needed to establish viable populations in invaded areas. Hence, sperm-dependent parthenogens may decisively affect large-scale biogeographic patterns of their sexual hosts that, even after an eventual extinction of asexuals, would not be able to expand into new habitats that might have been occupied by another species in the meantime.

The biogeography of European loaches of the genus *Cobitis* potentially offers an empirical example of such a process. While in many European freshwater fishes the postglacial recolonization of Central and Western Europe proceeded from Danubian/Pannonian refugia, *Cobitis* fishes show a contrasting pattern since the Danubian species *C. elongatoides* experienced only a limited postglacial expansion reaching only the upper Odra and Elbe river watersheds, while most of Europe was colonized by *C. taenia* rapidly expanding from Eastern refugia (Janko et al. 2005). Interestingly, *C. elongatoides* populations survived the last glacial maximum in Danubian refugia together with sperm-dependent parthenogenetic hybrids and co-expanded with them into northern areas, which might have delayed its colonization rate as compared to *C. taenia*, whose expansion was not burdened by sexual parasites (Janko and Eisner 2009).

In addition, sperm-dependent parthenogens may decisively affect the results of interspecific coexistence and competition among interacting sexual species. To appreciate this phenomenon, let us emphasize that many sperm-dependent asexuals originated by hybridization between several sexual species (Neaves and Baumann 2011; Choleva et al. 2012) and they can therefore simultaneously use (or parasitize) two or more sexual species for their own reproduction e.g. (Schlupp 2005; Choleva et al. 2008). In such cases, mathematical models of dispersal with competition showed that the sexual host species with better mate recognition ability or smaller niche overlap with coexisting parthenogens will be less negatively affected by their presence, giving it a potentially decisive advantage in competition with other sexual species, whose demographic performance is harmed to a greater extent (Janko et al. 2019). Gynogens can therefore mediate the so-called ***apparent competition*** (Glossary) among sexual species and cause an effect analogous to ***parasite-mediated competition*** (Glossary) (Thomas et al. 2000; Holt and Bonsall 2017). In their presence, even a stronger sexual competitor may be outcompeted by a weaker one if the latter is less negatively impacted by coexisting sperm-dependent parthenogens (Figure 5). It follows that the effect on the diversity of sexual species would remain even if the asexuals eventually go extinct.

On the other hand, as discussed above, some asexuals may also have a positive effect on the distribution of their sexual hosts as they can transmit their genes far away from their own distribution. The examples are hybridogenetic frogs *P. esculentus* which serve as a "vector" transmitting clonal genomes of a parental species, *P. ridibundus*, to western Europe, far beyond its original range (Arano et al. 1994; Pagano et al. 2001), gynogenetic *Cobitis* hybrids that transmit genes of its Danubian parent, *C. elongatoides,* hundreds of kilometers outside its range to the Rhine River region and to the southern Ukraine (Choleva et al. 2008), or *Corbicula* clams, whose asexual hermaphroditic reproduction increases invasive success (Pigneur et al. 2011, 2012). Similarly in plants, such as in the genus *Rubus*, polyploid apomicts may preserve ancestral alleles lost in their sexual ancestors during Pleistocene ice-age bottlenecks and spread younger alleles obtained from diploids via recent gene flow (Sochor et al. 2017).

Conclusions

Gregor Mendel was unable to replicate his findings on peas in the *Hieracium* model due to its asexual reproduction. Of course, he had no way of knowing, but nonetheless, this story illustrates how perilous it can be to ignore asexuals. Asexuals are worthy objects for studies by themselves, but their ecological and evolutionary influences on other species and biodiversity in general are perhaps even more important and should be more appreciated. Here, we listed several mechanisms how the very existence of asexuals, in particular sperm-dependent parthenogens, can have major effects on coexisting sexual species and biodiversity overall in terms of their 1) genetic architecture, 2) diversification and speciation, and 3) spatial distribution.

1) The genetic architecture of sexual species might be influenced in systems when a clonal genome finds its way into a sexual genepool. Such asexual-to-sexual gene flow differs from gene exchange between sexual species because asexuals transmit their genetic material without recombination. The recipient sexual genepool might be impacted negatively by introducing deleterious mutations but also positively by advantageous combinations of alleles that coevolved in linkage. Asexuals of hybrid origin can further serve as a bridge for introgression of alleles or

whole mitochondrial genomes between sexual species. Even without asexual-to-sexual gene flow, extensive mating between sperm-dependent parthenogens and their sexual hosts can reduce effective population size, increase the strength of genetic drift and thus decrease genetic variability and efficiency of natural selection in sexual populations.

2) Sperm-dependent parthenogens can contribute to differentiation of populations of sexual species by reducing their effective population size and increasing the strength of genetic drift but can also promote the accomplishment of speciation between hybridizing taxa. Since asexually reproducing hybrids restrict the gene flow between parental species to much higher extent than sexual hybrids, hybrid asexuality may be viewed as a special type of postzygotic incompatibility. It could be also predicted that sperm-dependent parthenogens reinforce the formation of prezygotic barriers by exerting selection pressure on mate-recognition systems in hybridizing sexual species, a process analogous to reinforcement in classical hybrid zones. Finally, asexuals can play an important role in speciation when, through an intermediate stage of polyploid forms, they can evolve into a new sexual species.

3) Asexuals may affect large-scale biogeographic patterns of related sexual species. They frequently outcompete their sexual counterparts in disturbed habitats, at higher latitudes and altitudes, or at the edge of distribution ranges (geographical parthenogenesis). Theoretical models also reveal that sperm-dependent asexuals reduce abundance and density of sexual populations and thus may reduce expansion speed of sexual host species. In complexes composed of two sexual species and their sperm-dependent hybrids, sperm-dependent asexuals may significantly affect competition between sexual species by a process analogous to parasite-mediated competition (or apparent competition) well known in classical host-parasite systems. Sperm-dependent parthenogens thus might be important players forming the structure of ecosystems.

Recent advances show that most proposed mechanisms do have support from empirical cases of asexual – sexual coexistence in nature. It indicates that even if the existence of individual clonal species may be ephemeral from an evolutionary point of view, their impact on sexual species likely lasts much longer than the existence of individual clonal lineages. These are all important population or species level effects that should be included into our research programs. We hope our review is going to stimulate further research into the questions we raise. In our review we elected to focus mainly on animals with some mentioning of plants. A combined review of the plant and animal literature is desirable but made exceedingly difficult by important differences in reproductive biology, as well as differences in terminology. We also listed several empirical examples supporting their relevance. Many such examples concerned our own work, but this was not out of vanity, but rather because the discussed aspects of asexual – sexual interactions have otherwise received little attention to date. Our review provides testable hypotheses with clear predictions that may be explored by other scientists in other systems, searching for potentially overlooked empirical examples.

We also hope that expanded research will create positive feedback for ecology and evolution in general as new tools are developed. As an example, consider testing the hypothesis that some current sexual organisms have passed through an asexual stage in their evolutionary history either because of an asexual bridge, or because they had an asexual phase during speciation. This would require the development of novel analytical tools incorporating not only population genetic approaches but also explicit models of asexual hereditary patterns. Such tools may eventually not just help finding influences of asexuals but will also improve tools for all of biology.

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Glossary

Allee effect: a phenomenon describing a positive correlation between population size or density and the mean individual fitness of a population. A higher mean population fitness in more abundant or dense populations may be associated with better mate finding, better cooperation among individuals, greater ability to change the environment in favor of the species or with a lower rate of inbreeding and higher genetic variability.

Apparent competition: a form of mostly negative indirect interactions between species that arise because they share a natural enemy (predators, parasites, pathogens or herbivores). When such an indirect competition is driven by a shared parasite, it is called **parasite-mediated competition**.

Asexual reproduction: reproductive mode in which an organism passes on its genome (or parts of it) clonally as a result of vegetative reproduction, polyembryony or by circumventing recombination during gametogenesis. The latter is gametic asexuality.

Clonal: this makes reference to a mode of inheritance where all or most of the genome is passed on unaltered.

Cybrids: hybrids containing a nucleus of one species and cytoplasm of another species.

Effective population size (N_e): reflects the rate at which genetic diversity will be lost following genetic drift, and this rate is inversely proportional to a population's N_e. N_e is reduced by unequal sex ratio, variation in reproductive success, and by the fluctuation of the population size in time.

Extended speciation continuum: a conceptual frame work linking the formation of asexual reproduction in hybrids with the classical speciation continuum assuming gradual formation of postzygotic reproductive barriers among diverging taxa. It posits that before accumulating genetic incompatibitlies between hybridizing species cause complete sterility or even inviability, they may occasionally distort hybrid's gametogenesis towards production of unreduced gametes, thereby sometimes alleviating problems in chromosomal pairing and rescuing hybrid's fertility, simultaneously triggering its (hemi-) clonal reproduction.

Geographical parthenogenesis: a phenomenon describing that asexual organism occupy larger ranges, occur at higher elevations or at higher latitudes, and colonize more frequently previously glaciated or otherwise disturbed areas than their sexual relatives.

Gynogenesis: females produce typically diploid eggs, which are pseudo-fertilized by sperm of males from a different species. The sperm genome is typically not incorporated, and inheritance is maternal.

Hybridogenesis: females produce haploid or diploid eggs, which are usually fertilized by males from a different species. The sperm genome is incorporated and expressed but excluded from the germ line during gametogenesis. The female genome is thus inherited clonally.

Mixis: well defined haploid and diploid phases that alternate.

Muller's ratchet: a process of the irreversible accumulation of deleterious mutations in a clonal genome because of the absence of recombination.

Red Queen Hypothesis: making reference to the red queen character in Lewis Carrolls' 1871 novel "Through the Looking Glass", the hypothesis posits that constant genetic change is needed to stay evolutionary alive under the continuous pressure from parasites.

Sexual reproduction: prevailing mode of reproduction in metazoans, characterized by production of offspring via syngamy of meiotically produced gametes. Recombination and segregation of chromosomes (alleles) during meiosis result in genetically variable offspring.

Sperm-dependent parthenogenesis: a form of clonal inheritance where eggs need to interact with sperm, either in gynogenesis or hybridogenesis. This is also called pseudogamy or sexual parasitism.

Figure 1

Modes of asexual reproduction, A, B, E) mechanisms of nuclear (C, F) and mitochondrial (G, H, I) introgression and polyploid speciation (D). Since asexual reproduction might be linked with interspecific hybridization, asexual forms in this scheme are hybrids (red and blue genomes originate from the parental species). **(A)** A parthenogenetic hybrid female (e.g. in lizards of the genus *Darevskia*) forms unreduced eggs from which a new generation of clonal daughters originate without any contribution of males. **(B)** Gynogenesis (e.g. in the genus *Cobitis*) is a similar mode of reproduction during which unreduced eggs must be activated by sperm of a sexual male. The sperm, however, don't fertilize the eggs and a new generation of daughters is clonal. **(C)** In gynogenetic systems (e.g., in the fish *Poecilia formosa*), microchromosomes (B chromosomes) might be incorporated to the clonal egg from the paternal sperm. **(D)** Incorporation of sperm to clonal triploid eggs (observed in the *Squalius alburnoides* complex) can lead to sexual tetraploid progeny, which is reproductively isolated from other ploidy forms. **(E)** A hybridogenetic hybrid female (e.g. in the *Pelophylax esculentus* complex) eliminates a genome of one parental species during gametogenesis and forms clonal eggs which are fertilized by sperm of a sexual male. **(F)** In triploid forms (e.g. in hybridogenetic *P. esculentus*) two different genomes belonging to one parental species (red ones in the scheme) can enter meiosis and recombine after premeiotic elimination of the genome of another parental species (blue genome). This process is called meiotic hybridogenesis. Here mating between a diploid hybrid female producing both diploid and haploid eggs and a triploid male is shown. This mating leads to diploid and triploid progeny of both sexes (in the scheme a male is triploid and a female is diploid just for simplicity) and enables the perpetuation of a population without the contribution of the parental species. **(G)** Mating between hybridogenetic hybrids *P. esculentus* and parental species leading to the origin of the parental species progeny with introgressed mtDNA. **(H)** In androgenetic *Corbicula* clams, the egg is fertilized by an unreduced biflagellate sperm. The entire maternal nuclear genome is then extruded from the oocyte, whereas mitochondria and other organelles from the egg are retained. Thus, the offspring inherit paternal nuclear genome and maternal mtDNA. **(I)** In the *Bacillus* stick insect, the whole hybrid genome is lost, two male pronuclei may fuse (since phasmid eggs are physiologically polyspermic) and produce a sexually reproducing progeny of one parental species with introgressed mitogenome.

Please note that we deliberately avoided reproductive schemes for plants in Fig. 1 since in apomictic plants (e.g. in *Hieracium*), asexual reproduction is a more complex process due to a switch from double fertilization (need for endosperm formation) in sexual species to diplospory, apospory or haploid parthenogenesis in asexuals.

Figure 2

The effect of coexisting sperm-dependent parthenogen on a sexual hosts effective population size and related phenomena: Compared to a purely sexual population (A), when a sexual population of the same census size coexists with sperm-dependent parthenogens (B), it suffers from increased variance in reproductive success since relatively fewer males have access to conspecific sexual females and 'waste' their reproductive effort on asexual females. This negatively affects the long-term effective size of sexual population. Such intensification of genetic drift also leads to faster population differentiation.

Effect on operational sex ratio (OSR) and mate-choice: Because males are in a minority when coexisting with a sperm-dependent all-female population, it changes the OSR. Simultaneously, given that mating with sperm-dependent females effectively 'wastes' males' reproductive effort, an intensified selection for mating preferences with conspecific is expected.

Figure 3

The classical scenario of postzygotic reproductive isolation assumes that as nascent species diverge (stage 1 in the scheme), their genomes (denoted as bicolored chromosomes) become progressively less compatible and interspecies barriers become more pronounced (as denoted by dotted to solid lines) until a stage is reached when species cannot produce fertile or viable hybrids and speciation is complete (stage 3 in the scheme). However, the ability to produce asexually reproducing hybrids probably also scales with genetic divergence between hybridizing taxa (Moritz et al. 1989). Empirical data (Janko et al. 2018) suggest that such a phase (stage 2 in our scheme) may occur generally at earlier stages of species differentiation before complete hybrid sterility occurs (stage 3). If so, asexual hybrids, although as fertile as "classical" sexual hybrids produced at early stages (stage 1 in the scheme), may turn into an effective barrier to interspecific gene flow due to their general inability to backcross into either parental species.

Figure 4

When sperm-dependent parthenogens coexist with a sexual population (B), they tend to decrease its effective population size and therefore hamper the population growth rate. Expansions of sexuals to a new environment thus occur at lower frequency as compared to purely sexual populations (A) and therefore they have a lower probability to find a proper mate to start a new generation of colonists. This ultimately decreases the growth rate and expansion rate of entire populations (Janko and Eisner 2009).

Figure 5

Compared to purely sexual competing species (A), when a stronger competitor (blue) outcompetes the weaker one (red), sperm dependent parthenogens may turn the result of interspecific competition (B). This occurs when the stronger sexual competitor invests more into mating with sperm dependent parthenognes (or is otherwise more vulnerable to their presence) than the weaker competitor, whose population growth is therefore faster and may ultimately outcompete the stronger one (Janko et al. 2019).

Supplementary Material

Figure S1

Phylogenetic relationships among metazoans showing lineages (phyla) where parthenogenesis secondarily evolved (red asterisk). A clade named Nematoda involves also the phylum Nematomorpha in which parthenogenetic species were also discovered. The tree was taken from the study of Laumer et al. (2019; Figure 2a). Information about parthenogenetic reproduction of particular taxa comes from works of Hummon (1984), Roe (1986), Read (1988), Lively and Johnson (1994), Bertolani (2001), Schön et al. (2009), Hanelt et al. (2012) and Schwarz (2017).

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Figure 1

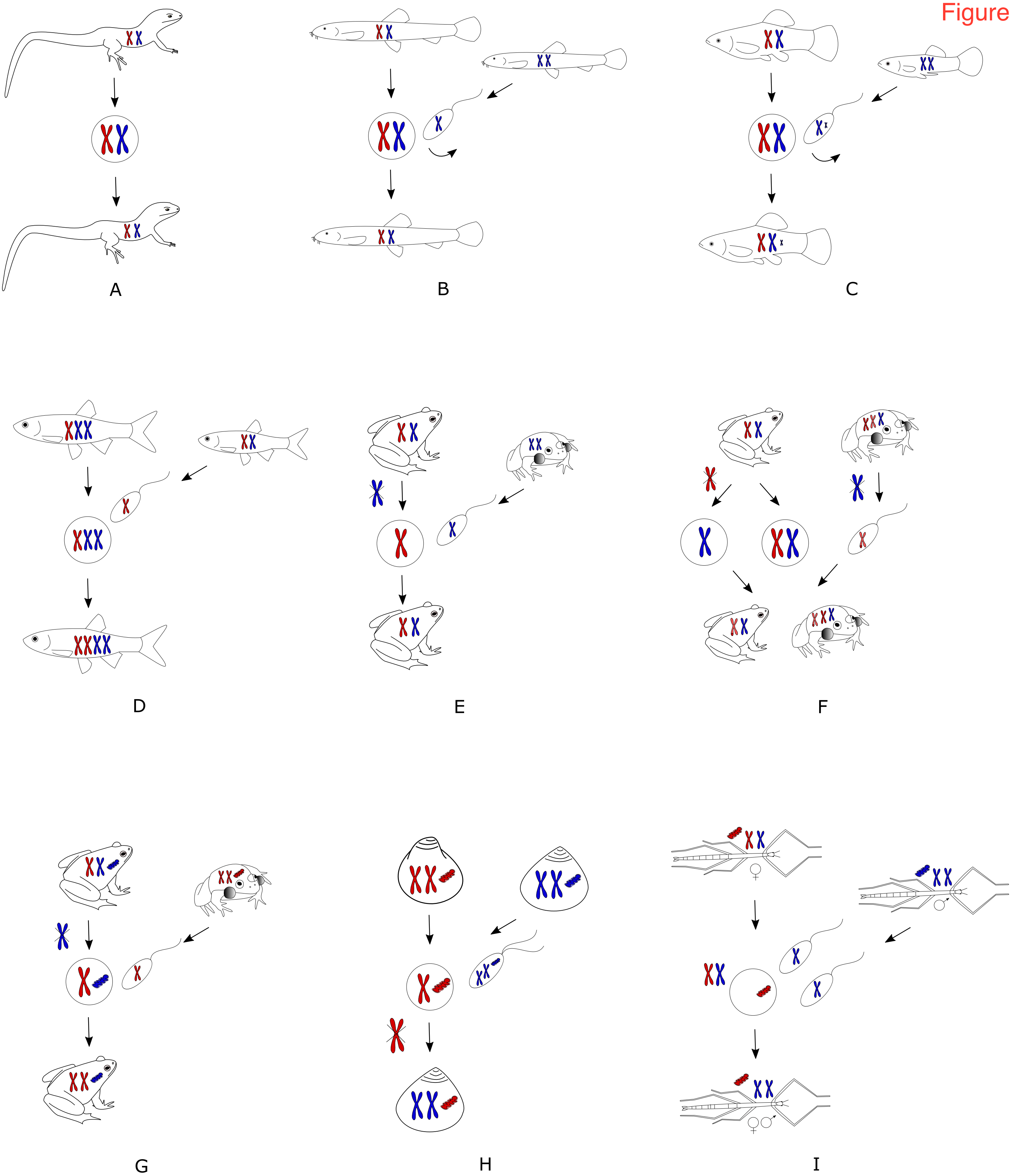


Figure 2

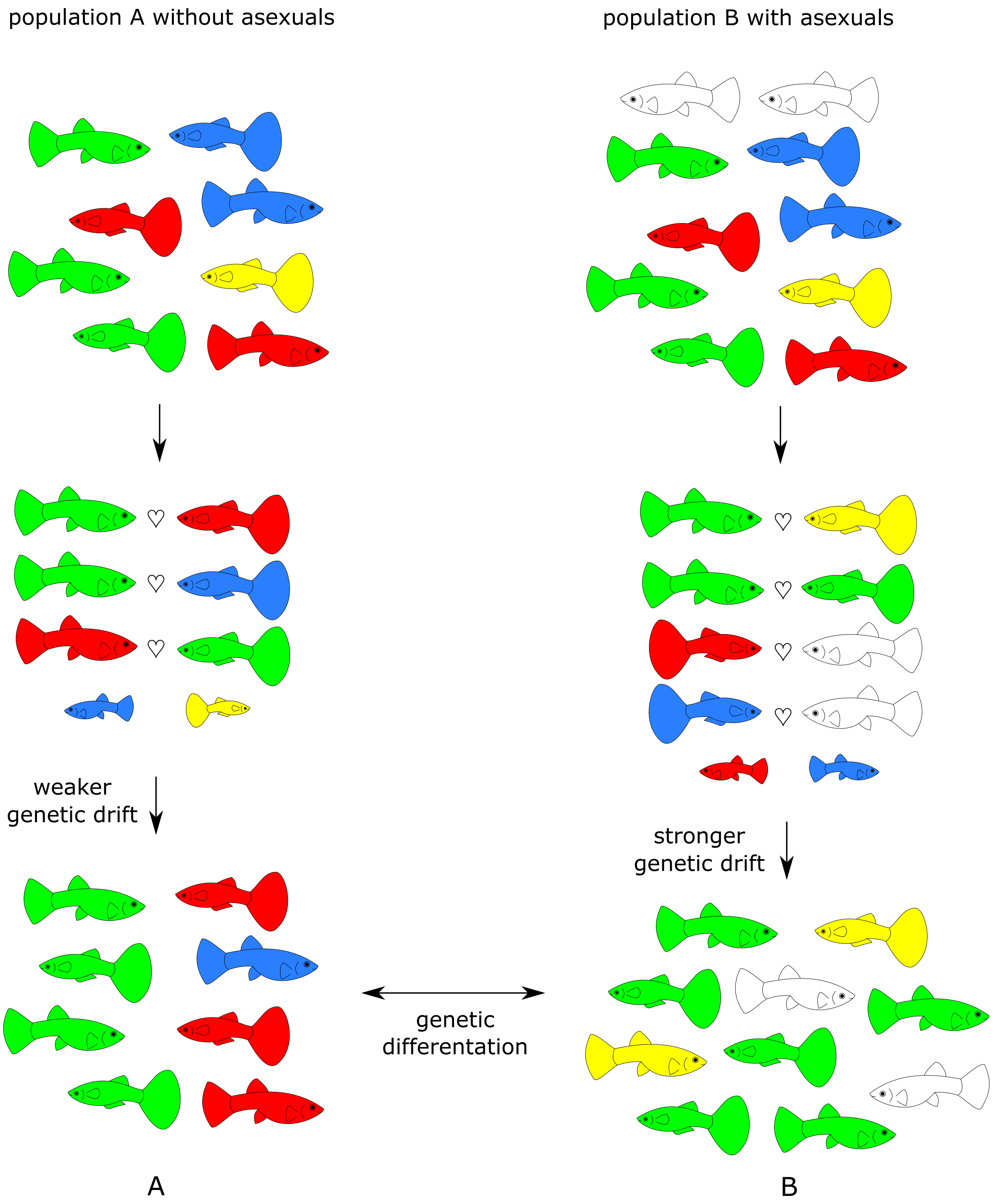

population A without asexuals
population B with asexuals
♡
weaker genetic drift
stronger genetic drift
genetic differentation
A
B

Figure 3

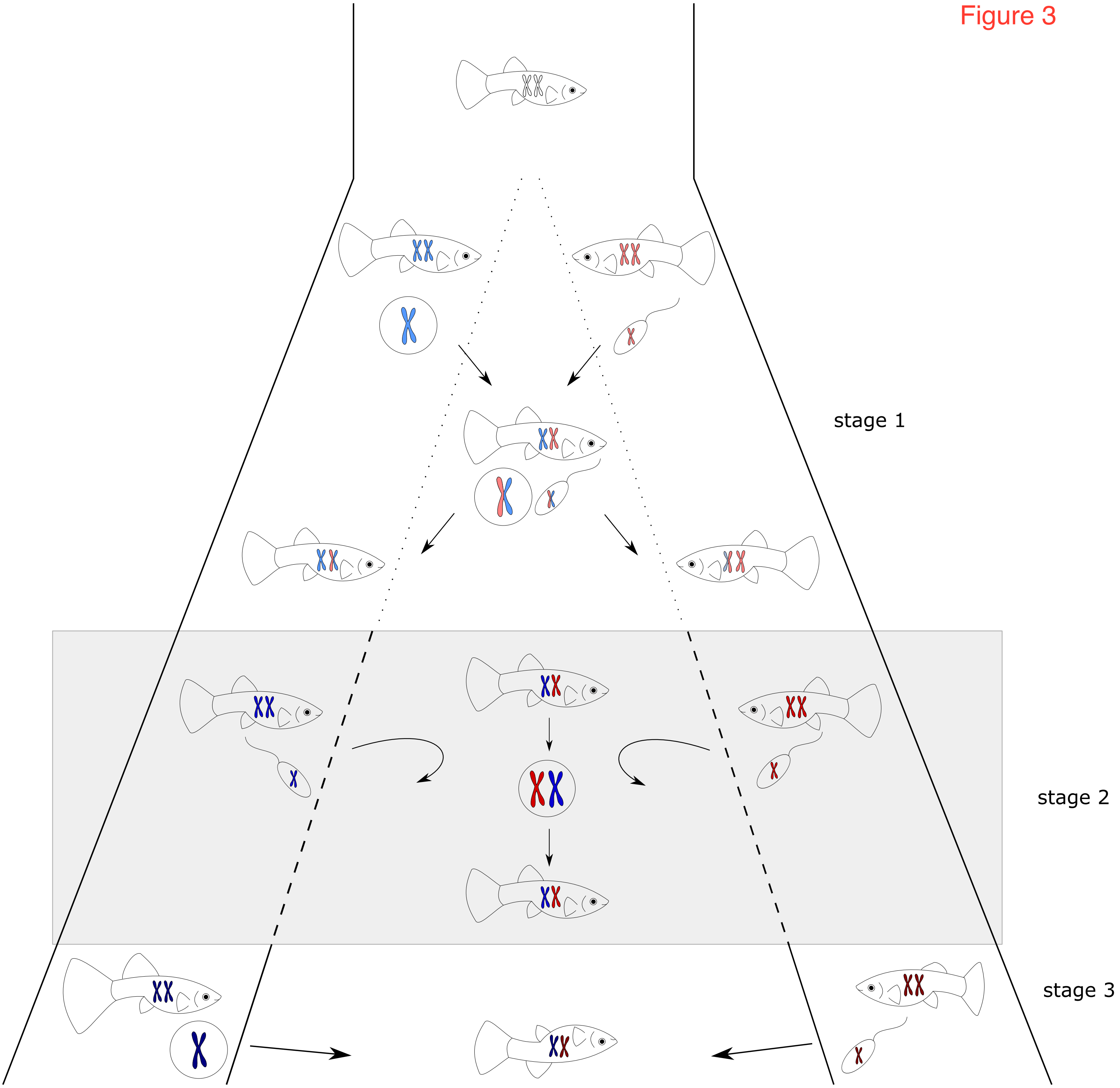


Figure 4

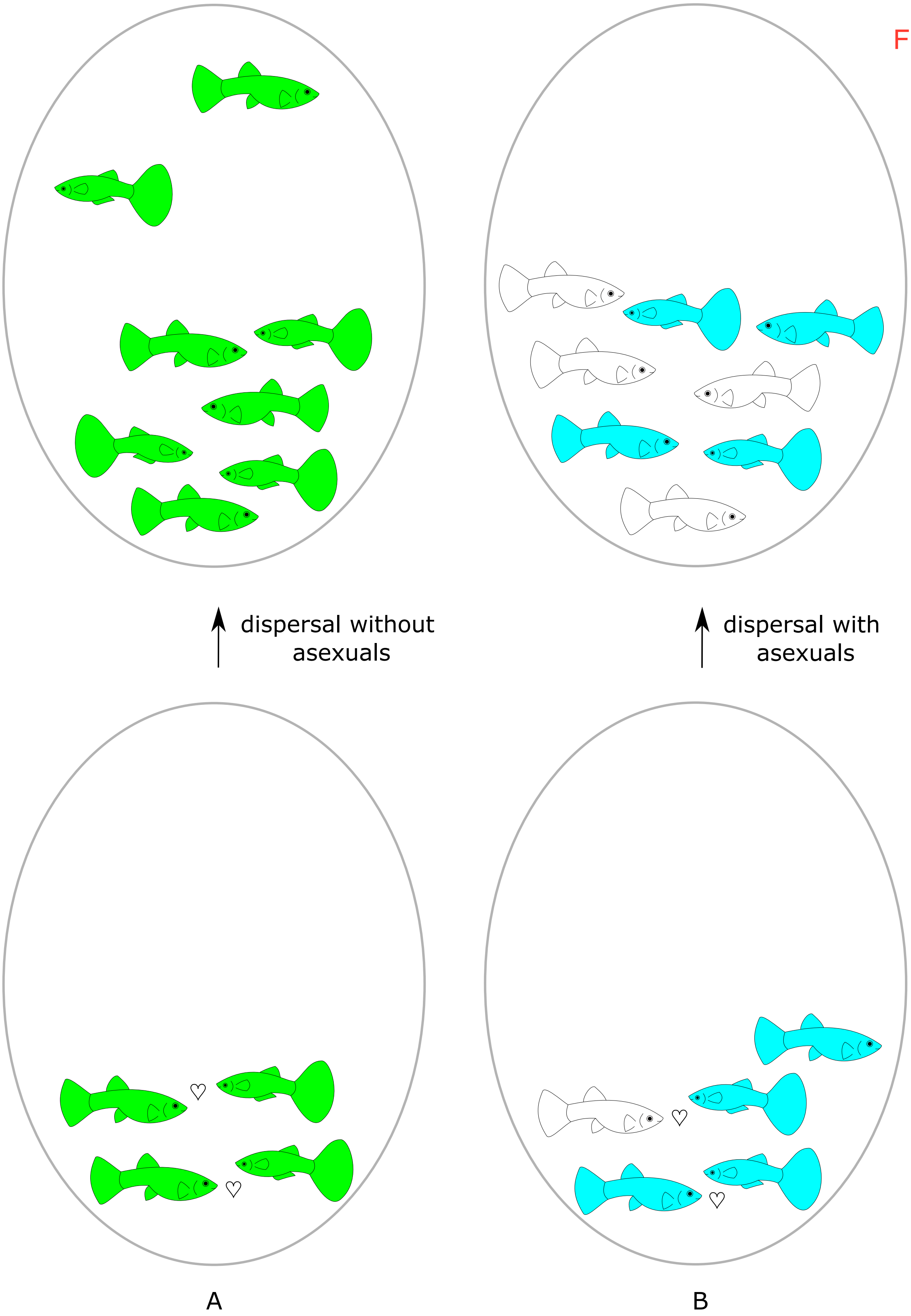
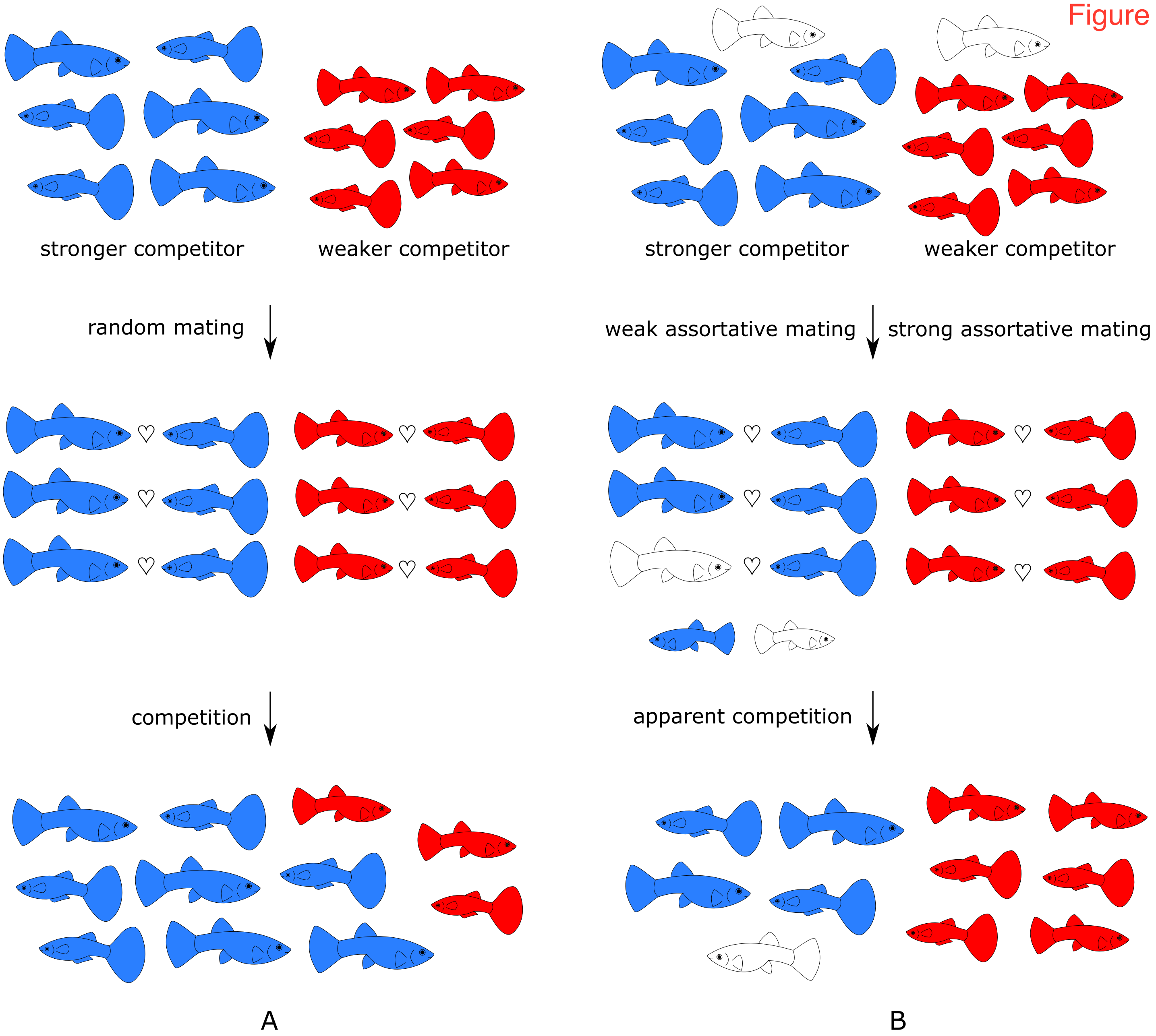


Figure 5


stronger competitor
weaker competitor
random mating
competition
A
stronger competitor
weaker competitor
weak assortative mating
strong assortative mating
apparent competition
B

Supplementary Figure 1