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

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Running Title: Sex in the wild

Keywords: sexual reproduction, asexual reproduction, parthenogenesis, Red Queen, niche differentiation, Muller's ratchet

Author contributions

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.

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

116 Here, we argue that these limitations of lab-based studies mean that field-focused
117 research must play a critical role in the resolution of the problem of sex. It is our hope that a
118 useful and synthetic overview of these “sex in the wild” studies will both provide some of the
119 credit that this body of work deserves and motivate researchers to continue and expand this type
120 of empirical research. Our overview –the first of which we are aware since Bell (1982)–
121 addresses this goal by performing a survey of relevant empirical literature on "sex in the wild" to
122 (1) assess the contributions of field studies towards resolving the sex problem, (2) identify what
123 we have learned from these studies and what we still need to know, and (3) provide some
124 concrete steps forward.
125

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

148 least part of their range. We made this choice because in these species, the maintenance of sex is
149 an active problem. We excluded all studies of sperm-dependent asexual taxa (e.g., *Ambystoma*
150 mole salamanders, *Ips* bark beetles, *Rubus* subgenus *Rubus* blackberries) because all-asexual
151 populations of sperm-dependent organisms are not evolutionarily stable.

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

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

171 *Categories of hypotheses for sex*

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

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

194 empirical methods are typically applied to detect evidence for ineffective adaptive evolution vs.
195 ineffective purifying selection.

196 *Parasites*

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

207 *Rate of adaptive evolution*

208 Selection works most effectively if beneficial and deleterious mutations occur in different
209 individuals because these individuals should experience larger differentials in relative fitness
210 than when mutations co-occur within individuals (Hill and Robertson 1966). Over time, drift in
211 the presence of selection may therefore lead to the accumulation of individuals where beneficial
212 and harmful alleles are linked. Sex can generate benefits in this situation in two ways: by
213 immediately exposing 'hidden variation' (both beneficial and harmful) to selection and by
214 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

236 generating a genetically diverse set of offspring that can make efficient use of a heterogeneous
237 habitat via reduction in competition between siblings for limited resources. Asexually produced
238 siblings, on the other hand, will compete for these same resources because they are genetically
239 similar (also predicted by the conceptually similar frozen niche concept (Vrijenhoek 1979). This
240 advantage of sexual reproduction is increasingly offset as asexual lineage diversity increases,
241 assuming that higher asexual diversity translates into more variable resource utilization by the
242 asexual population.

243 Results

244 Our literature survey of 66 studies (83 cases; some studies focused on multiple mechanisms)
245 addressing the mechanisms underlying the maintenance of sex in the wild revealed some clear
246 patterns (Table 1). First, there is a distinct majority of support (56 cases) vs. lack of support (27
247 cases), perhaps reflecting a publication bias towards positive results. The parasite and niche
248 differentiation hypotheses predominated amongst the studies featuring positive results; we
249 elaborate on these and other hypothesis-specific patterns below. Our survey also clearly showed
250 that some taxa have been the focus of far more investigation than others: the vast majority of
251 studies involved animal systems (54 studies; 82%), which themselves were dominated by
252 gastropods (23 studies), branchiopods (eight studies), reptiles (eight studies), and insects (six
253 studies). The remaining 16% of the studies were in plants (11 studies; all
254 Magnoliopsida/angiosperms) and fungi (one study). Some systems were particularly heavily
255 represented. For example, the gastropod *Potamopyrgus antipodarum* was featured in 16 studies
256 (see supplementary material, Table S1, for an overview). Other taxa common in our survey
257 included the branchiopod *Daphnia pulex* (seven studies), the gastropod *Melanoides tuberculata*

258 (four studies), and the angiosperm *Taraxacum officinale* (four studies). Only two studies applied
259 a broad taxonomic approach, using comparisons of the ecologies of hundreds of sexual and
260 asexual taxa (Ross et al. 2013, van der Kooi et al. 2017) to detect associations with, or
261 consequences of, reproductive mode variation that apply across taxa.

262 *Parasites*

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

273 *Rate of adaptive evolution*

274 Our survey identified only three cases that addressed rates of adaptive evolution in the context of
275 the maintenance of sex. All three of these cases took what we viewed as indirect approaches to
276 this question, addressing whether sexuals were more often found in unpredictable abiotic
277 environments that would likely demand rapid adaptation relative to the environments harboring
278 asexual counterparts. Two ostracod-focused cases reported evidence consistent with this
279 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.

303 *Niche differentiation*

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

315 *Coverage of niche space*

316 We identified eight cases where niche breadth was compared between asexual taxa and sexual
317 counterparts, representing five taxonomic groups. In all but one case, the asexuals were
318 characterized by broader niches than their sexual relatives. While most of these studies just
319 focused on one or a few systems, the two studies that evaluated hundreds of species reported the
320 same pattern (Ross et al. 2013, van der Kooi et al. 2017). Because the maintenance of sex via
321 differential coverage of niche space requires that *sexuals* cover more niche space (and not, as
322 found here, asexuals), our survey does not support the idea that niche-coverage related
323 hypotheses will provide substantial explanatory power with respect to the maintenance of sex in
324 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).

348 Another striking difference between our results and the typical focuses and outcomes of
349 lab-based studies on the maintenance of sex is with respect to the role (or lack thereof) of an
350 increased rate of adaptive evolution in sexual vs. asexual organisms. While there is substantial
351 theoretical (Barton 1995, Burt 2000) and lab-based (e.g., Kaltz and Bell 2002, Goddard et al.
352 2005, McDonald et al. 2016) support for an important role for sexual reproduction in facilitating
353 adaptive evolution, we only found three field-based studies that directly addressed whether
354 sexuals have an adaptability advantage relative to asexual counterparts. One possible explanation
355 for this distinct difference in focus between laboratory and field-focused research on the
356 maintenance of sex is that adaptability hypotheses are perceived to be difficult to rigorously test
357 in the wild and are thus difficult to propose, fund, or execute. We also cannot exclude the
358 possibility that publication bias (e.g., the challenges in publishing negative results) contributes to
359 this pattern. Finally, the possibility remains that the necessarily artificial nature of lab-based
360 studies may enhance or bias results and explain –at least in part– the different focuses and
361 outcomes of laboratory vs. field-focused research.
362 Most of the positive evidence in our survey comes from studies addressing the Red
363 Queen hypothesis, a particular formulation of the parasite hypothesis for sex. A distinct majority
364 of these Red Queen-focused studies found evidence that parasite-host interactions contribute to
365 the maintenance of sex. While the relatively large number and generally positive outcome of
366 these studies might be taken as evidence that the Red Queen can provide a general explanation
367 for the maintenance of sex in natural populations, the fact that most of these cases (15/ 27;
368 ~55%) involve a single study system, *Potamopyrgus antipodarum*, means that this conclusion
369 would be premature. The issues posed by dominance of a particular study system with respect to
370 tests of a particular hypothesis are highlighted by the fact that 15/15 cases in the *Potamopyrgus*

371 system are consistent with the expectations of the Red Queen, compared to only five of 12 cases
372 from other taxa (see Table S1 for more details). In general, our take-home message is that
373 emergence of any mechanism as one that confers broad explanatory power for understanding sex
374 in nature will require support from a diverse array of natural systems.

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

389 No single mechanism emerged as being important to the maintenance of sex across all
390 natural systems included in our survey. This result provides indirect support for the idea that
391 different mechanisms for sex might be important for different taxa (see also Neiman et al. 2017).
392 While the notion that multiple mechanisms are of relevance to the maintenance of sex in nature
393 would not surprise most of the researchers who study this topic, our survey results emphasize the

394 importance of including a variety of taxa and considering multiple mechanisms when studying
395 the maintenance of sex. Direct tests of the importance of this type of pluralism are conceptually
396 simple but logistically challenging: the simultaneous study of the importance of multiple
397 mechanisms across a diverse array of appropriate taxa in natural settings. The related but distinct
398 point regarding the existence of a variety of different evolutionary "schools" concerning the
399 maintenance of sex (Gouyon 1999, Meirmans and Strand 2010) also highlights the value of
400 research on the same mechanisms or systems by multiple independent investigator groups.

401 *Outlook*

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

414 With respect to other mechanisms for the maintenance of sex, our study suggests that
415 broader attention to niche differentiation mechanisms would likely turn out to be fruitful. In
416 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).

Acknowledgements

We acknowledge Curt Lively for useful discussions on the history and development of the Red Queen hypothesis for sex and members of the Neiman lab as well as two anonymous reviewers for helpful comments on earlier versions of the MS. TS was supported by SNSF grant PP00P3 139013.

Data archival location

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

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688 **Table Caption**

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

695

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

696