Editorial to the SCAPE Joint Special Issue

How should we think about the pollination crisis?

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This essay arose from a talk I gave at the SCAPE meetings in October 2023; it reflects my growing unease about the phenomenon called "the pollination crisis." That term has gained widespread recognition and tacit acknowledgement, despite the lack of a consistent definition and a general lack of conventional evidence, such as case studies. As an example, a Google search for "pollination crisis" on 14 February 2024 generated 2.7 million hits. Although the exact meaning of a Google hit is obscure, the idea is clearly receiving discussion. I have not pursued the sprawling literature carefully enough to provide an authoritative review, but I fear that the acceptance of the idea has outpaced the accumulation of evidence for it. Because my skepticism about the crisis does not seem to be widely shared (but see Ghazoul 2005), this essay will highlight some of the personal research experiences and perspectives that have led me to adopt a heterodox position. I hope that they will stimulate useful conversations. As a practicing pollination ecologist and a lay consumer of environmental news, I have three areas of concern.

First, the nature, scope, and timing of the crisis are elusive.

This phenomenon clearly refers to pollination by animals, not abiotic vectors such as wind, and its major impact is seen to lie in the future. The term "crisis" certainly implies a big bad thing that is serious enough to warrant action. Beyond that, references to it seldom delineate its defining hallmarks and seldom identify what stage its development has reached. Regarding the timing of the crisis, is it well underway now, or is it only lurking? How will we measure its progress? How far will it go? Are the effects ratchet-like and irreversible? Are the effects biome-specific? Does it have an endpoint?

Regarding the nature of the crisis, the driving force is seen to be declining populations of flower-visiting animals. The anticipated bad effects are principally (1) declines in agricultural productivity of human foods and (2) declines in populations of plant species in natural communities. Most of my research into the adequacy of pollination service has been in natural communities of perennial plants, so I will focus on that aspect of the crisis. Some of the questions I raise may also be applicable to agricultural situations, but those situations will tend to have crop-specific aspects that make them resistant to generalization. Some may benefit from technological approaches such as importing managed pollinators or even artificial pollination by humans or drones, depending on economic considerations. The pollination crisis in agriculture has recently received a critical review by Aizen et al. (2022, also see Aizen et al. 2008).

Turning to natural communities, the most alarming invocations of the crisis portray pollination as a brittle link that is necessary for holding up a fragile house of cards. The brittleness is attributed to the co-dependence of plants and pollinators. The envisioned outcomes are that plant species populations will be demographically devastated by insufficient pollination. Such insufficiency may be due to declining populations of pollinators or to disrupted phenological matches. The secondary or knock-on effects may

entrain extinction vortices: declines in zoophilous plant species may trigger further declines in flower-feeding animals, triggering further declines in pollination, etc. Influential early papers, now highly cited, raised the possibility of bleak prospects (e.g., "The predicted result of these disruptions is the extinction of pollinators, plants and their crucial interactions," Memmott et al. 2007), and subsequent retellings in the popular news media came to portray plant extinctions not as mere possibilities but as virtual inevitabilities. (A representative report from a respectable news medium is: https://www.cnn.com/2022/08/14/weather/food-risk-bee-butterfly-pollinator-decline-climate-scn/index.html)

My focus here is on the proposed negative effects of disrupted pollination on natural plant populations.

SECOND, CURRENT RESEARCH STRATEGIES ARE INCOMPLETE.

Having established what I hope is a fair sketch of how the crisis is perceived, I wish to raise several questions about the supporting evidence. More importantly, I will try to explain why too many current approaches are inadequate for estimating the scope of the crisis. To motivate this discussion, I will pose a conundrum. In flower-rich subalpine meadows of the West Elk Mountains of Colorado, flying insects caught in Malaise traps have declined by 61.5% in numbers and 47% in biomass over the period from 1986 to 2020 (Dalton et al. 2023). Numerous species of flower-visiting Diptera and Hymenoptera are included. This study's long duration and consistency of methodology qualify it as a "gold-standard" report on insect declines. In floristically similar meadows about 10 km away, however, I have annually estimated pollination deficits in one member of this plant community (*Erythronium grandiflorum* Pursh, Liliaceae), with similarly consistent methodology and extended duration (1993-present; Thomson 2019). This early-flowering plant is pollinated primarily by bumble bee queens, and frequently incurs pollination deficits, as shown by increased fruit and seed set following supplemental hand-pollination. Despite the substantial decline in insect activity, pollination deficits have not increased over the decades. This locally matched pair of unusually extensive studies could well have served as a harbinger case study for the pollination crisis, but it has not. Examining the assumptions that lead to predictions of crisis may help to clarify why demographic outcomes may remain uncoupled from their putative drivers. Given that we have seen examples of dramatic declines in animals that pollinate, shouldn't we be seeing a growing collection of well-publicized warning examples?

In fact, fears of the crisis depend not on an accumulation of dramatic, documented case studies, but rather on what I will call "the plausible relationship." Figure 1 depicts this relationship as a linear flow of driven consequences connected through three processes designated by numbered arrows. Observed disruptions or shortfalls at some of the linkage points are (1) assumed to be caused by the factors upstream and (2) predicted to cause

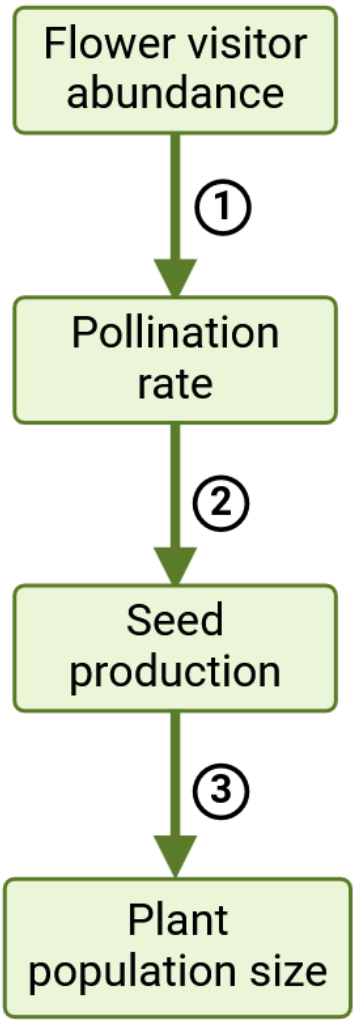

Figure 1. The "plausible relationship"

the effects downstream. The plausibility of this causal chain provides a "duty to warn" that undoubtedly underlies the wide adoption of the crisis terminology by scientists. However, I argue that all three arrows ought to be studied--ideally experimentally—rather than being taken on faith.

The best experimental design, by far, would be to manipulate pollinator abundance and to record the demographic response, in replicated experiments. In practice, pollination ecologists have overwhelmingly focused on Arrow 2, with much less attention to Arrows 1 and 3. For example, a very thorough recent attempt to estimate the consequences of declining pollination (Rodger et al. 2021) focused on predicting the effects of the most drastic possible change in pollination—complete cessation—on expected seed set. Although the study represents a bravura assault on Arrow 2, it does not address the consequences of more realistic, incremental, incomplete declines in populations of flower visitors. Nor does it address the consequences of reduced seed output on plant population responses.

Historically, the "plausible relationship" echoes a pioneering speculation in *The Origin of Species* by Darwin (1859), arising from his impression that bumble bees were the only effective pollinators of red clover. Adding his additional impressions that bumble bee populations were controlled by nest predation by mice, and that cats controlled mouse populations, he adduced a food-chain argument that cat densities could determine the prevalence of red clover:

"Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!"(Darwin 1859, p.74)

THIRD, HOW OFTEN DOES POLLINATOR ABUNDANCE DETERMINE PLANT POPULATION DYNAMICS?

The perception that plants are frequently "dependent" on animal pollination has contributed much to the adoption of the term crisis. I believe that some of this concern arises from careless interpretations of judicious reviews such as the widely-cited and exemplary treatment of crop pollination by Klein et al. (2007). In such reviews, the degree of "dependence" of, say, seed set on pollination rate is typically viewed as a continuous variable that may range from negligible to absolute. But in secondary treatments, especially in the media, the notion of "dependence" is at risk of being reduced to a binary, yes/no variable. The unwarranted exaggeration is that if a plant "depends on pollinators," it cannot reproduce in their absence. In fact, many species, even those with fairly strong self-incompatibility systems, are capable of eking out some seeds through autogamous selfing or autogamy. Vegetative reproduction through clonal spread, splitting, production of bulbils, etc., can also occur without pollination. And perennial plants can persist through seasons with no pollination.

It is likely that the relationship between animal visitation to flowers and female reproductive success (fruit and seed set) is not linear but rather saturating. At some abundant level of visitation, reproductive success becomes limited not by pollination but by other factors. Extending Bateman's principle to hermaphrodites, Bell (1985) argued that most plant populations should exist in the saturating portion of this relationship, with female reproductive success being limited by resources rather than mating opportunities. If this condition prevailed, a pollination crisis would be much farther away. However, scores of experiments have shown that wild plant populations are frequently pollination-limited (recent compilation by Bennett et al., 2018). If Bell's proposition were correct, finding so many populations with pollination deficits might be evidence that nature had already entered a crisis, with pollination rates deteriorating from some high levels in a previous Arcadian world. But other theorists (Haig 1988, Thomson 2001, Harder and Routley 2006, Rosenheim at al. 2016,) have offered convincing alternatives to Bell's proposition, so it seems parsimonious to presume that observed pollination deficits may represent an evolutionary equilibrium rather than a fall from grace.

The classical operational criterion for pollination limitation, used in virtually all of these assays of pollination deficits, is that supplemental hand-pollination raises female reproductive output above what is achieved by open-pollinated

controls. Despite the popularity of these straightforward experiments, there has been rather little recognition that they are biased toward showing pollination deficits (Thomson 2001, Aizen and Harder 2007). Supplemental hand pollinations will typically deliver virtually pure outcross pollen, whereas animal visits will very often deliver mixtures including self pollen. Therefore, the design intrinsically confounds variation in pollination quantity with variation in genetic quality. In the common case where outcross pollen is superior, the supplemented plants receive better pollination than any animal visitation rate would be able to deliver naturally. Therefore, a pollination deficit revealed in a supplementation experiment might *or might not* reflect an inadequate rate of visitation by pollinators.

In terms of Figure 1, this bias results from skipping over Arrow 1. Supplemental pollinations are tacitly assumed to mimic variation in animal visitation, but they do so inaccurately. The amount of bias depends on obscure variation in plants' breeding/compatibility systems, which would be impractical to quantify in each case study.

Spanning Arrow 1.

A more accurate approach would be to manipulate animal visitation rates directly, rather than trying to simulate such variation through hand-pollinations. Unfortunately, this is a much more difficult experiment to conduct, especially at the large spatial scales that would be necessary to rule out edge or source-sink effects. One successful example depended on a very special circumstance: the large-scale program of aerial insecticide spraying aimed at controlling the spruce budworm *Choristoneura fumiferana*, a forest pest in New Brunswick, Canada. Peter Kevan drew attention to the probable effects on pollinating insects, raising the possibility that depressed fruit set might also stress frugivorous birds (Kevan 1974). The regional scale of the spray operation allowed Thomson et al. (1985) to measure fruiting success of understory herbs in numerous sprayed blocks and numerous unsprayed control blocks. We focused on two ubiquitous species: *Maianthemum canadense* (Asparagaceae) was visited by an array of small bees and flies, while *Cornus canadensis* (Cornaceae) attracted those same insects plus bumble bee queens. In exposure trials, bumble bees survived insecticide treatment, but the smaller insects did not. *Maianthemum* fruit set was depressed in sprayed blocks while *Cornus* fruit set was not. Therefore, this study is a rare large-scale experiment that spans Arrows 1 and 2, without resorting to artificial pollinations. The lack of effect on *C. canadensis* further demonstrates that a plant may incur substantial losses of pollinator numbers and species diversity without depression of reproduction, as long as some potent pollinators are spared. Such experiments could be very valuable in assessing the scope of the pollination crisis, but they require extraordinarily favorable circumstances. Attempts to employ insecticide treatments on the smaller scales that are typical of pollination-ecological research would often be complicated by source-sink dynamics of animals moving from unsprayed plots into sprayed ones.

Therefore, pollination deficits recorded by single-season supplemental pollination experiments will not precisely mimic the consequences of a drop in pollinator numbers or a phenological displacement. I would argue, though, that repeating such experiments over many seasons could provide robust assessments of whether pollination service is changing over time in a single locality.

Spanning Arrow 3.

It may be noteworthy that classical accounts of plant community ecology seldom considered pollination as a strong force in determining population dynamics. For example, Harper's magnum opus *Plant Population Biology* (Harper 1977) contains only five indexed references to "pollination": all are brief and none relate to population size. Historically, broad floristic surveys of species abundances over environmental gradients (e.g., Curtis 1959) tend to support the Gleasonian "individualistic" hypothesis that species occur wherever local abiotic conditions suit their ranges of tolerance, unless they have been kept out by inadequate dispersal. This pollination-blind view of plant community composition is certainly oversimplified, and sadly reflects the formerly siloed nature of botany and zoology. Nevertheless, it might be an appropriate null hypothesis for investigating the role of pollination.

It is reasonable to assume that increases in seed production due to better pollination would boost

population growth, but there are many ecological hurdles—subsumed under Arrow 3---that can complicate the relationship. Reviewing seed augmentation experiments, Turnbull et al. (2000) concluded that only about half of such studies caused population increases. Factors such as limited safe sites, seed banks, self-thinning, and density-dependent attacks by natural enemies get plant demographers excited but are often overlooked by pollination ecologists. Nevertheless, this sort of ecological noise will weaken the plausible relationship embodied in Arrow 3. Beyond adding noise, these processes might interact in counter-intuitive ways. Imagine, for example, a mid-successional plant species. As the first members of the species arrive in a newly suitable habitat, their rarity and novelty may cause them to experience low pollination rates and therefore produce few seeds. Because those seeds are released into a favorable environment, however, they establish successfully, and the population grows. The increase in density probably increases attractiveness to flower visitors, so pollination and seed production may increase as the population establishes itself. As succession proceeds, however, conditions for successful establishment may decline, and populations of natural enemies may burgeon. During this hypothetical successional transition, pollination gets better and seed production increases, but recruitment through seeds declines. Shifting ecological circumstances of this kind might not only weaken the expected positive correlation between seed production and recruitment; they could in principle transform it into a negative correlation.

Other scenarios of negative correlations caused by "complicated ecology" can probably be imagined, but the most consistent disruptor of Arrow 3, at least for perennial plants, is probably the cost of reproduction through female function. If a perennial plant fails to set fruit because of pollination failure, it saves the material and energetic resources that would have been needed to develop fruits and seeds. As mentioned above, flowers of the glacier lily *Erythronium grandiflorum* often fail to set fruit because of pollination deficits or frost damage. However, the failure of a single fruit allows about 10% more growth of the plant's perennating corm in that season (Thomson 2024, unpublished but archived data). The additional stored resources increase the probability of flowering—and the number of flowers—in the following season. These cost-of-fruiting studies were conducted in a transplant garden in which seeds could not be allowed to germinate, so the net effect of pollination failure on population growth could not be measured.

A more desirable experimental design would be to vary pollination rates in study plots and then follow the consequences through demographic measurements of recruitment, growth, and survival. This would constitute a "two-arrow" study spanning arrows 2 and 3. The only example of this approach of which I am aware is unpublished work by Amy Iler and colleagues (personal communication; in preparation). Working on perennials in subalpine meadows (also near the Rocky Mountain Biological Laboratory), they established three levels of pollination: *increased* pollination via supplemental hand-pollinations, *reduced* pollination via bagging flowers to exclude visitors, and unmanipulated controls. They combined demographic measurements of flower production, seed production, growth, and survival to estimate a net reproductive rate (λ). The several study species responded individualistically, but all showed some vegetative compensation for reduced fruiting. The most dramatic response was by *Hydrophyllum fendleri* (Boraginaceae): *increased* pollination yielded an increase in seed production over controls, but caused a significant *decline* in λ due to substantial reductions in growth and survivorship. Compared to controls, the *reduced* pollination treatment produced a slight, non-significant increase in λ. In this study, the substantial cost of fruiting meant that more pollination actually jeopardized the species' foothold in the community.

Although Iler et al. have been exceptionally thorough, their study does not span all three arrows; their increased-pollination treatment was achieved by hand-pollination, and is confounded to some extent by genetic variation in the pollen delivered, and therefore is vulnerable to the bias described earlier.

SUMMARY AND POSSIBLE WAYS FORWARD.

To answer the question posed in my title, I suggest that we will think about "the pollination

crisis" more clearly if we avoid thinking of "pollination ecology" as an isolated area of study. Rather than viewing the pathway from flowers to seeds as a pivotal but fragile force that determines the composition of plant communities, we should think of it as only one cog in the complicated interplay among life history, population dynamics, and community ecology that determines how well particular plant species can persist in communities. The prediction of a pollination crisis rests on the proposition that the pollination cog is of central importance, but maybe it is not. Indeed, given the relentless anthropogenic onslaught on ecology and climate, perhaps we ought to be considering pollination as a surprisingly *resilient* component of communities, rather than one that is intrinsically fragile. For example, the rapid decline of certain bumble bee species in North America (e.g., *Bombus affinis* and *B. franklini*) is one of the best-documented and most shocking cases of pollinator loss (Colla et al. 2012), but there are other bumble bee species in those communities that may well have taken up much of the slack. The prevalence of generalization in plant-pollinator interactions (Waser et al. 1996) is likely to provide some resilience through redundancy: flower-feeders tend to be exploratory, opportunistic, and adept at finding food; anthers are good at dusting animals with pollen grains, and stigmas are good at snagging those grains. Even at the opposite extreme of the generalization scale, hyper-specialized fig trees colonized lifeless Krakatau islands and persisted long before the arrival of the hyper-specialized wasps that are their only possible pollinators (Compton et al. 1988). In this case, it was the life history of the trees, rather than opportunistic alternative pollinators, that conferred resilience. Given the ubiquitous natural variation in things like phenological timing and weather conditions, it is not surprising that pollination relationships have evolved elasticity and escape hatches. Some of this flexibility will also make anthropogenic change more tolerable.

Pollination ecologists are understandably predisposed to consider pollination an important force in nature. This is surely true in the case of floral evolution, as demonstrated by Darwin and innumerable followers. However, evolutionary importance does not necessarily imply ecological importance in the assembly of communities. At the start of my career (Thomson 1980, p.723), I pontificated with youthful assurance that "the connections between pollination rate and plant population size are incredibly complex," and I criticized arguments that proposed, "without particularly strong evidence, that pollination is the determinant of plant numbers." Over four decades later, I conclude—reluctantly and wearily--that we have not yet compiled a compelling body of case histories to establish the strength of that relationship.

If we are to move from "thinking about the pollination crisis" to doing something about it, one recommendation obviously springs from the organization of this paper: in mechanistic studies, we should pursue all three of the arrows of the plausible relationship, not just Arrow 2. Ideally, we should assess the entire causal chain in replicated experiments that experimentally manipulate pollinator populations and follow the consequences all the way to the demographic responses of the plants. As mentioned, I am not aware of any studies that do this, but the examples of the New Brunswick spray program and of the demographic work of Iler et al. show that both Arrows 1 and 3 can in principle be linked to arrow 2. Still, such studies will require hard work and fortuitously favourable situations. Such situations should be exploited when they occur, because they will help us understand mechanisms, but opportunities and funding are likely to be scarce.

An alternative approach is to leave the complex interactions in a black box and focus instead on the principal response variable of the pollination crisis—population sizes of plants—over time. If we are indeed experiencing a pollinator crisis because deteriorating pollination is reducing populations of animal-pollinated plants, we should expect to see the species compositions of mixed plant communities to be increasingly dominated by abiotically reproducing species such as anemophilous graminoids. It should be possible to test this proposition by establishing permanent study plots in mixed communities, and monitoring their species composition over time. Ideally, common designs could be followed in places that vary in anthropogenic impact, e.g., close to or distant from agricultural systems that depend on insecticides. Attention would have to be paid to the effects of other drivers of community change, such as drought, but those challenges ought to be

addressable by locally appropriate side experiments, such as providing extra water, hand pollination, etc. It would take time for trends to become apparent, but the gravest effects would be revealed the quickest.

Monitoring a set of such plots once a season need not be expensive in time or money, especially at established field or agricultural stations that already attract students seeking research experience. Given progress in image analysis, it seems possible that the field work might not require more than the acquisition of good digital images of plots, to undergo automated analysis later. Compared to other monitoring efforts such as pan-trapping insects, such a program would focus directly on the response variables that define the crisis, rather than on indirect components. I would advise young ecologists to consider whether their professional goals could be advanced by contributing to a coordinated network of such studies.

It seems fitting to conclude by returning to Darwin's early invocation of "the plausible relationship." After learning from some of his correspondents that red clover could also be successfully pollinated by honey bees, he rejected his hasty speculation in an emphatically worded 1862 *mea culpa* to his neighbour, Sir John Lubbock:

"I beg a million pardons. Abuse me to any degree but forgive me - it is all an illusion (but almost excusable) about the Bees. I do so hope that you have not wasted any time for my stupid blunder. I hate myself, I hate clover and I hate bees." (Darwin Correspondence Project).

I suggest that modern pollination biologists need not imitate Darwin in hating plants, bees, or themselves, but we should heed his warning that "illusions" might arise from uncritically accepting simplified caricatures of pollination relationships.

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