Self-incompatibility (SI) is a genetic barrier to inbreeding that is broadly distributed in angiosperms. In finite populations of SI plants, the loss of S-allele diversity can limit plant reproduction by reducing the availability of compatible mates. Many studies have shown that small or fragmented plant populations suffer from mate limitation. The advent of molecular typing of S-alleles in many species has paved the way to address quantitatively the importance of mate limitation, and to provide greater insight into why and how SI systems breakdown frequently in nature. In this review, we highlight the ecological factors that contribute to mate limitation in SI taxa, discuss their consequences for the evolution and functioning of SI, and propose new empirical research directions.

The multi-faceted perils of rarity
Small populations often face instability owing to demographic and environmental fluctuations that increase the probability of local extinction [1]. When such populations are composed of self-incompatible (SI) plants, limitation in the numbers of genetically compatible mates can contribute to population decline. In this paper, we review theory and data pertaining to mate limitation in finite populations of SI species, and consider the effects of mate limitation on the evolutionary stability of SI. We suggest that the use of molecular approaches for typing diversity at the S-locus (‘S’ denotes self-sterility) will provide tools for addressing questions about the importance of mate limitation in SI taxa. By combining traditional ecological approaches for studying mating systems with the application of molecular biological approaches, a deeper understanding of the generality of limited mate availability can be gained, as well as the mechanisms by which this inbreeding barrier has been lost.

Mate limitation in SI taxa
SI systems have long been studied by plant evolutionary biologists because they strongly influence the distribution of genetic variation in populations [2,3]. SI probably evolved early during the diversification of angiosperms, and is found in nearly half of all flowering plant species [4]. Despite the variation among SI systems, most share one fundamental property: SI is controlled by a linked cluster of genes collectively known as the ‘S-locus’, and individual plants that share recognition alleles at this locus are incapable of successfully producing offspring [5]. In homomorphic gametophytic or sporophytic SI systems, mate recognition occurs when maternal S-alleles match those expressed in the haploid or diploid life stages of pollen parents, respectively. In heteromorphic SI systems, incompatibility prevents matings between individuals of the same floral morph, although matings between morphs can occur. Regardless of the specific type of SI system, sexual reproduction within populations is dependent upon the number and distribution of alleles at the S-locus. In the next two sections, we discuss factors that exacerbate the negative fitness consequences of mate limitation in small populations of SI taxa, including reductions in the number of S-alleles, population fragmentation, local pollen dispersal and limited pollinator availability.

Reduced population size, S-allele diversity and mate limitation
Population size is an important determinant of the amount of genetic variation. Theory has shown that in effectively large populations, many S-alleles should be maintained by negative-frequency-dependent selection, and surveys of allelic variation have supported this hypothesis [3,6,7] (Figure 1). In the model, it is assumed that there is sufficient compatible pollen available to plants to ensure that all ovules are fertilized. In moderately sized or small populations, however, variation at the S-locus can be lost owing to genetic drift. This is an important change in population-genetic structure because the total number of S-alleles maintained in a group of breeding individuals can strongly influence the seed production of individual plants. When compatible mates are limiting, not all ovules are fertilized, and seed production per plant will be greatest for the rarest S-locus genotypes; this has been termed ‘fecund-
ity selection’ [8]. A clear example of this phenomenon is the low seed production of the common morph in distylous *Hottonia palustris*, which was especially pronounced in the smallest of populations examined [9].

Some studies suggest that in small or low density populations, mate limitation causes extreme variation among plants in seed production [10,11] (Figure 2a–c). Direct manipulation to reduce S-allele number in experimental *Raphanus sativus* populations led to pronounced declines in seed production in small populations with high inbreeding coefficients [12]. Population studies of *Hymenoxys herbacea* found a tight relationship between the size of natural populations and the average mate-compatibility [13]. Surveys have examined patterns of mate-compatibility and seed production in natural populations of *Cochlearia bavarica* and *Ranunculus reptans*, two restricted European endemics. These experiments found a collapse in the average fruit set in populations with fewer than one-hundred individuals [14,15]. The endemic species *Rutidosis leptorrhynchoiides* has experienced strong habitat fragmentation in southeastern Australia over the past 100 years. In the smallest of populations, allozyme allele diversity in the pollen pool of *R. leptorrhynchoiides* was found to be a reduced subset of the diversity of parental genotypes, suggesting that mate limitation occurs simply because not all individuals donate gametes through pollen [16].

The stochastic loss of S-alleles in small populations will also cause an increase in population structure (FST) at the S-locus [17,18]. In a metapopulation where individual populations have lost S-locus diversity, interpopulation crosses should more often alleviate mate limitation compared to crosses between plants from the same population. Interpopulation crosses were used to determine whether seed production could be rescued in populations of *C. bavarica*, *R. reptans* and *R. leptorrhynchoiides* [19–21]. In each of these endemic species, interpopulation crosses led to increased fruit and seed set, and this effect was greatest in populations that were the smallest or had the lowest levels of genetic variation, as estimated using neutral markers [19,20]. Patterns of seed production have also been studied in remnant prairie patches of *Echinacea angustifolia* [22]. Lower levels of fertilization were observed in areas of the population with the lowest local densities. A model incorporating the effects of habitat fragmentation and stochastic loss of S-alleles showed that bottlenecks of several hundred or fewer plants might have caused the levels of mate limitation observed in small local patches of *E. angustifolia* [22].

**Pollinator activity and the strength of mate limitation realized within populations**

The amount by which seed production declines in small populations can also depend upon the activity of pollinators. In theory, if SI plants are capable of continually sampling the pollen pool until they encounter a compatible pollen grain (i.e. because they receive many visits from pollinators), these plants will compensate for lost reproductive opportunities caused by mating with plants sharing the same S-allele(s) [23]. Complete reproductive compensation is expected in populations of SI plants in which pollinators are abundant and bring about transfer of pollen between many individuals. If, however, flowers are visited by few pollinators, then they might receive pollen from one or a few pollen donors [24]; because few S-alleles would be sampled in the process, cross-incompatibility is probable (Figure 2d–f). Pollen limitation of seed set is a common phenomenon in populations of SI plants [25], and smaller or less dense populations have been shown to attract fewer pollinators [26–28]. Lower levels of pollinator service in small populations and the resulting effects on individual seed production is a specific manifestation of the Allee effect (see Glossary) [29,30]. Although declines in pollinator visitation in small or low density natural populations are generally expected to exacerbate mate limitation in SI species [31], a recent study found that elevated pollinator activity in small populations did, in fact, attenuate the effects of limited S-allele diversity [13].

Because field and theoretical studies demonstrate that both the size of natural populations and the level of polli-
nator activity can influence mate limitation, it will be important for future investigators to account for variation in both S-allele diversity and pollinator activity in studies aimed at understanding the ecology of mate limitation in SI populations.

Evolutionary consequences of mate limitation
Mate limitation lowers individual reproductive output and increases the probability of population extinction [29]. Once populations have lost a sufficient number of S-alleles and individual seed production declines, per-capita population growth rates should fall. Under these conditions, natural selection should favor new mutations that disable or modify the SI reaction because these alleles will have higher intrinsic rates of increase. Below, we discuss the potential evolutionary pathways taken by populations that can experience the selective loss of SI, either through the evolution of pseudo self-compatibility (PSC) or self-compatibility (SC).

Population declines and the possibility of extinction
Low individual seed production in mate-limited populations can endanger population persistence. If the population suddenly declines in size, few S-alleles will survive the bottleneck, and extinction can be inevitable unless pre-existing SC mutations spread and ‘rescue’ reproduction. This ‘filtering’ mechanism was originally invoked to explain the evolution of SC on islands, where a single SC seed can establish a new population following colonization [32–34]. There is compelling evidence to suggest that precipitous population declines do, in fact, occur in natural populations. Populations of the endangered lakeside daisy, Hymenoxys acaulis var. glabra, were monomorphic at the S-locus and were incapable of producing fruit [35]. Complete or nearly complete losses of S-allele diversity require catastrophic bottlenecks, which are possible in populations inhabiting a fragmented landscape. Less severe bottlenecks are probably more likely to occur in nature, although these will also cause S-alleles to be lost from populations.

Figure 2. Distributions of mean fruit set in 250 simulated populations possessing a sporophytic SI system with codominant allele expression. (a–c) In each trial, the mutation rate to new alleles is $\mu = 0.0001$ and populations of size $N = 250$ (a), 50 (b) and 25 (c) plants. (d–f) The number of pollinator visits was varied in populations of 100 individuals, with 3 (d), 2 (e) or 1 (f) visits per flower; in cases of multiple visits per flower, the pollinator could visit a different pollen donor each time with probability $1/N$. In each simulation trial, populations were enabled to attain the quasi-equilibrium number and frequency distribution of S-alleles expected before assessing fruit-set distributions.
owing to genetic drift [22]. Population declines of varying severity were implicated in limiting the seed production of individuals in populations of *Aster furcatus*, a restricted endemic [36]. In some of these populations, the majority of individuals produced little or no fruit, suggesting the nearly complete loss of allelic diversity at the S-locus.

**The evolution of PSC**

Quantitative variation in the strength of the SI response is a phenomenon that has long been recognized in various SI systems [37–40]. In other words, the SI response of a plant can be 'leaky', such that it exhibits PSC. PSC can be caused by S-allele products that are expressed at low levels in flowers [41], the action of one or several modifiers that influence the efficacy of the SI reaction [38], or be associated with post-pollination mechanisms such as floral abscission and fruit abortion [23]. A common indicator of PSC in species with SI systems is the production of small fruits with few or small seeds following natural or enforced self-pollination, or the weakening of the SI response in older flowers [40,42,43]. PSC mechanisms seem to be widespread among species with SI systems (for a review, see [37]). This is perhaps not too surprising because modifiers of S-allele expression can enable selfing once opportunities for outcrossing have elapsed; in fact, delayed selfing should nearly always be favored by natural selection because it enables for the 'best of both worlds' (i.e. plants outcross first and self if no other pollen is available [44,45]). Recent theoretical papers have confirmed this idea, showing that quantitative variation in SI might reflect an evolutionary stable mating strategy in the face of variable pollen delivery [23,46].

The emerging picture from research into the multiple losses of SI in the genus *Arabidopsis* supports the idea that PSC can be an evolutionary transition to high levels of self-fertilization. There is marked variation among individuals and populations in the strength of the SI response in *Arabidopsis lyrata* var. *lyrata* in North America [47]. Populations that have experienced the loss of SI are genetically less variable [48]. In this species, there does not seem to be a strong indication that the loss of SI occurs more frequently in smaller populations – it does seem, however, that the recent history of post-glacial colonization was important. The historical chain of events that seem to have led to the loss of SI and the evolution of self-fertility in *A. thaliana* is similar to that invoked in the case of *A. lyrata*, although there is more information on the genetic modifications that have disabled SI in *A. thaliana*. The loss of SI might have started with the weakening of the incompatibility response in older flowers [43], which would be selectively favored during the post-glacial colonization of habitats by this weedy plant [47]. Moreover, it seems that, within this species, there were several independent losses of the SI reaction [49–51], and the loss of variation at the S-locus has been gradual [52]. In support of this idea, the S-locus pseudo-genes of *A. thaliana* are still extremely variable in comparison to the genomic average [53]. Taken together, these independent pieces of evidence suggest that natural selection, facilitated by a lack of mates during colonization, might have led to the gradual fixation of multiple, independent mutations that weakened or disabled the SI system throughout the geographic range of *A. thaliana*.

**Selective spread of non-functional S-alleles enabling SC**

It has often been suggested that SI systems breakdown when non-functional S-alleles (causing SC) invade natural populations and are swept to fixation [49,54,55]. In many natural systems, it might be possible for both PSC and SC mutations to be present in populations [47,56–59] because both will be selectively favored under conditions of mate limitation. However, even in populations that do not experience mate limitation, SC mutations should equilibrate at some intermediate frequency dictated by the level of inbreeding depression and rate of selfing [54]. With mate limitation, SC mutations should be quickly driven to high frequencies unless inbreeding depression is extreme [23,46]. Given the widespread occurrence of pollen limitation of seed set, one would expect that there should be many observations of SC mutations that have been fixed by natural selection, thereby disabling the SI mechanism. Interestingly, although there have been indications of a low frequency of SC individuals within natural populations of SI plants [47,56–63], as well as direct genetic evidence of SC mutations segregating at low frequency in populations or cultivars [64–68], there is also evidence that the loss of SI might not always be caused by the rapid fixation of SC mutations at the S-locus [47,53].

Theory makes specific predictions regarding the specific kinds of SI-disabling mutations that should be recruited
when SC is favored. In particular, mutations that disable the pollen component of recognition should have the highest rates of increase when they appear in natural populations; such mutations reduce mate limitation through both pollen and seed if they enable self-fertilization [69]. By contrast, mutations that disable maternal recognition do not alleviate mate limitation as a pollen parent, although they do enable self-fertilization. Molecular investigations into the genetic basis of SC mutations have found support for the occurrence of mutations that disable pollen function [62,64–66], maternal function [60,64–67] or both [61]. Perhaps the most compelling generality from these studies is that there are often several independent mutations conferring SC within a single species. Although it is clear that SI systems are lost recurrently, there is a need to determine whether mate limitation plays a role in this repeated evolutionary trend at the population level.

**Recessive S-alleles in sporophytic SI systems**

In sporophytic (as opposed to gametophytic) SI systems, there is the further possibility for a unique evolutionary response to mate limitation and limited S-allele diversity. In these systems, some alleles have recessive phenotypes. If two mates are heterozygous for the same recessive S-allele, they can still produce offspring; this enables recessive S-alleles to be found at relatively high frequencies in natural populations. Empirical studies of S-allele diversity in nature and in cultivars have found evidence in favor of

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**Box 2. Neutral genomic variation and S-allele diversity**

The variation found at neutral loci should reflect the balance of mutation and genetic drift. Putatively neutral nuclear genetic markers (e.g. allozymes, non-coding sequences and microsatellites) can provide estimates of effective population size (\(4N_e\)), which will reflect recent historical bottlenecks or fluctuations in overall number. Using microsatellite loci in populations of the Corsican endemic *Brassica insularis*, a recent study examined both S-allele diversity and estimated parameters describing genetic variation (Figure I) [71]. Estimates of microsatellite heterozygosity and effective population size were markedly reduced in the smallest population (Punta Calcina; Table I). Interestingly, positive inbreeding coefficients across microsatellite loci indicated departures from random mating even in three of the larger populations; this might be the result of many recessive S-alleles that are broadly distributed throughout the range of the species. Indeed, each of the two recessive S-alleles in this species are distributed in at least four of the studied populations, whereas alleles with more codominant expression are restricted to fewer locales.

It is also evident from this study that populations must be small (and, therefore, that genetic drift must be strong) so as to promote the loss of S-alleles. The Punta Gobaghiola and Punta Calcina populations have approximately three- to fourfold reductions in effective size compared with the other studied populations. However, S-allele diversity seems to have declined only in Punta Calcina, which currently harbors 80 plants, of which about half were flowering. Interestingly, Punta Calcina harbors a single recessive S-allele at high frequency (ranging from 45–90%, depending upon details concerning assumptions about inferring homozygous S-locus genotypes). A shift in this population toward one high frequency recessive allele is consistent with mate limitation of reproduction in Punta Calcina.

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**Table I. Estimates of population-genetic parameters in Brassica insularis**

<table>
<thead>
<tr>
<th>Population</th>
<th>Population size</th>
<th>% flowering</th>
<th>S-allele # (range)</th>
<th>(H_e)</th>
<th>(F_{IS})</th>
<th>(\Theta)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Teghime</td>
<td>2000</td>
<td>17</td>
<td>18 (15–19)</td>
<td>0.58</td>
<td>0.217*</td>
<td>10.48</td>
</tr>
<tr>
<td>Caporalino</td>
<td>1500</td>
<td>27</td>
<td>24 (19–31)</td>
<td>0.63</td>
<td>0.158*</td>
<td>8.43</td>
</tr>
<tr>
<td>Inzecca</td>
<td>500</td>
<td>55</td>
<td>15 (11–31)</td>
<td>0.48</td>
<td>–0.003</td>
<td>6.25</td>
</tr>
<tr>
<td>Punta Gobaghiola</td>
<td>300</td>
<td>70</td>
<td>16 (12–16)</td>
<td>0.50</td>
<td>0.147*</td>
<td>2.38</td>
</tr>
<tr>
<td>Punta Calcina</td>
<td>80</td>
<td>56</td>
<td>8 (5–19)</td>
<td>0.22</td>
<td>0.045</td>
<td>1.08</td>
</tr>
</tbody>
</table>

*Reproduced, with permission, from Ref. [71].

*Expected heterozygosity \((H_e)\), the scaled effective population size parameter \(\Theta = 4Ne\), and inbreeding coefficients \((F_{IS} = 1 – \frac{H_0}{H_e})\) (where \(H_0\) is observed heterozygosity) were estimated using 11 microsatellite markers.

*Asterisks denote significant departures from random mating.*
the hypothesis that mate limitation can cause populations to experience shifts toward a higher frequency of recessive alleles [69]. For instance, in the small populations at the western and eastern edge of the species range of Ipomoea trifida, there are fewer S-alleles maintained, and the relative frequency of the most recessive S-allele is nearly double that observed in larger, more geographically central populations [70]. In another study, the smallest population of the Corsican endemic Brassica insularis maintained few alleles, with the most common one being recessive [71]. Work on the Oxford ragwort (Senecio squalidus) also suggests that bottlenecks-induced losses of S-allele diversity drive shifts toward recessive alleles [72–75], although the selective enrichment of recessive alleles has also been invoked to explain increased mate availability in introduced populations of Senecio inaequidens [76]. In general, there has been much recent progress in our understanding of the forces influencing the evolution of dominance in sporophytic SI systems [77] (Box 1).

Empirical research directions
Molecular approaches to studying S-locus diversity are likely to be useful for addressing how and why mate limitation occurs in natural SI populations and its evolutionary consequences. Recent identification of the proteins involved in SI has made it possible to employ S-allele variation as a direct tool to study the functioning of mating systems in populations of a growing number of wild species in the Brassicaceae (Arabidopsis [78], Capsella [79] and Leavenworthia [80]) and the Solanaceae (Petunia [62], Solanum [41] and Witheringia [63]). These species might serve as models for understanding the strength of mate limitation, and the spread of mutations that weaken or disable SI. Below, we propose several exemplary experiments that we believe will further our understanding of mate limitation as a selective force in SI populations.

Are most SI populations mate-limited?
The generality of mate limitation in SI species is an important issue. It is possible that it is important only in geographically restricted species or in populations that have become fragmented. By determining the S-locus genotypes of individuals via direct amplification of S-linked loci, it should be possible to relate variation in S-allele diversity to reproductive success. Once mate limitation has been quantified, it should then be possible to relate this phenomenon to potential explanatory variables (e.g. population size, stability, isolation and/or loss of pollinator service, etc.). These experiments could provide a starting point for identifying threats to the persistence of individuals and populations, particularly in SI species with restricted ranges [19–21].

How important are historical bottlenecks in causing mate limitation?
Population genetic theory suggests that population size crashes limit S-allele diversity and cause mate limitation. Identification of populations for the study of mate limitation can be facilitated by acquiring estimates of the effective population size using neutral genetic markers; this measure encapsulates fluctuations in the recent demographic history [47,71,75]. If mate limitation has caused a shift toward greater amounts of mating between relatives or self-fertilization in a leaky SI system, estimation of population mating system parameters and

Box 3. Natural selection of SC mutations via pollen and seed
Once one identifies a mutation causing SC, it should be possible to study the evolutionary forces acting on it. This is a potentially important approach because it could enable investigators to measure directly how natural selection operates on the strength of SI. Although we might expect transient positive (negative) selection on S-alleles as they fluctuate below (above) their deterministic equilibria, persistent positive selection on a SC mutation might be expected for two reasons. First, SC alleles have a natural transmission advantage through paternal function because SC pollen grains should, in theory, not be recognized by functional S-alleles. Second, if mate limitation is restricting the seed production of maternal plants with functional S-alleles, then SC genotypes should enjoy a seed benefit because they enable self-fertilization.

The relative fitness advantage of a SC mutation via either of these pathways can be quantified if one genotypes individuals at the S-locus using PCR-based amplification of specific S-alleles [78]. For example, assume that the population contains n alleles (S₁, S₂, ..., Sₙ), which occur at frequencies (p₁, p₂, ..., pₙ) in the parents. In the absence of selection via male function, the frequency of any given S-allele in the pollen pool should be equal to its relative frequency among the parent plants in the population. Thus, for a focal S-genotype (e.g. S₁S₁) one can calculate the observed frequency of the nth S-allele in the progeny and compare it to that expected in the absence of selection (p₁(expected)).

If the nth allele is a SC mutation that is spreading because it avoids rejection by functional S-alleles, then one should observe a greater number of these alleles transmitted to progeny via pollen than expected in the absence of selection (p₁(observer) > p₁(expected); Figure I). It is easier to show that the nth S-allele confers a selective advantage through seeds. Natural selection of an S-allele via a seed advantage is implicated whenever the average seed production of the nth haplotype is significantly greater than the average seed production of all haplotypes (Figure II).
inbreeding coefficients should also reflect departures from patterns expected under random mating [48]. A recent study of B. insularis (Box 2) provides an excellent example of this approach because it used highly variable microsatellite markers to infer historical population sizes and to motivate future studies of a population that might be experiencing mate limitation [71].

**Does mate limitation drive the loss of SI in natural populations?**

Although the recurrent loss of SI systems has often been invoked as a major evolutionary trend in angiosperms [81], our ability to understand the population-level mechanisms that underlie such losses has increased in the past decade. It will be important to determine whether mate limitation selects against SI genotypes by studying plant species where the evolution of PSC or SC has occurred recently. Recent breakdown of SI, where SI and SC (or PSC) genotypes co-occur in the same population, provides an important opportunity to compare seed production of both SI and SC (PSC) genotypes directly [47,56,57,59], and, therefore, gives investigators the ability to implicate natural selection in the evolution of the mating system. For example, a study of Solanum carolinense identified a ‘leaky’ S-allele causing PSC [41]. Given this evidence and the ability to amplify the allele directly, it should now be possible to determine whether this allele enjoys a selective advantage in natural populations, and to determine whether selection is strongest in populations experiencing mate limitation (Box 3).

Traditional approaches, such as the genetic analysis of hybrids and phylogenetic studies of mating system transitions, have advanced our understanding of the evolutionary paths taken between SI and SC. For example, the historical chain of events involved in the evolution of PSC or SC has been illuminated by creating experimental hybrids between plants from closely related SI and SC species [79]. This approach recently implicated a mutation causing delayed selfing in the loss of SI in A. thaliana [43]. However, it can sometimes be difficult to identify the mutation(s) causing the initial loss of SI because all of the genes in this signaling pathway should evolve neutrally once the SI system ceases to function [82]. Phylogenetic studies have provided, and will continue to provide, important insights into the loss of SI because these studies continue to provide valuable information on the minimum number of times SI has been lost, as well as the ecological correlates that might have favored or disfavored the maintenance of inbreeding barriers [54,82–85]. Direct studies of selection on S-alleles should complement these approaches by implicating the selective processes that disable SI systems or stabilize mixtures of SI, PSC and/or SC genotypes at the population level.

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**References**

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