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Inbreeding and Outbreeding Depression in Wild and Captive Insect Populations

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Abstract

Major changes in genetic variation are generally considered deleterious to populations. The massive biodiversity of insects distinguishes them from other animal groups. Insect deviant effective population sizes, alternative modes of reproduction, advantageous inbreeding, endosymbionts, and other factors translate to highly specific inbreeding and outbreeding outcomes. We review the evidence for inbreeding and outbreeding depression and consequences across wild and captive insect populations, highlighting conservation, invasion, and commercial production entomology. We not only discern patterns but also explain why they are often inconsistent or absent. We discuss how insect inbreeding and outbreeding depression operates in complex, sometimes contradictory directions, such as inbreeding being detrimental to individuals but beneficial to populations. We conclude by giving recommendations to (*a*) more comprehensively account for important variables in insect inbreeding and outbreeding depression, (*b*) standardize the means of measuring genetic variation and phenotypic impacts for insect populations so as to more reliably predict when inbreeding or outbreeding depression applies, and (*c*) outline possible remediation options, both nongenetic and genetic, including revision of restrictive international trade laws.

1. INTRODUCTION: INSECT-SPECIFIC DIFFERENCES FOR INBREEDING AND OUTBREEDING DEPRESSION

1.1. The Importance of Inbreeding and Outbreeding Depression for Insects

Insects are critical to ecosystems and food security, and knowledge of inbreeding and outbreeding depression is important for maintaining the health of wild and captive populations. Wild insect populations are rapidly undergoing extinctions and biomass loss (147), but the contributions of genetic variation changes are complicated and variable. For example, genetic variation reduction from habitat loss and fragmentation is often linked to species declines (147), yet some insects have become the most problematic invasive species in the world with only a few founding individuals (12). Meanwhile, insects are increasingly being reared for conservation or for commercial purposes such as biological control, pollinator services, feed and food, and technical products (111, 144). However, breeding programs are sustainable only when the dynamics of genetic variation in maintaining population health or desirable traits are understood. Thus, it is important that we have working knowledge of how to predict, detect, and remediate in- and outbreeding depression in insects.

1.2. Problems of Defining Inbreeding and Outbreeding Depression for Insects

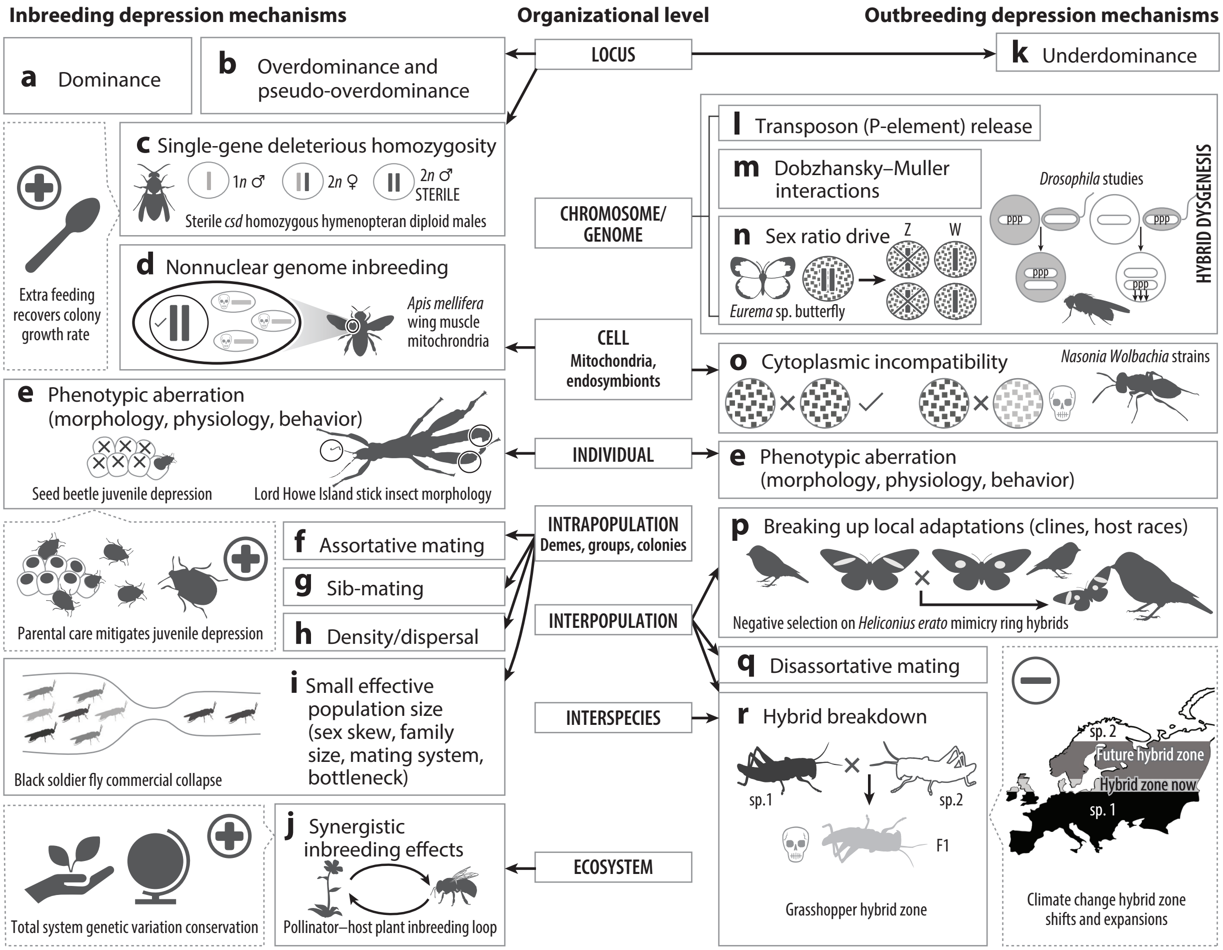
In the extensive history of research on livestock species, threatened mammals, birds, and plants (112, 156), inbreeding and outbreeding depression studies have yielded generally consistent results of deterioration in fitness with inbreeding (27, 78, 85, 97). For numerous reasons, the consistency among results is less applicable to insects. Understanding the control of invasive insects and breeding optimization for threatened and commercial insects is hindered by the low number of inbreeding and outbreeding studies proportionate to their massive diversity and by the enormous variability of their reproductive systems and life histories.

The general principles of in- and outbreeding depression also apply to insects: Inbreeding depression refers to detrimental effects in the offspring of closely related individuals, and outbreeding depression is the offspring of two populations that have lower fitness than either purebred parental population (93). The mechanisms of inbreeding depression are within-locus interactions of deleterious recessive allele accumulation (dominance theory) and increased frequency of disadvantaged homozygotes over advantaged heterozygotes (overdominance theory). In contrast, outbreeding depression arises from interloci interactions (93), the breaking up of gene complexes that coevolved for optimal fitness (hybrid dysgenesis) (**Figure 1**). Classic examples from *Drosophila* are interline cross-negative epistatic interactions (Dobzhansky–Muller interactions) (115) and deleterious transposons (P-elements) being released in new backgrounds, as co-evolved suppressor elements are no longer present (61). Outbreeding depression can also dilute the number of beneficial mutations that went to fixation under specific conditions and local adaptation (31). An interesting case is that of the butterfly *Heliconius erato*, whose mimicry rings produce perfectly viable hybrids that nonetheless have an increased predation rate because their intermediate phenotypes are no longer recognizable as either toxic mimic species (55).

Both for insects and in general, there have been far more studies of inbreeding than outbreeding. Insect inbreeding studies often report on heterozygosity loss (but also often report no genetic variation data at all). Usually, dominance (recessive allele accumulation) is assumed to be the causal mechanism for inbreeding depression, but it is difficult to distinguish from overdominance (heterozygote advantage). In addition, fundamental inbreeding and outbreeding depression centers on the concept of population fitness (i.e., the level of viable offspring production across all individuals) (42, 112, 156). This idea, however, is inadequate to capture the complexities of inbreeding and outbreeding depression concepts across applied and theoretical entomology for the reasons described below (**Figure 2**).

1.2.1. Various types of measures, yet few values for insect genetic variation. Inbreeding indisputably reduces genetic variation and outbreeding increases it, but there are different means of quantifying genetic variation. Neutral genetic diversity markers include microsatellites, synonymous single-nucleotide polymorphisms (SNPs), and genome-wide heterozygosity markers. In contrast, the genetic diversity of specific segregating phenotypes is measured with heterozygote frequency for a given gene, allele frequency, or genome-wide quantitative trait locus. These are distinct interpretations of diversity; an important but understudied aspect of inbreeding and outbreeding depression is differentiating the importance of overall genome diversity versus specific key loci.

Critically, however, there are few measures of insect genetic diversity. For example, a review (112) of inbreeding depression in wild populations covered only 54 insect studies. This small number may be due to the lingering misconception that insects are generally resilient to extinction and are less urgently in need of in- and outbreeding depression study than other groups (113). Captive



(Caption appears on following page)

Figure 1 (*Figure appears on preceding page*)

Mechanisms of insect inbreeding and outbreeding depression across biological levels of life. Dashed-line boxes with plus and minus signs indicate ameliorative and exacerbative factors, respectively. (*a*–*j*) Inbreeding mechanisms. (*a*) The accumulation of deleterious recessive alleles. (*b*) The loss of advantageous heterozygosity. If it occurs at multiple loci (pseudo-overdominance), it can mask the purging of deleterious recessive alleles (149). (*c*) A single gene can cause inbreeding depression. An example is hymenopteran *csd*, which produces sterile diploid males if homozygous (145). Extra feeding helps overcome colony growth reduction from these useless males because their resource consumption is compensated for (10). (*d*) Inbreeding of the nonnuclear genome can cause inbreeding depression, as with inbred mitochondrial genomes that impair the metabolism of honey bee flight muscles (107). (*e*) Inbreeding depression phenotypes include morphological aberration of the Lord Howe Island stick insect (43). However, parental care at the juvenile stage can help these individuals with developmental inbreeding depression survive to adulthood, as in the case of caregiving *Nicrophorus* spp. beetles (118). (*f*) Assortative mating, (*g*) sib-mating, and (*h*) low-density/limited dispersal reduce genetic variation. Whether they induce inbreeding depression versus tolerance depends on the species. (*i*) Small effective population size (N_e) indicates heightened extinction or inbreeding depression risk, as with population crashes of commercial black soldier fly (121). Caution must be taken when interpreting N_e, which can range widely for healthy insect populations. (*j*) Inbreeding loops between insects and their hosts can compound, making total system conservation important. (*k*–*r*) Outbreeding mechanisms. (*k*) Heterozygosity is more deleterious than either homozygote. (*l*) Deleterious transposable elements are released when different strains are crossed because suppressive elements from a parental strain are no longer present, as in *Drosophila* (61). (*m*) Negative epistatic interactions between genes that have not coevolved (115). (*n*) A chromosomal or endosymbiotic element that selfishly eliminates one parental genome to maximize transmission, as is the case for *Wolbachia* driving the elimination of masculinizing Z chromosomes from mothers in *Eurema mandarina*, making all-female offspring (77). Outcrossing nonclonal lines may be lethal. (*o*) Cytoplasmic incompatibility, as with nonmatching endosymbiotic *Wolbachia* strains driving a genetic bottleneck in North American *Nasonia vitripennis* populations (120). (*p*) Hybrid phenotypes may experience stronger negative selection. For example, hybrids of separate mimicry rings of the butterfly *Heliconius erato* are fully viable and fertile, but their wing patterns expose them to increased predation risk because they do not match the protective pattern of either parental population (55). (*q*) Disassortative mating increases genetic variation, which can be deleterious for systems favoring inbreeding, such as those maximizing parent–offspring fitness. (*r*) F1 European grasshopper hybrids have smaller male testes and higher mortality. Hybrid zones may expand from climate change (5), although there are instances of hybrid vigor in invasive species (125).

or commercial insect populations are logically more subject to bottlenecks and breeding concerns, yet they also have few measures of genetic diversity. The most comprehensive overview to date (for biological control agents; 36) identified only 105 measures of standing genetic variation (in association with specific traits) in 69 papers, which may be due to a lack of incentive unless threshold production values are not met (as with the investigation linking inbreeding to population crashes of black soldier fly; 121). Without these data, it is hard to definitively link in- or outbreeding depression with changes in population genetic variation. Genetic variation changes in populations are also detectable only with reference data from past or origin populations, which can be inaccessible due to international trade restrictions for biomaterials (notably the Nagoya Protocol; 15).

1.2.2. Deviations from fitness as the focal trait, or the trait being measured at the population level. The classic measure of population fitness directly relates to the success of conservation programs and commercial production, but many insect studies instead report on other traits such as immune response (155), morphology (43), and even personality (109). The reason for this discrepancy may be that population fitness is not realistically scorable, as insects have a high lifetime reproduction, so these latter traits stand in as indirect measures of fitness. Alternatively, these traits may have more direct contextual relevance. For example, for commercial entomology, in- or outbreeding depression is sometimes characterized as a decline in applied performance or profitability, without fitness being measured at all. More than one trait at a time may also be investigated, and the traits may have oppositional outcomes (e.g., one trait is selected at the expense of another). Such trade-offs are a form of inbreeding depression even though one trait benefits. Notably, though, insect life-history traits such as developmental time, adult size, fecundity, and lifespan tend to be the ones that experience a cost (44), whereas morphological traits are less sensitive to inbreeding depression (122). Regardless, these traits also are often not measured

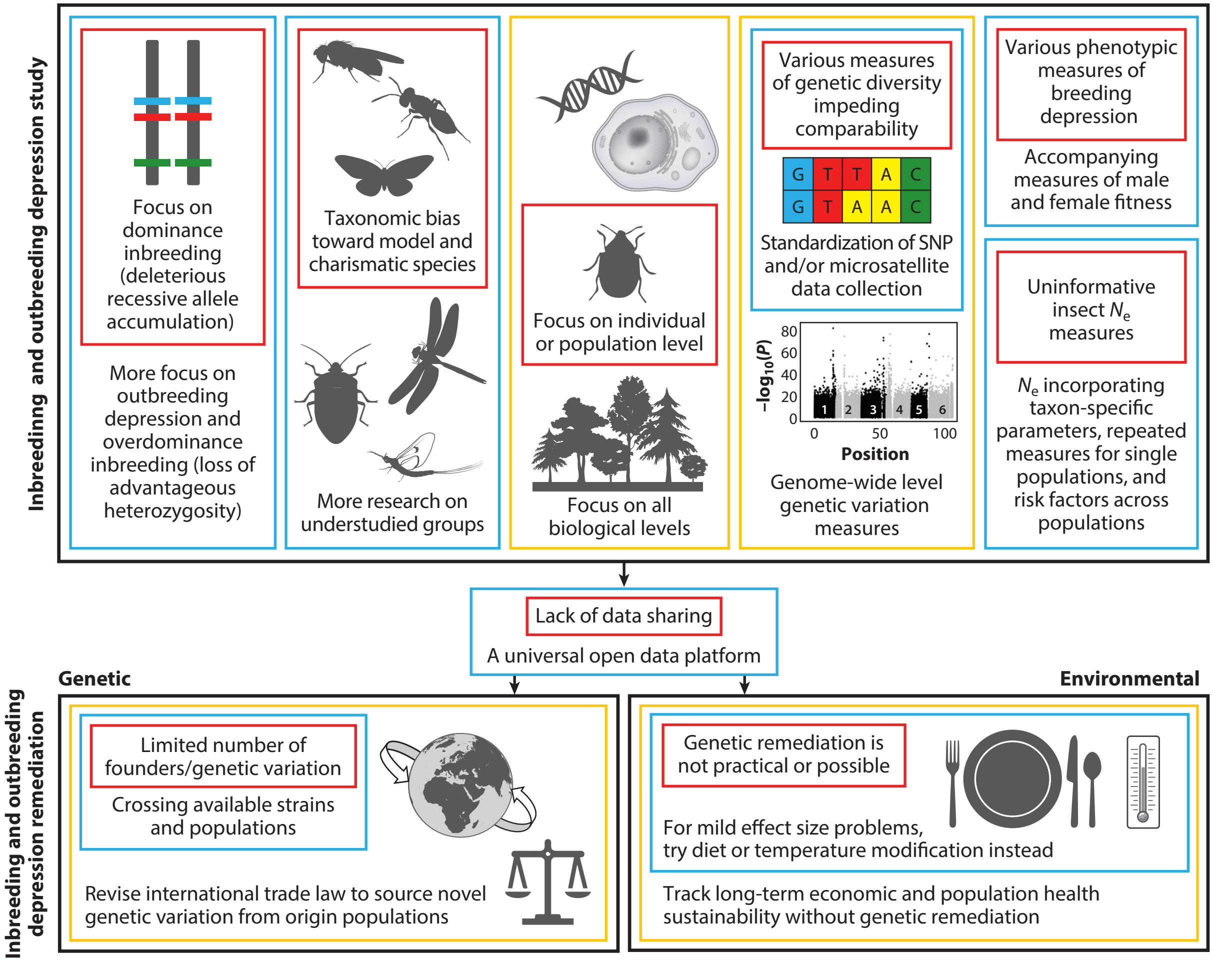


Figure 2

Problems and solutions of insect inbreeding and outbreeding depression study and remediation. Red boxes signify current problems. Blue boxes indicate immediately feasible resolutions. Yellow boxes symbolize large-scale resolutions that require long-term time investment, greater expense or workload, or technological advances. Abbreviations: N_e, effective population size; SNP, single-nucleotide polymorphism.

at the population level, despite population fitness being part of the archetypical definitions of in- and outbreeding depression, because the effect manifests at some other biological organization of life, from the subindividual level (e.g., cellular effects) to the suprapopulation level (e.g., total ecosystem) (**Figure 1**). Detrimental effects may compound across levels from the bottom up, but contradictory effects also occur at different levels. For example, in introduced insect populations, inbreeding depression may reduce individual fitness but benefit the population by purging deleterious alleles. The complex ways to interpret the manifestation of breeding depression limits comparability between studies.

1.2.3. Problems with using effective population size to approximate insect breeding depression.

Effective population size (N_e) is a cornerstone parameter for breeding and conservation. Census size N represents every individual of a population, but N_e is a measure of individuals that genetically contribute to the next generation. Low N_e/N values are a standard for identifying populations at heightened risk for inbreeding, genetic drift, and extinction. Three major factors cause low N_e/N: unequal sex ratios, variable lifetime offspring production, and population size stability. For some animal groups, these parameters are generally stable. For example, with few exceptions (46), mammals have a one-to-one male-to-female sex ratio, are diploid, and have low lifetime fecundity. These characteristics contribute to N_e/N for distantly related, healthy mammal populations being in the same order of ~0.1–1.0 (41).

In contrast, the massive inter- and intraspecific diversity in insect life histories greatly complicate the interpretation of N_e. For example, many insects have different ploidies for males and females (haplodiploidy), with important consequences for deleterious allele dynamics (104). Skewed sex ratios are also common and often inherent to the reproductive biology of the species, so even though a skewed sex ratio reduces population genetic variation, it does not necessarily cause breeding depression. High within-species variation in fecundity is also found across insects: Body size directly determines female fecundity and sometimes ovariole number (66), and sperm count and competition are highly variable among males (67). Many insects also have strongly fluctuating population sizes that depend on climate, population density, and resource availability, so capturing insect baseline population values needed to project trends of growth or decline is a major problem (26). These additional factors mean that even if N_e/N values for an insect population are drastically lower than previous measures, it can be hard to determine whether this reflects enhanced risk of inbreeding depression or typical biology. For example, N_e estimates for wild and laboratory *Drosophila* species suggest that robust insect populations can have highly variable N_e values across multiple orders of magnitude (41, 80).

Below, we provide recommendations to address these problems (**Figure 2**), but at present these issues make it difficult to infer any patterns of insect inbreeding and outbreeding depression. As an immediate solution, we look more closely at specific sectors (invasion, conservation, and commercial entomology). These include subdivisions of life history and reproductive mode, interspecific relationships, and nongenetic factors to better mark trends of inbreeding and outbreeding depression in an insect-specific framework.

2. PATTERNS (AND THEIR ABSENCE) IN INSECT INBREEDING AND OUTBREEDING DEPRESSION

2.1. Inbreeding and Outbreeding Depression in Insect Conservation

Insect extinctions are difficult to document because of their enormous diversity, small body size, and large population sizes. Only 70 extinctions were recognized even into the 2000s (29). Insect conservation has concentrated on a few specific groups, such as endemic island taxa (101) or indicator or charismatic species, particularly butterflies (113). However, a major global insect extinction crisis has long been underway, and scientific and public awareness is expanding (53, 82, 147). There is a consensus that invasive species, habitat loss, climate change, and pesticides are important factors (147), but there is less clarity on how often population recoveries are hindered by genetic variation loss.

Inbreeding depression may be a serious danger to conservation because a limited number of individuals may prevent successful captive breeding or wild reintroductions. Documented inbreeding depression effects include captive-bred butterflies laying far fewer eggs than wild-caught counterparts. This finding has been attributed to an increased genetic load of deleterious alleles (52, 106, 124), but the authors of these studies acknowledged that further investigations for overdominance are warranted. Egg laying has also decreased for captive inbred Lord Howe Island stick insects (*Dryococelus australis*) (65), which also have malformed legs and sensory organs (eyes, antennae, cercal organs) that would likely impair survival upon release (43, 103). For rare bumble bees, susceptibility to the gut parasite *Crithidia bombi* has increased for *Bombus muscorum* (154), and susceptibility to the parasitic mite *Locustacarus buchneri* for *Bombus jonellus* and *B. muscorum* (155) has increased with population homogeneity. Interestingly, for *Locustacarus buchneri*, susceptibility did not increase with homogeneity at the individual level, suggesting that population diversity is key for a bumble bee group immunity effect. Caste-specific expression can also play a role in inbreeding depression severity, as inbred reproductive gynes of the threatened wood ant *Formica exsecta* have lower immune defenses than workers despite genetic similarity (146).

Outbreeding has been suggested as a means of genetic rescue, but there is a danger of outbreeding depression. A 2007 review (31) indicated that, for several butterflies and a beetle, outbreeding depression is just as deleterious as inbreeding depression, particularly for egg viability and juvenile development. Notably, intra-/inter-insect hybrid zones are shifting or expanding as a result of climate change (5), possibly increasing natural opportunities for outbreeding and outbreeding depression. Sterility and lethality hybrid breakdown effects for subspecies or interpopulation crosses have been repeatedly observed for European grasshopper hybrid zones, for example (51).

There are counterexamples in conservation where breeding depression is not a problem. A release of only 50 inseminated females of the butterfly *Erebia epiphron* surprisingly established a population as genetically diverse as its source, according to alloenzyme data (although another replicate died out) (129). Another reintroduction, of Hawaiian yellow-faced bees (*Hylaeus anthracinus*), used only 100 individuals per site. Establishment did not seem to depend on genetic diversity but rather on the presence or absence of predatory invasive ants (98). Other studies have shown that threatened populations that are presumed to be inbred are not. For example, isolation from habitat fragmentation is expected to promote inbreeding, and the limited dispersal ability of small-sized insects would intuitively put them at higher risk of isolation. But, as in the case of the endangered heath bush cricket (*Gampsocleis glabra*) scattered across Europe, there may be more gene flow than assumed (58). Inbreeding must be confirmed through adequate genetic sampling of a population before its effects can be accurately interpreted.

Far too little is known about the role of genetic variation in insect conservation, but efforts to close this critical knowledge gap are underway. A recent review advises using population genomics to define discrete units for conservation (species, subspecies, populations), measure genetic variation, and identify genetic load (151). Future studies should use comprehensive approaches that integrate genetic and phenotypic measurement because the implications of the amount of genetic variation for the conservation of insect populations have so far been highly context dependent. Inadequate knowledge of all these factors may have major consequences. An illustrative case is the butterfly model *Bicyclus anynana*, in which inbred males have reduced flight ability and mating pheromones but any negative impacts on breeding success are masked in captivity because the free-flying of females is constrained, inflating mating success (72, 143). If this phenotype were to emerge in a reintroduction program without foreknowledge, the population would seemingly decline inexplicably.

2.2. Invasive Species Tolerance to Inbreeding Depression

Aided by anthropogenic spread and high reproductive rates, insects represent a major class of invasive species. By competing with or predating on natives, spreading disease, and destroying crops, they cause an estimated US$80 billion of damage per year (12). These populations thrive outside their native range despite being bottlenecked, an invasion paradox that seemingly contradicts inbreeding depression theory (28). Studies suggest that invasive species use diverse means of exhibiting inbreeding tolerance, with population genetic mechanisms often at play. For example, certain hymenopteran species (and at least some Lepidoptera with a similar mechanism; 142) should be critically vulnerable to inbreeding because homozygosity at a single sex-determining locus (CSD) results in sterile males (145). This assumption predicts rapid extinctions (161), but severely bottlenecked invasive populations of *Bombus terrestris* bumble bees (128), *Lasioglossum leucozonium* solitary bees (160), and *Vespula* wasps (127) nevertheless expand. Genetic rescue may arise from strong balancing selection favoring rare alleles and from the generation of de novo variation through mutation, as in the case of invasive bees (48, 56, 160). For the invasive ladybird *Harmonia axyridis* (35, 81) and the ant *Brachyponera chinensis* (33), inbreeding initially increased mortality and decreased fitness in invasive populations, limiting early population size, but in so doing purged deleterious alleles, allowing an advantageously selected population to rapidly expand afterward. Phenotypic plasticity and epigenetic mechanisms in invasive species may also be an important tool for them to escape inbreeding depression. For example, five geographically and environmentally distinct independent introductions of parthenogenic *Naupactus* weevils are genetic clones, but they have adapted to different hosts as reflected in gene expression variation, elements of which persist in their offspring (96).

Inbreeding may also reinforce beneficial behavior changes. Social insects, among the worst and most widespread invasives (34, 50), inherently have low genetic variation within colonies. However, genetic variation loss and the corresponding high level of relatedness reduce aggression and increase cooperation between colonies, improving invasion success. This process can lead to supercolony formation for many species, including supercolonies of the Argentine ant, *Linepithema humile*, that occur worldwide (139). Inbreeding phenotypes that would be deleterious in the native range may also be modulated by lower-selection-pressure environments. Invasives, for example, often no longer encounter coevolved predators or pathogens (as is the case for some invasive *Solenopsis invicta* that have lost their microbial natural enemies; 159). Thus, weakened defense mechanisms or immune systems from inbreeding may not be as disadvantageous; indeed, in such cases it is a form of directional selection, eliminating extraneous expenditure on metabolically expensive traits.

The success of invasive species thus appears to be a strong counterargument to inbreeding depression in insects, but this interpretation warrants caution. First, we can study only the extant invasions, not the ones that may have rapidly gone extinct from inbreeding depression and were never documented. Therefore, it is not always known whether inbreeding has occurred at all or, if so, whether it is sustained. Using mitochondrial and microsatellite markers, some studies have affirmed that introduced populations have reduced genetic variation in comparison to the native population [e.g., human-spread gall midge *Asynapta groverae* (74) and potato tuber moth *Tecia solanivora* (119)]. However, it is often difficult to determine how invasions start and spread and whether genetic isolation persists. Repeated introductions with infusions of novel genetic variation are possible. Separate invasive ranges can also merge to become a more genetically variable admixed population, as occurred for the highly damaging Asian brown marmorated stink bug (*Halymorphus halys*) in Europe (19). Gene flow may also be higher than realized. Surprisingly, multiple examples exist of interspecies gene flow between invasive species, which resulted in hybrids that violate expectations of hybrid breakdown by being hardier or having faster population growth than parent populations (125). In contrast, population genetic analyses of the cosmopolitan fruit fly *Drosophila melanogaster* show a clear effect of ancient migration history on genetic diversity measures, even with relatively mild population differentiation (100). Collectively, the general resistance of invasive species to breeding depression makes these species a rich resource for identifying mitigative mechanisms.

2.3. The Danger of Inbreeding and Outbreeding Depression in Commercial Populations

Inbreeding and outbreeding could endanger commercial insect populations by altering desired traits or overall fitness. The three major areas of industrial insect production are (*a*) products for goods, food, and feed; (*b*) biological control/sterile insect technique (SIT); and (*c*) pollinators (bees) for agriculture. Surprisingly few publications address the role of genetic variation in these sectors, even though they often aim to optimize desirable fitness traits. This paucity of research may be because breeding depression problems are truly uncommon, but it may also be because they are underreported in order to protect company confidentiality. It is likely that most commercial populations were founded with a limited number of individuals for one or a few strains.

2.3.1. Mass-rearing of insects for feed and food requires genetic variation. Various insects are mass-reared for human food and animal feed, such as mealworms, crickets, and flies. Studies of breeding depression have focused on the black soldier fly *Hermetia illucens*, used to convert waste products to protein and animal feed. Few strains are in use, with little genetic variation, and population crashes have occurred (76). Effects of inbreeding, however, can differ drastically. In one study (121), colonies collapsed after a few generations following introduction into the laboratory, which correlated with genetic diversity loss as measured with microsatellites. Another study (16) reported a positive effect of higher egg production following inbreeding of a laboratory strain. Such variation between studies is to be expected, as genetic drift is unpredictable at the strain level. Although fitness can be retained or even improved with early purging of deleterious alleles, populations with low genetic variation are likely to be more susceptible to, for instance, diseases (95). While breeders are wary of introducing wild-caught individuals and diluting selected or domesticated traits, there is growing interest in screening natural source populations for genetic variants to avoid inbreeding and improve selectability of other beneficial traits (47, 90, 126). One caveat is that a favored trait may need work-intensive continual selection. Passive upkeep of inbred, previously selected lines can accumulate deleterious mutant alleles that, for example, reduce fitness in food and feed (*Musca domestica*) (14) and SIT (*Anastrepha ludens*) (126) fly populations.

2.3.2. Risks of inbreeding and outbreeding depression in biological control and sterile insect technique species. Various insect species are being reared for biological control and SIT to control pest species. Biological control uses entomophagous predator or parasitoid natural enemies that are either native or introduced to the geographic area of the pest. Predators tend to be diploid Coleoptera (e.g., ladybirds) or Heteroptera (e.g., Anthocorid bugs) and haplodiploid mites (Acari), whereas parasitoids are mainly haplodiploid hymenopterans. SIT uses mass-produced, sterilized males of the pest species itself that are released to outcompete wild males and reduce pest population size.

Corresponding to these different biologies, inbreeding outcomes have been variable in biocontrol and SIT species. Deleterious alleles associated with inbreeding depression for development time, survival, and reproduction in native populations were quickly purged in introduced biocontrol populations of the Asian ladybird *Harmonia axyridis* (35). The biocontrol agent, the spined soldier bug *Podisus maculiventris* (Pentatomidae), seemingly does not suffer inbreeding depression (23). In contrast, lines of *Nesidiocoris tenuis* (Miridae) did not survive forcible inbreeding in attempts to create highly homozygous individuals to facilitate whole-genome sequencing (K. Leung, personal communication regarding Reference 37). Such inbreeding depression has also been observed in the sweetpotato weevil *Cylas formicarius* used in SIT, which can be selected for higher progeny production but has reduced progeny when inbred (79). Interestingly, studies of the haplodiploid predatory mite *Phytoseiulus persimilis* (Phytoseiidae) suggest that intermediate relatedness is optimal. Both in- and outbreeding depression occur in F1 for female fecundity, and siblings are reluctant to mate. However, long-term outbred lineages are the most productive (6, 18). Some groups of hymenopteran parasitoids, the most prevalent biocontrol agent class, have complementary sex determination (CSD) (54, 59, 145). They are subject to the same ambiguous inbreeding-driven population declines as bees. In the case of at least one parasitoid, *Cotesia rubecula*, there is evidence that CSD allele loss has driven higher production of sterile diploid males (22). Non-CSD species show mixed results: *Muscidifurax* species demonstrated inbreeding depression for lifespan and fecundity (83), but neither outbreeding nor inbreeding affected the commonly used *Trichogramma* species (9, 136). These studies show that breeding depression outcomes in biocontrol and SIT require careful assessment and case-specific action.

2.3.3. Pollinators are theoretically at high risk for breeding depression. Sharp population declines for pollinators are particularly high profile in the insect extinction crisis (25). Studies of inbreeding impacts to commercial pollination ability have focused on honey bees (*Apis* spp.), bumble bees (*Bombus* spp.), and to a lesser extent stingless bees (*Melipona* spp.). The relationship between genetic diversity and bee declines is complicated by the fact that all bees have CSD sex determination, whereby homozygosity of the CSD gene results in sterile diploid males. However, our understanding of CSD molecular mechanisms is limited; the molecular mechanism has been only partially delineated in the honey bee *Apis mellifera* (11, 116). Various mitigating factors across species include juvenile diploid male executions and a hypothesized rapid CSD de novo mutation rate (88). Therefore, it remains unclear what role the specific extreme form of CSD inbreeding depression has in bee declines worldwide. On the whole-genome level, no general pattern to inbreeding depression in bees has been observed. One study found that outbred *A. mellifera* lived longer and stored food faster than their inbred counterparts (13), but modeling predicted that a 20% gain in complex pollinator traits could be achieved through selection, at the cost of a 25–50% increase in inbreeding (108). Another study found metabolic impairment of *A. mellifera* flight muscles due to inbred mitochondria, even though the effect from the inbred nuclear genome was negligible (107). Inbreeding depression in *B. terrestris* for hibernation survival, colony size, and fitness was specific to the family line, with other lines exhibiting outbreeding depression (45). Yet another study found that inbred *B. terrestris* colonies did not differ phenotypically from outbred controls, but those that produced diploid males (signifying inbreeding specifically at the CSD locus) had slower colony growth, lower fitness, and lower field survival (153).

These studies highlight the importance of considering segregating effects in all insect breeding depression, as there are different outcomes relating to distinct mitochondrial and nuclear genomes, and at the locus versus the whole-genome level. But strikingly, even continual inbreeding may not have apparent detrimental effects, as *Melipona scutellaris* populations inbred for 10 years nevertheless continued to grow (3). A hint as to the underlying mechanism may be that honey bees that have undergone 20 years of clonal breeding still have a strikingly high level of heterozygosity, as 30% of more than 10,000 genes have a signature of heterozygote advantage (overdominance) (135).

2.4. Impacts of Reproductive Systems on Inbreeding and Outbreeding Depression

The reproductive system is a strong determiner of the presence or absence of insect breeding depression. Many insects have reproductive systems that deviate from random sexual mating and greatly reduce genetic variation. For example, many insects will mate with a limited number of individuals, as in territorial or lek-mating systems where only few males control access to females [e.g., the tarantula hawk wasp (2) and the calopterygid damselfly (21)]. Other insects, such as bed bugs (38) and fig wasps (49), routinely perform sib-mating or mate with other close relatives. The extreme is parthenogenetic (asexual) reproduction, which occurs in all insect orders except Odonata and the suborder of Hemiptera (99, 137). In many such species, sexual reproduction is also possible; however, asexual populations have less genetic variation than their sexual counterparts, as was confirmed in a stick insect study (8).

Some authors have proposed that the prevalence of insect inbreeding reproductive systems are rooted in the evolutionary advantage of maximizing parent–offspring fitness (30). Another possibility is patchy (demic) or fragmented distribution resulting in local mating groups, or the fact that offspring are produced in clutches and have few dispersal capabilities (157). In either case, it is unclear whether such species have inherent inbreeding tolerance or whether inbreeding tolerance evolves over time. A clue may be found in the haplodiploids. All Hymenoptera and Thysanoptera (and some Coleoptera and many mites) are haplodiploid, in which males are haploid and females are diploid. Theory and empirical evidence support the idea that haplodiploids have less genetic variation but suffer less from inbreeding depression than diploids (62, 152). It is widely accepted that this is due to purging of recessive deleterious alleles in haploid males. Loss of deleterious alleles is not without consequence, though, as bidirectional sexual conflict occurs. Diploid females may still suffer from inbreeding for female-specifically expressed and maternal-effect genes (138). In contrast, recent studies have demonstrated that *Polistes fuscatus* paper wasps (104) and invasive *Nylanderia fulva* ants (33) show an overrepresentation of female heterozygosity acting as a reservoir for male-deleterious alleles. This finding suggests a trade-off to benefit from this form of inbreeding-tolerant reproduction. However, there is evidence for specific mechanisms to avoid inbreeding in insects for which it is deleterious. Some authors have claimed that postcopulatory behaviors have evolved to actively avoid sib-mating, such as (sex-specific) dispersal after emergence (4), asynchronous reproductive activity of both sexes (148), female remating intervals (140), parental care (102, 118), and skewed sex ratio to reduce the likelihood of sib-mating (133).

The emerging picture is that the severity of inbreeding depression varies considerably across species, depending on specific aspects of their mating systems. The same may be true for outbreeding depression. A comprehensive review of the animal and plant literature on outbreeding depression (156) found clear negative effects on fitness in response to intraspecific outbreeding but gave only one insect example (a grasshopper). Other studies found outbreeding depression in species with inbreeding adaptation and preference: ambrosia beetles (117), the common bed bug *Cimex lectularius* (38), haplodiploid *Coccotrypes dactyliperda* beetles (105), and *Nasonia vitripennis* wasps (92). In summary, insects with certain reproductive characteristics have higher breeding depression tolerance, but there are limits.

3. NONGENETIC FACTORS OF INSECT INBREEDING AND OUTBREEDING DEPRESSION

Scientific discourse on breeding depression has understandably focused on classic population genetics principles. However, an increasing number of nonheritable factors are proving important. These range from abiotic factors to interspecific interactions. Importantly, the external nature of these factors sometimes implies easier routes to reduce breeding depression than genetic remediation.

3.1. Environmental and Ecological Effects Can Mitigate or Exacerbate Breeding Depression

Several environmental factors mask or exacerbate breeding depression, particularly for captive populations. For example, better nutrition slightly reduced inbreeding depression for pathogen resistance to the bacterium *Serratia marcescens* in *D. melanogaster* (although not for development or body size) (141). In social hymenopterans with CSD, inbreeding is predicted to slow colony growth, as the resultant noncontributory sterile diploid males consume resources (88). However, researchers have found that captive inbred colonies can be rescued when they are given ample food resources to make up for diploid male consumption in *Meliponini* species (114) and *Apis* species (10). Effects of inbreeding depression may also scale to abiotic stressors, as with fitness for the seed beetle *Callosobruchus maculatus* with heat (39). A recent study with corroborating results for the same system suggested that the inbreeding depression of wild populations may be magnified by climate change (69). However, heat did not worsen inbreeding depression across fitness and developmental traits for the butterfly *Bicyclus anynana* (40). Thus, modifications such as extra food, temperature adjustment, and other environmental variables may help reduce or eliminate effects of breeding depression. Although more study is needed, in a captive breeding setting, altering environmental conditions could be a financially and logistically feasible alternative or supplement to genetic-based programs reintroducing genetic diversity.

For wild populations, ecological relationships have complex consequences for breeding depression. If host plants and prey have inbreeding depression themselves, they can have downstream effects on the population health of their closely associated insects. For example, inbred flowers may be less attractive and have lower nutritional value for pollinators (17, 68, 75, 131), which can then drive pollinator population declines and genetic variation loss. A direct example is inbreeding compounding in a negative-feedback loop between the herbivore moth *Abrostola asclepiadis* and its plant host, swallow-wort (73). Such connectivity supports the conservation of total biodiversity as a preventive measure for insect inbreeding depression.

3.2. The Influence of Sex Distorters, Chromosomal Elements, and Endosymbionts

In many insects, the mode of reproduction and offspring sex ratios can be manipulated by genetic elements and endosymbionts. The resultant sex skew might act as an inbreeding avoidance strategy by reducing sib-mating (63). This mechanism has been proposed, for example, for meiotic drive sex chromosomes, known predominantly from dipterans and lepidopterans (70), which bias population sex ratios toward one sex (with balancing drive suppressors preventing total population extinctions; 60). This effect of inbreeding-preventing sex ratio skew has also been suggested for *Rickettsia* and *Spiroplasma* male-killing bacteria, common in Diptera, Coleoptera, Hymenoptera, and Lepidoptera (63), and for widespread *Wolbachia* and *Cardinium* endosymbiotic bacteria, which have a range of effects but can induce parthenogenesis in, for example, parasitoids and mites (94). These bacteria can also act as a meiotic drive, as *Wolbachia* eliminates masculinizing Z chromosomes from mothers in *Eurema mandarina*, resulting in female-only progeny (77). Different strains of *Wolbachia* in individuals can also act as a precopulatory or postzygotic mating barrier, for example, through cytoplasmic incompatibility, thereby reducing outbreeding. However, evidence that these distorters and endosymbionts prevent breeding depression is mixed. There is little documentation, for instance, that species with male killers experience inbreeding depression in the first place (63). In contrast, a recent study of the parasitoid *Habrobracon hebetor* found that sib-mating reduces female offspring production as a postcopulatory inbreeding avoidance mechanism but that *Wolbachia* infection alleviates this inbreeding depression effect, increasing the production of sib-produced female offspring and, thus, its own transmission (7).

An alternative explanation is that these chromosomal distorters and endosymbionts are selfish elements driven to maximize production of the transmissive sex. Sometimes such sex ratio distortion is at the expense of the host through genetic variation reduction or maladaptation. For example, much lower mitochondrial (but not nuclear) DNA variation in North American *N. vitripennis* populations relative to European populations was attributed to a *Wolbachia* sweep driving a cytoplasmic-incompatibility bottleneck (120). Furthermore, *Wolbachia*-induced parasitoid parthenogenesis operates through gamete duplication, resulting in genome-wide homozygosity (female isolines). This process results in immediate inbreeding depression via expression of recessive deleterious alleles for female traits, as with *Asobara japonica* (94) and *Trichogramma* species (162) traits, including sexual attractiveness, mating behavior, fecundity, lifespan, and body size. In addition, as a parasite, *Wolbachia* can worsen inbreeding depression effects in the host through competition or resource consumption (89). Collectively, these studies demonstrate that the role of reproductive manipulators in breeding depression needs further exploration, as some evidence suggests that they modulate it and other evidence argues that they exacerbate it.

3.3. Mitigative Impacts of Parental Care

Independently of their contribution to offspring genetics, parental condition can influence breeding depression, especially when close parent–offspring interactions such as parental care are occurring. This is because breeding depression often manifests at the juvenile stage (e.g., lower weight, developmental delay), but individuals may be functional and reproductive if they survive to adulthood. In the burying beetle *Nicrophorus vespilloides*, parental care reduces inbreeding depression for larval survival, dispersal, and lifespan (118). However, in the related species *Nicrophorus orbicellus*, the effects of inbreeding depression on offspring brood size, survival, and lifespan did not worsen even when older parents provided lower-quality care (130). In contrast, inbreeding depression of hatch rate, development time, and survival worsens in the noncaregiving seed-burying beetle *Callosobruchus maculatus* as maternal age advances, which could be the result of reduced resource provisioning to eggs (39) or late-acting deleterious mutations (20).

Currently, whether parent–offspring dynamics can be purposely exploited to lessen breeding depression is hypothetical. The genetic basis of these behaviors is likely complex, so it may be difficult to select for such behaviors to reduce breeding depression. A more immediate possibility could be to choose species with this behavior as a preemptive mitigating factor when inbreeding depression is inevitable, such as when starting a new production insect line. However, juvenile care is not a foolproof predictor of reduced breeding depression for all traits. For instance, while inbred *Forficula auricularia* earwigs deprived of typical maternal care had worse nymphal development inbreeding depression, they did not have a higher degree of inbreeding depression for male fitness (102).

4. FUTURE RECOMMENDATIONS FOR INSECT BREEDING DEPRESSION

The breadth of the above studies has hopefully illustrated the difficulty of obtaining a standardized understanding of insect inbreeding and outbreeding depression. However, they offer lessons on how to study and remediate insect breeding depression in a more nuanced manner (**Figure 2**).

4.1. Future Insect Breeding Depression Study

First, we must address study gaps. Outbreeding depression is understudied and thus may be underreported. It is especially important in commercial breeding, as outcrossing is a common way to resolve inbreeding depression (32). Careful study design is needed to account for outbreeding depression, as a fitness increase in F1 can mask subtler negative effects (e.g., loss of local adaptation or introduction of genetic incompatibilities) that take more effort or generations to observe (93). For inbreeding depression specifically, the likelihood of overdominance (heterozygote advantage) should be given the same weight as dominance (recessive allele accumulation). Although difficult to distinguish, detection of overdominance is becoming more possible with genome-wide studies; for instance, a study of clonal honey bees detected a ubiquitous signature of overdominance (135). There is also a taxonomic bias in breeding depression study efforts, with especially high representation of charismatic species or genetic model organisms such as *Drosophila*, *Nasonia*, and *Bicyclus.* Taxonomy can be a strong predictor for breeding depression; for example, Lepidoptera seem to have an outsized vulnerability to inbreeding depression (63). Thus, the lack of studies for the orders Odonata, Ephemeroptera, Orthoptera, and Hemiptera, among others, must be addressed to gain even a basic understanding (64). Lastly, complex breeding depression interactions across all biological levels should be kept in mind. In this review, the pollinators are perhaps the most illustrative example, as they have complex incongruencies between the mitochondrial and nuclear genome and between the CSD gene and the whole genome, and they have possible inbreeding loops with host plants.

Second, it is important to standardize genetic and phenotypic breeding depression data. Although many context-specific considerations for insect breeding depression clearly exist, some standardization of data collection is recommended to facilitate comparability and trend prediction across studies, such as meta-analyses. To detect genetic variation changes, reference data sets of origin populations or historical museum specimens are needed for comparison with focal conservation, invasive, or commercial populations. In the future, large-scale analyses such as genome-wide association studies may become standard (151). This has already occurred with threatened bumble bees (91, 110), and genome-level resolution might even be essential in some cases (e.g., in accurate gene flow tracking in the invasion history of the global fruit pest *Drosophila suzukii*; 1). For now, however, a generally cost-effective approach is the use of mitochondrial genome marker cytochrome oxidase I (COI), microsatellites, or SNPs. Note that these measures report different things: COI reflects only matrilineal lineage, whereas nuclear markers can be chosen genome-wide. We recommend the use of SNPs as the standard because they are more uniformly distributed across the genome and are more precise for population differentiation. However, microsatellites, or randomly distributed repeats, might carry a higher level of heterozygosity important for tracking, for instance, parental lineage that could be relevant for highly pedigreed applications such as conservation breeding (57). We also suggest that, regardless of the breeding depression trait of interest, which can range from morphology to immunity, companion measures of male and female fitness should always be made, as such measures would adhere more closely to the classic definition of breeding depression for cross-study analyses.

Third, N_e must be accurately estimated. Improvements in calculations of N_e are needed for more accurate interpretation of healthy versus alarmingly decreasing insect numbers. Such improvements could be brought about with more comprehensive incorporation of taxon-specific parameters. A classic example is haplodiploid N_e. Because haploids are exposed to deleterious recessive alleles, their N_e approximates X-linked traits (158). More recently, a study of several eusocial insects found that vertebrate-like life-history features, such as slow generational turnover, increase their genetic load and decrease their N_e, and this effect increases with degree of sociality (123). Repeated measures of N_e for a given insect population or species over time are also necessary in order to determine the range of normal versus concerning values. Lastly, in conservation, insect N_e needs to be calculated in association with a specific risk factor. For instance, a study of the endangered damselfly *Coenagrion mercuriale* found that its variable reproductive success and habitat area sizes yielded N_e/N values between 0.006 and 0.42 and that smaller populations surprisingly had the largest values, suggesting a possible genetic compensation mechanism (150).

Fourth, studies should use a standardized database. Pattern recognition in insect breeding depression to make proactive decisions would be greatly facilitated by the use of a single platform to upload genetic diversity measures and corresponding phenotypic data (15). Efforts toward this end are underway; for example, the open data portal ShareTrait (84) can be parsed into subcategories such as insects, followed by biological control traits. Some parties (e.g., breeders who want to keep the genetic data of their populations confidential) may be reluctant to share data openly. However, conservation programs and commercial breeders are more likely to perform repeated measures on the same population, which would be valuable for making robust inferences on genetic variation effects over time. In such cases, we suggest using data anonymization with labels such as "commercial population X."

4.2. Future Insect Breeding Depression Remediation

Genetic remediation is most immediately relevant for captive populations in conservation and commercial breeding. Unfortunately, many programs start with the objective of being able to successfully mass-rear the focal insect, without considering downstream genetic consequences. In conservation, this may be inevitable if there is limited genetic diversity to start with. For example, inbreeding depression in key sensory organs of the Lord Howe Island stick insect is assumed to be a severe founder effect, as the colony was founded by only four reproductive individuals (43, 103). In the future, commercial species breeding programs should ideally be established with several populations from various locations so as to maximize the amount of genetic variation in the founding population (100). Ideally, source populations should also be maintained separately, in case of, for instance, outbreeding depression. A selection or domestication process is often undertaken to make the commercial insects easier to handle, have higher production, or have better applied functions, but this process reduces genetic variation. In at least some cases, commercial in- or outbreeding depression has occurred with effects ranging from impaired life-history traits to total population crashes (22, 45, 87, 121). The richest resource to infuse novel genetic variation is origin populations, but their use is currently constrained by the Nagoya Protocol, which requires access and benefit-sharing agreements between countries of origin and countries of use for biological materials (87, 132). Navigating the Nagoya Protocol has impeded biodiversity research (24, 132) and the sourcing of individuals needed for corrective breeding, so revision is necessary to account for these shortcomings while also preserving its mission of correcting global trade inequities (15, 132). For now, the Centre for Agriculture and Bioscience International provides a template for access and benefit-sharing agreements for nonprofit and research objectives (134). An alternative solution is the use of between-strain crosses of available lines (32), but mixing variants in breeding cultures may cause outbreeding depression or reverse beneficial selection. Another possibility is to maintain several subpopulations or strains that have been optimized for the same trait, but these will have random fixation and loss of genetic variation. Such populations can be recombined to restore overall health, a traditional breeding principle from livestock (86).

Another idea is to take no action with regard to genetics but instead to consider whether the effect size of the breeding depression is small enough to be affordably and feasibly mitigated through environmental treatment. For example, diet changes or higher temperature could be used to compensate for a developmental delay, or production scale-up could make up for a minor loss of fitness (71). Caution is warranted, though, as there has been little assessment of whether environmental approaches are viable in the long term, as then the population's genetic variation and corresponding inbreeding depression remains impaired and may even worsen.

SUMMARY POINTS

1. Insect inbreeding and outbreeding depression mechanisms and outcomes are highly variable. Conservation and commercial species are more vulnerable. Invasive species, and species with reproductive modes driving sex skew and parthenogenesis, are more tolerant.

2. A more comprehensive understanding of insect breeding depression will incorporate more outbreeding depression, overdominance in inbreeding depression, standardized data collection, corrected N_e and taxonomic biases, and interactive effects at different organizational levels of life.
3. A universal database will facilitate pattern prediction and actions. Practical actions against insect inbreeding and outbreeding depression include genetic remediation, which will require revision of international biomaterial trade law to facilitate sourcing. Environmental remediation may be an easier alternative or supplement, but its long-term sustainability needs assessment.

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