

Title: Sexual harassment sustains biodiversity via producing negative density-dependent population growth.

Running head: Sexual harassment sustains biodiversity

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Abstract

1. Mechanisms for maintaining biodiversity are still mysterious despite the considerable amount of research. The classic theory predicts that stable co-occurrence of competitive species requires niche differentiation. In fact, the co-occurring species are often differentiated from each other. However, the neutral theory assuming equivalence of the reproductive rate of all individuals regardless of the species in a biological community has successfully recreated observed patterns of species abundance distribution. This success is based on the unrealistic assumption suggesting that some mechanisms eliminate interspecific differences in the reproductive rates.

2. Here, I present sexual harassment as a candidate of the mechanisms by constructing analytical and simulation models. Sexual harassment is the traits that increase mating success even at the expense of fecundity when the species is abundant. Contrary, when the species is relatively low density, this negative effect on the fecundity is mitigated because less competition for mating occurs in the rare species.

3. The analytical model of this effect on fecundity predicted that sexual organisms stop population growth before exhausting resources due to the effect. This prediction was confirmed by simulation models. The simulations also showed that hundreds of competitive species with interspecific differences in reproductive potential can co-exist over 10,000 generations. Moreover, the species abundance distributions obtained from the simulations were similar to the patterns observed in the field data as those of the neutral theory does. Given the generality of sexual reproduction in nature, sexual harassment will play a significant role to sustain the biodiversity over a broad range of environments.

4 *Synthesis*. Evolution doesn't always maximize population growth rate. This study shows that evolution of sexual harassment controls the population growth rate according to density and stabilizes the population size. This stabilizing effect has a potential to rescue endangered species from extinction, prevent overgrowth of common species, promote coexistence of competitive species and successfully recreate observed patterns of species abundance distribution.

Key words: Density-dependence, Eco-evolutionary dynamics, Game theory, Mating competition, Neutral theory, Rank-abundance diagram, Population dynamics, Sexual harassment, Evolutionary ecology

Introduction

Biodiversity has long been a source of wonder and scientific curiosity (Tilman, 2000). An important measure of biodiversity at a particular trophic level is the species abundance distribution, which is usually illustrated in a rank-abundance diagram (RAD), where the logarithm of abundance is plotted against the rank of species in abundance (Hubbell, 2001, 2006). The RADs show a certain pattern, i.e. S-shaped form, over a wide range of ecological communities, which suggests that a general theory of biodiversity can be applied. One of the hypotheses to explain this pattern is the neutral theory of biodiversity, which assumes that all individuals have the same demographic parameters regardless of their species identity (Hubbell, 2001, 2006). Although this assumption appears seemingly unrealistic, the neutral theory has successfully recreated RADs observed in nature (Hubbell, 2001; Rosindell, Hubbell, & Etienne, 2011), which has generated a vigorous debate among ecologists because the success of the neutral theory appears paradoxical as a result of the manifest differences among species. This seemingly unrealistic assumption of the neutral theory will be explained by negative density-dependent population growth which can buffer against species differences in population growth rates. Previous theoretical works showed that this negative density-dependence is necessary to sustain complex and large ecological communities stably for a long time (Allesina & Tang, 2012; Barabás, Michalska-Smith, & Allesina, 2017; May, 1972). Otherwise the species with low abundance will be extinct stochastically. The density-dependent population growth is generally explained by the two mechanisms: predation pressure from their natural enemies (Elton, 1927; Murdoch, 1969) and/or intraspecific competition over resources (Gause, 1934). However, the mechanism controlling demography of each species on a scale sufficient to explain the biodiversity in nature remains obscure. Integrating these previous studies suggests the existence

of unknown mechanisms causing negative density-dependent population growth, which will be able to support the assumption of the neutral theory. In this paper, it is revealed that sexual harassment is one of the candidates to provide negative density-dependent population growth, and that the model supposing sexual harassment can recreate RADs observed in nature.

Sexual harassment is a trait of one sex (usually male) to increase its fertilization success rate at the expense of the fecundity of its mating partners (Gosden & Svensson, 2009; Shine, Wall, Langkilde, & Mason, 2005; Takahashi, Kagawa, Svensson, & Kawata, 2014). In flowering plants, sexual harassment occurs in the pistil after pollination but before fertilization because of pollen tube competition via chemicals that inhibit the growth of other pollen tubes (Brandvain & Haig, 2005; Lankinen & Karlsson Green, 2015). Sexual selection favors the pollen traits that increase the fertilization success rate and even damage the stigma, which may result in abortion. Without competitors (other pollen grains on the stigma), such harassment is disadvantageous for the harasser because of the increment of the abortion rate; therefore, the optimal amount of harassment depend on the number of competitors on the stigma. Thus, we can expect that evolutionary dynamics of the sexual harassment will stabilize population size of sexual organisms via regulating abortion rate of the species.

In this study, focusing on the sexual harassment, the relationship between sexual harassment and population dynamics is revealed by constructing several analytical and simulation models. Moreover, from the simulations with multiple species that suppose a biological community, it is demonstrated that this model can recreate the S-shaped RAD that is generally observed in nature.

Models

First, to clarify the relationship between sexual harassment and population dynamics, an analytical model was constructed. Supposing a structured population of self-compatible flowering plants in which individuals belong to one of the local populations that corresponds to the pollen dispersal area, and they produce pollen with harassment level h , the fitness of a mutant individual with the harassment level h^* is

$$W = \frac{h^*}{h^* + (n-1)h} nF [1 - h^* - (n-1)h] + F [1 - h^* - (n-1)h] \dots (1)$$

where n is the number of individuals in the local population (pollen dispersal area), and F is the fecundity per individual (amount of seeds) without harassment. The first term is the fitness as male, which is obtained by the multiplication of the fertilization success rate for the individual (proportion of the harassment of the mutant individual in the total harassment), the total fecundity of the local population without harassment and the total effect of harassment. The second term is the fitness as female, which represents the fecundity including the effect of harassment. To determine the evolutionarily stable strategy for the harassment level, take the derivative of W with respect to h^* and set $h^* = h$ and the value equal to zero:

$$\left. \frac{\partial W}{\partial h^*} \right|_{h^*=h} = \frac{(n-1)F}{nh} - (n+1)F = 0 \dots (2).$$

This expression provides the following solution:

$$h = \frac{(n-1)}{n(n+1)} \dots (3).$$

The second derivative of W with respect to h^* is

$$\frac{\partial^2 W}{\partial h^{*2}} = \frac{-2nFh}{[h^* + (n-1)h]^3} \dots (4).$$

This is negative because reproduction doesn't occur without individuals ($n \geq 1$) and the fecundity

and the harassment levels are positive ($F, h^*, h > 0$). Then, assuming that all individuals adopt the evolutionary stable strategy (equation 3), the realized fecundity of each individual R is as follows:

$$R = F(1 - nh) = F \left(1 - \frac{n-1}{n+1} \right) = \frac{2F}{n+1} \dots\dots (5).$$

To test this analytical model and to survey the effect on biological community, an individual-based simulation was also constructed, which supposes haploid annual plant species in a homogeneous environment. The spatial structure followed an island model in which individuals belonged to one of the local populations that corresponded to the pollen dispersal area. Each individual produced pollen with a harassment level h that was dependent on the individuals' genetic value ($0 < h < 1$). This pollen was equally transferred to each stigma within the local populations. Then, each seed was fertilized by a single pollen grain, and the fertilization rate of each of the pollen grains was determined by the relative harassment level (see equation 1). Individuals in the next generation were randomly selected from the pool of seeds produced in the entire population, and they inherited genes randomly from either the mother or father. The total number of available sites for germination was fixed in the simulations. Random mutation occurred at a constant probability per generation per locus (i.e., 0.01), and then the genetic value (h) was added as a small random value (normal distribution: $\mu = 0, \sigma = 0.001$). When this value became negative, it was replaced by the minimum positive value. All the seeds that were not selected as the individuals of the next generation died, which assumed that a seed bank was not available in this simulation. After the blooming season, all the flowered individuals died and the next generation started. The simulations began with individuals with a minimal harassment level. The simulation code is available at the Dryad repository (doi:10.5061/dryad.n05rj44).

Results

The analytical result (equation 5) revealed the strong negative density-dependent effect of sexual harassment on the population growth and matched well with that of the simulation results (Fig. 1). If three individuals occur within the pollen dispersal area, then the species will lose half of the seeds because of harassment. Note that this negative density-dependent effect on population growth rate was qualitatively the same in self-incompatible and dioecious conditions (see Supporting information). In either model, R approaches zero as n increases.

To reveal this density-dependent effect of sexual harassment on the biological community, the simulation began with the individuals randomly deciding their species as one of ten species at an equal probability, and the species-specific fecundity (amount of seeds: F in the analytical model) was sequentially set from 2 to 1.1 at an equal interval (0.1). This species-specific fecundity corresponds to differences in the level of adaptation to the environment for each species, e.g., photosynthetic capabilities under certain light conditions. The competition over fertilization on the stigma occurs within species, and another competition over space for germination occurs among all the seeds in the entire community. Despite the apparent species differences in reproductive potential, these 10 species co-occurred over 10,000 generations, even in the homogeneous environment (Fig. 2A). Although the dominant species had a potential to produce the largest amount of seeds in the community, their high density led to an evolution of strong sexual harassment because of intraspecific competition over fertilization (Fig. 2B), which rapidly reduced their population growth rates (Fig. 2C). In contrast, species with relatively low reproductive potential could not achieve such high density, which resulted in less harassment (Fig. 2B). Thus, the evolution of sexual harassment induced invariant fecundity (= population

growth rates) among these species (Fig. 2C), which led to the stable co-occurrence of multiple species, even without niche differentiation.

Similarly, in the simulations that began with 1,000 species and for the species-specific fecundity that was sequentially set from 2 to 1.001 at an equal interval, the rank-abundance diagrams exhibited an S-shaped form irrespective of the community size (Fig. 3). The qualitatively same results were also obtained from the simulations supposing a lower mutation rate (Fig. S1), a normal distribution for the species-specific fecundity (Fig. S2), a limitation for the seed dispersal range (Fig. S3) and a community of self-incompatible species (Fig. S4).

Discussion

This study showed that evolutionary dynamics of sexual harassment results in a strong negative density-dependent effect on population growth rate over a broad range of conditions including self-compatible species (Fig. 1-2 and equation 5), self-incompatible species (Fig. S4 and equation 10 in supporting information) and dioecious species (equation 15 in supporting information). The self-incompatible model will also cover the condition of plants with separate male and female flowers if the function of unisexual flowers is to avoid self-pollination. Thus, these analytical models covers most of sexual reproductive systems in flowering plants. The models showed the realized fecundity of each individual R approaches zero as the density (number of individuals in a local mating population: n) increases (equation 5, 10, 15). Because R indicates the fecundity of each individual, $R < 1$ indicates that the population decreases and thus n becomes smaller in the next generation. Similarly, $R > 1$ indicates n becomes larger in the next generation. This population dynamics arising from sexual harassment changes optimal strength of sexual harassment because it alters density of the species (n). Therefore, mating competition

with sexual harassment has a potential to stabilize population dynamics of the species even when there are enough amount of available resources.

Considering this negative density-dependent effect at the community level, the evolutionary dynamics of sexual harassment regulates population growth rates of each species via density-dependent evolution, counteracts species differences in reproductive potential and thus causes invariance in population growth rates among the species in the community as far as the species reproduce sexually (Fig. 2, 3). Thus, the seemingly unrealistic assumption of the neutral theory may be common in nature due to this negative density-dependent effect. Notably, this negative density-dependence arising from sexual harassment had the effect consistently to make the community structure S-shape in RAD under the various conditions (Fig. 3 and S1-4). Therefore, this study presented the mechanism to remove the interspecific difference in population growth rates and succeeded in reproducing the pattern observed in the actual biological communities, which indicates that sexual harassment is a hopeful candidate as the general mechanism for controlling the biodiversity.

Sexual organisms must compete for mates at high densities regardless of the available resources (or niche space). Thus, the mechanism provided in this study allows huge number of competitive species to co-occur without niche differentiation as far as there are enough space to germination (Fig.3 and S1-4). Indeed, the number of species co-occurring over 10,000 generations was increased with the number of available sites in the community (Fig. 3). This finding has shown that competitive species can co-occur more easily than previously thought. Especially in the case of cryptic species that share most of resources, sexual harassment will be a prospective candidate for the mechanism to promote their coexistence. Note that such co-occurrence depending only on this mechanism will be rare in natural condition because niche

differentiation is favored by natural selection for these competitive species. Thus, under field conditions, the density-dependent effect of sexual organisms on population growth will be arising simultaneously from both intraspecific resource competition and mating competition.

The classic competitive exclusion principle predicts that stronger intraspecific competition than interspecific competition is a necessary condition for coexistence (Gause, 1934). This condition is easily achieved when the intraspecific competition over mating is supposed. Given the biological species concept, which defines species as groups of interbreeding natural populations that are reproductively isolated from other such groups (Abbott, Ritchie, & Hollingsworth, 2008; Mayr, 1970; Rabosky, 2016), mating competition must occur within the species. Therefore, the occurrence of sexual harassment will always make intraspecific competition stronger than interspecific competition.

Since Darwin's era, sexual selection has been recognized as a cause of evolution of the trait that is beneficial for mating but sometimes harmful for survival (Darwin, 1859, 1871). Although it has been an extremely popular topic in evolutionary ecology (Andersson, 1994; Jones & Ratterman, 2009; Trivers, 1972), the relationship between the sexual selection and the population dynamics remains obscure (Kokko & Brooks, 2003; Kokko & Rankin, 2006). One exception is the sex allocation theory, more precisely, the local mate competition theory that predicts female-biased allocation at low density and unbiased allocation at high density due to mating competition among sons (Hamilton, 1967; West, 2009). This adaptive dynamics of sex allocation (increment of females at low density) provides the negative density-dependent effect on population growth, and thus results in the stable co-occurrence of competitive species (Hassell, Waage, & May, 1983; Kobayashi, 2017; Zhang & Jiang, 1995). This mechanism is similar to that of sexual harassment in that it is arising from mating competition among males.

Moreover, sexual selection causes evolution of broad ranges of traits, such as mate choice and direct competition among males. Because these traits will evolve depending on the number of mating opportunities, even if these traits can evolve independently of each other, a closely related evolutionary pattern among them will be found under field conditions. What happens when these traits evolve at the same time is very interesting as a future research topic.

By explicitly including the effect of species abundance on the strength of sexual harassment, the model of sexual harassment presented here provides several qualitatively testable predictions. For examples, the relationships between number of mating partners and fecundity (equation 5, 10, 15) and between abundance and evolutionary optimal harassment level (equation 3, 8, 13) will be suitable for empirical tests. As shown in above, empirical tests of these equations in broad taxonomic groups are important not only for evolutionary biology but also for community ecology.

Understanding the process that maintains species diversity is a central problem in ecology and has implications for the conservation and management of ecosystems(Kraft, Godoy, & Levine, 2015). Considering the generality of sexual reproduction and sexual selection in plants and animals, the theoretical framework revealed here will be a significant step to understand ecosystems from the evolutionary view point.

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Data Accessibility

Data deposited in the Dryad repository: <http://datadryad.org/resource/doi:10.5061/dryad.n05rj44>

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Figure legends

Figure 1. Negative density-dependent effect of sexual harassment on fecundity.

The analytical results are drawn from equation 5: $R = 2F / (n+1)$, where $F = 10$. In these simulations, the number of the local population (pollen dispersal area) was 10^6 and each of the local populations contained n individuals. The simulation results were obtained after 10^4 th generation.

Figure 2. Sexual harassment promotes the stable coexistence of competitive species over 10^4 generations. Ten species' demographics (A), the evolutionary dynamics of sex harassment (B) and the realized fecundity per individual (C) are drawn. Each colored line corresponds to the dynamics of each species. In this simulation, the number of the local population (pollen dispersal area) and the total number of available sites for germination (community size) were 10^4 and 10^7 , respectively. Thus, each local population contained 10^3 available sites. The realized fecundities hardly changed after the 40th generation, which were stabilized around 1.0.

Figure 3. Species rank-abundance diagrams drawn from the simulation results at 10^4 th generation. Light- and dark-colored lines correspond to the results of a single simulation run and the mean of 100 simulation runs, respectively.

1 Supporting information

2 Additional Models

3 Supposing self-incompatible species, the fitness of a mutant individual with the harassment level h^* is

$$4 \quad W = \frac{h^*}{h^* + (n-2)h} (n-1)F[1-h^* - (n-2)h] + F[1-(n-1)h] \dots\dots (6)$$

5 To determine the evolutionarily stable strategy for the harassment level, take the derivative of W with
6 respect to h^* and set $h^* = h$ and the value equal to zero:

$$7 \quad \left. \frac{\partial W}{\partial h^*} \right|_{h^*=h} = \frac{(n-2)F}{(n-1)h} - (n-1)F = 0 \dots\dots (7).$$

8 This expression provides the following solution:

$$9 \quad h = \frac{n-2}{(n-1)^2} \dots\dots (8)$$

10 The second derivative of W with respect to h^* is

$$11 \quad \frac{\partial^2 W}{\partial h^{*2}} = \frac{-2(n-2)(n-1)Fh}{[h^* + (n-2)h]^3} \dots\dots (9).$$

12 This value is negative because reproduction doesn't occur if there are at least two individuals ($n \geq 2$) and
13 the fecundity and the harassment levels are positive ($F, h^*, h > 0$). Then, assuming that all individuals
14 adopt the evolutionary stable strategy (equation 8), the realized fecundity of each individual R is as
15 follows:

$$16 \quad R = F[1-(n-1)h] = F\left(1 - \frac{n-2}{n-1}\right) = \frac{F}{n-1} \dots\dots (10).$$

17 This realized fecundity is also a decreasing function of density. Note that $n > 1$ because of self-
18 incompatibility.

19 Similarly, for dioecious species, the fitness of a mutant individual (male) with the harassment level h^* is
20 as follows:

$$W = \frac{h^*}{h^* + (n-1)h} F[1 - h^* - (n-1)h] \dots\dots (11)$$

where n is the number of males in the local population (the number of pollen-donors for each stigma or number of mating trials for each female in animals). Taking the derivative of W with respect to h^* and set $h^* = h$ and the value equal to zero gives

$$\left. \frac{\partial W}{\partial h^*} \right|_{h^*=h} = \frac{(n-1)F}{n^2 h} - F = 0 \dots\dots (12).$$

Then, it gives

$$h = \frac{n-1}{n^2} \dots\dots (13)$$

The second derivative of W with respect to h^* is

$$\frac{\partial^2 W}{\partial h^{*2}} = \frac{-2(n-1)Fh}{[h^* + (n-1)h]^3} \dots\dots (14).$$

This value is negative because reproduction doesn't occur without males ($n \geq 1$) and the fecundity and the harassment levels are positive ($F, h^*, h > 0$). Then, assuming that all individuals adopt the evolutionary stable strategy (equation 13), the realized fecundity of each female R is as follows:

$$R = F[1 - nh] = F \left[1 - \frac{n-1}{n} \right] = \frac{F}{n} \dots\dots (15).$$

This realized fecundity is also a decreasing function of density.

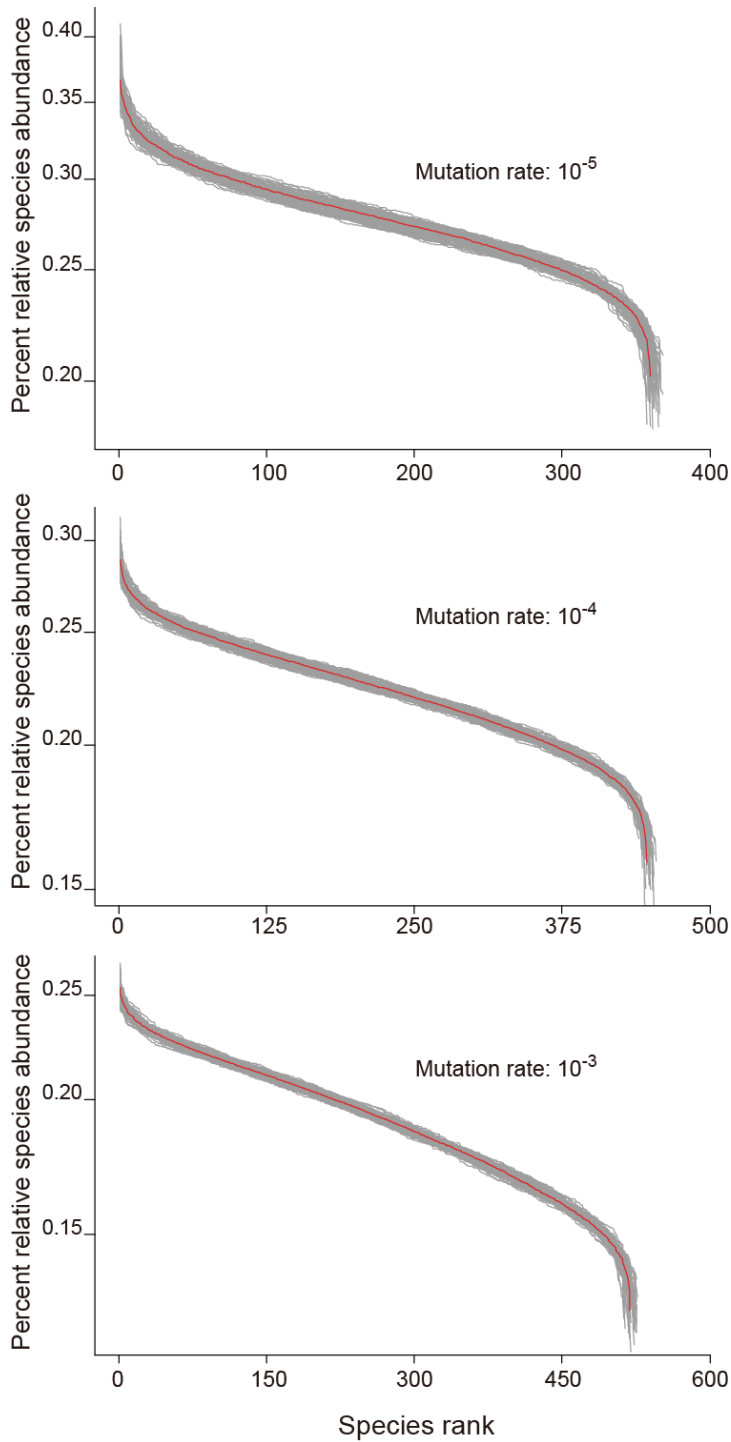


Figure S1. Species rank-abundance diagrams drawn from the simulation results supposing lower mutation rates.

The gray and red lines correspond to the results of a single simulation run and the median of 100 simulation runs, respectively. The total number of available sites for germination is 10^7 . Other parameters were the same as in Fig.3. The data was obtained at 10^4 th generation.

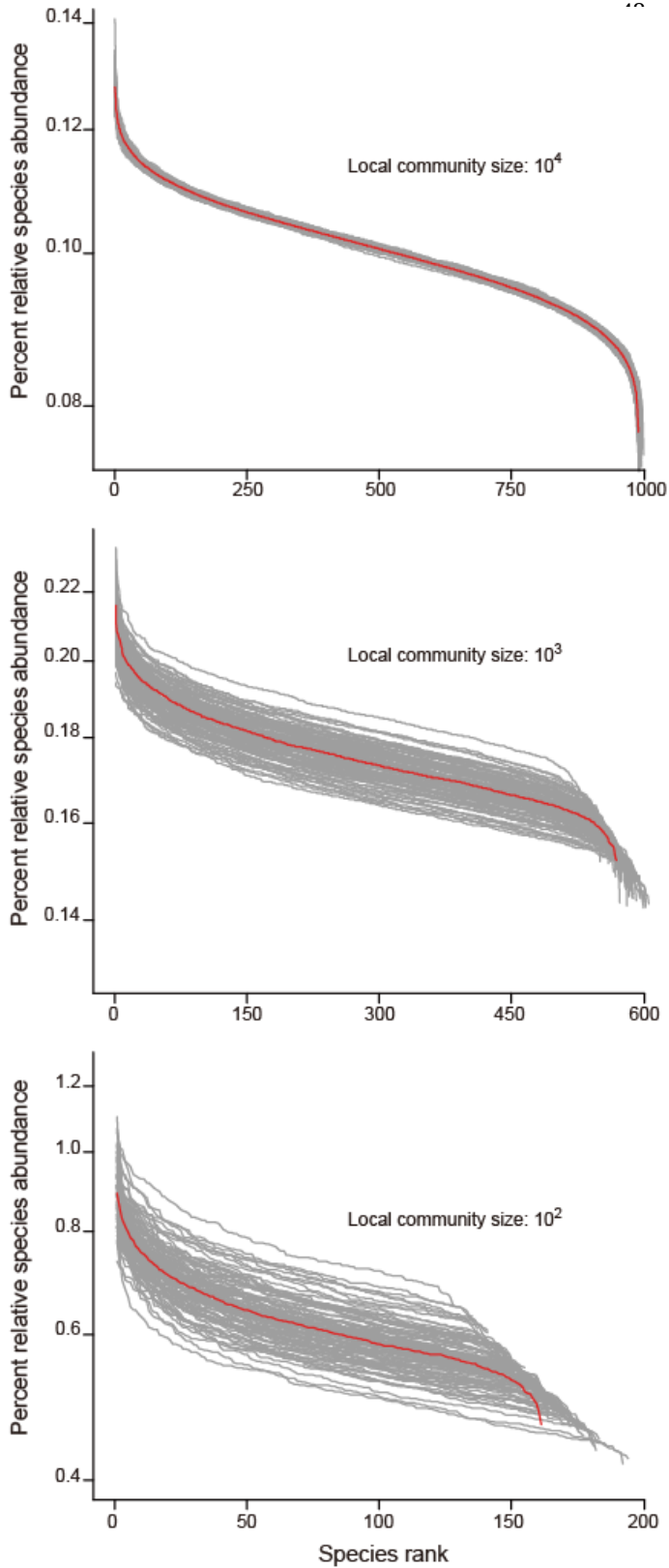


Figure S2. Species rank-abundance diagrams drawn from the simulation results using a normal distribution for the species-specific fecundity (mean = 2, s.d. = 0.1).

The gray and red lines correspond to the results of a single simulation run and the median of 100 simulation runs, respectively. The total number of available sites for germination is 10^7 . Other parameters were the same as in Fig.3. The data was obtained at 10^4 th generation.

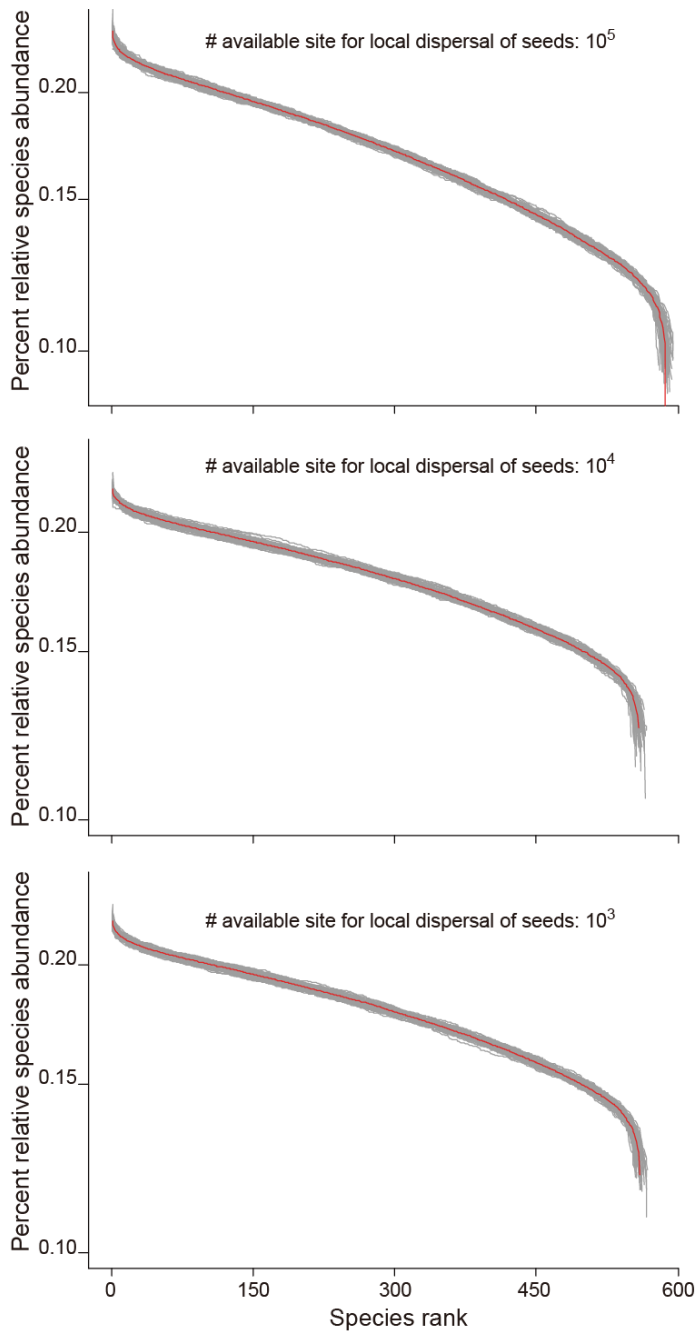


Figure S3. Species rank-abundance diagrams drawn from the simulation results supposing a limitation of seed dispersal.

In the other models, the individuals of the next generation were randomly chosen from the seeds produced in the entire community, which is unlikely to occur in nature because the dispersal distance of seeds is generally shorter than that of pollen.

Therefore, the model was modified as follows: the probability of randomly selecting individuals of the next generation from seeds produced throughout the entire community (long-distance dispersal) is small (d), and the remaining individuals will be selected from seeds produced in the local area (short-distance dispersal). In this simulation, the number of the local population (pollen dispersal area), the total number of available sites for germination (community size) and dispersal rate (d) were 10^4 , 10^7 and 0.1, respectively. The gray and red lines correspond to the results of a single simulation run and the median of

100 simulation runs, respectively. Other parameters were the same as in Fig.3. The data was obtained at 10^4 th generation.

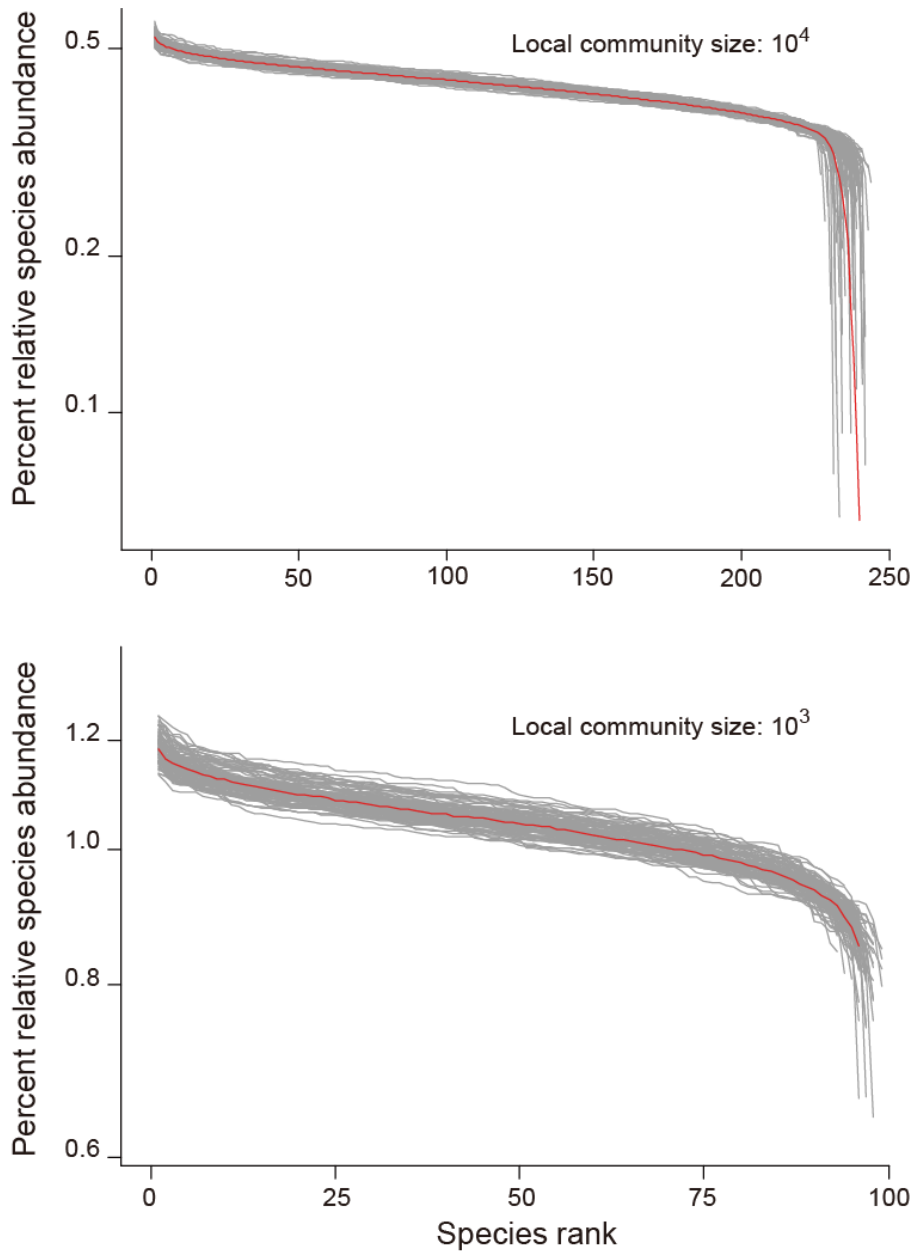


Figure S4. Species rank-abundance diagrams drawn from the simulation results supposing self-incompatible species.

The gray and red lines correspond to the results of a single simulation run and the median of 100 simulation runs, respectively. The total number of available sites for germination is 10^7 . Other parameters were the same as in Fig.3. When the local population size is 10^2 , all species extinct within 10 generations because there were almost no conspecific individuals in the local population and most of individuals fail to pollination. The data was obtained at 10^4 th generation.