1 **The article category: Review Article**

2 **Title: Sexual reproduction and diversity: connection between sexual selection and biological**

3 **communities via population dynamics**

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10 **Abstract:** Sexual reproduction is a mysterious phenomenon. Most animals and plants invest in

11 sexual reproduction, even though it is more costly than asexual reproduction. Theoretical studies

12 suggest that occasional or conditional use of sexual reproduction, involving facultative switching

13 between sexual and asexual reproduction, is the optimal reproductive strategy. However, obligate

14 sexual reproduction is common in nature. Recent studies suggest that the evolution of facultative

15 sexual reproduction is prevented by males that coerce females into sexual fertilization; thus, sexual

16 reproduction has the potential to enforce costs on a given species. Here, the effect of sex on

17 biodiversity is explored by evaluating the reproductive costs arising from sex. Sex provides atypical

18 selection pressure that favors traits that increase fertilization success, even at the expense of

19 population growth rates, i.e., sexual selection. The strength of sexual selection depends on the

20 density of a given species. Sexual selection often causes strong negative effects on the population

21 growth rates of species that occur at high density. Conversely, a species that reduces its density is

22 released from this negative effect, and so increases its growth rate. Thus, this negative density-

23 dependent effect on population growth that arises from sexual selection could be used to rescue

24 endangered species from extinction, prevent the overgrowth of common species, and promote the

25 coexistence of competitive species. Recent publications on sexual reproduction provide several

26 predictions related to the evolution of reproductive strategies, which is an important step towards

27 integrating evolutionary dynamics, demographic dynamics, and community dynamics.

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Why sexual reproduction is widespread in animals and plants remains a long-standing mystery in evolutionary ecology. Sex is associated with numerous short-term costs that asexual organisms mostly avoid (Maynard Smith 1971; Williams 1975; Bell 1982; Lehtonen et al. 2012). Theoretical studies have demonstrated that investing in small quantities of sexual reproduction represents the optimal reproductive strategy in predominantly parthenogenetic organisms (Charlesworth et al. 1993; Green and Noakes 1995; D'Souza and Michiels 2010). However, obligate sex is the dominant reproductive system in nature. Therefore, the mystery of sex is the prevalence of obligate sexual reproduction (Burke and Bonduriansky 2017). Recent studies have provided the notable hypothesis that males force asexual females to reproduce sexually (Dagg 2006; Kawatsu 2013b, a, 2015), which is a very simple but powerful solution for the mystery of sex. Males cannot reproduce by themselves without sexual reproduction, so they must forcibly mate with females, even if coercion is required. Consequently, facultative and obligate asexual reproduction are removed from the population. If this scenario is correct, the various costs of sexual reproduction arise from forced mating by males. This type of selection pressure that arises from sexual reproduction has been documented since Darwin's era, because males often have traits that are useless for survival, but beneficial for mating. This pressure is named sexual selection to distinguish it from natural selection (Darwin 1859, 1871). If the evolutionary dynamics driven by the sexual selection affect the population growth rates of sexual organisms, this effect of sexual selection must influence a broad range of biological communities, because sexual reproduction is common in eukaryotes. However, just as the effects of sexual selection have long been overlooked in the context of the mystery of sex, they have not been adequately explored in biological communities. Thus, in this review, I discuss two hypothetical mechanisms, in which sexual traits regulate population dynamics, along with suggestion of remaining problems and potential experimental approaches that could be used to test model predictions of the hypotheses.

One of the greatest challenges in ecology is elucidating the conditions under which biodiversity

56 may sustained over long timeframes (Tilman 2000). Self-regulation mechanisms of population size

57 are known as fundamental to sustain ecological communities (May 1972; Yodzis 1981; Barabás et al.

58 2017; Gavina et al. 2018). These mechanisms are achieved by a negative density-dependent effect

59 (NDDE) on population growth rates. If an NDDE exists, the density of species with low densities

60 will increase, which prevents extinction. In comparison, overgrowth is prevented in species with high

61 densities. An NDDE is generally explained by two mechanisms: predation pressure from natural

62 enemies (Elton 1927; Murdoch 1969) and intraspecific competition for resources (Gause 1934;

63 Macarthur and Levins 1967). Recently, the importance of sexual selection on population dynamics

64 has been pointed out (Kokko and Brooks 2003; Kokko and Rankin 2006; Kobayashi 2018). NDDE

65 arising from sexual selection results from competition for mating or fertilization success. At high

66 densities, where strong mating competition is expected, sexual selection favors traits that increase

67 mating success, even at the expense of population growth rates. In contrast, at low densities, this

68 negative effect on growth rate is mitigated, because there is less competition for mating in rare

69 species. Thus, the coexistence of many competitive species becomes possible, because sexual

70 selection has the potential to control the reproductive rate of any sexual species. This mechanism is

71 similar to the resource competition mechanism, because both arise from intraspecific interactions.

72 However, when considering niche theory, these mechanisms differ slightly, because sexual selection

73 promotes coexistence without niche partitioning between species. Given the biological species

74 concept, which defines species as groups of interbreeding natural populations that are reproductively

75 isolated from other groups (Mayr 1970), mating competition must occur within a given species;

76 consequently, sexual selection works depending on the density of each species. Therefore, even if

77 competitive species share the same niche space, the NDDE arising from sexual selection allows them

78 to coexist stably, as long as the biological species concept holds and the mechanisms arising from

79 resource competition do not. This case will be rare under natural conditions, because niche

80 differentiation is favored by the natural selection of competitive species to reduce competition for

81   resources.

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83   The first example that causes NDDE related to sexual reproduction is sex allocation. The most

84   renowned sex allocation theory predicts equal allocation to male and female reproductive functions

85   for the optimal division of resources (Fisher 1930). Because of this allocation, the production of

86   males is considered as one of the largest costs of sex (Maynard Smith 1971; Lehtonen et al. 2012).

87   However, equal allocation occurs under certain conditions, such as random mating and large mating

88   populations. In situations where sons compete with each other for mating partners in a local

89   population, the allocation to sons (or male functions, such as pollen in plants) reduces the mating

90   success rate for each son, because strong mating competition occurs among sons for a limited

91   number of mating partners. In comparison, greater allocation to daughters creates more mating

92   partners for the sons. This situation is called local mate competition and was modeled by Hamilton

93   (1967). In this model, the evolutionarily stable allocation to females is $(n + 1)/2n$, where n represents

94   the number of mothers in a local mating population. When n is sufficiently large, equal allocation

95   (0.5) occurs. In contrast, if a single mother is present in the local mating population ($n = 1$), this

96   female should allocate most of its resources to daughters. Thus, this intraspecific competition for

97   mating promotes the evolution of highly female-biased allocation, depending on the number of

98   mothers in the local mating population (Hamilton 1967; West 2009). Because the allocation to

99   females is strictly linked to the population growth rate, adaptive sex allocation results in an NDDE

100   on population growth, leading to the stable co-occurrence of competitive species (Hassell et al. 1983;

101   Zhang and Jiang 1995; Kobayashi and Hasegawa 2016; Kobayashi 2017). Models that incorporate

102   this mechanism have demonstrated that hundreds of species can co-occur over 10,000 generations

103   even in homogeneous environments, recreating the observed patterns of biodiversity (Kobayashi

104   2017). This study (Kobayashi 2017) clearly showed that sexual reproduction has the potential to

105   influence the ecological community via the evolutionary dynamics of sex allocation. At present, it is

106   not clear whether this mechanism works well under natural condition. Recent eco-evolutionary

107   feedback studies demonstrate the importance of genetic variation (Pelletier et al. 2009; Post and

108   Palkovacs 2009). However, there is insufficient information about genetic variation related to sex

109   allocation at the population level. The exception is haplodiploid species that can alter sex allocation

110   without genetic difference by controlling fertilization. Some wasps under the condition of local mate

111   competition theory are able to adequately alter their sex allocation, depending on the number of

112   competitors (Werren 1983; Herre 1985). Thus, hymenopteran species that exhibit local mate

113   competition could be good material to test the relationship between NDDE and sex allocation.

114   Another example is sexual harassment, which is a trait of one sex (usually male) that increases

115   its fertilization success rate but reduces the fecundity of its mating partners. Although previous

116   empirical studies have provided evidence of the density or frequency dependence of sexual selection

117   (Andersson 1994; Levitan 2004; Gosden and Svensson 2009; Takahashi and Kawata 2013), the

118   relationship between the density dependence of sexual selection and population growth rate remains

119   obscure (Kokko and Brooks 2003; Kokko and Rankin 2006), but see also (Mikami et al. 2004;

120   Takahashi et al. 2014). Sexual harassment creates an NDDE similar to that resulting from sex

121   allocation. For high-density species, sexual selection favors males that utilize strong harassment to

122   increase their fertilization success rate, even at the expense of the fecundity of their mating partners.

123   At low densities, which means fewer competitors are present, such too strong harassment becomes

124   disadvantageous for the harasser, because it decreases the fecundity of the mating partners despite

125   the fertilization success is secured to some extent without harassing; therefore, sexual selection

126   generally has an NDDE on the population growth rate of sexual organisms. This situation was

127   modeled in a recent study, which also revealed that sexual harassment has an NDDE on the

128   population growth rate, promoting the stable co-occurrence of competitive species (Kobayashi

129   2018). Thus, as shown by the model of sex allocation (Kobayashi 2017), this recent study

130   demonstrated that the evolution of sexual harassment reduces the fecundity per individual, depending

131   on the density, allowing hundreds of species to co-occur without niche differences.

132   Both of these examples show that sexual organisms, generally, have the ability to self-regulate

133   the size of their populations. Of note, these two mechanisms generate slightly different population

134   dynamics from the time-scale perspective. In the case of sex allocation, a change in the abundance of

135   each species promotes an evolutionary change in sex allocation, and vice versa. Thus, NDDE arising

136   from sex allocation takes time, because a change is required in the average sex allocation depending

137   on genetic variation and mutations within the species. Because small populations have low

138   evolutionary potential (few genetic variations within populations and low mutation rates per

139   generation at the population level), relatively rare species tend to show greater variation in

140   population dynamics than common species (Fig. 1a). In the sexual harassment models, when

141   abundance increases, the numbers of copulation, courtship and pollinated pollen grains increase;

142   consequently, the amount of harassment to which each individual is subjected increases immediately

143   without any evolutionary processes, and vice versa. Because NDDE arising from sexual harassment

144   does not require evolutionary change, and mostly depends on the abundance of a given species,

145   sexual harassment models show relatively stable population dynamics (Fig. 1b). These two

146   mechanisms are not mutually exclusive. Further research is required to clarify the dynamics that

147   occur when both of these mechanisms occur simultaneously.

148   Harassment models suggest that flowering plants represent ideal model systems in future

149   research on this topic. Compared with animals, it is difficult for plant species to interact directly with

150   other conspecific individuals; consequently, most sexual harassment will occur in the pistils, where

151   pollen and pistils directly interact. Thus, competition between pollen tubes in pistils could be used to

152   explore mechanism of harassment (Prasad and Bedhomme 2006; Lankinen et al. 2016). Sexual

153   selection favors pollen traits to ensure fertilization success, even at an expense of some seeds from

154   the pistils. Thus, artificial pollination experiments could prove useful for clarifying the validity of

155   assumptions in modelling the effect of reducing seed production in parallel to increasing pollen grain

156   number on a stigma. Moreover, the model predicts that the optimal strength of harassment depends

157   on the number of competitors; thus, it is important to obtain information on the density of

158   conspecific individuals in sexual organisms. As direct interactions are restricted in plants, it is more

159   difficult for plants than animals to detect density, due to the lack of eye-like sensors. A stigma of a

160   flowers represents important sensor that could be used to detect the density of conspecific

161   individuals, because it can detect the presence of pollen grains on the surface. Thus, the traits of

162   pollen and flowers might change depending on the numbers of pollen donors and pollen grains after

163   pollination. Therefore, the artificial pollination experiments could provide a way of elucidating the

164   evolution of sexual harassment in plant species.

165   Various sexual traits are considered to evolve depending on density, which, in turn, impact

166   population dynamics (Kokko and Brooks 2003; Kokko and Rankin 2006). These traits evolve at the

167   same time, due to density fluctuation, even if the traits have independent genetic bases. Some of

168   these traits might improve population growth, as opposed to sexual harassment. Thus, it is important

169   to consider multiple sexual traits to clarify the generality of NDDE arising from sexual selection, and

170   to obtain an accurate interpretation of the effect of sexual selection on the biological community.

171   Next I explore three situations that several traits could evolve simultaneously.

172   There are many options to remove the negative effects of harassment (e.g., escape, physical

173   rejection of mating and physiological tolerance); however, these options are qualitative, making it

174   difficult to construct analytic models that can be applied to real organisms. One possible counter-

175   strategy for female is the evolution of tolerance to harassment, which reduces the effect of

176   harassment at the expense of reproductive cost. However, knowledge on the efficiency of tolerance is

177   required (reduction of harassment effect per reproductive cost). Studies of efficiency in real

178   organisms would be an interesting topic to explore in evolutionary biology, but might not be

179   important in community ecology because sexual harassment causes NDDE, even when the evolution

180   of tolerance is considered. Although evolutionary optimal tolerance is obscure, whenever the

181   evolution of a counterstrategy improves the fecundity of females, a given species must increase its

182   density. As a result, individuals would be subject to stronger harassment, depending on their

183   abundance. Thus, from the perspective of community ecology, models that incorporate the evolution

184   of tolerance should provide qualitatively similar results, due to the effect of NDDE.

185   Similarly, mate choice should evolve as a counterstrategy to harassment, which might reduce the

186   number of mating partners, leading to a decline in harassment. One of the simplest processes to reject

187   a part of pollen is the evolution of self-incompatibility. Removing harassment from self-pollination is

188   beneficial when harassment is strong. Thus, self-incompatibility might be adaptive when density is

189   sufficiently high, which is intuitive and easy to understand. High-density causes the fecundity of

190   females to decrease, because of male-male competition causing fertilization success rates to decline.

191   Therefore, securing seed production by an individual via the elimination of self-harassment becomes

192   relatively important. Evolution in the opposite direction, from self-incompatible to self-compatible at

193   low densities, is also explained by the model, which is similar to the classical argument that self-

194   compatible is adaptive because of reproductive assurance when pollinators or mates are scarce

195   (Darwin 1876; Tsuchimatsu et al. 2010). Around the density where the optimal strategy switches

196   between self-compatible and incompatible, the evolution of a mixed strategy might support a smooth

197   transition between them. Even when considering these transitions, sexual selection consistently

198   causes NDDE because models assuming both reproductive systems show NDDE(Kobayashi 2018).

199   Therefore, when considering the transition of mating systems, sexual selection has the potential to

200   cause NDDE consistently.

201   Other potential traits influencing population growth rates related to sexual selection exist in

202   animals, such as infanticide by males, paternal brood care, and nuptial gifts. The first example,

203   infanticide, occurs when an immigrating male encounters a mature female with siblings (Swenson et

204   al. 1997), which affects population growth rate depending on density (Moller 2004). The others are

205   cooperative behaviors of males to females and might improve the population growth rates of a given

206 species. Thus, the density dependence of these various options related to sexual reproduction and

207 mating must be considered to clarify the relationship between sexual selection and population

208 dynamics in actual communities.

209   Sexual selection theory has made a number of fundamental contributions to evolutionary

210 ecology; however, its impact on biological communities remains poorly understood. Compared to

211 tests of hypothetical mechanisms that explain the sustainability of biodiversity at the community

212 level, it is easy to explore how strongly NDDE arising from sexual harassment affects the population

213 dynamics of a certain species. By assimilating information on the conditions required for NDDEs in

214 various organisms, we might be able to ascertain when and how the stability of a given biological

215 community and ecosystem collapses. Thus, multiple disciplines of ecology must be integrated,

216 including behavioral ecology, population ecology, and community ecology, to conduct appropriate

217 experiments that clarify the properties of individual species stabilizing an ecosystem. When

218 considering the generality of sexual reproduction in nature, sexual selection theory represents a

219 central topic in multi-discipline ecology. I hope this perspective will stimulate and contribute to the

220 further development of ecology.

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328 Figure legends:

329 Figure 1.

330 Simulation results showing the demographics and evolutionary dynamics. Each plot shows 10

331   species co-occurrence over 2,000 generations by the evolutionary dynamics of **a** sex allocation and **b**

332   harassment. Each colored line corresponds to the dynamics of each species and starts from

333   approximately **a** 10^5 individuals with equal allocation (0.5), and **b** 10^6 individuals with no

334   harassment (relative productivity = 1). The number on each colored line indicates the amount of

335   available resources for the species. Using the data for **a** is the same with figure 1 in Kobayashi 2017,

336   and for **b** the same with figure 2 in Kobayashi 2018, respectively. The x axis of **b** indicates

337   productivity compared with no sexual harassment, which was decreasing due to evolution of

338   harassment.