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Abstract: Sexual reproduction is a mysterious phenomenon. Most animals and plants invest in sexual reproduction, even though it is more costly than asexual reproduction. Theoretical studies suggest that occasional or conditional use of sexual reproduction, involving facultative switching between sexual and asexual reproduction, is the optimal reproductive strategy. However, obligate sexual reproduction is common in nature. Recent studies suggest that the evolution of facultative sexual reproduction is prevented by males that coerce females into sexual fertilization; thus, sexual reproduction has the potential to enforce costs on a given species. Here, the effect of sex on biodiversity is explored by evaluating the reproductive costs arising from sex. Sex provides atypical selection pressure that favors traits that increase fertilization success, even at the expense of population growth rates, i.e., sexual selection. The strength of sexual selection depends on the density of a given species. Sexual selection often causes strong negative effects on the population growth rates of species that occur at high density. Conversely, a species that reduces its density is released from this negative effect, and so increases its growth rate. Thus, this negative density-dependent effect on population growth that arises from sexual selection could be used to rescue endangered species from extinction, prevent the overgrowth of common species, and promote the coexistence of competitive species. Recent publications on sexual reproduction provide several
predictions related to the evolution of reproductive strategies, which is an important step towards
integrating evolutionary dynamics, demographic dynamics, and community dynamics.

**Keywords:** biological community; intraspecific competition; density dependence; population
dynamics; sexual selection
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
may sustained over long timeframes (Tilman 2000). Self-regulation mechanisms of population size are known as fundamental to sustain ecological communities (May 1972; Yodzis 1981; Barabás et al. 2017; Gavina et al. 2018). These mechanisms are achieved by a negative density-dependent effect (NDDE) on population growth rates. If an NDDE exists, the density of species with low densities will increase, which prevents extinction. In comparison, overgrowth is prevented in species with high densities. An NDDE is generally explained by two mechanisms: predation pressure from natural enemies (Elton 1927; Murdoch 1969) and intraspecific competition for resources (Gause 1934; Macarthur and Levins 1967). Recently, the importance of sexual selection on population dynamics has been pointed out (Kokko and Brooks 2003; Kokko and Rankin 2006; Kobayashi 2018). NDDE arising from sexual selection results from competition for mating or fertilization success. At high densities, where strong mating competition is expected, sexual selection favors traits that increase mating success, even at the expense of population growth rates. In contrast, at low densities, this negative effect on growth rate is mitigated, because there is less competition for mating in rare species. Thus, the coexistence of many competitive species becomes possible, because sexual selection has the potential to control the reproductive rate of any sexual species. This mechanism is similar to the resource competition mechanism, because both arise from intraspecific interactions. However, when considering niche theory, these mechanisms differ slightly, because sexual selection promotes coexistence without niche partitioning between species. Given the biological species concept, which defines species as groups of interbreeding natural populations that are reproductively isolated from other groups (Mayr 1970), mating competition must occur within a given species; consequently, sexual selection works depending on the density of each species. Therefore, even if competitive species share the same niche space, the NDDE arising from sexual selection allows them to coexist stably, as long as the biological species concept holds and the mechanisms arising from resource competition do not. This case will be rare under natural conditions, because niche differentiation is favored by the natural selection of competitive species to reduce competition for
The first example that causes NDDE related to sexual reproduction is sex allocation. The most renowned sex allocation theory predicts equal allocation to male and female reproductive functions for the optimal division of resources (Fisher 1930). Because of this allocation, the production of males is considered as one of the largest costs of sex (Maynard Smith 1971; Lehtonen et al. 2012). However, equal allocation occurs under certain conditions, such as random mating and large mating populations. In situations where sons compete with each other for mating partners in a local population, the allocation to sons (or male functions, such as pollen in plants) reduces the mating success rate for each son, because strong mating competition occurs among sons for a limited number of mating partners. In comparison, greater allocation to daughters creates more mating partners for the sons. This situation is called local mate competition and was modeled by Hamilton (1967). In this model, the evolutionarily stable allocation to females is \((n + 1)/2n\), where \(n\) represents the number of mothers in a local mating population. When \(n\) is sufficiently large, equal allocation (0.5) occurs. In contrast, if a single mother is present in the local mating population \((n = 1)\), this female should allocate most of its resources to daughters. Thus, this intraspecific competition for mating promotes the evolution of highly female-biased allocation, depending on the number of mothers in the local mating population (Hamilton 1967; West 2009). Because the allocation to females is strictly linked to the population growth rate, adaptive sex allocation results in an NDDE on population growth, leading to the stable co-occurrence of competitive species (Hassell et al. 1983; Zhang and Jiang 1995; Kobayashi and Hasegawa 2016; Kobayashi 2017). Models that incorporate this mechanism have demonstrated that hundreds of species can co-occur over 10,000 generations even in homogeneous environments, recreating the observed patterns of biodiversity (Kobayashi 2017). This study (Kobayashi 2017) clearly showed that sexual reproduction has the potential to influence the ecological community via the evolutionary dynamics of sex allocation. At present, it is
not clear whether this mechanism works well under natural condition. Recent eco-evolutionary feedback studies demonstrate the importance of genetic variation (Pelletier et al. 2009; Post and Palkovacs 2009). However, there is insufficient information about genetic variation related to sex allocation at the population level. The exception is haplodiploid species that can alter sex allocation without genetic difference by controlling fertilization. Some wasps under the condition of local mate competition theory are able to adequately alter their sex allocation, depending on the number of competitors (Werren 1983; Herre 1985). Thus, hymenopteran species that exhibit local mate competition could be good material to test the relationship between NDDE and sex allocation.

Another example is sexual harassment, which is a trait of one sex (usually male) that increases its fertilization success rate but reduces the fecundity of its mating partners. Although previous empirical studies have provided evidence of the density or frequency dependence of sexual selection (Andersson 1994; Levitan 2004; Gosden and Svensson 2009; Takahashi and Kawata 2013), the relationship between the density dependence of sexual selection and population growth rate remains obscure (Kokko and Brooks 2003; Kokko and Rankin 2006), but see also (Mikami et al. 2004; Takahashi et al. 2014). Sexual harassment creates an NDDE similar to that resulting from sex allocation. For high-density species, sexual selection favors males that utilize strong harassment to increase their fertilization success rate, even at the expense of the fecundity of their mating partners. At low densities, which means fewer competitors are present, such too strong harassment becomes disadvantageous for the harasser, because it decreases the fecundity of the mating partners despite the fertilization success is secured to some extent without harassing; therefore, sexual selection generally has an NDDE on the population growth rate of sexual organisms. This situation was modeled in a recent study, which also revealed that sexual harassment has an NDDE on the population growth rate, promoting the stable co-occurrence of competitive species (Kobayashi 2018). Thus, as shown by the model of sex allocation (Kobayashi 2017), this recent study demonstrated that the evolution of sexual harassment reduces the fecundity per individual, depending
on the density, allowing hundreds of species to co-occur without niche differences.

Both of these examples show that sexual organisms, generally, have the ability to self-regulate the size of their populations. Of note, these two mechanisms generate slightly different population dynamics from the time-scale perspective. In the case of sex allocation, a change in the abundance of each species promotes an evolutionary change in sex allocation, and vice versa. Thus, NDDE arising from sex allocation takes time, because a change is required in the average sex allocation depending on genetic variation and mutations within the species. Because small populations have low evolutionary potential (few genetic variations within populations and low mutation rates per generation at the population level), relatively rare species tend to show greater variation in population dynamics than common species (Fig. 1a). In the sexual harassment models, when abundance increases, the numbers of copulation, courtship and pollinated pollen grains increase; consequently, the amount of harassment to which each individual is subjected increases immediately without any evolutionary processes, and vice versa. Because NDDE arising from sexual harassment does not require evolutionary change, and mostly depends on the abundance of a given species, sexual harassment models show relatively stable population dynamics (Fig. 1b). These two mechanisms are not mutually exclusive. Further research is required to clarify the dynamics that occur when both of these mechanisms occur simultaneously.

Harassment models suggest that flowering plants represent ideal model systems in future research on this topic. Compared with animals, it is difficult for plant species to interact directly with other conspecific individuals; consequently, most sexual harassment will occur in the pistils, where pollen and pistils directly interact. Thus, competition between pollen tubes in pistils could be used to explore mechanism of harassment (Prasad and Bedhomme 2006; Lankinen et al. 2016). Sexual selection favors pollen traits to ensure fertilization success, even at an expense of some seeds from the pistils. Thus, artificial pollination experiments could prove useful for clarifying the validity of assumptions in modelling the effect of reducing seed production in parallel to increasing pollen grain
number on a stigma. Moreover, the model predicts that the optimal strength of harassment depends on the number of competitors; thus, it is important to obtain information on the density of conspecific individuals in sexual organisms. As direct interactions are restricted in plants, it is more difficult for plants than animals to detect density, due to the lack of eye-like sensors. A stigma of a flowers represents important sensor that could be used to detect the density of conspecific individuals, because it can detect the presence of pollen grains on the surface. Thus, the traits of pollen and flowers might change depending on the numbers of pollen donors and pollen grains after pollination. Therefore, the artificial pollination experiments could provide a way of elucidating the evolution of sexual harassment in plant species.

Various sexual traits are considered to evolve depending on density, which, in turn, impact population dynamics (Kokko and Brooks 2003; Kokko and Rankin 2006). These traits evolve at the same time, due to density fluctuation, even if the traits have independent genetic bases. Some of these traits might improve population growth, as opposed to sexual harassment. Thus, it is important to consider multiple sexual traits to clarify the generality of NDDE arising from sexual selection, and to obtain an accurate interpretation of the effect of sexual selection on the biological community.

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

There are many options to remove the negative effects of harassment (e.g., escape, physical rejection of mating and physiological tolerance); however, these options are qualitative, making it difficult to construct analytic models that can be applied to real organisms. One possible counter-strategy for female is the evolution of tolerance to harassment, which reduces the effect of harassment at the expense of reproductive cost. However, knowledge on the efficiency of tolerance is required (reduction of harassment effect per reproductive cost). Studies of efficiency in real organisms would be an interesting topic to explore in evolutionary biology, but might not be important in community ecology because sexual harassment causes NDDE, even when the evolution of tolerance is considered. Although evolutionary optimal tolerance is obscure, whenever the
evolution of a counterstrategy improves the fecundity of females, a given species must increase its density. As a result, individuals would be subject to stronger harassment, depending on their abundance. Thus, from the perspective of community ecology, models that incorporate the evolution of tolerance should provide qualitatively similar results, due to the effect of NDDE.

Similarly, mate choice should evolve as a counterstrategy to harassment, which might reduce the number of mating partners, leading to a decline in harassment. One of the simplest processes to reject a part of pollen is the evolution of self-incompatibility. Removing harassment from self-pollination is beneficial when harassment is strong. Thus, self-incompatibility might be adaptive when density is sufficiently high, which is intuitive and easy to understand. High-density causes the fecundity of females to decrease, because of male-male competition causing fertilization success rates to decline. Therefore, securing seed production by an individual via the elimination of self-harassment becomes relatively important. Evolution in the opposite direction, from self-incompatible to self-compatible at low densities, is also explained by the model, which is similar to the classical argument that self-compatible is adaptive because of reproductive assurance when pollinators or mates are scarce (Darwin 1876; Tsuchimatsu et al. 2010). Around the density where the optimal strategy switches between self-compatible and incompatible, the evolution of a mixed strategy might support a smooth transition between them. Even when considering these transitions, sexual selection consistently causes NDDE because models assuming both reproductive systems show NDDE(Kobayashi 2018). Therefore, when considering the transition of mating systems, sexual selection has the potential to cause NDDE consistently.

Other potential traits influencing population growth rates related to sexual selection exist in animals, such as infanticide by males, paternal brood care, and nuptial gifts. The first example, infanticide, occurs when an immigrating male encounters a mature female with siblings (Swenson et al. 1997), which affects population growth rate depending on density (Moller 2004). The others are cooperative behaviors of males to females and might improve the population growth rates of a given
species. Thus, the density dependence of these various options related to sexual reproduction and mating must be considered to clarify the relationship between sexual selection and population dynamics in actual communities.

Sexual selection theory has made a number of fundamental contributions to evolutionary ecology; however, its impact on biological communities remains poorly understood. Compared to tests of hypothetical mechanisms that explain the sustainability of biodiversity at the community level, it is easy to explore how strongly NDDE arising from sexual harassment affects the population dynamics of a certain species. By assimilating information on the conditions required for NDDEs in various organisms, we might be able to ascertain when and how the stability of a given biological community and ecosystem collapses. Thus, multiple disciplines of ecology must be integrated, including behavioral ecology, population ecology, and community ecology, to conduct appropriate experiments that clarify the properties of individual species stabilizing an ecosystem. When considering the generality of sexual reproduction in nature, sexual selection theory represents a central topic in multi-discipline ecology. I hope this perspective will stimulate and contribute to the further development of ecology.

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Figure legends:

Figure 1.

Simulation results showing the demographics and evolutionary dynamics. Each plot shows 10
species co-occurrence over 2,000 generations by the evolutionary dynamics of a sex allocation and b harassment. Each colored line corresponds to the dynamics of each species and starts from approximately a $10^5$ individuals with equal allocation (0.5), and b $10^6$ individuals with no harassment (relative productivity = 1). The number on each colored line indicates the amount of available resources for the species. Using the data for a is the same with figure 1 in Kobayashi 2017, and for b the same with figure 2 in Kobayashi 2018, respectively. The x axis of b indicates productivity compared with no sexual harassment, which was decreasing due to evolution of harassment.