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Competition for Pollination and the Evolution of Flowering Time

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The first American Naturalist *appeared in March 1867. In a countdown to the 150th anniversary, the editors have solicited short commentaries on articles from the past that deserve a second look.*

Imagine a time before smart phones, the Internet, and even personal computers. Am I thinking of the 1860s, with this journal *in statu nascendi*? No, I have in mind 1975, toward the end of my PhD work. In those days before web searches, I had delved into the literature by a method that is still worth the trouble—starting with recent papers and working through their citations and the citations in the cited papers. The pollination literature at that point was relatively small, so that a mere mortal could absorb much of it. This old-fashioned sleuthing sometimes led to obscure papers—haltingly read in French perhaps (an 1899 paper by Félix Plateau that had been misinterpreted for decades) or in German (a 1943 paper by Hans Kugler, published as Lancasters and B-17s were bombing Germany)—and then, to my amazement, a February 1895 *American Naturalist* paper closely foreshadowing the topic of my PhD. My emotions were excitement and pleasure (magnified, I am sure, by the fact that the guy who had scooped me by 80 years was not competing on the job market). Here is the paper by Charles Robertson (fig. 1): "The Philosophy of Flower Seasons, and the Phaenological Relations of the Entomophilous Flora and the Anthophilous Insect Fauna." In modern terms this title might begin as "A Hypothesis to Explain Flowering Times. . . ."

What makes Robertson's 1895 paper worthy of notice as we approach the 150th birthday of *The American Naturalist*? It lays out a strikingly prescient view of the adaptive significance of flowering times of plant species within a community, and it leaves one with ideas for an exciting research agenda that is still only partly fulfilled.

Robertson's stated motivation is to question an earlier contribution to *The American Naturalist* on the same topic, in which a Mr. Clarke from the University of Chicago proposed that species flower in succession during the growing season "from the lower to the higher." Clarke defined "higher" as "a higher character of development" (read: evolutionarily more advanced) but also as "more perfect" or "more specialized." Robertson objects to this hypothesis on three grounds, all of which remain useful to contemplate today. First, Clarke's hypothesis is so vague that the flowering time of any plant can be shown to fit some inter-

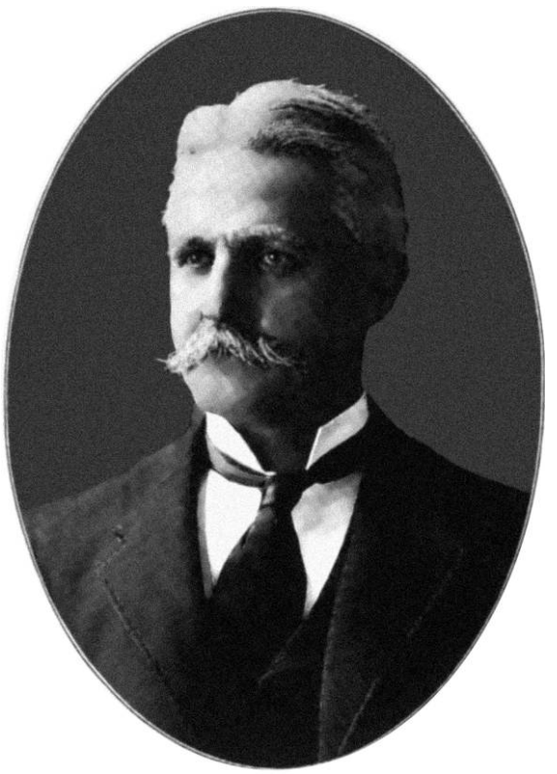

Figure 1: Ideas ahead of their time: Charles Robertson ca. 1910.

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pretation of it; it explains everything and therefore nothing. Second, if one makes the hypothesis more operational by equating "higher" only with a reasonable definition of "more specialized," Clarke's hypothesis fails to be supported by phenological patterns in one locale, the landscape around Carlinville in west central Illinois—a landscape destined to become remarkably well studied thanks to Robertson's long-term surveys of flowers and pollinators (J. C. Marlin and W. E. LaBerge, 2001, "The Native Bee Fauna of Carlinville, Illinois, Revisited after 75 Years: A Case for Persistence," *Conservation Ecology* 5:9. http://www.consecol.org/vol5/iss1/art9/). I will return to this below. Third, Clarke's hypothesis is not Darwinian, as any acceptable hypothesis of flowering times (or other such patterns) must be.

As he lays out these concerns, Robertson presents his alternative, which today we might think of as a scenario for community assembly. As plant species populate a region, they bring with them ancestral seasonal flowering phenologies, which sometimes can be explained in terms of other habits of the species (such as growing on the forest floor) or may seemingly be mysterious. These species ultimately give rise to lineages that diversify to a greater or lesser degree, and members of different lineages initially express the phenologies of their ancestors. From this starting point, however, natural selection modifies flowering times to match flight times of pollinators, especially in species that are relatively specialized to one functional type (e.g., bumblebees). Notice here the proposition that plants evolve to match pollinators (an idea one finds also in Verne Grant and Karen Grant's famous 1965 book *Flower Pollination in the Phlox Family*, Columbia University Press, New York) rather than that the mutualistic partners coevolve.

But Robertson adds another major idea: plant species that flower at the same time will compete for successful pollination, insofar as they rely on the same functional type(s) of pollinator, and this should select for evolutionary divergence in flowering time. This is a prescient recognition of the phenomenon (and possible outcome) of "interaction at a distance" among sessile plants effected by mobile animals. Robertson went so far as to opine that "In the interaction of organisms in the struggle for existence it strikes me that a law of avoidance of competition is more obvious than that of the survival of the fittest."

Robertson's clear statement of competition for pollination services surprised me in 1975 in another way. He hinted at an idea that also had dawned on me, that such competition went beyond competition for "pollinators" (i.e., for the attention of flower visitors) and could include other mechanisms—such as loss of pollen transferred by pollinators to flowers of a different, "wrong" species, or disruption of a flower's female function (e.g., disruption of germination or growth of conspecific pollen) following receipt of the "wrong" pollen. Robertson is not explicit about these indirect mechanisms, but his discussion of competition among wind-pollinated plants strongly suggests that he recognized them.

After meeting with some skepticism in the 1970s, the phenomenon of interaction at a distance via both direct and indirect mechanisms has gained wider acceptance and has expanded to include facilitation as well as competition among coflowering plants. But much remains to be explored, not only in the smaller "competition" insight of Robertson (e.g., R. J. Mitchell et al., 2009, "New Frontiers in Competition for Pollination," *Annals of Botany* 103: 1403–1413), but also in the much larger philosophy of the flower seasons. Reviews of flowering phenology in 1985 by B. Rathcke and E. P. Lacey ("Phenological Patterns of Terrestrial Plants," *Annual Review of Ecology, Evolution, and Systematics* 16:179–214) and, also in 1985, by R. B. Primack ("Patterns of Flowering Phenology in Communities, Population, Individuals, and Single Flowers," in *The Population Structure of Vegetation*, edited by J. White, Junk, Dordrecht) bolster what Robertson suggested about combined effects of phylogenetic signal and adaptation to local conditions but leave many questions to be answered (e.g., What explains most of the "ancestral" flowering times that characterize different plant families? What determines the length of species' flowering seasons?).

I must somewhere have discovered a pointer to the 1895 paper that led me to it, and when I examine the numbering of my paper reprints (remember those?), I find that the pointer most likely was a 1975 article by D. F. Austin ("Bird Flowers in the Eastern United States," *Florida Scientist* 38:1–12). Austin discusses the synchrony between flowering and hummingbird migration—something that has fascinated me since the 1970s—and notes Robertson's earlier treatment of the topic. Thus Robertson's "philosophy" anticipated not only the current general interest in phenological match and mismatch between plants and pollinators (and indeed between interacting species of all kinds, e.g., C. Parmesan, 2006, "Ecological and Evolutionary Responses to Recent Climate Change," *Annual Reviews of Ecology, Evolution, and Systematics* 37:637–669) but also the specific interest in pollinators whose fate depends on intact migratory pathways.

Soon after discovering the 1895 paper, I encountered Robertson's self-published book (1928, *Flowers and Insects: Lists of Visitors to Four Hundred and Fifty-Three Flowers*, Carlinville, IL), which represents more than three decades of surveys around Carlinville and which draws on his expertise in the biology of pollinators (especially solitary bees) and on his dedication to careful natural history observation (an art that seems, luckily, to be returning to favor). The information it contains was transformed recently—in an era of computer power not available to earlier workers—into the largest qualitative plant-pollinator

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interaction network available to date. Exploring this network and returning to Carlinville for additional field surveys more than a century after Robertson drove around with horse and buggy is providing new insights into the opposite of Robertson's topic, namely, community disassembly, occurring as it now appears to be in a time of climate change (e.g., L. A. Burkle et al., 2013, "Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-occurrence, and Function," *Science* 339:1611–1615).

Acknowledgments

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In *The American Naturalist*

Robertson, C. 1895. The philosophy of flower seasons, and the phaenological relations of the entomophilous flora and the anthophilous insect fauna. American Naturalist 29:97–117.



"In ornithophilous pollination the pollen is carried in such diverse ways that this together with other data combine to make it possible that the humming-bird is the most wonderful distributor of pollen known to the animal world. We are not content to leave the subject without noticing, that as compared with insects, the local range of flight of humming-birds is undoubtedly greater and during the regular migrations they make extensive flights." From "Ornithophilous Pollination" by Joseph L. Hancock (*The American Naturalist*, 1894, 28:679–683).

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