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Emerging Themes from the ESA Symposium Entitled “Pollinator Nutrition: Lessons from Bees at Individual to Landscape Levels”

Vanessa Corby-Harris , Julia H. Bowsher , Morgan Carr-Markell, Mark J. Carroll , Mary Centrella, Steven C. Cook, Margaret Couvillon, Gloria DeGrandi-Hoffman, Adam Dolezal, Julia C. Jones, Christina L. Mogren , Clint R. V. Otto , Pierre Lau , Juliana Rangel , Roger Schürch and Ashley St. Clair

Introduction

Pollinator populations are declining (Biesmeijer et al., 2006; Brodschneider et al., 2018; Cameron et al., 2011; Goulson, Lye, & Darvill, 2008; Kulhanek et al., 2017; National Research Council, 2007; Oldroyd, 2007), and both anecdotal and experimental evidence suggest that limited access to high quality forage might play a role (Carvell, Meek, Pywell, Goulson, & Nowakowski, 2007; Deepa et al., 2017; Goulson, Nicholls, Botias, & Rotheray, 2015; Potts et al., 2003, 2010; Vanbergen & The Insect Pollinators Initiative, 2013; Vaudo, Tooker, Grozinger, & Patch, 2015; Woodard, 2017). Multiple researchers are earnestly addressing this topic in a diverse array of insect-pollinator systems. As research continues to be published, increased communication among scientists studying the topic of nutrition is essential for improving pollinator health.

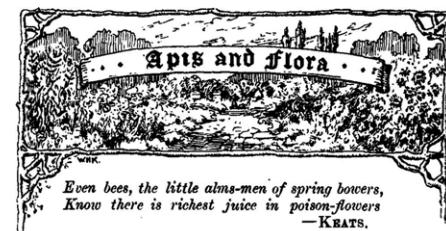
The 2017 meeting of the Entomological Society of America convened the first week of November in Denver, CO, USA. The meeting included a variety of symposia across a diverse set of insect study systems, including bees and other insect pollinators. In the member symposium “*Pollinator Nutrition: Lessons from Bees at Individual to Landscape Levels*”, researchers convened to discuss innovative areas of research in this area, with the goal of inspiring novel, information-based ideas for improving pollinator health. The research that was presented addressed the

nutritional needs of native and introduced (i.e., *Apis mellifera* in the United States) bee pollinators at both individual and population levels, and how stressors like disease, landscape change, and pesticides influence these nutritional needs. The symposium included 12 oral and 13 poster presentations. The attendance in the room consistently reached more than 100 people from academia, government, industry, and private organizations, all with an interest in pollinator conservation.

The purpose of this review and summary is two-fold. First, we want to communicate the major themes covered in the symposium for a wider audience, including researchers, the beekeeping community, natural resource managers, policymakers, and members of the public. Second, we are keen to highlight potential areas for future study that emerged from our discussions. Each theme that we discussed is highlighted below, with permission from the researcher. We conclude with a note on how this information could be applied in the context of land use and conservation and discuss areas of future study.

Defining the Nutritional Requirements of Bees

The first section of the symposium dealt with the nutritional requirements of bees and the role of seasonality in defining these requirements. Honey bee nutrition has been reviewed extensively elsewhere (Brodschneider & Crailsheim, 2010;



Crailsheim, 1990; Vaudo et al., 2015; Wright, Nicolson, & Shafir, 2018). We summarize bee nutrition information while highlighting current efforts to understand novel aspects of bee nutrition. We stress that throughout the symposium it was clear that more data are needed on the requirements of non-honey bee taxa to meet our goal of providing adequate, nutritious landscapes for all bees. Nonetheless, many (but not all) of the presentations addressed nutrition work that is being done on honey bees.

Like most insects that undergo metamorphosis, honey bees acquire most of the nutrition and energy stores required for growth, development, and reproduction during the larval stages. For early instar larvae, these nutrients come exclusively from worker and royal jelly that is provided by the young nurse bees that support the larvae, the queen, and other adults in the hive. Jelly is comprised of secretions from the nurses' hypopharyngeal and mandibular glands. In later instars, worker jelly is combined with pollen and nectar, while royal jelly only contains nurse secretions (Haydak, 1970).

In the last larval instar, the wax cell is capped by the workers, and so bees do not consume any food as pupae and quite possibly as very young (<12 h old) adults. The excess nutritional resources consumed as juveniles, if not used during pupal development, are stored in the developing bee's fat body. Adult workers can live on a diet containing carbohydrates and minimal to no protein (Altaye, Pirk, Crewe, & Nicolson, 2010; Paoli et al., 2014; Pirk, Boodhoo, Human, & Nicolson, 2010), suggesting that, when needed, fat body stores alone can provide the sufficient protein, lipid, and micronutrients required for basic survival and maintenance.

However, because many bees are social, self-preservation alone may not maximize their fitness.

Honey bees perform additional tasks that maximize the inclusive fitness of the colony, and thus have additional nutritional requirements beyond ensuring their own individual survival. Newly emerged workers, for example, consume the bulk of the pollen between 2 and 8–10 days postemergence (Haydak, 1970) in order to fuel the synthesis of the jelly that is fed to the larvae and queen. Diets severely limited in pollen, protein, or fat lead to smaller jelly-secreting hypopharyngeal glands (Arien, Dag, Zarchin, Masci, & Shafir, 2015; Corby-Harris et al., 2016; Crailsheim & Stolberg, 1989), early foraging (Schulz, Huang, & Robinson, 1998; Toth, Kantarovich, Meisel, & Robinson, 2005), irregular nurse physiology (Corby-Harris, Jones, Walton, Schwan, & Anderson, 2014), and reduced brood rearing through fewer nurse visits, larval cannibalism, and early capping of late instar larvae (Haydak, 1935; Schmickl & Crailsheim, 2001, 2002). Thus, although individuals can persist when nutrition is limited, colony function may suffer and the needs of both groups must be considered when thinking about hive nutrition.

Forage contains macronutrients (protein, lipids, and carbohydrates) in suboptimal amounts and/or ratios. Many animals actively regulate their nutrient intake in order to meet current nutritional demands when a range of different resources are available (Behmer, 2009; Lihoreau et al., 2014; Raubenheimer, Simpson, & Mayntz, 2009; Waldbauer & Friedman, 1991). Anthony Vaudo (Penn State University) shared his work on bumble bee nutritional ecology, showing that they preferred pollens containing certain protein-to-lipid ratios that also maximized survival

(Vaudo, Patch, Mortensen, Tooker, & Grozinger, 2016; Vaudo et al., 2016). It is somewhat controversial whether honey bee colonies also self-select (Corby-Harris, Snyder, Meador, & Ayotte, 2018; Hendriksma & Shafir, 2016; Paoli et al., 2014; Pernal & Currie, 2001, 2002; Zarchin, Dag, Salomon, Hendriksma, & Shafir, 2017). It is also unclear how this could work. How do nurse bees, who consume the pollen, communicate information on the quality of incoming pollen to the foragers, who consume primarily carbohydrates? (Camazine et al., 1998; Corby-Harris et al., 2018).

Honey bee larval nutrition was also discussed. Although the mechanism is unclear, nurses can modulate the nutrient content of jelly so that the jelly fed to worker larvae differs from that fed to queen larvae (Wang et al., 2016). Julia Bowsher (North Dakota State University) showed that the nutrient content of jelly impacts not only caste but also larval survival. Larvae successfully reached metamorphosis *in vitro* on a wide range of diets with varying ratios of protein to carbohydrate (P:C), but diets with very low or very high protein were harmful to larval growth and survival. Larvae survived the best when the P:C ratio of their diet was 1:4 (Helm et al., 2017). This ratio is similar to the 1:3 ratio that honey bee foragers seek out when collecting food for a colony that is rearing brood (Pirk et al., 2010).

The Seasonality of Bee Nutrition

The symposium included two talks addressing the seasonal component of honey bee nutrition. Honey bee colonies are perennial and must survive periods of harsh conditions (i.e., winter) and/or nutrient shortage. Honey bees prepare for nutrient dearths by amassing food resources when they are abundant, either by storing it in their hives, or in their fat bodies and hemolymph (Döke, Frazier, & Grozinger, 2015). The annual life cycle of a honey bee colony includes distinct phases of colony growth and reproduction in the spring and summer, reduced brood production into the later summer and fall, and overwintering during the colder months (reviewed in Döke et al., 2015). Individual honey bees also exhibit seasonal differences. For example, winter bees live for several months, while spring and summer bees live ~30 days. Winter bees also resemble

the nurse workers of spring and summer, with low levels of juvenile hormone and larger amounts of the lipoprotein vitellogenin compared to foragers. Like nurses, winter bees also have large hypopharyngeal glands, but unlike nurses the secretory activity of these glands is low, suggesting that they might be used as storage organs in the winter (Brouwers, 1983). According to unpublished work presented by Steven Cook [United States Department of Agriculture (USDA)], the cell membrane fatty acid profiles of winter bees also mirror long-lived queens.

As colonies cycle through the seasons and as the physiology of the bee changes, one question that arises is whether individual and colony physiology reflects the nutrition of seasonal food resources or is an inherent annual cycle that the bees experience irrespective of seasonal food resources. In ants, seasonality influences foraging behavior and physiology and is not shaped purely by the nutrient content of available foods (Cook, Eubanks, Gold, & Behmer, 2011, 2016). This may also be true in honey bees. Gloria DeGrandi-Hoffman (USDA) showed that spring nurse-aged honey bees performed better when consuming spring rather than fall pollen, while fall bees were not sensitive to pollen type. This sensitivity was also true in the context of a *Nosema* infection: spring bees responded differently to *Nosema* infection depending on pollen type, whereas fall bees showed the same level of response to infection irrespective of pollen type (DeGrandi-Hoffman et al., 2018). Cook also showed that spring and fall honey bees have distinct seasonal preferences for certain types of dietary fatty acids. If a bee's choice reflects her nutritional needs, then this suggests that colonies need different fatty acids depending on the season. Seasonality may also affect honey bee's requirements for micronutrients; researchers have demonstrated that honey bees can regulate their micronutrient intake by consuming floral resources and mineralized water at a rate that changes with season (Bonoan, O'Connor, & Starks, 2018). These examples indicate that bees in different seasons have different nutritional requirements that reflect, or are dictated by, the colony's annual cycle and are not simply a product of the forage that is available. As more information on seasonal nutritional requirements comes in, it can be used to provide bees with forage matched more closely to their circannual needs.

High-Throughput Methods Offer Additional Clues to the Consequences of Nutritional Deprivation

The symposium also highlighted ways in which modern, high-throughput, methods are being used to study the consequences of different nutritional regimes. High-throughput biological markers, specifically those based on DNA sequences or gene and protein expression libraries, allow researchers to analyze the large amounts of data that are needed to further understand and quantify the consequences of nutrient deprivation at the individual, colony, and landscape level. DeGrandi-Hoffman's presentation (discussed above) also included results from a transcriptome library, which offered a deeper look into the physiological consequences of seasonal pollen consumption and *Nosema* infection (DeGrandi-Hoffman et al., 2018). One of the most interesting results of this was how energy, particularly fat metabolism, influences *Nosema* resistance.

Julia Jones (Uppsala University) presented the results of a high-throughput bacterial DNA sequencing project that looked at the relationship between honey bee gut microbial community and environmental landscape (i.e., patch type). Jones and colleagues found that patch type (oilseed rape where neonicotinoid pesticides were used versus agricultural farmland distant from oilseed rape where no neonicotinoids were used) was correlated with the relative abundances of certain key bacteria in the bee's gut. Some of the bacteria that were less abundant in bees exposed to oilseed rape farms may also be beneficial for bees (Chouaia et al., 2012; Engel et al., 2016; Engel & Moran, 2013; Koch & Schmid-Hempel, 2011), suggesting a negative consequence of this patch type to microbial community structure and bee health. Other potentially beneficial gut bacteria were more abundant in bees foraging on oilseed rape, suggesting that some bacteria may be selected for in such environments. Although it is not yet clear why these changes happen or how they might impact bee health, Jones's work provides a framework for future functional studies directly linking the landscape patch type to the gut bacterial community and bee health.

Quantifying the Nutritional Value of Landscapes for Bees

Agricultural crop production continues to be a driving force of declining habitat for pollinators, particularly in states that are critical for honey production in the USA (Koh et al., 2016; Smart, Pettis, Euliss, & Spivak, 2016; Spivak et al., 2017). Landscape conversion to agricultural monocultures negatively affects pollinator diversity and habitat by reducing forage availability and increasing pesticide exposure risk (Krupke, Hunt, Eitzer, Andino, & Given, 2012; Mogren, Rand, Fausti, & Lundgren, 2016; Otto, Roth, Carlson, & Smart, 2016). In these intensively managed areas, conservation easements are critically important for maintaining pollination services of honey bees (Gallant, Euliss, & Browning, 2014; Otto et al., 2016; Schulte et al., 2017; Smart et al., 2016) and native bees (Benjamin, Reilly, & Winfree, 2014). In order to develop clear plans for designing or conserving pollinator-friendly landscapes, the impact that these different land types (farmland versus conservation land or nonagricultural) have on pollinator health must be quantified. The next set of presentations highlighted the various ways in which this objective is being addressed for native and introduced bee taxa.

Transition of landscapes from natural ecosystems to those dominated by one or a few agriculturally important crops is exemplified by the "corn belt" of the agricultural Midwestern United States, where vast tracts of land are dominated by just a few commodity crops. In Iowa, a corn belt state, crops like corn and soybean occupy ~65% of the landscape, replacing a landscape that was predominantly tallgrass prairie (Fausti, 2015). Adam Dolezal (University of Illinois) showed that landscape composition surrounding apiaries (agricultural versus uncultivated) relates to colony success, but in unexpected ways. Hives surrounded by *more* cropland produced more brood, more bees, and accumulated more honey than those in uncultivated areas. This trend was also observed in a separate study by Sponsler and Johnson (2015), who compared honey bee colonies surrounded by farmland to those in urban and forested environments. Hives from agricultural areas collected mostly clover, a plant that predominantly grows in field edges and that is not found in uncultivated areas composed mostly of forest, which supports fewer flowers for bees to

forage upon. Therefore, agricultural areas may provide better forage simply from the clover contained within field edges and margins. But no matter what land type surrounded the hives, all apiaries exhibited a period of late summer dearth that coincided with the end of the clover bloom, hive weight decrease, and a physiological decline of the bees that made them unlikely to survive the winter. Access to prairies and their late-summer forage may reverse this trend. Ashley St. Clair (Iowa State University) showed that stress and loss of colony reserves faced by honey bees in agricultural landscapes was reversed if colonies were provided access to prairies in the late summer. Focusing on queen quality, St. Clair found that queens in colonies placed in prairie landscapes in late summer laid 41% more eggs than those in soybean fields. Workers in prairie colonies also reared 50% more eggs into capped pupae compared to those in soybean. St. Clair's research suggests that access to prairie habitat in the late summer leads to larger colony populations, and that prairies may provide more nutritious resources compared to monoculture landscapes.

Clint Otto [United States Geological Survey (USGS)] showed how land-use change affects forage availability and honey bee health in another area of the USA, the Northern Great Plains (NGP). This area supports diverse, yet relatively unknown, native pollinator communities and more than one million honey bee colonies for honey production annually (Spivak et al., 2017). The NGP has undergone substantial land-cover change due to cropland expansion and weakening of conservation programs like the Conservation Reserve Program (CRP; Morefield, LeDuc, Clark, & Iovanna, 2016; Wright & Wimberly, 2013). Otto found that over 160,000 ha of conservation grassland around apiaries was converted to row crop from 2007 to 2012 in North Dakota and South Dakota alone. Through simulations he showed that future limitations on CRP acreage will be harmful for commercial apiaries in the NGP. Reducing CRP lands to 7.7 M ha nationally would reduce the number of Dakota apiaries that meet the defined forage criteria by 28%, while increasing the CRP lands to 15 M ha nationally would increase the number of apiaries that meet these criteria by 155%. Strategic placement of CRP lands near existing apiaries increased the number of apiaries that meet the forage criteria by 182%. Otto's analyses showed how future changes to the CRP

affect the environment's carrying capacity for supporting honey bee colonies and supports ongoing efforts to quantify the value of landscapes for honey bee colony health (Otto et al., 2018).

While efforts toward quantifying the value of landscapes for honey bees is important, we must also consider how the same landscapes impact other important pollinators that might have very different foraging and life history strategies. Wild pollinators (i.e., not managed in the USA, like honey bees) strongly influence crop output (Garibaldi et al., 2013) and maintain ecosystem function, so it is crucial to consider their response to different landscape management efforts and to consider how their response might relate to that of honey bees. In particular, efforts to enhance pollinator habitat should not assume that the habitat enhancements made for honey bees will also benefit native bees. Christina Mogren (University of Hawaii) showed us how diet and land use impact the health (glycogen, lipid, and protein concentrations) of two different bees, the polylectic eusocial honey bee (*Apis mellifera*) and the native, solitary, oligolectic thistle long-horned bee (*Melissodes desponsa*). While their diets did overlap somewhat, honey bees foraged more on introduced weedy species while the thistle long-horned bee foraged more on native wildflowers. The health of both bee taxa was unaffected by dietary diversity but was sensitive to differences in land use. Honey bees performed better in landscapes with larger contiguous areas of floral resources, while thistle long-horned bees performed better in landscapes dominated by single, larger resource patches. This might reflect key differences in species-specific life histories. Honey bees may forage for miles from their colony in search of resources and recruit other bees to promising locations. Solitary bees such as the thistle long-horned bee forage more closely to their nests, and thus require patches where abundant resources are immediately present. Mary Centrella (Cornell University) also showed that the introduced solitary and polylectic mason bee (*Osmia cornifrons*) was negatively impacted by agricultural landscapes, in which their pollen provisions were comprised of fewer plant species with higher pesticide loads. In order to preserve the health of all bees throughout agricultural landscapes, conservation plans should consider the life history and foraging strategies of every bee in the landscape while maximizing floral diversity, especially of native annuals and perennials plants. Such a strategy could enhance bee

nutrition while encouraging resource partitioning between competing bee species.

Two presentations showed how foraging behavior itself can be used to measure the nutritional value of landscapes. Pierre Lau (Texas A&M University) discussed the use of palynology to quantify the dominant bee-forage plant taxa. Several labs represented in this symposium and elsewhere are currently using pollen identification to study the foraging behavior of bees and the nutritional value of landscapes (Barth, 2005; Baum et al., 2004; Bell et al., 2016; Corby-Harris et al., 2018; de Vere et al., 2017; DeGrandi-Hoffman et al., 2018; Smart et al., 2017). Lau et al. (2018) showed that 200–500 pollen grains should be microscopically identified and enumerated in order to accurately characterize honey bee pollen diets. Morgan Carr-Markell (University of Minnesota) also addressed how bees evaluate the nutritional value of landscapes in her work with the honey bee waggle dance (von Frisch & Chadwick, 1993), which functions as a bioindicator of landscape value (Couvillon & Ratnieks, 2015). The waggle dance has been used to measure how honey bees respond to different land uses and resource availability (Balfour & Ratnieks, 2017; Couvillon & Ratnieks, 2015; Couvillon, Schürch, & Ratnieks, 2014; Danner, Keller, Härtel, & Steffan-Dewenter, 2017; Sponsler, Matcham, Lin, Lanterman, & Johnson, 2017). Carr-Markell showed that foragers with easy access to restored prairies in the Midwestern US advertise nonprairie sites and collect most of their food from nonprairie flowers, especially in the spring and early summer. This somewhat counterintuitive result that nonprairie resources were more highly preferred and possibly more nutritious agreed with Adam Dolezal's results from earlier in the symposium.

Science and Support Tools for Improving Bee Nutrition

The main goal of the symposium was to inspire novel, information-based ideas for improving pollinator health. We were especially interested in hearing how studies involving the nutritional value of forage and foraging landscapes can influence land management activities that balance the needs of pollinators with those of growers and other stakeholders. This is a formidable task, but one that needs to be addressed more fully in order to curb ongoing pollinator declines (Iovanna et al., 2017;

Spivak et al., 2017). The science highlighted in this symposium provides policy makers and natural resource managers with information needed to make more informed decisions with respect to pollinator forage and nutrition. For example, several studies in our symposium demonstrated how land use and habitat quality affect bee health, honey production, and pollination services. The need for heterogeneous land cover that provides continuous bloom for bees was a common theme among our presenters. We hope that future policies and habitat restoration plans can be based on the best available science to improve pollinator forage in agricultural systems. Policy makers and land managers can also employ decision-support tools that our scientists develop to evaluate the cost of restoring pollinator habitats. Clint Otto (USGS) showed an example of such a tool, the USGS Pollinator Library (United States Geological Survey – Northern Prairie Wildlife Research Center, 2015), which catalogues how bees and other pollinators use different plant species on private and federal conservation lands in North Dakota. Otto found significant variability in the complexity of plant-pollinator communities across different land types (CRP, Waterfowl Production Areas, and National Wildlife Refuges), which highlighted the need for heterogeneous land cover in maintaining diverse pollinator communities. He then provided an example of how data from the Pollinator Library can be combined with seed cost data to develop cost-effective seeding mixes to support wild and managed bees (Otto et al., 2017). Collectively, the research presented in our symposium can be used to improve pollinator nutrition across multiple spatial scales.

Departing Thoughts

The organizers of this symposium sought to identify creative research opportunities and collaboration among researchers. We are glad to report that this goal was largely met. The symposium attendants left emboldened and inspired to continue researching these topics, while discussions between talks hinted at possible collaborations among researchers to address topics in transformative ways. One of the most important results of the symposium was a refined vision for areas that should be investigated more fully in order to meet the challenge of increasing pollinator health through improved nutrition. We suggest that increased research effort should be devoted to the following areas in particular:

1. The nutritional needs of *all* bees, especially non-honey bee taxa, at different life stages and different seasons.
2. How a pollinator's life history contributes to their sensitivity to land use and change.
3. Strategies for avoiding, preventing, or mitigating seasonal nutrient dearths.
4. Defining the economic value of landscapes in the context of pollinator ecosystem services, both for nonmigratory and migratory bees.
5. Developing decision support tools for policy makers that incorporate information gleaned from point 4.
6. A synthesis of ongoing pollinator habitat and land use research in agricultural and urban landscapes.

We are grateful for the opportunity to disseminate the main points of our discussion on pollinator health to a wider audience.

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Maria Ziaja, Bożena Denisow, Małgorzata Wrzesień & Tomasz Wójcik:
Availability of food resources for pollinators in three types of lowland meadows.

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The availability of floral resources is considered a key factor for the maintenance and conservation of pollinators. We compared the forage floral diversity of three types of lowland meadows (Molinia meadows, tall herb fringe meadows, and hay meadows)

located in south eastern Poland. The total number of plant species was 125, including 84 species (67.2%) classified as plants visited by insects. The richness and diversity of forage flora differed between the types of meadow. The Molinia meadows and hay meadows were preferred by pollinators. However, different taxonomic groups of pollinators can respond to the variability and availability of floral resources in a different way. Molinia meadows are of particular importance for the abundance of *Bombus* spp., solitary bees, and flies. The RDA ordination model demonstrated that the floral community composition, plant species abundance, plant species richness, and floral attributes (size, shape, phenology) were all important for the abundance of insect visitors in the mosaic of meadows. The cluster analysis showed that most plant species were visited by similar groups of insects; however, their proportion differed considerably. Our results present arguments for inclusion of semi-natural meadows into conservation plans and for efforts of protection of highly effective floral resources aimed at maintenance of pollinators.

Ida Conti, Piotr Medrzycki, Antonio Iannone, Francesca Vittoria Grillenzoni, Francesca Corvucci, Davide Dagnino, Gabriele Casazza, Carlo Montanari & Mauro Giorgio Mariotti: **Preliminary survey of the nutritional and palynological traits of honey bee-foraged pollen from Liguria (Italy).**

<https://doi.org/10.1080/00218839.2018.1460910>

It is known that the palynological features, and consequently the nutritional quality, of bee-foraged pollen vary according to several factors such as sampling site and period of year. In our two year study, carried out as part of the COLOSS CSI Pollen study between April and September in the eastern province of Genova (Italy), we explored the relationships between the palynological spectra and the protein content of corbicular pollen. We found that the differences are mainly driven by the collection season rather than by the site. This observation allowed us to employ the sample's palynological traits for the identification of foraging seasons characterized by different protein content in pollen. The outcome of our study provides a useful tool for beekeepers, helping them to cautiously program certain apiary management practices. This work also provides suggestions for future monitoring programs, regarding the advantages of studying the seasonal pattern not only of the floral origin of pollen but also of its nutritional traits.