

Aging asexual lineages and the evolutionary maintenance of sex

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Finite populations of asexual and highly selfing species suffer from a reduced efficacy of selection. Such populations are thought to decline in fitness over time due to accumulating slightly deleterious mutations or failing to adapt to changing conditions. These within-population processes that lead nonrecombining species to extinction may help maintain sex and outcrossing through species level selection. Although inefficient selection is proposed to elevate extinction rates over time, previous models of species selection for sex assumed constant diversification rates. For sex to persist, classic models require that asexual species diversify at rates lower than sexual species; the validity of this requirement is questionable, both conceptually and empirically. We extend past models by allowing asexual lineages to decline in diversification rates as they age, that is nonrecombining lineages “senesce” in diversification rates. At equilibrium, senescing diversification rates maintain sex even when asexual lineages, at young ages, diversify faster than their sexual progenitors. In such cases, the age distribution of asexual lineages contains a peak at intermediate values rather than showing the exponential decline predicted by the classic model. Coexistence requires only that the average rate of diversification in asexuals be lower than that of sexuals.

KEY WORDS: Adaptation, asexual lineage age, diversification rate, evolution of sex, extinction rate, lineage age dependence, Muller’s ratchet.

Asexual and selfing species exhibit low effective rates of recombination, which reduces the efficacy of selection on deleterious and beneficial mutations due to Hill-Robertson effects (Hill and Robertson 1966; Charlesworth and Charlesworth 1995; Charlesworth 2012; Hartfield 2015). This can cause the continuous accumulation of deleterious mutations and the resulting reduction in fitness a process known as Muller’s ratchet (Muller 1964; Haigh 1978; Heller and Maynard Smith 1979). In addition, low recombination rates reduce the probability of fixing beneficial mutations, lowering adaptive potential (Barton 1995; Orr 2000). It has long been speculated that these processes will elevate extinction rates in asexual or highly selfing species relative to their outcrossing counterparts (Fisher 1930; Maynard Smith 1976). As a result, it has been proposed that outcrossing and sexual lineages can be maintained by selection occurring at the species level (Fisher 1930; van Valen 1975; Maynard Smith 1976; Nunney 1989). Research on the maintenance of sex through species selection has been somewhat neglected because only lower levels of

selection can explain the persistence of sex in populations exhibiting variation in reproductive mode (Williams 1975). Within populations, sexual individuals suffer a twofold disadvantage in their genetic contribution to the next-generation relative to asexuals (Maynard Smith 1971; Williams 1975). This problem has generated extensive work in search of genetic processes that favours sex in populations despite its costs (Otto 2009). However, the presence of extant asexual and selfing species implies that individual selection does not always favor sex and outcrossing. Species selection remains a plausible explanation for the distribution of low recombining species at the tips of phylogenies (Judson and Normark 1996; Butlin 2002; Rice 2002). Here, we examine how species selection maintains sex when incorporating time-dependence in the diversification rate of asexual lineages. Specifically, we ask how such time-dependence alters the conditions for maintenance of sex at the macro level, the abundance of asexuals relative to sexuals, and the age distribution of asexual species. We primarily use the language of sex/asex but the results are also pertinent to

outcrossing/selfing as highly selfing species have low effective recombination rates and suffer a similar reduction in the efficacy of selection as asexuals. Though the model we present below is motivated by reproductive mode as the focal trait (i.e., sex/asex, outcrossing/selfing), the model applies to any trait with one-way transitions that involve age-dependent declines in the diversification rate in the derived state.

In species levels models, the diversification rate is used to describe the net change in species abundance over time due to speciation and extinction. van Valen (1975) formulated a model where sexual species gave rise to asexual species at rate, μ . If the diversification rate of asexual species is less than sexuals by a factor $1-s$, the equilibrium proportion of asexuals is μ/s assuming $0 < \mu < s < 1$. Higher transition rates to asexuality and smaller reductions in asexual diversification rate increase their equilibrium proportion. If there is variation in the transition rate among sexual lineages, selection can also reduce the transition rate because lineages with lower transition rates give rise to less asexual descendants (Nunney 1989; de Vienne et al. 2013). In this model, if transitions occur at all ($\mu > 0$), sexuals must diversify faster than asexuals ($s > 0$), else sexuals will be eventually completely eliminated. However, this requirement of lower diversification rate of asexuals may not be satisfied because nonrecombining lineages can do very well initially (as discussed below). This concern might be alleviated by the widely held belief that nonrecombining lineages will eventually perform poorly. Such statements imply that asexual diversification rates are time-dependent but this feature has not been modeled explicitly, which is our goal here.

For sexuals to persist, the classic model requires sexuals to diversify faster than asexuals. This requirement is viewed as plausible because sexual species do not suffer elevated mutation accumulation rates from processes such as Muller's ratchet that can raise the extinction rate of asexuals. Sexual populations can also diversify into novel habitats more quickly than asexual populations when adaptation involves multiple genes or is associated with sexual selection (Fisher 1930; Barton 1995; Ritchie 2007; Schluter 2009). However, there are plausible reasons to believe the reverse that newly created asexual lineages may diversify faster than their sexual counterparts. Newly created asexual lineages could have either a higher speciation rate or a lower extinction rate than their sexual progenitor. Gene flow between populations is a major barrier to speciation (and ecological divergence) in sexual taxa but is irrelevant to asexuals (Gavrilets 1999; Barraclough et al. 2003). Young asexual species can potentially diversify at high rates because speciation is unrestricted by gene flow. Asexuals may possess lower extinction rates because they do not suffer mate limitation when recovering from population crashes (Stephens and Sutherland 2000; Knight et al. 2005). Similarly, asexual migrants can colonize (and diverge in) new habitats more

easily because they do not require mates. Phylogenetic analyses of *Solanaceae* (Goldberg et al. 2010) and *Onagraceae* (Johnson et al. 2011) revealed self-compatible and asexual species have higher speciation rates than their self-incompatible and sexual counterparts, respectively (see Discussion). This hints at the possibility that the loss of sex and outcrossing may promote higher speciation rates and perhaps higher diversification rates at least initially. If true, then classic models of species selection cannot explain the maintenance of sex; highly diversifying asexuals will drive sexuals extinct. However, the longer term consequences of reduced recombination may be negative.

We do not expect the diversification rate of asexuals to remain constant over time; rather, it should decline. Extinction rates of asexual species are likely to increase over time because they are more susceptible to processes that lower population fitness than sexual species. First, slightly deleterious mutations accumulate at higher rates in asexual populations due to selective interference (Muller 1964; Hill and Robertson 1966; Charlesworth 2012). Second, environmental change may alter the optimum phenotype over time. Inefficient selection on beneficial alleles within asexual species can cause them to lag behind the optimum (Charlesworth 1993; Burger 1999). Sexual populations are less vulnerable to either process and maintain high fitness due to efficient response to both negative and positive selection. Relaxed negative selection is evident in asexual species (Paland and Lynch 2006; Barraclough et al. 2007; Neiman et al. 2010; Henry et al. 2012; Hollister et al. 2014) and highly selfing species (Cutter et al. 2008; Qui et al. 2011; Ness et al. 2012; Arunkumar et al. 2015). Positive selection is also more efficient in outcrossers compared to their highly selfing relatives (Slotte et al. 2010; Burgarella et al. 2015). In addition to increasing extinction risk, elevated rates of deleterious mutation accumulation and reduced rates of adaptation may reduce the chance of asexual speciation when colonizing new habitats. Asexual individuals from species that have accumulated deleterious mutations and exhibit low absolute fitness, perhaps realized as a low population growth rate, may be more susceptible to stochastic loss and less likely to establish in new areas, especially if this requires rapid adaptation to novel conditions. In sum, multiple mechanisms likely contribute to declining rates of diversification in asexual lineages. We expect this decline to have quantitative and qualitative consequences on the abundance and coexistence of asexual and sexual species, especially when young asexual lineages diversify faster than sexuals.

We aim to determine the conditions for sex to persist in a community of asexual and sexual species where diversification rates are dependent on lineage age. We assume that frequent recombination in sexuals prevents processes that cause age-related declines in diversification rates in asexuals. Sexual species diversify at a constant rate but occasionally give rise to asexual

species that suffer reductions in diversification rates as the lineage age due to inefficient selection; they “senesce” with respect to diversification rates. Contrary to past models, we find that coexistence between asexual and sexual species permit the presence of asexuals with (initially) higher diversification rates than sexuals. Coexistence merely requires the average diversification rate of asexual species be lower than that of sexual species.

Model and Results

We consider an evolutionary time scale relevant for speciation and extinction to occur at appreciable rates. Here, we define the diversification rate more generally as the net effect of speciation and extinction, such that the number of species within a lineage changes by a factor of its diversification rate at each time step. Sexual species suffer much less from Hill-Robertson effects and are assumed to possess a constant diversification rate, e^S . At each time step, sexuals transition to new asexual species at rate, $e^U \ll 1$; we assume transitions in the reverse direction are not possible. Transition occurs when a newly arisen asexual individual outcompetes its progenitor sexual species. Given the twofold cost of sex, we assume the transition occurs instantaneously on our time scale. An asexual species that has newly arisen from a sexual progenitor has a basal diversification rate, e^A ; asexual speciation events can be thought of as resulting in the formation of two distinct genetic clusters from one (e.g., Fonteneto et al. 2007). We define $R_0 = e^A/(e^S - e^U)$ as the basal diversification rate of asexual relative to the realized rate of change for sexual species (i.e., at each time step, sexual species grow by a factor of their diversification rate minus their transition rate to asexuals). We assume $e^S - e^U > 1$ so that sexual species always have a positive growth rate.

An asexual species progresses through age classes with each time step and we allow the diversification rate to change across age classes. We assume that asexual species have declining diversification rates over time, which are inherited by any daughter species they produce. Declining diversification rates may be due to accumulating deleterious mutations or reduced rates of adaptation, either or both of which could increase the extinction rate or reduce the speciation rate. We do not specify the mechanism through which asexual diversification rates decline; we simply assume that it does. Because the diversification rates of asexuals decreases with the age of their lineage we think of asexual lineages as “senescing” with respect to their diversification rates. If there are $n_x(t)$ asexual species in age class x at time t , then there will be $n_x(t) e^A z_x$ in age class $x + 1$ at time $t + 1$. The senescence function, z_x , reduces the diversification rate of species in age class x relative to the basal rate and declines with age, $z_{x+1} \leq z_x$.

We model the number of sexual and asexual species, in different age classes, using a system of linear equations.

$$\begin{pmatrix} N_S(t+1) \\ N_{A,0}(t+1) \\ N_{A,1}(t+1) \\ N_{A,2}(t+1) \\ N_{A,3}(t+1) \\ N_{A,4}(t+1) \\ \vdots \end{pmatrix} = \begin{pmatrix} e^S - e^U & 0 & 0 & 0 & 0 & 0 & \dots \\ e^U & 0 & 0 & 0 & 0 & 0 & \dots \\ 0 & e^A z_0 & 0 & 0 & 0 & 0 & \dots \\ 0 & 0 & e^A z_1 & 0 & 0 & 0 & \dots \\ 0 & 0 & 0 & e^A z_2 & 0 & 0 & \dots \\ 0 & 0 & 0 & 0 & e^A z_3 & 0 & \dots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix} \begin{pmatrix} N_S(t) \\ N_{A,0}(t) \\ N_{A,1}(t) \\ N_{A,2}(t) \\ N_{A,3}(t) \\ N_{A,4}(t) \\ \vdots \end{pmatrix} \tag{1}$$

$N_S(t)$ and $N_{A,x}(t)$ represents the number of sexual species and asexual species in age class x at time t , respectively; all age classes are assumed to be of equal length (i.e., one time step). The timespan within a class can be made arbitrarily short by having many age classes. If time steps are short, the diversification rate may change little (or not at all) between successive classes, as specified by the choice of z_x . Importantly, we allow for any finite number of asexual age classes but the transition matrix is truncated at an arbitrary, but very old, age class; this only negligibly affects the steady-state approximations when $R_0 < 1$ and/or when asexual diversification rate senesce (Supplementary File 1). Our form of truncation precludes a steady-state equilibrium where only asexual species exist. However, we are interested in the conditions that lead to coexistence, so we do not discuss the asexual-only equilibrium.

We solve for the only positive eigenvalue of this system, $e^S - e^U$ and the corresponding right eigenvector to obtain the stable age class distribution, \vec{u} . By normalizing all classes in \vec{u} relative to the sexual class, we obtain $\vec{u} = \{1, f_0, f_1, f_2, \dots, f_{max}\}$, where f_x represent the frequency of asexual species in class x relative to the abundance of sexual species (f_{max} is the frequency of an extremely old age class that will be very rare if net diversification rates of old lineages is less than unity). We now specify the senescence function as $z_x = e^{-2\alpha x}$, where $\alpha \geq 0$. α scales the effects of accumulating deleterious mutations (or a reduced rate of adaptation) as the asexual lineage ages and higher values of α represent faster senescence in diversification rates. We assume an exponentially decaying diversification rate (linear decay shows similar results, Supplementary File 1). We find the relative abundance of asexuals of age x at equilibrium is

$$f_x = e^U e^{(A+\alpha)x} (e^S - e^U)^{-(x+1)} e^{-\alpha x^2} \tag{2}$$

Figure 1 shows the distribution of f_x for several parameter values. Increasing senescence rates reduces the frequency of all age classes except for the first class, which transitions from sexual species. Finally, total relative frequency of asexual species, F , is

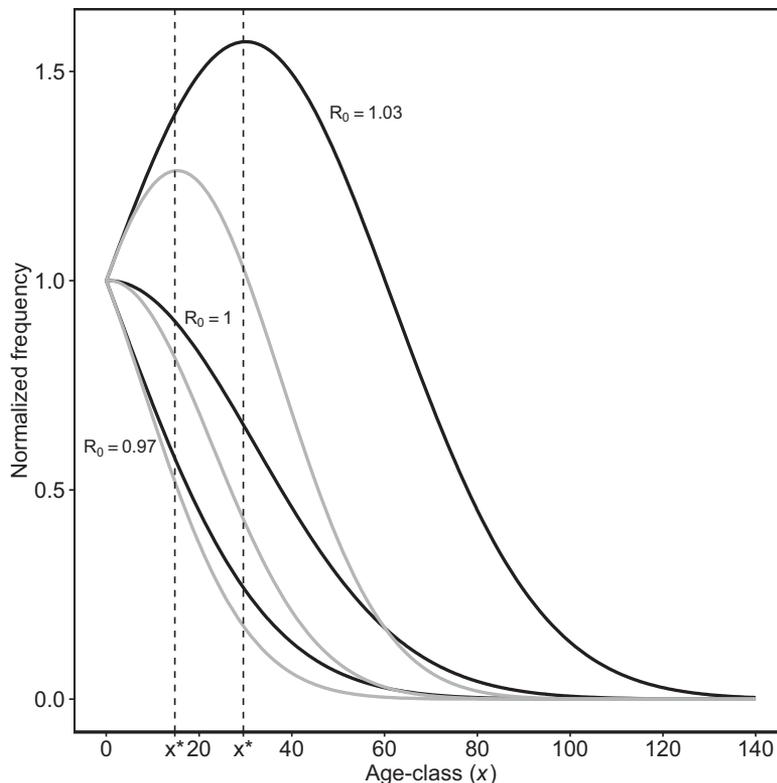


Figure 1. Distribution for the frequency of asexual species in age class x normalized to the frequency of asexual age class 0, f_x/f_0 . Black and gray lines represents case where $\alpha = 0.0005$ and 0.001 , respectively. There is a peak in f_x at class x^* when R_0 is larger than 1 (vertical dashed line).

found by summing over all asexual age classes. The frequency of asexual species among all species is then simply $F/(1+F)$.

We assume all diversification, transition, and senescence rates are sufficiently small to approximate our discrete time model with a continuous time model (as would be true if we make a sufficiently large number of short age classes). We also assume the diversification rate of asexuals never increases with lineage age ($\alpha \geq 0$). These assumptions allow our model to approximate a system with an infinite number of age classes (detailed in Supplementary File 1). Now we examine when senescence is relevant and what conditions allow sexuals and asexuals to coexist.

Constant Diversification Rates

We first ignore senescence and allow all asexual species to diversify at a constant rate by setting $\alpha = 0$ and consequently $R_x = R_0$ for all x , where $R_x = e^A z_x J(e^S - e^U)$. Note that without senescence all asexual age classes become equivalent (as in classic models), but we keep this notation for consistency when comparing to subsequent models. The total relative frequency of asexual species when we assume $R_0 < 1$ is given by

$$F_{const} = \frac{e^U}{e^S - e^U} \frac{1}{1 - R_0} \quad (3)$$

The frequency of asexual species is then equal to $F_{const} / (1 + F_{const}) = e^{U-S} / (1 - e^{A-S})$, which resembles the classical result of van Valen (1975), μ/s , described in the Introduction as $1 - e^{A-S}$ is equivalent to s and e^{U-S} is equivalent to μ . (μ can be thought of as the rate that sexuals generate new asexuals relative to generating more sexuals.) Importantly, this solution for equation (2) only converges when $R_0 < 1$, implying coexistence requires all asexual species to diversify at a slower rate than sexual species (Fig. 2A).

Strongly Senescing Diversification Rates

A limiting case occurs when senescence is very strong ($\alpha > 1$), such that most age classes contribute negligibly to the total frequency of asexuals. The total relative frequency of asexuals as α approaches infinity is

$$\lim_{\alpha \rightarrow \infty} F_{senesce} = \frac{e^U}{e^S - e^U} (1 + R_0) \quad (4)$$

With strong senescence, asexuals consists of only the first two age classes. Class 0 arises from sexuals and diversify at rate R_0 to produce class 1; class 1 and all subsequent classes diversify at negligible rates. The rate of senescence becomes irrelevant for asexual frequency once α is large enough.

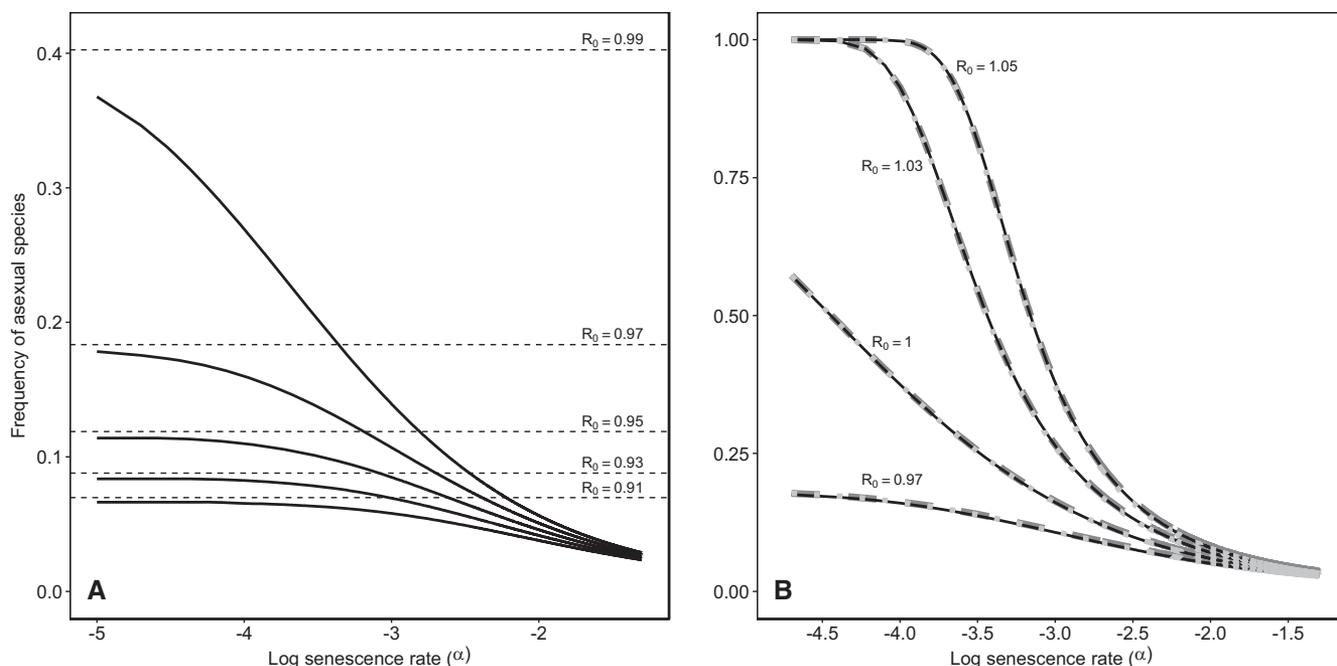


Figure 2. The frequency of asexual species, $F_{senesce}/(1 + F_{senesce})$, for a range of senescence rates (α) with $\ln(e^U/(e^S - e^U)) = -5$. (A) $R_0 = 0.91, 0.93, 0.95, 0.97, 0.99$ (top to bottom). The solid lines represent equation (5) and converge to the dashed lines, equation (3) (no senescence), with decreasing senescence rates. (B) $R_0 = 1.05, 1.03, 1, 0.97$ (top to bottom). The solid black line represents equation (5) and the dashed dark gray line indicates the numerical solution to $F_{senesce}$. The gray dotted line represents equation (3) but substituting \bar{R} obtained from equation (7) for R_0 . These three lines are difficult to distinguish because they are highly overlapping.

Weakly Senescing Diversification Rates

For weak senescence, we utilize an integral approximation to obtain the total relative frequency of asexual species, $F_{senesce} = \int_0^\infty f_x dx$. This assumes there are many extant age classes to apply a continuous approximation to the class distribution. The integral approximation fails in two scenarios where there are few extant classes. First, when R_0 is small and less than one, asexual species are very rare relative to sexual species. Senescence does not reduce asexual frequencies much further and equation (3) is sufficient to approximate $F_{senesce}$. The second case occurs under strong senescence ($\alpha > 1$). Asexual species mostly consist of the first two age classes and equation (4) approximates $F_{senesce}$. Numerical tests indicate that our integral approximation applies when the basal asexual diversification rate is comparable to or larger than that of sexuals, $R_0 > 0.8$, and when senescence is intermediate in strength, $0 < \alpha < 1$.

Under the integral approximation, the total frequency of asexual species is

$$F_{senesce} = \frac{e^U}{e^S - e^U} e^{\left(\frac{\ln(R_0) + \alpha}{2\sqrt{\alpha}}\right)^2} \frac{\sqrt{\pi}}{2\sqrt{\alpha}} \left(1 + \operatorname{erf}\left(\frac{\ln(R_0) + \alpha}{2\sqrt{\alpha}}\right)\right), \quad (5)$$

where erf represents the error function. Under our assumptions, the solution converges for all values of R_0 . As expected, increasing senescence reduced the frequency of asexual species (Fig. 2A, B). When $R_0 < 1$, $F_{senesce}$ approaches equation (3) as α goes to 0 (Fig. 2A). Coexistence of sexual and asexual lineages does not require senescence when asexuals diversify at lower rates than sexuals (van Valen 1975); senescence merely reduces asexual frequencies further. When $R_0 \geq 1$, $F_{senesce}$ approaches ∞ as α approaches 0, implying the elimination of sexual taxa (Fig. 2B) because sexuals transition into asexuals that subsequently diversify at high rates. Importantly, the inclusion of senescence, $\alpha > 0$, permits coexistence even when asexual species at the beginning of a lineage diversify at higher rates than their sexual progenitors (Fig. 2B). As discussed above, increasing α causes $F_{senesce}$ to converge toward equation (4).

We observe qualitative changes in the distribution of asexual age classes when $R_0 > 1$ compared to classic models where $R_0 < 1$. With $R_0 < 1$, the youngest asexual lineages are the most abundant and each subsequent class is rarer (i.e., $f_x > f_{x+1}$). For $R_0 > 1$, f_x initially increases with lineage age x , but once $R_x \leq 1$, each older class is less abundant than the one before due to elevating extinction rate. This forms a peak in the distribution of f_x at class $x^* = \ln R_0 / (2\alpha)$, whereby asexual species younger than x^* diversify at higher rates than sexual species

(Fig. 1). The proportion of asexual species with $R_x > 1$ is given by

$$\begin{cases} \frac{\operatorname{erf}\left(\frac{\ln(R_0)+\alpha}{2\sqrt{\alpha}}\right) - \operatorname{erf}\left(\frac{\alpha}{2\sqrt{\alpha}}\right)}{1 + \operatorname{erf}\left(\frac{\ln(R_0)+\alpha}{2\sqrt{\alpha}}\right)}, & R_0 > 1 \\ 0, & R_0 \leq 1 \end{cases} \quad (6)$$

We can summarize the growth of asexual lineages by finding the average diversification rate in asexuals relative to the realized rate of change of sexual species, $\bar{R} = \frac{1}{e^S - e^U} \int_0^\infty \frac{f_x}{F_{\text{senesce}}} e^{A_z x} dx$,

$$\bar{R} = \frac{1 + \operatorname{erf}\left(\frac{\ln(R_0)-\alpha}{2\sqrt{\alpha}}\right)}{1 + \operatorname{erf}\left(\frac{\ln(R_0)+\alpha}{2\sqrt{\alpha}}\right)} \quad (7)$$

Despite values of $R_0 > 1$, \bar{R} remains below unity provided $\alpha > 0$, because the numerator in equation (7) is less than the denominator due to the “ $-\alpha$ ” versus “ $+\alpha$ ” in the monotonically increasing error function. Coexistence with senescing diversification rates allows young asexuals to diversify faster than sexual species ($R_0 > 1$), but the average diversification rate of asexuals still falls below the realized rate of change of sexual species ($\bar{R} < 1$). Using this average rate in the classical (“no senescence”) model by substituting $R_0 = \bar{R}$ in equation (3), we recover the result for F_{senesce} given in equation (5) (Fig. 2B). This means that effects of senescence on the frequency of asexual species can be fully captured by the average growth of asexuals (though this average growth rate depends on senescence).

Variable Senescence Rates

Our model above assumes a constant senescence rate, α , implying diversification rate decays uniformly throughout the lineage’s lifetime. This may not be biologically realistic, but the extent to which genetic processes reducing individual fitness also affects ecological success and diversification is unknown. Even if asexual lineages accumulate mutations at a linear rate, the effects on extinction may not be linear (see similar discussion in Agrawal and Whitlock 2012). For example, if extinction rates only change after passing a threshold of accumulated mutations, species may initially experience no senescence followed by strong senescence. Conversely, fitness may decline initially but then stop declining in the presence of compensatory or beneficial mutations (Goyal et al. 2011), causing extinction rates to remain constant after a period of senescence. Clearly, assuming a constant senescence rate would become inappropriate and may not reflect biologically relevant dynamics in extinction rates.

To accommodate such scenarios, we allow flexibility in how diversification rate changes with lineage age. Specifically, we model diversification rate as a piece-wise function consisting of n pieces or intervals, each can be of any length encompassing one to many age classes. In principle, the piece-wise model can approximate any monotonic function of diversification rates. Within each interval, diversification rate declines exponentially with age (the rate of decline could be made zero to model constant diversification rates). Within the i^{th} interval, the diversification rate senesces at

$$\alpha_i = \begin{cases} \alpha_0, & y_0 = 0 \leq x < y_1 \\ \alpha_1, & y_1 \leq x < y_2 \\ \alpha_2, & y_2 \leq x < y_3 \\ \vdots & \vdots \\ \alpha_n, & y_n \leq x < y_{n+1} = \infty \end{cases} \quad (8)$$

where y_i represents the threshold age class where senescence rate changes for the i^{th} time, that is if age class x falls in the interval $y_i \leq x < y_{i+1}$ then its diversification rate senesces at rate α_i . We define $\alpha_i = \alpha_0 + \sum_{j=1}^i \delta_j$, such that $\delta_j = \{\delta_1, \delta_2, \dots, \delta_n\}$ denote effects of the i^{th} change in senescence rate. We now construct a continuous piecewise function, containing $n+1$ subfunctions, to describe the asexual diversification rate of age class x , D_x . The i^{th} subfunction governs the diversification rate following the i^{th} change in senescence rate and over the age class interval $y_i \leq x < y_{i+1}$, analogous to the senescence rate step function.

$$D_x = \begin{cases} e^{A-2\alpha_0 x}, & y_0 = 0 \leq x < y_1 \\ e^{A-2(\alpha_0 x + \Delta_1)}, & y_1 \leq x < y_2 \\ e^{A-2(\alpha_0 x + \Delta_2)}, & y_2 \leq x < y_3 \\ \vdots & \vdots \\ e^{A-2(\alpha_0 x + \Delta_n)}, & y_n \leq x < y_{n+1} \end{cases} \quad (9)$$

where $\Delta_i = \sum_{j=1}^i \delta_j(x - (y_j - 1))$.

Analogous to the model with a constant senescence rate, we construct a system of linear equations and use the piecewise D_x function to build the subdiagonal of the transition matrix, which describes the diversification rate of asexuals in successive age classes. As before, we find the eigenvector corresponding to the sole positive eigenvalue, $e^S - e^U$, to obtain the stable age class distribution. The relative frequency of asexual species within class x normalized to the abundance of sexual species, f_x can be written analytically as

$$\begin{aligned}
 & (e^U / (e^S - e^U))^{-1} f_x \\
 & = \begin{cases} (e^S - e^U)^{-x} e^{-\alpha_0 x^2} e^{(A-\alpha_0)x}, & y_0 = 0 \leq x \leq y_1 \\ (e^S - e^U)^{-x} e^{-\alpha_1 x^2} e^{(A-\alpha_1)x} e^{L_1 x} e^{M_1}, & y_1 < x \leq y_2 \\ (e^S - e^U)^{-x} e^{-\alpha_2 x^2} e^{(A-\alpha_2)x} e^{L_2 x} e^{M_2}, & y_2 < x \leq y_3 \\ \vdots & \vdots \\ (e^S - e^U)^{-x} e^{-\alpha_n x^2} e^{(A-\alpha_n)x} e^{L_n x} e^{M_n}, & y_n < x < y_{n+1} \end{cases} \quad (10)
 \end{aligned}$$

where $L_i = \sum_{j=1}^i 2\delta_j(y_j - 1)$ and $M_i = \sum_{j=1}^i -\delta_j y_j (y_j - 1)$. The total relative frequency of asexuals described by each subfunction of f_x is approximated by integrating over all age classes within the corresponding interval,

$$\begin{aligned}
 & (e^U / (e^S - e^U))^{-1} F_i = \int_{y_i}^{y_{i+1}} f_x dx \\
 & = \begin{cases} \frac{e^{M_i} (e^{K_i y_{i+1}} - e^{K_i y_i})}{K_i}, & \alpha_i = 0 \\ e^{\left(\frac{K_i + \alpha_i}{2\sqrt{\alpha_i}}\right)^2 + M_i} \left(\frac{\sqrt{\pi}}{2\sqrt{\alpha_i}}\right) \left(\operatorname{erf}\left(\frac{K_i - \alpha_i (2y_i - 1)}{2\sqrt{\alpha_i}}\right) - \operatorname{erf}\left(\frac{K_i - \alpha_i (2y_{i+1} - 1)}{2\sqrt{\alpha_i}}\right) \right), & \alpha_i > 0 \end{cases}, \quad (11)
 \end{aligned}$$

where $K_i = \ln R_0 + L_i$; L_i and M_i are slightly different when considering age classes on a continuous scale (Supplementary File 1). The integral approximation requires the same assumptions as that for weak senescence rates in equation (5). Similarly, the average diversification rate of asexual species relative to the realized rate of change of sexual species for each subfunction, \bar{R}_i , is given by

$$\bar{R}_i = \begin{cases} R_0 e^{L_i}, & \alpha_i = 0 \\ \frac{\operatorname{erf}(K_i - \alpha_i (2y_i + 1)) - \operatorname{erf}(K_i - \alpha_i (2y_{i+1} + 1))}{\operatorname{erf}(K_i - \alpha_i (2y_i - 1)) - \operatorname{erf}(K_i - \alpha_i (2y_{i+1} - 1))}, & \alpha_i > 0 \end{cases}. \quad (12)$$

The total relative frequency of asexuals is $F_{senesce} = \sum_0^n F_i$ and the average diversification rate relative to sexual species is $\bar{R} = \sum_0^n (F_i / F_{senesce}) \bar{R}_i$. As discussed below, $F_{senesce}$ is finite and thus sex is maintained as long as $\bar{R}_n < 1$, which is satisfied when $R_0 e^{L_n} < 1$ or $\alpha_n > 0$ due to the negative curvature of the error function. Similar to the model with constant senescence rates, the analytical solution for $F_{senesce}$ matched well with numerical solutions and by substituting \bar{R} into the nonsenescent model, equation (3) (results not shown).

We illustrate the effects of changing senescence rates with a simple example involving a single change in the rate of senescence: α_0 changes to $\alpha_1 = \alpha_0 + \delta_1$ at age class y_1 . Compared to a case with no change in α , altering α_0 by δ_1 changes the relative frequency of asexual age class subsequent to y_1 (Fig. 3A). The age class where senescence rates changes can have dramatic impacts

for $F_{senesce}$. Increasing α_0 to α_1 at a young age class drastically reduces $F_{senesce}$ compared to increasing the senescence rate at a later age (Fig. 3B). Changes in senescence rates contribute to the average diversification rate of asexuals, \bar{R} , in proportion to $F_i / F_{senesce}$ (eq. (12)). When $\alpha_1 > \alpha_0 > 0$, the effect of δ_1 decreases with increasing y_1 because the proportion of age classes that will experience α_1 also decreases with time.

Discussion

Species with low rates of recombination suffer a reduced efficacy of selection due to Hill-Robertson interference, which is speculated to lead inevitably to extinction (Hill and Robertson 1966; Haigh 1978; Lynch et al. 1993; Charlesworth and Charlesworth

1997; Bürger 1999). Our model is inspired by selective interference under little or no recombination causing the accumulation of deleterious alleles and low rates of adaptation over the lifetime of an asexual lineage, spanning multiple potential diversification events. With senescing diversification rates in asexual species, we

show that species selection maintains sex even if young asexual species diversify faster than sexuals. A value of $R_0 > 1$ is compatible with coexistence and creates a peak in asexual species frequency at intermediate age classes (Fig. 1). In contrast, coexistence in past models assuming constant diversification rates require all asexual species diversify slower than sexuals ($R_0 = R_x < 1$). Furthermore, we extend our model to accommodate age-dependent senescence, allowing diversification rates to change in almost any manner as asexual lineages age. In a lineage already undergoing senescence, a change in the rate of senescence has the most impact on asexual frequencies and average diversification rates when it occurs early on in the lineage's lifetime.

We show for both the simple and extended senescence model that maintaining sex merely requires the average growth rate of

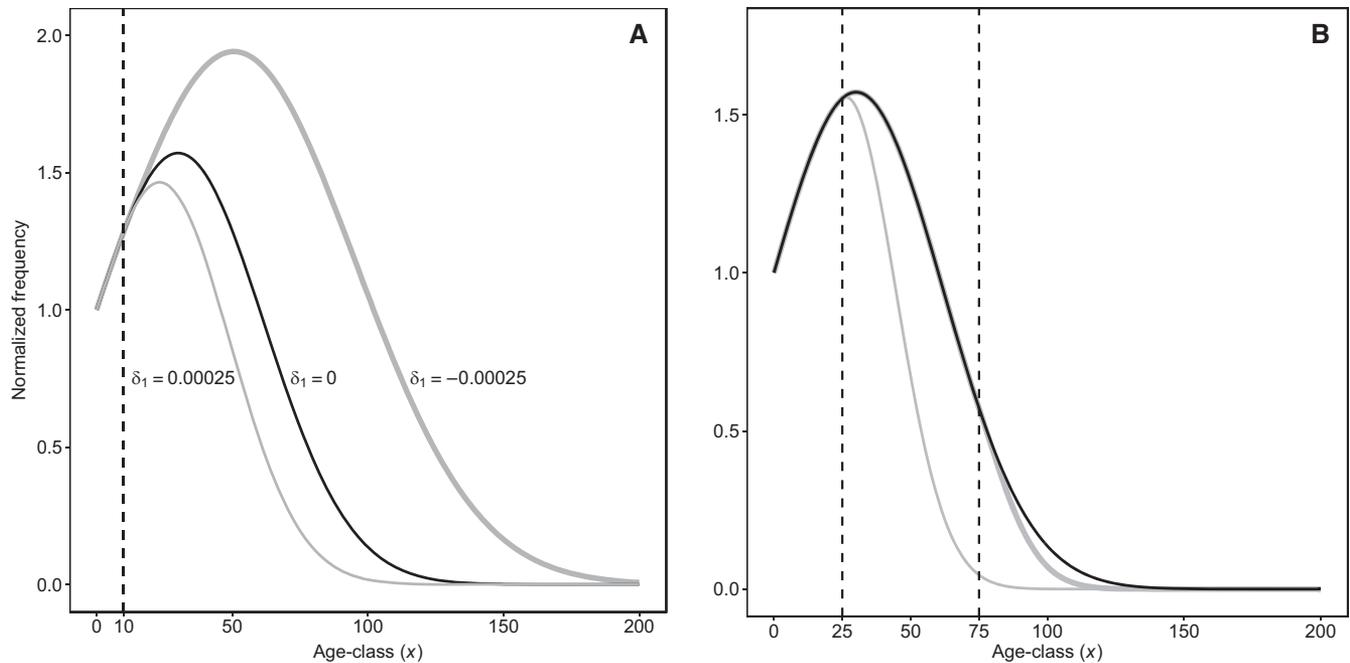


Figure 3. Distribution of the relative frequency of asexual species in age class x normalized to the frequency of age class 0, f_x/f_0 , in a model possessing two senescence rates. Here $R_0 = 1.03$ with an initial senescence rate of $\alpha_0 = 0.0005$. The solid lines in both panels indicate a case with no change in senescence rates. (A) The effects of altering senescence rate at age class 10 by $\delta_1 = 0.00025$ (gray thin line) or by $\delta_1 = -0.00025$ (gray thick line). (B) The effects of altering the senescence rate by $\delta_1 = 0.001$ at age class 25 (thin gray line) or age class 75 (thick gray line). Vertical dashed lines indicate the age class where senescence rate is altered.

asexuals relative to sexuals fall below one ($\bar{R} < 1$). This conclusion is not specific to our choice of the senescence function. A model that assumes a linear senescence function also shows that $\bar{R} < 1$ when there is senescence (Supplementary File 1). More generally, one can argue that any monotonically decreasing senescence function in which the asexual diversification rate falls below 1 beyond some age class $x_{critical}$ should allow the coexistence of sexuals and asexuals in the type of deterministic framework used here. This is because any given asexual lineage will eventually reach the age $x_{critical}$ and is then doomed to extinction. The growth of asexuals as a class is thus limited by a required replenishment from sexuals; consequently, asexuals cannot become infinitely more common than sexuals. Given coexistence, it must be the case that $\bar{R} < 1$ because at steady-state asexuals and sexuals grow at the same total rate ($e^S - e^U$) but asexuals receive input from sexual transitions ($(1/F_{senesce})e^U$) in addition to their own diversification ($(1/F_{senesce})\int_0^\infty f_x e^A z_x dx$) whereas sexuals reach this same total rate on their diversification rate alone. By this logic, the average diversification rate of asexuals is $(e^S - e^U) - (1/F_{senesce})e^U$.

The argument above for coexistence (provided that $R_x < 1$ for $x \geq x_{critical}$) does not consider interspecific competition or the discrete nature of species numbers. In reality, if young asexual lineages are very successful ($R_0 \gg 1$), they could drive all sexual lineages extinct before the asexual lineages themselves get old and evolve towards extinction. We speculate that these types of

processes do not strongly alter the conclusions in our model under conditions when the predicted equilibrium frequency of asexuals is not too high.

Two major questions arise when considering the relevance of senescence in asexual lineages. First, how large is R_0 ? If R_0 is low ($R_0 \ll 1$), then even new asexual lineages diversify more slowly than sexual ones and the long-term success of asexuals is unimportant making senescence irrelevant. Second, how much would diversification rate decline over time in a nonrecombining lineage due to accumulation of deleterious mutations and reduced adaptation?

Senescing diversification rates affect species selection when the basal diversification rate of asexual species is comparable to or larger than that for sexuals (eq. (5)). Low diversification rates of asexuals on long-time scales do not preclude high diversifying species at the base of lineages. For example, a lack of gene flow between populations and reproductive assurance can promote higher speciation and lower extinction rates in young asexual species relative to sexual species (Barraclough et al. 2003). To assess the relevance of senescing diversification rates, we can estimate diversification rates from phylogenies. Using the BiSSE model, Johnson et al. (2012) found asexual *Onagraceae* possessed higher diversification rates than sexual species but Goldberg et al. (2010) found self-compatible (SC) *Solanaceae* diversified at half the rate of self-incompatible (SI) species. At face value, we may suspect that

senescence is not important for maintaining self-incompatibility because SC *Solanaceae* have a low diversification rate. However, BiSSE does not incorporate time varying diversification rates, so the estimates may be more comparable to the time-averaged (\bar{R}) rather than the basal (R_0) rate (i.e., observed rates would underestimate R_0). Asexual *Onagraceae* and SC *Solanaceae* both possess higher speciation and higher extinction rates than their sexual and self-compatible counterparts. The estimated speciation rates are likely similar or an underestimate of the basal rate because we have no reason to believe that asexual speciation rates should increase with lineage age. In contrast, if extinction increases with lineage age, the estimated extinction rates are an overestimate of the basal rate. For these reasons, we suspect the basal diversification rate (R_0) of asexual *Onagraceae* and self-compatible *Solanaceae* are likely higher than BiSSE estimates. The low realized diversification rate in SC *Solanaceae* may actually be a result of senescence, rather than a low basal rate. Estimating basal rates awaits statistical models that account for lineage age dependence. Nonetheless, current evidence, at the very least, does not refute the idea that rates of diversification in asexual or highly selfing taxa are initially high.

Whether diversification rates change with lineage age remains difficult to test. Empirical evidence supports the assumption that asexual and selfing species suffer from inefficient positive and negative selection (Cutter et al. 2008; Slotte et al. 2010; Qui et al. 2011; Ness et al. 2012; Hollister et al. 2014; Arunkumar et al. 2015; Burgarella et al. 2015). Projections using realistic mutation rates and selection strengths predict Muller's ratchet reduces the lifetime of asexual and selfing lineages (Lynch et al. 1993; Loewe and Lamatsch 2008; Loewe and Cutter 2008). However, inferring the fitness effects of nucleotide substitutions is difficult, even if informed by protein structure changes (Lambert and Moran 1998; Henry et al. 2012). More challenging is determining whether mutations reducing individual fitness will reduce diversification rates of the species. Fontaneto et al. (2012) offer evidence that asexual bdelloid rotifers decline in diversification rates over time but the cause is unknown. Our model accommodates a wide range of relationships between age class and diversification rates. It remains a challenge to test and parameterize the effects of lineage age on speciation and extinction rates.

Lastly, we consider if current data show signatures of senescing diversification rates. Using the distribution of asexual species age, Neiman et al. (2009) revealed that asexuals have a large age variation and the so-called "scandalously" old species are not actually outliers. Alexander et al. (2016) applied a likelihood model to self-compatible (SC) clades of *Solanaceae* (Goldberg et al. 2010), and found that extinction rates decreased with species age. However, it is unclear how results may change when implementing age-dependence in extinction rates that define age from a character transition event (sex to asex) rather than a spe-

ciation. In our model, diversification rates depend on the time since an asexual lineage transitioned from sexuality; this formulation of age-dependence diversification is similar to that in the Bayesian Analysis of Macroevolutionary Mixtures model of Rabosky (2014). For the *Solanaceae* dataset, we could consider whether diversification depends on the age of an SC clade since it transitioned from self-incompatibility (SI). Following a helpful reviewer suggestion, we examine whether there is a relationship between diversification rate and clade age among the 73 SC clades in the *Solanaceae* dataset (Goldberg et al. 2010); the largest dataset, to our knowledge, that exists for this purpose. If diversification rate senesces over time, we expect a negative relationship between our estimates of diversification rate and clade age. We estimate clade age, t , as the time since an SC clade transitioned from self-incompatibility (SI) assuming no transitions from SI back to SC, which is the oldest possible age for the SC lineage (discussed below). We estimate diversification rate as $d = \log(S)/t$, where S is the number of species in a clade (Supplementary File 2). We then fit a generalized linear model assuming a quasi-Poisson error distribution for d against the absolute clade age or the rank clade age. The relationship is negative. However, measurement error in t will create a negative correlation between our estimates of d and t because the estimate of d is inversely proportional to the estimate of t . After attempting to account for this correlation via performing permutation tests, we found no evidence of clade age or rank clade age being more negatively associated with d than would be expected from the inherent negative correlation; excluding singletons does not alter our conclusions (Supplementary File 2). Although we found no evidence of senescing diversification rates in SC *Solanaceae*, there were multiple factors that obscured our efforts to detect a significant relationship between d and t . First and most importantly, SC species are not necessarily highly selfing (Wright and Barrett 2010). Old SC lineages may not senesce if they contain a single species with a modest amount of outcrossing as low rates of outcrossing are sufficient to prevent most of the negative effects associated with prolonged selfing (Hartfield 2015). Second, our estimates of clade age, which traces the clade to the nearest SI ancestor node, will overestimate the true age if the SI ancestors of SC clades went extinct or if transitions did not occur at the root. Third, sampling incompleteness may cause an underestimation of diversification rates, especially for small clades. Fourth, we are overestimating diversification rates by ignoring extinction events (Magallon and Sanderson 2001). However, accounting for extinctions in our estimation of diversification rates does not change our conclusions (Supplementary File 2). Lastly, there are factors other than senescence that can introduce rate variation among SC clades, such as the ecological conditions at the time and place of origin (Rabosky and McCune 2010) and species-specific factors attributable to themselves or their SI ancestors. Crucially, standard methods of phylogenetic

reconstruction have more statistical power for detecting signatures of temporally changing diversification rates (Rabosky et al. 2014; Hagen et al. 2015; Alexander et al. 2016). Simply using the number of species and branch lengths as we have done discards much of the information.

The role for species selection on the evolutionary maintenance of sex remains controversial. Our model expands the parameter space where asexual and sexual species coexists in a simplified world. Detecting lineage age dependence in diversification rates awaits statistical methods that confidently distinguish effects of senescence from other factors intrinsic or extrinsic to lineages. Lack of well-constructed phylogenies containing asexual/sexual or selfing/outcrossing clades also limit the scope of these analyses. Although empirical data is much needed to parameterize species selection models, we believe that our model explores a credible parameter space where senescing diversification rates affect the maintenance of sex.

AUTHOR CONTRIBUTIONS

EKHH and AFA conceived the idea and wrote the paper. EKHH performed the analyses.

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DATA ARCHIVING

The doi for data used in the figures is <https://doi.org/10.5061/dryad.6p87s>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Relationship between estimated diversification rate, d_1 , and age of SC clades.

Figure S2. Relationship between estimated diversification rate, d_2 , and age of SC clades.