Sex in the wild: why field-based studies play a critical role in resolving the problem of sex

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SM and MN conceived the paper idea, SM, PM, MN, and TS designed the review strategy, reviewed and analysed the literature, and wrote the manuscript. All authors gave final approval for publication.

Abstract

Why and how sexual reproduction is maintained in natural populations, the so-called "queen of problems", is a key unanswered question in evolutionary biology. Recent efforts to solve the problem of sex have tended to emphasize results generated from laboratory settings and traditional model systems. Here, we use a literature survey of representative "sex in the wild" literature to argue that even though these laboratory-based studies have provided important insights, understanding the maintenance of sex ultimately requires an empirical focus in natural populations. Our survey revealed several substantial ways in which field-based research into the maintenance of sex has departed from the emphasis and outcomes of laboratory studies, including relatively strong support for mechanisms involving niche differentiation and an almost complete absence of attention towards adaptive evolution. We conclude by suggesting steps forward, emphasizing tests of niche differentiation mechanisms and adaptive evolution-focused hypotheses in the wild and leveraging the growing body of genomic resources for non-model taxa to address whether molecular evolution in natural populations proceeds as expected under various hypotheses for sex.

Introduction

Ask evolutionary biologists about unresolved problems in evolution, and many will question why so many species reproduce via sexual reproduction ("sex"). The predominance of sex was first identified as a major unanswered question by leading twentieth century evolutionary biologists such as George Williams and John Maynard Smith, who developed theory demonstrating that sexual reproduction should be at a substantial disadvantage vis-à-vis asexual reproduction and thus be rapidly replaced by the latter (Maynard Smith 1971, 1978, Williams 1975). This theory is based on the recognition that sex should impose a variety of costs (e.g., males, recombination, for a recent overview see Lehtonen et al. 2012, Meirmans et al. 2012) that should translate into major advantages for asexual reproduction. The central place of the problem of sexual reproduction in evolutionary theory is illustrated by Graham Bell's 1982 statement that the maintenance of sex is the "queen of problems" in evolutionary biology (Bell 1982). Within a decade or so after the paradox of sex was first identified, dozens of hypotheses for sex had been proposed (Kondrashov 1993). Most of these hypotheses focused on direct or indirect benefits of sexual reproduction that can outweigh (at least in principle) the costs of sex (reviewed in Neiman and Schwander 2011) and that are linked to genetic consequences of meiotic recombination and segregation (e.g., Agrawal 2009a,b). Despite all of this attention and the forty or so years that have passed since the problem of sex was identified, the evolutionary mechanisms underlying the maintenance of sex remain hotly debated (e.g., Sharp and Otto 2016, Neiman et al. 2017).

The crux of the problem of the maintenance of sex is the persistence of sexual reproduction in so many species, and especially the maintenance of sex in natural populations of organisms for which asexual reproduction is an option. This means that natural populations are ultimately the empirical setting in which to seek solutions to sex. While the critical importance of field-based research to the resolution of the problem of sex might seem obvious, most recent attention towards empirical tests of the maintenance of sex has focused on results generated by experimental evolution in laboratory settings. Laboratory studies are very powerful because the processes underlying the focal mechanisms can be manipulated and isolated. Indeed, these lab-focused studies, which nearly always use genetic model systems (e.g., *Drosophila melanogaster* (Singh et al. 2015), *Saccharomyces cerevisiae* (McDonald et al. 2016), *Tribolium castaneum* (Lumley et al. 2015), *Brachionus calyciflorus* (Becks and Agrawal 2012)), have provided important tests of the potential for particular mechanisms for sex to be applicable under specific circumstances (e.g., sexual selection-facilitated clearance of mutational load, strong selection for adaptation to new environments; reviewed in Sharp and Otto 2016).

Though we agree that laboratory studies are valuable, it should be obvious that these studies are ultimately limited by the distinct possibility that their results are confounded by influences emerging from the lab setting itself. In other words, it can be difficult to impossible to determine whether the outcomes of lab-based studies can be extrapolated to natural conditions, exemplified by a recent example of a case where field and lab studies addressing the same mechanisms for sex generated opposite results (Lavanchy et al. 2016). The solution to the challenge posed by the limitations of laboratory-focused research is conceptually simple but often empirically challenging: (1) determine whether the patterns or processes that emerged from laboratory insights apply similarly in natural populations, and (2) use field studies to parameterize or focus laboratory experiments.

There are some specific issues that are likely to be particularly difficult to address in a laboratory setting. For example, most laboratory studies use model organisms (typically small organisms with short generation times), which do not represent the diversity of eukaryotes.

Model organisms –often the products of decades of laboratory culture– are also almost certainly adapted to laboratory conditions (e.g., Sterken et al. 2015). Another limitation of laboratory studies is that factors that are typically present in nature and likely relevant to the realized costs and benefits of sexual reproduction are often difficult to replicate in the lab. Examples of such factors include naturally occurring and locally adapted parasites and predators, extreme abiotic conditions, and unpredictable environmental changes. Even efforts to include these factors in laboratory experiments could in principle translate into conditions that are unlikely to characterize natural populations, e.g., unrealistically high doses of infectious parasites or the imposition of direct competition between sexual and asexual individuals that experience niche differentiation in the wild.

Here, we argue that these limitations of lab-based studies mean that field-focused research must play a critical role in the resolution of the problem of sex. It is our hope that a useful and synthetic overview of these “sex in the wild” studies will both provide some of the credit that this body of work deserves and motivate researchers to continue and expand this type of empirical research. Our overview –the first of which we are aware since Bell (1982)– addresses this goal by performing a survey of relevant empirical literature on "sex in the wild" to (1) assess the contributions of field studies towards resolving the sex problem, (2) identify what we have learned from these studies and what we still need to know, and (3) provide some concrete steps forward.

Methods

Literature survey approach

We began our survey by establishing a set of *a priori* criteria for study inclusion. These criteria were formulated with the goal of only including studies that could directly inform the maintenance of sex in natural populations. First of all, this meant that the study had to be performed in the field or use field-collected individuals that were not subsequently subject to the potential for selection in a laboratory environment. We included studies with laboratory-reared individuals only in those cases where lab rearing was not likely to influence the factors that are the focus of testing (e.g., establishment of phylogenetic relationships). We therefore excluded studies where the potential for laboratory-imposed selection could confound the ability to interpret the study outcome, e.g. via laboratory-cultured lineages (e.g., Xu et al. 2011).

Second, we decided to confine our survey to studies explicitly focused on testing or investigating a particular mechanism for the maintenance of sex. We chose to adopt this mechanism-centered approach because this type of research takes place in a structured framework that facilitates meaningful comparisons among studies. Our strategy does have some limitations in excluding other valuable types of studies, including but not limited to evaluation of population genetic principles in natural populations (e.g., Menken et al. 1995, Lo et al. 2009), establishing the biogeographic distribution of sexual vs. asexual reproduction (e.g., geographic parthenogenesis; see Tilquin and Kokko 2016 for a recent overview), or describing unusual natural manifestations of reproductive strategies (e.g., Aanen et al. 2016).

Finally, we chose to only include those studies that featured obligately asexual individuals and facultatively or obligately sexual individuals that are sympatric in nature in at least part of their range. We made this choice because in these species, the maintenance of sex is an active problem. We excluded all studies of sperm-dependent asexual taxa (e.g., *Ambystoma* mole salamanders, *Ips* bark beetles, *Rubus* subgenus *Rubus* blackberries) because all-asexual populations of sperm-dependent organisms are not evolutionarily stable.

We then classified and described each study according to the question/hypothesis that the study addressed (as outlined below), the methods used to address study goals, the study outcomes, whether the study supported or did not support the focal question/hypothesis, and the taxonomic group that the study represented (see supplementary material; Table S1). We included an "Other" category to account for studies that addressed mechanisms or conditions with the potential to favor sex that did not easily fit under the umbrella of an established hypothesis (e.g., reproductive assurance, which is largely confined to asexuals but needs to be tested by comparing sexuals and asexuals). We classified the species by class, following the U.S. Interagency Taxonomic Information System; when species from multiple classes were addressed, we used the lowest shared taxonomic level.

We included individual studies in more than one hypothesis category if (a) the study found evidence for or against multiple hypotheses or (b) whether and how the study tested hypotheses was not clear enough to identify a single hypothesis that was the focus of the paper. In the latter situation, we assessed each study carefully and then assigned the study to each hypothesis that in our view was tested by the study design and/or was supported by the evidence delivered by the study. We termed each incidence of a distinct test of a distinct hypothesis a "case", which meant that some studies are represented by more than one case. We use this terminology consistently throughout the rest of the paper. We concluded our survey at the end of the summer of 2017, meaning that only papers published by this time were able to be included.

Categories of hypotheses for sex

Sex, via segregation and recombination, breaks up linkage disequilibria (LD) within and across loci (Hill and Robertson 1966). This consequence of sexual reproduction is the reason that most hypotheses for the maintenance of sex focus on identifying conditions or situations associated with benefits of breaking up LD. Theoretical analyses have highlighted situations where selection changes over time and over space or when linkage is generated by the combination of selection and drift as the conditions that are most likely to produce such benefits (Barton 2009). Field-based studies of sex that address benefits of LD breakup have typically focused on ecological situations (e.g., coevolving parasites or spatially structured niches, see below) that are expected to translate into changes in selection over space or time, but do not generally establish explicit links to the genetic mechanisms conferring benefits to sex. For this reason we *a priori* delineated the major hypotheses for sex by ecological mechanisms or scenarios that can generate or are associated with changes in selection.

We acknowledge that some of these categories feature conceptual overlap (e.g., “parasites” and “increased rate of adaptive evolution”, from the perspective that sexuals that can adapt more quickly to parasites might be at an advantage), that other categories could be combined to make even broader categories (e.g., all niche-based hypotheses; all hypotheses generated by genetic linkage), and that not all evolutionary biologists would necessarily produce the same classification system. We decided to separate hypotheses involving disadvantages to asexual lineages via reduced rate of adaptive evolution and increased rate of accumulation of harmful mutations into separate categories because, even though both phenomena are the consequence of the reduction in efficacy of selection at linked sites in the absence of recombination (Hill-Robertson effect; Hill and Robertson 1966, Felsenstein 1974), different empirical methods are typically applied to detect evidence for ineffective adaptive evolution vs. ineffective purifying selection.

Parasites

Biological antagonism –what we henceforth refer to as "parasites" or parasite pressure"– is potentially connected to the maintenance of sex because parasites can generate rapid changes in the direction of selection. Most prominent of the parasite mechanisms is the hypothesis that parasites can help maintain sex by imposing negative frequency-dependent selection favouring rare host genotypes (the "Red Queen"; Bell 1982, Jaenike 1978, Hamilton 1980). Links between sex and biological antagonism can be driven by other mechanisms (e.g., Haafke et al. 2016), though the Red Queen-sex connection seems to be the most theoretically robust (e.g., Hamilton et al. 1990, Howard and Lively 1994, Peters and Lively 1999) and has received more empirical attention and support than other parasite-driven mechanisms for sex (reviewed in Neiman and Koskella 2009, Lively and Morran 2014).

Rate of adaptive evolution

Selection works most effectively if beneficial and deleterious mutations occur in different individuals because these individuals should experience larger differentials in relative fitness than when mutations co-occur within individuals (Hill and Robertson 1966). Over time, drift in the presence of selection may therefore lead to the accumulation of individuals where beneficial and harmful alleles are linked. Sex can generate benefits in this situation in two ways: by immediately exposing 'hidden variation' (both beneficial and harmful) to selection and by enabling more effective adaptive evolution at longer time scales.

Harmful mutations

Hill-Robertson effects are expected to translate into increased rates of harmful mutation accumulation via relatively ineffective purifying selection in asexual vs. sexual lineages. Muller's ratchet, which will cause irreversible mutation accumulation in small populations, is also expected to disproportionately affect asexual lineages (Muller 1964).

Niche differentiation

One of the simplest mechanisms that enables coexistence between asexuals and their sexual relatives is niche differentiation. In the most extreme case of non-overlapping sexual and asexual niches, there is no competition between sexuals and asexuals, rendering costs of sex irrelevant (Meirmans et al. 2012). Perhaps because of its simplicity, there exist only a few theory-focused papers on this topic. One exception is the modelling study by Case and Taper (1986), who showed that niche differentiation can arise through character displacement after invasion of a sexual population by an asexual lineage. In practice, however, this hypothesis is difficult to test: it is challenging to estimate the degree of niche overlap in natural populations and to determine whether the observed degree of niche differentiation between sexuals and asexuals is enough to prevent competition-driven extinction of one of the reproductive modes.

Coverage of niche space

There are a variety of formulations of the overarching hypothesis that sex can be maintained in situations where sexual individuals, lineages, or populations cover larger fractions of the available niche space than asexual counterparts. The most prominent example is the Tangled Bank hypothesis (Bell 1982), which postulates that sexual reproduction can be favored by generating a genetically diverse set of offspring that can make efficient use of a heterogeneous habitat via reduction in competition between siblings for limited resources. Asexually produced siblings, on the other hand, will compete for these same resources because they are genetically similar (also predicted by the conceptually similar frozen niche concept (Vrijenhoek 1979). This advantage of sexual reproduction is increasingly offset as asexual lineage diversity increases, assuming that higher asexual diversity translates into more variable resource utilization by the asexual population.

Results

Our literature survey of 66 studies (83 cases; some studies focused on multiple mechanisms) addressing the mechanisms underlying the maintenance of sex in the wild revealed some clear patterns (Table 1). First, there is a distinct majority of support (56 cases) vs. lack of support (27 cases), perhaps reflecting a publication bias towards positive results. The parasite and niche differentiation hypotheses predominated amongst the studies featuring positive results; we elaborate on these and other hypothesis-specific patterns below. Our survey also clearly showed that some taxa have been the focus of far more investigation than others: the vast majority of studies involved animal systems (54 studies; 82%), which themselves were dominated by gastropods (23 studies), branchiopods (eight studies), reptiles (eight studies), and insects (six studies). The remaining 16% of the studies were in plants (11 studies; all Magnoliopsida/angiosperms) and fungi (one study). Some systems were particularly heavily represented. For example, the gastropod *Potamopyrgus antipodarum* was featured in 16 studies (see supplementary material, Table S1, for an overview). Other taxa common in our survey included the branchiopod *Daphnia pulex* (seven studies), the gastropod *Melanoides tuberculata* (four studies), and the angiosperm *Taraxacum officinale* (four studies). Only two studies applied a broad taxonomic approach, using comparisons of the ecologies of hundreds of sexual and asexual taxa (Ross et al. 2013, van der Kooi et al. 2017) to detect associations with, or consequences of, reproductive mode variation that apply across taxa.

Parasites

Our search revealed 30 cases (representing 29 studies; one study with mixed results contributed two cases) that considered the maintenance of sex from the perspective of selection imposed via parasitism, by far the most frequently tested of the five main hypothesis categories that we distinguished. Twenty of these cases reported results consistent with the expectations of situations where parasites are contributing to the maintenance of sex. Nearly all cases (27/30) focused at least in part on the Red Queen. A distinct majority of these Red Queen cases (15/27) involved the interaction between the snail *Potamopyrgus antipodarum* and the trematode parasite *Microphallus* 'livelyi'. The three parasite-focused papers that did not explicitly address the Red Queen considered broader formulations of the parasite/antagonism hypothesis (e.g., "parasitism rate", "herbivory").

Rate of adaptive evolution

Our survey identified only three cases that addressed rates of adaptive evolution in the context of the maintenance of sex. All three of these cases took what we viewed as indirect approaches to this question, addressing whether sexuals were more often found in unpredictable abiotic environments that would likely demand rapid adaptation relative to the environments harboring asexual counterparts. Two ostracod-focused cases reported evidence consistent with this prediction, with sexual ostracods associated with relatively harsh and unpredictable environments (Schmit et al. 2013a,b). By contrast, parasites seemed to be a more likely explanation of patterns of distribution of sexual vs. asexual New Zealand freshwater snails than rapidly changing abiotic components of the environment (Lively 1987). Direct empirical evaluation of whether sexual organisms feature higher rates of adaptive evolution than their asexual relatives in natural populations clearly deserves future attention. Despite ample evidence for the importance of drift in natural populations (e.g., all studies supporting the ‘mutation accumulation’ mechanism), we found no field-based studies that investigated whether sex generates short-term benefits by exposing hidden genetic variation to selection.

Mutation accumulation

The prediction that deleterious mutations accumulate more rapidly in asexual than sexual lineages has been tested in a number of different organisms. In most cases (14 out of 19 cases; Table 1) there was support for the hypothesis that asexuals do accumulate deleterious mutations more rapidly than sexual lineages. Even so, nearly all (15/19) cases are based on a handful of genes, raising the question of the extent to which these results are likely to hold for the genome as a whole. Only four studies thus far have extended analyses of deleterious mutation accumulation to the genome scale (Hollister et al. 2015, Ament-Velásquez et al. 2016, Brandt et al. 2017, Lovell et al. 2017). Three of these studies (Hollister et al. 2015, Ament-Velásquez et al. 2016, Lovell et al. 2017) found that, as expected, asexuals had a higher load of deleterious mutations than sexuals. The fourth study (Brandt et al. 2017) found that *sexual* taxa experienced more mutation accumulation than asexual counterparts. This latter study focused on asexual lineages that are extremely old (tens of million years since derivation from sexual ancestors), suggesting that the absence of deleterious mutation accumulation may have contributed to the long-term persistence of these lineages in the absence of sex.

Niche differentiation

We identified 17 cases that considered the maintenance of sex from the perspective of niche differentiation. Together with harmful mutations, these studies featured the broadest taxonomic support of the hypothesis categories, representing six of the 11 taxonomic classes in Table 1. Tests for niche differentiation were most common in angiosperms, representing six of 17 cases. Thirteen of these 17 cases found at least some support for niche differentiation between sexuals and asexuals. Only three of these cases took the critical and perhaps most challenging additional step of determining whether the observed niche differentiation is enough to eliminate competition between sexuals and asexuals (O'Connell and Eckert 2001, Lehto and Haag 2010, Schmit et al. 2013a). All three cases did indeed suggest that niche differentiation between sexuals and asexuals was substantial enough that direct competition is unlikely, which should in turn resolve the problem of sex by rendering costs of sex irrelevant.

Coverage of niche space

We identified eight cases where niche breadth was compared between asexual taxa and sexual counterparts, representing five taxonomic groups. In all but one case, the asexuals were characterized by broader niches than their sexual relatives. While most of these studies just focused on one or a few systems, the two studies that evaluated hundreds of species reported the same pattern (Ross et al. 2013, van der Kooi et al. 2017). Because the maintenance of sex via differential coverage of niche space requires that *sexuals* cover more niche space (and not, as found here, asexuals), our survey does not support the idea that niche-coverage related hypotheses will provide substantial explanatory power with respect to the maintenance of sex in the wild.

Discussion

Our survey revealed that the conceptual focus and outcomes of field-focused studies on the maintenance of sex were different from their lab-focused counterparts, emphasizing a critical need for continued empirical research on sex in natural settings. Perhaps most prominently, our survey results highlight an important role for niche differentiation mechanisms in the maintenance of sex. This finding is also consistent with the many examples of geographical parthenogenesis and the observation that sexual and asexual individuals or lineages often differ in other key elements of their biology or ecology (e.g., hybrid status, polyploidy, production of resting eggs) (see also Meirmans et al. 2012). Evidence for the potential importance of niche differentiation from the field is striking in light of what seems like the near absence of laboratory studies focused on this mechanism. Indeed, we are not aware of any laboratory-focused study that has specifically addressed niche differentiation. While we do not know why this hypothesis has received so little attention in the laboratory, we speculate that the fact that niche differentiation departs from most other prominent hypotheses for sex in the absence of a specific advantage generated by or associated with sexual reproduction might be a contributing factor.

In contrast to niche differentiation, there was very little support for the related but distinct niche space-coverage mechanisms such as Tangled Bank (Bell 1982). While these niche space-focused mechanisms have been the focus of quite a bit of theoretical attention (e.g., Bell 1982, Case and Taper 1986, Pound et al. 2002), these mechanisms seem to have very little empirical backing: in our survey, we found seven examples of negative results and only one example of support among the eight niche-space focused cases in our survey. This finding is in agreement with the general sentiment from earlier sex-focused research that revealed little evidence for Tangled Bank-like mechanisms (Ellstrand and Antonovics 1985, Burt and Bell 1987).

Another striking difference between our results and the typical focuses and outcomes of lab-based studies on the maintenance of sex is with respect to the role (or lack thereof) of an increased rate of adaptive evolution in sexual vs. asexual organisms. While there is substantial theoretical (Barton 1995, Burt 2000) and lab-based (e.g., Kaltz and Bell 2002, Goddard et al. 2005, McDonald et al. 2016) support for an important role for sexual reproduction in facilitating adaptive evolution, we only found three field-based studies that directly addressed whether sexuals have an adaptability advantage relative to asexual counterparts. One possible explanation for this distinct difference in focus between laboratory and field-focused research on the maintenance of sex is that adaptability hypotheses are perceived to be difficult to rigorously test in the wild and are thus difficult to propose, fund, or execute. We also cannot exclude the possibility that publication bias (e.g., the challenges in publishing negative results) contributes to this pattern. Finally, the possibility remains that the necessarily artificial nature of lab-based studies may enhance or bias results and explain –at least in part– the different focuses and outcomes of laboratory vs. field-focused research.

Most of the positive evidence in our survey comes from studies addressing the Red Queen hypothesis, a particular formulation of the parasite hypothesis for sex. A distinct majority of these Red Queen-focused studies found evidence that parasite-host interactions contribute to the maintenance of sex. While the relatively large number and generally positive outcome of these studies might be taken as evidence that the Red Queen can provide a general explanation for the maintenance of sex in natural populations, the fact that most of these cases (15/ 27; ~55%) involve a single study system, *Potamopyrgus antipodarum*, means that this conclusion would be premature. The issues posed by dominance of a particular study system with respect to tests of a particular hypothesis are highlighted by the fact that 15/15 cases in the *Potamopyrgus* system are consistent with the expectations of the Red Queen, compared to only five of 12 cases from other taxa (see Table S1 for more details). In general, our take-home message is that emergence of any mechanism as one that confers broad explanatory power for understanding sex in nature will require support from a diverse array of natural systems.

While many cases (12/17) demonstrate at least some support for mutation accumulation hypotheses, most of the confirmatory evidence comes from only three study systems: *Daphnia*, *Potamopyrgus*, and *Campeloma*. All directly relevant genome-scale analyses of deleterious mutation accumulation of which we are aware have found considerable among-gene variation with respect to the rate of deleterious mutation accumulation in sexual and asexual lineages. Because of this among-gene variation, the inferences generated by the 15 cases that only included a handful of genes must be viewed with caution. Indeed, one of the four cases that did investigate mutation accumulation at the whole-genome scale in the wild found that, contrary to predictions, sexual taxa experienced more mutation accumulation (Brandt et al. 2017). Finally, although there appears to be some tentative general support for deleterious mutation accumulation in asexual lineages, it is important to note that even broad support for this mechanism is unlikely to explain the maintenance of sex. The reason for this caveat is that mutation accumulation generates a long-term disadvantage for asexuality, whereas short-term advantages are required for the maintenance of sex within populations (Maynard Smith 1978).

No single mechanism emerged as being important to the maintenance of sex across all natural systems included in our survey. This result provides indirect support for the idea that different mechanisms for sex might be important for different taxa (see also Neiman et al. 2017). While the notion that multiple mechanisms are of relevance to the maintenance of sex in nature would not surprise most of the researchers who study this topic, our survey results emphasize the importance of including a variety of taxa and considering multiple mechanisms when studying the maintenance of sex. Direct tests of the importance of this type of pluralism are conceptually simple but logistically challenging: the simultaneous study of the importance of multiple mechanisms across a diverse array of appropriate taxa in natural settings. The related but distinct point regarding the existence of a variety of different evolutionary "schools" concerning the maintenance of sex (Gouyon 1999, Meirmans and Strand 2010) also highlights the value of research on the same mechanisms or systems by multiple independent investigator groups.

Outlook

Important steps forward for field-based research on the maintenance of sex will ideally come from several angles, which should perhaps most prominently include rigorous evaluation of the Red Queen hypothesis for sex in a diverse array of systems and direct tests for adaptive evolution (especially short-term effects) in natural settings. Especially insightful results with respect to the latter could be obtained from field experiments where sexuals and asexuals are transferred to (1) relatively harsh and/or unpredictable habitats, and (2) a relatively stable habitat, and where adaptation to the environment is tracked over multiple generations. Other useful tests could come from creative leveraging of unpredictable events (e.g., floods, fire, or even climate change) that might be expected to enable the detection of rapid adaption. Finally, researchers could evaluate whether sex generates short-term benefits via the exposure of hidden genetic variation to selection by comparing genetic variation for fitness in naturally occurring and coexisting sexual and asexual organisms over multiple generations.

With respect to other mechanisms for the maintenance of sex, our study suggests that broader attention to niche differentiation mechanisms would likely turn out to be fruitful. In particular, the application of mesocosm approaches, which can come closer to reflecting natural complexity, could bridge field and laboratory insights (e.g., Ganz and Ebert 2010). Throughout, we expect that an increasing availability of genomic resources for non-model taxa that have achieved prominence as the focus of "sex in the wild" studies (e.g., *Potamopyrgus antipodarum* (Bankers et al. 2017); *Taraxacum officinale*, E. Schranz pers. comm.) will provide a critical means of testing hypotheses for sex that make specific predictions regarding molecular evolution. We also believe that "pluralist" approaches that explicitly consider the possibility that different mechanisms might be important for different taxa or that separate mechanisms can operate simultaneously or in concert will also provide key advances (recently reviewed in Neiman et al. 2017).

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Data archival location

The results of our literature survey are provided as electronic supplementary material.

References

Aanen D, Beekman M, Kokko H. 2016 Introduction: Weird sex: the underappreciated diversity of sexual reproduction *Phil. Trans. R. Soc. B* **371**, 20160262.

Agh N, Abatzopoulos TJ, Kappas I, Van Stappen G, Razavi Rouhani SM, Sorgeloos P. 2007 Coexistence of sexual and parthenogenetic *Artemia* populations in Lake Urmia and neighboring lagoons. *Int. Rev. Hydrobiol.* **92**, 48-60.

Agrawal AF. 2009a Differences between selection on sex versus recombination in Red Queen models with diploid hosts. *Evolution* **63**, 2131-2141.

Agrawal AF. 2009b Spatial heterogeneity and the evolution of sex in diploids. *Am. Nat.* **174**, S54-S70.

Ament-Velásquez SL, Figuet E, Ballenghien M, Zattara EE, Norenburg JL, Fernández-Álvarez, Bierne J, Bierne N, Galtier N. 2016. Population genomics of sexual and asexual lineages in fissiparous ribbon worms (Lineus, Nemertea): hybridization, polyploidy and the Meselson effect. *Mol. Ecol.* **25**, 3356-3369.

Bankers L, Fields P, McElroy KE, Boore JL, Logsdon JM Jr, Neiman M. 2017 Genomic evidence for population-specific responses to co-evolving parasites in a New Zealand freshwater snail. *Mol. Ecol.* **26**, 3663-3675.

Barraclough TG, Fontaneto D, Ricci C, Herniou EA. 2007 Evidence for inefficient selection against deleterious mutations in cytochrome oxidase I of asexual bdelloid rotifers. *Mol. Biol. Evol.* **24,** 1952-1962.

Barton NH. 1995 A general model for the evolution of recombination. *Genet. Res.* **65**, 123-144.

Barton NH. 2009 Why sex and recombination? *Cold Spring Harb. Symp. Quant. Biol* **74**, 187-95.

Bast J, Schaefer I, Schwander T, Maraun M, Scheu S, Kraaijeveld K. 2016 No accumulation of transposable elements in asexual arthropods. *Mol. Biol. Evol.* **33**, 697-706.

Becks L, Agrawal AF. 2012 The evolution of sex is favoured during adaptation to new environments. *PLoS Biol.* **10**, e1001317.

Bell G. 1982 *The masterpiece of nature*. London, UK: Croon Helm.

Ben-Ami F, Heller J. 2008 Sex versus parasitism versus density. *Biol. J. Linn. Soc.* **93**, 537-544.

Ben-Ami F, Heller J. 2005 Spatial and temporal patterns of parthenogenesis and parasitism in the freshwater snail *Melanoides tuberculata*. *J. Evol. Biol.* **18**, 138-146.

Ben-Ami F, Heller J. 2007 Temporal patterns of geographic parthenogenesis in a freshwater snail. *Biol. J. Linn. Soc.* **91**, 711-718.

Brandt A, Schaefer I, Glanz J, Schwander T, Maraun M, Scheu S, Bast J. 2017. Effective purifying selection in ancient asexual oribatid mites. *Nat. Comm* ***8,*** 873.

Brown SG, Kwan S, Shero S. 1995 The parasitic theory of sexual reproduction: parasitism in unisexual and bisexual geckos. *Proc. Roy. Soc. Lond. B* **260**, 317-320.

Bruvo R, Adolfsson S, Symonova R, Lamatsch DK, Schön I, Jokela J, Butlin RK, Müller S. 2010 Few parasites, and no evidence for *Wolbachia* infections, in a freshwater ostracod inhabiting temporary ponds. *Biol. J. Linn. Soc.* **102**, 208-216.

Burt A. 2000 Perspective: sex, recombination, and the efficacy of selection – was Weismann right? *Evolution* **54**, 337-351.

Burt A, Bell G. 1987 Mammalian chiasma frequencies as a test of two theories of recombination. *Nature* **326**, 803-805.

Case TJ. 1990 Patterns of coexistence in sexual and asexual species of *Cnemidophorus* lizards. *Oecologia* **83**, 220-227.

Case TJ, Taper ML. 1986 On the coexistence and coevolution of asexual and sexual competitors. *Evolution* **40**, 366-387.

Crummett LT, Sears BF, Lafon DC, Wayne ML. 2013 Parthenogenetic populations of the freshwater snail *Campeloma limum* occupy habitats with fewer environmental stressors than their sexual counterparts. *Freshw. Biol.* **58**, 655-663.

Cuellar O. 1979 On the ecology of coexistence in parthenogenetic and bisexual lizards of the genus *Cnemidophorus*. *Am. Zool.*, **19**, 773-786.

Dagan Y, Liljeroos K, Jokela J, Ben-Ami F. 2013 Clonal diversity driven by parasitism in a freshwater snail. *J. Evol. Biol.* **26**, 2509-2519.

Dybdahl MF, Lively CM. 1995 Host-parasite interactions: infection of common clones in natural populations of a freshwater snail (*Potamopyrgus antipodarum*). *Proc. Roy. Soc. Lond. B Biol. Sci.* **260**, 99-103.

Dybdahl MF, Lively CM. 1998 Host-parasite coevolution: evidence for rare advantage and time-lagged selection in a natural population. *Evolution* **52**, 1057-1066.

Ellstrand NC, Antonovics J. 1985 Experimental studies of the evolutionary significance of sexual reproduction II. A test of the density-dependent selection hypothesis. *Evolution* **39**, 657-666.

Elzinga JA, Chevasco V, Mappes J, Grapputo A. 2012 Low parasitism rates in parthenogenetic bagworm moths do not support the parasite hypothesis for sex. *J. Evol. Biol.* **25**, 2547-2558.

Felsenstein J. 1974 The evolutionary advantage of recombination. *Genetics* **78**, 737-756.

Fox JA, Dybdahl MF, Jokela J, Lively CM. 1996 Genetic structure of coexisting sexual and clonal subpopulations in a freshwater snail (*Potamopyrgus antipodarum*). *Evolution* **50**, 1541-1548.

Ganz HH, Ebert D. 2010 Benefits of host genetic diversity for resistance to infection depend on parasite diversity. *Ecology* **91**, 1263–1268.

Gibson AK, Xu JY, Lively CM. 2016 Within-population covariation between sexual reproduction and susceptibility to local parasites. *Evolution* **70**, 2049-2060.

Goddard MR, Godfray H, Burt A. 2005. Sex increases the efficacy of natural selection in experimental yeast populations. *Nature* **434**, 636-40.

Gouyon, P-H. 1999 Sex: a pluralistic approach includes species selection. (One step beyond and it's good.). *J. Evol. Biol.* **12**, 1029-1030.

Grishkan I, Korol AB, Nevo E, Wasser SP. 2003 Ecological stress and sex evolution in soil microfungi. *Proc. Roy. Soc. Lond. B Biol. Sci.* **270**, 13-18.

Haafke J, Chakra MA, Becks L. 2016 Eco-evolutionary feedback promotes Red Queen dynamics and selects for sex in predator populations. *Evolution* **70**, 641-652.

Hamilton WD. 1980 Sex vs. non-sex vs. parasite. *Oikos* **35**, 282-290.

Hamilton WD, Axelrod R, Tanese R. 1990 Sexual reproduction as an adaptation to resist parasites (A review). *Proc. Nat. Acad. Sci. USA* **87**, 3566-3573.

Hanley KA, Bolger DT, Case TJ. 1994 Comparative ecology of sexual and asexual gecko species (*Lepidodactylus*) in French Polynesia. *Evol. Ecol.* **8**, 438-454.

Hanley KA, Fisher RN, Case TJ. 1995 Lower mite infestations in an asexual gecko compared with its sexual ancestors. *Evolution* **49**, 418-426.

Henry L, Schwander T, Crespi BJ. 2012 Deleterious mutation accumulation in asexual *Timema* stick insects. *Mol. Biol. Evol.* **29**, 401-408.

Hill WG, Robertson A. 1966 The effect of linkage on limits to artificial selection. *Genet. Res.* **8**, 269-294.

Hollister JD, Greiner S, Wang W, Wang J, Zhang Y, Wong GK, Wright SI, Johnson MT. 2015. Recurrent loss of sex is associated with accumulation of deleterious mutations in *Oenothera*. *Mol. Biol. Evol.* **32**, 896-905.

Howard RS, Lively CM. 1994 Parasitism, mutation accumulation, and the maintenance of sex. *Nature* **367,** 554-557.

Innes DJ, Ginn M. 2014 A population of sexual *Daphnia pulex* resists invasion by asexual clones. *Proc. Roy. Soc. Lond. B* **281**, 20140564.

Jaenike J. 1978 An hypothesis to account for the maintenance of sex within populations. *Evol. Theor.* **3**, 191-194.

Jiang X, Tang H, Ye Z, Lynch M. 2017 Insertion polymorphisms of mobile genetic elements in sexual and asexual populations of *Daphnia pulex*. *Genome Biol. Evol.* **9**, 362-374.

Johnson SG. 1994 Parasitism, reproductive assurance and the evolution of reproductive mode in a fresh-water snail. *Proc. Roy. Soc. Lond. B Biol. Sci.* **255**, 209-213.

Johnson SG, Howard RS. 2007 Contrasting patterns of synonymous and nonsynonymous sequence evolution in asexual and sexual freshwater snail lineages. *Evolution* **61**, 2728-2735.

Johnson MTJ, Smith SD, Rausher MD. 2009 Plant sex and the evolution of plant defenses against herbivores. *Proc. Nat. Acad. Sci. USA* **106**, 18079-18084.

Jokela J, Lively CM. 1995 Parasites, sex, and early reproduction in a mixed population of freshwater snails. *Evolution* **49**, 1268-1271.

Jokela J, Dybdahl MF, Lively CM. 2009 The maintenance of sex, clonal dynamics, and host-parasite coevolution in a mixed population of sexual and asexual snails. *Am. Nat.* **174**, S43-S53.

Kaltz O, Bell G. 2002. The ecology and genetics of fitness in *Chlamydomonas*. XII. Repeated sexual episodes increase rates of adaptation to novel environments. *Evolution* **56**, 1743-1753.

Kearney MR, Moussalli A, Strasburg J, Lindenmayer D, Moritz C. 2003 Geographic parthenogenesis in the Australia arid zone: I. A climatic analysis of the *Heteronotia binoei* complex (Gekkonidae). *Evol. Ecol. Res.* **5**, 953-976.

Killick SC, Obbard DJ, West SA, Little TJ. 2008 Parasitism and breeding system variation in North American populations of *Daphnia pulex*. *Ecol. Res.* **23**, 235-240.

King KC, Lively CM. 2009 Geographic variation in sterilizing parasite species and the Red Queen. *Oikos* **118**, 1416-1420.

King KC, Jokela J, Lively CM. 2011 Parasites, sex, and clonal diversity in natural snail populations. *Evolution* **65**, 1474-1481.

Kondrashov AS. 1993 Classification of hypotheses on the advantage of amphimixis. *J. Hered.* **84**, 372-387.

Külköylüoğlu O, Sari N, Akdemir D, Yavuzatmaca M, Altinbağ C. 2012 Distribution of sexual and asexual ostracoda (Crustacea) from different altitudinal ranges in the Ordu region of Turkey: Testing the Rapoport Rule. *High Alt. Med. Biol.* **13,** 126-137.

Lavanchy G, Strehler M, Roman MNL, Lessard-Therrien M, Humbert JY, Dumas Z, Jalvingh K, Ghali K, Fontcuberta García-Cuenca A, Zijlstra B, Arlettaz R, Schwander T. 2016 Habitat heterogeneity favours asexual reproduction in natural populations of grassthrips. *Evolution* **70**, 1780-1790.

Lehto MP, Haag CR. 2010 Ecological differentiation between coexisting sexual and asexual strains of *Daphnia pulex*. *J. Anim. Ecol.* **79**, 1241-1250.

Lehtonen J, Jennions MD, Kokko H. 2012 The many costs of sex. *Trends Ecol. Evol.* **27**, 172-178.

Lively CM. 1987 Evidence from a New Zealand snail for the maintenance of sex by parasitism. *Nature* **328**, 519-521.

Lively CM. 1992 Parthenogenesis in a freshwater snail: reproductive assurance versus parasitic release. *Evolution* **46**, 907-913.

Lively CM, Morran LT. 2014 The ecology of sexual reproduction. *J. Evol. Biol.* **27**, 1292-1303.

Lo EY, Stefanović S, Dickinson TA. 2009. Population genetic structure of diploid sexual and polyploid apomictic hawthorns (*Crataegus*; Rosaceae) in the Pacific Northwest. *Mol. Ecol.* **18**, 1145–1160.

Lovell JT, Williamson RJ, Wright SI, McKay JK, Sharbel TF. 2017 Mutation accumulation in an asexual relative of *Arabidopsis*. *PLoS Genet*. **13**, e1006550.

Lumley AJ, Michalczyk Ł, Kitson JJN, Spurgin LG, Morrison CA, Godwin JL, Dickinson ME, Martin OY, Emerson BC, Chapman T, Gage MJJ. 2015 Sexual selection protects against extinction. *Nature* **522**, 470-473.

Mark Welch DB, Meselson MS. 2001 Rates of nucleotide substitution in sexual and anciently asexual rotifers. *Proc. Nat. Acad. Sci. USA* **98**, 6720-6724.

Mau M, Lovell JT, Corral JM, Kiefer C, Koch M, Aliyu OM, Sharbel TF. 2015 Hybrid apomicts trapped in the ecological niches of their sexual ancestors. *Proc. Nat. Acad. Sci. USA* **112**, E2357-E2365.

Maynard Smith J. 1971 What use is sex? *J. Theor. Biol.* **30**, 319-335.

Maynard Smith J. 1978 *The evolution of sex*. London, UK: Cambridge University Press.

McDonald MJ, Rice DP, Desai MM. 2016 Sex speeds adaptation by altering the dynamics of molecular evolution. *Nature* **531**, 233-236.

McKone MJ, Gibson AK, Cook D, Freymiller LA, Mishkind D, Quinlan A, York JM, Lively CM, Neiman M. 2016 Fine-scale association between parasites and sex in *Potamopyrgus antipodarum* within a New Zealand lake. *NZ J. Zool.* **40**, 330-333.

Menken S, Smits E, Den Nijs JCM. 1995 Genetical population structure in plants: gene flow between diploid sexual and triploid asexual dandelions (*Taraxacum* section *Ruderalia*). *Evolution* **49**, 1108–1118.

Meirmans PG. 2005 Ecological and genetic interactions between diploid sexual and triploid apomictic dandelions. Ph.D. Thesis. Instituut voor Biodiversiteit en Ecosysteem Dynamica, Universiteit van Amsterdam.

Meirmans PG, Calame FG, Bretagnolle F, Felber F, den Nijs JCM. 1999 Anthropogenic disturbance and habitat differentiation between sexual diploid and apomictic triploid *Taraxacum* sect. *Ruderalia*. *Folia Geobot.* **34**, 451-469.

Meirmans S, Strand R. 2010. Why are there so many theories for sex, and what do we do with them? *J. Hered*, **101**, S3-S12.

Meirmans S, Meirmans PG, Kirkendall LR. 2012 The costs of sex: Facing real-world complexities. *Q. Rev. Biol.* **87**, 19-40.

Moritz C, McCallum H, Donnellan S, Roberts JD. 1991 Parasite loads in parthenogenetic and sexual lizards (*Heteronotia binoei*): support for the Red Queen hypothesis. *Proc. Roy. Soc. Lond. B Biol. Sci.* **244**, 145-149.

Muller HJ. 1964 The relation of recombination of mutational advance. *Mutat. Res.* **106**, 2-9.

Neiman M, Koskella B. 2009. Sex and the Red Queen. In *Lost Sex* (eds Schön I, Martens K, van Dijk P), pp. 133-159. Amsterdam: Springer.

Neiman M, Schwander T. 2011 Using parthenogenetic lineages to identify advantages of sex. *Evol. Biol.* **38**, 115-123.

Neiman M, Jokela J, Lively CM. 2005 Variation in asexual lineage age in *Potamopyrgus antipodarum*, a New Zealand snail. *Evolution* **59**, 1945-1952.

Neiman M, Lively CM, Meirmans S. 2017 Why sex? A pluralist approach revisited. *Trends Ecol. Evol.* **32**, 589-600.

Neiman M, Hehman G, Miller JT, Logsdon JM Jr, Taylor DR. 2010 Accelerated mutation accumulation in asexual lineages of a freshwater snail. *Mol. Biol. Evol.* **27**, 954-963.

Normark BB, Moran NA. 2000. Testing for the accumulation of deleterious mutations in asexual eukaryote genomes using molecular sequences. *J. Nat. Hist.* **34**, 1719-1729.

O'Connell LM, Eckert CG. 2001 Differentiation in reproductive strategy between sexual and asexual populations of *Antennaria parlinii* (Asteraceae). *Evol. Ecol. Res.* **3**, 311-330.

Paczesniak D, Adolfsson S, Liljeroos K, Klappert K, Lively CM, Jokela J. 2014 Faster clonal turnover in high-infection habitats provides evidence for parasite-mediated selection. *J. Evol. Biol.* **27**, 417-428.

Paland S, Lynch M. 2006 Transitions to asexuality result in excess amino acid substitutions. *Science* **311**, 990-992.

Pellino M, Hojsgaard D, Schmutzer T, Scholz U, Hörandl E, Vogel H, Sharbel TF. 2013 Asexual genome evolution in the apomictic *Ranunculus auricomus* complex: examining the effects of hybridization and mutation accumulation. *Mol. Ecol.* ***22***, 5908-5921.

Peters AD, Lively CM. 1999 The red queen and fluctuating epistasis: a population genetic analysis of antagonistic coevolution. *Am. Nat.* **154**, 393-405.

Pound GE, Doncaster CP, Cox SJ. 2002 A Lotka–Volterra model of coexistence between a sexual population and multiple asexual clones. *J. Theor. Biol*. **217**, 535–545.

Rho M, Schaack S, Gao X, Kim S, Lynch M, Tang H. 2010 LTR retroelements in the genome of *Daphnia pulex*. *BMC Genomics* **11**, 425.

Ross L, Hardy NB, Okusu A, Normark BB. 2013 Large population size predicts the distribution of asexuality in scale insects. *Evolution* **67**, 196-206.

Schmit O, Adolfsson S, Vandekerkhove J, Rueda J, Bode SNS, Rossetti G, Michalakis Y, Jokela J, Martens K, Mesquita-Joanes F. 2013a The distribution of sexual reproduction of the geographic parthenogen *Eucypris virens* (Crustacea: Ostracoda) matches environmental gradients in a temporary lake. *Can. J. Zool.* **91**, 660-671.

Schmit O, Bode SNS, Camacho A, Horne DJ, Lamatsch DK, Martens K, Martins MJF, Namiotko T, Rossetti G, Rueda-Sevilla J, Schön I, Vandekerkhove J, Mesquita-Joanes F. 2013b Linking present environment and the segregation of reproductive modes (geographical parthenogenesis) in *Eucypris virens* (Crustacea: Ostracoda). *J. Biogeog.* **40**, 2394-2408.

Sharp N, Otto SP. 2016 Evolution of sex: Using experimental genomics to select among competing theories. *Bioessays* **38**, 751-757.

Singh ND, Criscoe DR, Skolfield S, Kohl KP, Keebaugh ES, Schlenke TA. 2015 Fruit flies diversify their offspring in response to parasite infection. *Science* **349**, 747-750.

Stefani, R. 1956. *Il problema della partenogenesi in* "*Haploembia solieri*" Ramb. (Embioptera-Oligotomidae). *Memorie dell'Accademia Lincei Rome Sez IIIa* **5**, 127-201.

Stefani, R. 1959. *Aspetti zoogeografici di un problema evolutivo*. *Bollettino di Zoologia Torino* **26**, 105-114.

Steiner BL, Armbruster GFJ, Scheepens JF, Stöcklin J. 2012 Distribution of bulbil- and seed-producing plants of *Poa alpine* (Poaceae) and their growth and reproduction in common gardens suggest adaptation to different elevations. *Am. J. Bot.* **99**, 2035-2044.

Sterken MG, Snoek LB, Kammenga JE, Andersen EC. 2015 The laboratory domestication of *Caenorhabditis elegans*. *Trends Genet.* **31**, 224-231.

Tarkhnishvili D, Gavashelishvili A, Avaliani A, Murtskhvaladze M, Mumladze L. 2010 Unisexual rock lizard might be outcompeting its bisexual progenitors in the Caucasus. *Biol. J. Linn. Soc.* **101**, 447-460.

Tilquin A, Kokko H. 2016. What does the geography of parthenogenesis teach us about sex? *Phil. Trans. Roy. Soc. Lond.* B **371**, 20150538.

Tucker A, Ackerman M, Eads B, Xu S, Lynch M. 2013 Population-genomic insights into the evolutionary origin and fate of obligately asexual *Daphnia pulex*. *Proc. Nat. Acad. Sci. USA* **110**, 15740-15745.

van der Kooi CJ, Matthey-Doret C, Schwander T. 2017 Evolution and comparative ecology of parthenogenesis. *Evol. Lett., in press,* DOI: 10.1002/evl3.30.

Verduijn MH, Van Dijk PJ, Van Damme JMM. 2004 The role of tetraploids in the sexual-asexual cycle in dandelions (*Taraxacum*). *Heredity* **93**, 390-398.

Vergara D, Lively CM, King KC, Jokela J. 2013 The geographic mosaic of sex and infection in lake populations of a New Zealand snail at multiple spatial scales. *Am. Nat.* **182**, 484-493.

Vergara D, Jokela J, Lively CM. 2014 Infection dynamics in coexisting sexual and asexual host populations: support for the Red Queen hypothesis. *Am. Nat.* **184**, S22-S30.

Verhoeven KJF, Biere A. 2013 Geographic parthenogenesis and plant-enemy interactions in the common dandelion. *BMC Evol. Biol.* **13**, 23.

Vrijenhoek RC. 1979 Factors affecting clonal diversity and coexistence. *Am. Zool.* **19**, 787-797.

West SA, Lively CM, Read AF. 1999 A pluralist approach to sex and recombination. *J. Evol. Biol.* **12**, 1003-1012.

Williams GC. 1975 *Sex and evolution*. Princeton, USA: Princeton University Press.

Xu S, Omilian AR, Cristescu ME. 2011 High rate of large-scale hemizygous deletions in asexually propagating *Daphnia*: Implications for the evolution of sex. *Mol. Biol. Evol.* **28**, 335-342.

Table Caption

Table 1. Summary of the results of our literature survey. We list the number of studies that provided support (green) or no support (red) for the different categories of hypotheses for sex, separated by taxonomic group. In total, 66 studies and 83 cases were included; studies that tested multiple hypotheses or included multiple taxonomic groups were counted as "cases" multiple times. Numbers in brackets after the name of the taxonomic group indicate the number of studies for each group.

Class/clade	Parasites	Rate of adaptive evolution	Harmful Mutations	Niche differentiation	Coverage of niche space	Other
Reptiles (8)	2 / 1	-	-	2 / 2	0 / 2	-
Insects (6)	0 / 2	-	2 / 1	-	0 / 2	-
Branchiopods (8)	0 / 1	-	4 / 0	2 / 0	0 / 1	1 / 0
Ostracods (4)	0 / 1	2 / 0	-	2 / 1	0 / 2	-
Arachnids (1)	-	-	0 / 1	-	-	-
Arthropods; general (1)	-	-	0 / 1	-	-	-
Gastropods (23)	17 / 4	0 / 1	4 / 0	1 / 0	1 / 0	3 / 1
Rotifers (2)	-	-	1 / 1	-	-	-
Anopla (1)	-	-	1 / 0	-	-	-
Magnoliopsida (11)	2 / 0	-	2 / 1	5 / 1	-	1 / 0
Fungi (1)	-	-	-	1 / 0	-	-
TOTAL	21 / 9	2 / 1	14 / 5	13 / 4	1 / 7	5 / 1