— Opinion —

THESIS, DECONSTRUCTION AND NEW SYNTHESIS: THE CHANGING FACE OF APPLIED POLLINATION

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Abstract—A quarter millennium of the changing face of pollination biology from 18th Century discovery (thesis) to 21st Century crisis is presented in six overlapping, interdigitating facets. Pollination biology was not regarded as serious science at its onset, but acceptance of the Darwinian theory of evolution has shown its biological value. Disciplinary issues in pollination (i.e. deconstruction) have produced a wealth of knowledge but with botanical and zoological solitudes. At the same time botany and zoology tend to be separate within agronomy and apiculture. Philosophical, social, scientific, technical, political and business agendas have variously hampered, and continue to hamper, objective science in each facet. Nevertheless, interdisciplinary approaches to pollination ecology, its inherent co-evolutionary principles, and the current "pollination" crisis have become a scientific and social unifying force that cannot but lead to new knowledge, insights and, I hope, wisdom (new synthesis).

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Pollination biology can be viewed as having started as **thesis** (i.e. a premise to be maintained or proved), having grown in depth and breadth through **deconstruction** (i.e. critical analysis of ideas and knowledge) and is entering a new phase of **synthesis** (i.e. combining components, old and new, to form a connected whole). Throughout the generally constructive history of pollination biology there have been detractions, distractions, and antagonisms. I present a brief compilation and commentary, in six overlapping and interdigitating facets, of the quarter millennium's changing face of pollination biology from non-applied and applied viewpoints. Whilst philosophical, social, scientific, technical, political and business agendas have variously hampered, and continue to hamper, objective science in each facets, these challenges have provided stimulus to deeper research. Certainly, pollination biology has grown in scientific respectability, influence, rigour and utility. Nowadays, it is generally acknowledged that there are enough instances, and mounting evidence, of the erosion of pollination services in many environments and locations that science and society should take, and is taking, notice.

Pollination biology has a venerable history of about one quarter of a millennium (see Baker 1979, 1983; Proctor et al. 1996; Waser 2006). From early days practical issues have not escaped the attentions of pollination biologists. Philip Miller as horticulturalist extraordinaire and Arthur Dobbs with his deep appreciation of agriculture both described pollination *per se* as early as the mid-18th Century (Vogel 1996). Christian Konrad Sprengel, the author of the first text book on pollination (1793), also considered the practical implications of his discoveries and generalizations (Endress 1992; Vogel 1996). During the latter half of the 19th Century, the subject burgeoned. Knuth's (1909) Handbook of Pollination Biology (three volumes in incomplete translation but four in the original German) lists over 2,000 references to scientific publications. Other important textbooks and compendia have since been published, notably those by Faegri & van der Pijl (1979), Proctor et al. (1996) and Willmer (2011). Also, over the years, the importance of pollination to agriculture became increasingly recognized, especially because of the expansion and intensification of mechanized and chemically oriented crop production. Reviews of crop pollination by insects are exemplified by McGregor (1976) and Free (1993). The need for pollinators (especially western honeybees (*Apis mellifera*)) in agroecosystems has become ever more evident as has the need for their protection, especially from pesticide applications (e.g. Brittain (director) 1933, ICPPR over 3 decades and most recently 2015; NRCC 1981; Johansen & Mayer 1990; Fischer & Moriarty (eds) 2014).

While practical facets of pollination were becoming more and more incorporated into agricultural practice, and alternative (non *Apis*) pollinators were being considered with methods of husbandry developed, it was becoming clear that major issues were starting to confront pollination in natural, quasi-natural and managed systems (NRCC 1981). The seminal publication of the book "The Forgotten Pollinators" (Buchmann & Nabhan 1996) brought the plight of pollinators across ecosystems (including agroecosystems) and the world into stark focus. It launched contemporary international concern for the role of pollination as an ecosystem service. The São Paulo Declaration on Pollinators (Dias et al. 1999; Kevan & Imperatriz-Fonseca (eds) 2002; 2006) led to the assimilation of ecosystem interrelations and

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services, as exemplified by pollination, into the agenda of the Convention on Biological Diversity (CBD) in 2002. The potential economic consequences of pollination deficits to human food and fibre production have created international concern (Kevan & Phillips 2001; Aizen et al. 2009; Melathopoulos et al. 2015).

With the above overview in place, I present the six overlapping, but certainly not mutually exclusive, facets of the general development of pollination biology and introduce the detractions from advancement and how they have been answered.

I consider **Facet I** to be that of Discovery. It started and continues energetically with ***Theses*** (as mentioned above and as are basic to the other Facets identified). Facet I continues actively today through ***Deconstruction*** (i.e. the critical analysis of ideas (theses) and knowledge by observation and experimentation). Initial 18th Century explanations of floral and pollinator form and function were viewed as contrary to some special-creationist beliefs and pollination studies were often considered as non-serious science (Vogel 1996). Other difficulties may have resided in the detailed exposés that plants had sex, as advanced much earlier by Linnaeus (1729) and put down as "loathsome harlotry" (www.ucmp.berekely.edu/history/linnaeus.html). Both Linnaeus and Sprengel accepted the creationist beliefs of their days. Certainly, that early resistance was foiled by acceptance of the Darwinian theory of evolution through natural selection, even as exemplified through pollination (Darwin 1862, 1877).

As biology became increasingly subdivided, pollination zoology (apiculture, entomology) and botany (agronomy, plant reproductive needs) became increasingly the purviews of detailed and subdisciplinary life sciences: pollination biology, for all its productivity, became poorly integrated. Late in the 20th and now in the early 21st Century pollination biology is expanding with recognition of the "pollination crisis", but the environmental focus has stressed animal pollinators, especially bees (Kevan & Imperatriz-Fonseca (eds) 2002, 2006; Stubbs & Drummond (eds) 2001; Strickler & Cane (eds) 2003; STEP 2015) rather than botanical aspects until recently (IPBES 2014 ongoing).

Facet II constitutes the application of pollination biology to human food and fibre production. Although some scientists recognized that pollination was directly important to food and human well-being, it was not widely applied until agriculture and beekeeping became mechanized in the mid-19th Century. It culminated with the publication of several major treatises, notably those of McGregor (1976) and Free (1993). It is useful to parse out, as **Facet III**, the issues of intensive renewable natural resources exploitation (farming and forestry) and pesticide use as having additional ramifications in pollination biology. In Facet III, pesticides, notably insecticides, became increasingly used in food and fibre production in the early 20th Century. Concern for pollinators stemmed primarily from honeybee kills (Anderson & Atkins 1968), but Brittain (1933), as director of a major study on pollination of apples, as early as the 1920s recognized broader concerns. Regulatory requirements for the registration of pesticides have become increasingly rigorous (often including needs for studies on safety for pollinators) and widespread since the 1970s (see Fisher & Moriarty (eds) 2014).

Apicultural concerns (e.g. colony collapse disorder, other pests and diseases of the apiary, neonicotinoid insecticides, overwintering losses in temperate countries) have tended to draw attention away from overarching, and ultimately more serious, environmental problems.

In both Facets II and III, the lack of integration between agronomy (botanical) and apiculture (zoological) is evident. At the same time, studies in basic and applied pollination tended to follow separate paths. Within agronomy, plant breeders have promoted, and continue to promote, pollinator-independent crops to assure yield. That applies strongly to crop breeding (which has probably been going on for millennia) for self-pollinating, self-compatible, and apomictic cultivars of crop plants that ancestrally required pollination by insects (see Shivanna & Sawhney (eds) 1997; Sleper & Poehlman 2006) and to a lesser extent to wind-pollinated cereals. Meanwhile, apidologists and beekeepers have advocated the almost exclusive use of the western honeybee (*A. mellifera*) to solve issues of pollination deficits, an attitude that is fast changing (Strickler & Cane (eds) 2003). Throughout Facets II and III the pesticide industries have mostly and vociferously denied responsibility for the demise of managed and wild pollinators.

The recognition in the mid 20th Century of the value of non-*Apis* species as managed pollinators constitutes the start of **Facet IV** (Strickler & Cane (eds) 2003). Alfalfa leafcutting bees (*Megachile rotundata*) became important in the 1950s. Bumblebees (*Bombus* spp.) became domesticated for greenhouse pollination in the 1990s. Mason bees (*Osmia* spp.) are being exploited in Europe, Asia and North America. Stingless bees (Meliponini) are being investigated for their utility for crop pollination in South America. Even so, some beekeepers and apidologists, now seemingly a decreasing minority, remain antagonistic, opining that alternative pollinators do not do the job and are too pricey. I am not aware of studies that have fully tested those opinions as scientific hypotheses. There are various studies that show that non-*Apis* pollinators are more efficient in terms of their capacities to move pollen (Javorek et al. 2002: Cane & Schifhauer 2003; Artz & Nault 2011; Ne'eman et al. 2011).

The adoption of non-*Apis* pollinators for some cropping systems suggests that they are capable of doing the job and are economically superior. Full analyses of costs and benefits remain to be made whereby the relations between pollination and yield deficits are linked to costs and benefits of managed (*Apis* or non-*Apis*) and/or unmanaged pollination. Recent studies across continents, landscapes and farming systems strongly suggest the economic value of wild populations of pollinators to agricultural sustainability (Garibaldi et al. 2014).

Facet V expands the purviews of Facets I to IV because attention to ecosystem function enters the picture. Although initially this Facet was restricted to agriculture (e.g. Brittain (director) 1933) it became expanded in the 1970s to include forest environments (NRCC 1981; Kevan & Plowright

1995), general ecosystems (Kevan 1999, 2001; Kevan & Baker 1983) and economics (Kevan & Phillips 2001). Even so, the broader issues remained largely unrecognized until the late 1990s when syntheses through Buchmann & Nabhan's book (1996) *The Forgotten Pollinators* and the *São Paulo Declaration on Pollinators* (Dias et al. 1999) heralded today's global concerns. Nearly two decades later, problems in pollinator conservation and management, pollination itself and apiculture (parasites, pathogens, pesticides) continue to intensify. Ecosystem function is receiving increasing recognition, especially with expanded studies of connectance patterns, or webs, of pollinators and plants. Those patterns are being used to understand the extents and strengths of interactions between flowers and flower visitors (e.g. Moreira et al. 2015) even if the additional dimensionalities as to how they function and their importance to pollination remain relatively poorly understood.

Facet VI, the new synthesis, is the here and now, and what may be envisioned for the future.

It is generally acknowledged that there are enough instances, and mounting evidence, of the erosion of pollination services in many environments and localities that science and society should take notice. In fact, since the acknowledgement that pollination services for agriculture and wildlife are at risk, major international and national initiatives are addressing the interdisciplinarity of the emergent problems (e.g. US-NAS 2007; IPI 2009; CANPOLIN 2009 – 2014; STEP 2015). Formal risk analyses are now being applied widely for assessing the effects of pesticide use on managed pollinator health (Fischer & Moriarty (eds) 2014; ICPPR 2015) and are being seriously considered for application to pollination ecology in its environmental contexts.

Most recently, the IPBES (2014 and ongoing) (Intergovernmental Panel on Biodiversity and Ecosystem Services) has taken on the task of producing a synthetic and scientifically based review, ranging from biology and ecology to economics and societally-based knowledge aimed at policy and pollination (publication expected in 2016). The ***new synthesis*** **(Facet VI)** takes on the evolving integrative and transdisciplinary approaches as they are embraced by forward-looking scientific teams around the world and in industry-sponsored environmental programs. Narrow disciplinary approaches will continue to contribute to the broader issues. Some vested interests might deny responsibilities and so detract from progress. In some countries, government policies require commercial involvement in research, and so detract from real or perceived objectivity. Scholarly disagreements will continue but, ultimately, they are the grist for the advancement of knowledge.

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