Pollen report: Quantitative review of pollen crude protein concentrations offered by bee pollinated flowers in agricultural and non-agricultural landscapes

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To ease nutritional stress on managed as well as native bee populations in agricultural habitats, agro-environmental protection schemes aim to provide alternative nutritional resources for bee populations during times of need. However, such efforts have so far focused on quantity (supply of flowering plants) and timing (flower-scarce periods) while ignoring the quality of the two main bee relevant flower-derived resources (pollen and nectar). As a first step to address this issue we have compiled a geographically explicit dataset focusing on pollen crude protein concentration, one measurement traditionally associated with pollen quality for bees. We attempt to provide a robust baseline for protein levels bees can collect in- (crop and weed species) and off-field (wild) in agricultural habitats around the globe. Using this database we identify crop genera which provide sub-optimal pollen resources in terms of crude protein concentration for bees and suggest potential plant genera that could serve as alternative resources for protein. This information could be used by scientists, regulators, bee keepers, NGOs and farmers to compare the pollen quality currently offered in alternative foraging habitats and identify opportunities to improve them. In the long run we hope that additional markers of pollen quality will be added to the database in order to get a more complete picture of flower resources offered to bees and foster a data-informed discussion about pollinator conservation in modern agricultural landscapes.

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Abstract

To ease nutritional stress on managed as well as native bee populations in agricultural habitats, agro-environmental protection schemes aim to provide alternative nutritional resources for bee populations during times of need. However, such efforts have so far focused on quantity (supply of flowering plants) and timing (flower-scarce periods) while ignoring the quality of the two main bee relevant flower-derived resources (pollen and nectar). As a first step to address this issue we have compiled a geographically explicit dataset focusing on pollen crude protein concentration, one measurement traditionally associated with pollen quality for bees. We attempt to provide a robust baseline for protein levels bees can collect in- (crop and weed species) and off-field (wild) in agricultural habitats around the globe. Using this database we identify crop genera which provide sub-optimal pollen resources in terms of crude protein concentration for bees and suggest potential plant genera that could serve as alternative resources for protein. This information could be used by scientists, regulators, bee keepers, NGOs and farmers to compare the pollen quality currently offered in alternative foraging habitats and identify opportunities to improve them. In the long run we hope that additional markers of pollen quality will be added to the database in order to get a more complete picture of flower resources offered to bees and foster a data-informed discussion about pollinator conservation in modern agricultural landscapes.

Introduction

The green agricultural revolution during the mid-20th century drastically increased productivity in agriculture and changed land use on a global scale (Evenson and Gollin 2003). The combination of high yield crop varieties, chemical fertilizer, plant protection products and intensified mechanization have amplified crop biomass production, which in turn has enabled the support of an ever-growing human population (Evenson and Gollin 2003, Pingali 2012). At the same time, the associated reduction in plant diversity in intensified agricultural habitats (e g. large scale mass flowering crop-cultures) has been suggested to adversely affect pollinator populations which provide essential ecosystem services (Potts, Biesmeijer et al. 2010, Roulston and Goodell 2011, Goulson, Nicholls et al. 2015). In particular, bees (Hymenoptera: Apoidea), a diverse group of primary phytophagous insects inhabiting most major habitats around the globe (Wcislo and Cane 1996, Michener 2000), have recently come into focus because they provide a large share of pollination services in agricultural habitats and some populations are apparently in decline (Goulson, Nicholls et al. 2015). Bees rely solely on plant derived resources (pollen and nectar) to satisfy their nutritional needs (Michener 2000, Brodschneider and Crailsheim 2010, Roulston and Goodell 2011), which can be problematic in agricultural landscapes because bee species foraging outside the restricted flowering period of pure culture dominated agricultural settings might be deprived of adequate alternative food sources. This phenomenon has been termed nutritional mismatch and has been suggested as one potential direct driver for the apparently observed decline in some bee populations (Vaudo, Tooker et al. 2015).

In order to ease nutritional stress on bee populations in modern agricultural settings the establishment of alternative foraging habitats has been incentivized via agro-environmental management schemes in the EU and elsewhere (Phillips and Lowe 2005, Vaughan and Skinner 2008, Lye, Park et al. 2009, Goulson, Nicholls et al. 2015, Potts, Biesmeijer et al. 2015). Such schemes seek to provide bees with complementary flower resources outside the mass flowering periods of commercial crops, but have traditionally focused solely on providing plants to attract and sustain social bees, particularly bumblebees (Vaudo, Tooker et al. 2015). Only recently has the important role of solitary

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bees in this context been recognized (Scheper, Bommarco et al. 2015). However, in all cases the quantity of flowering plants and the timing of flowering alone is likely insufficient to maintain healthy bee populations (Vaudo, Tooker et al. 2015). The quality of floral resources (including sugar concentration in nectar and protein content of pollen) also plays a major role in bee health with direct consequences for at least for social bees (Tasei and Aupinel 2008, Brodschneider and Crailsheim 2010, Di Pasquale, Salignon et al. 2013, Vaudo, Tooker et al. 2015, Vaudo, Patch et al. 2016) fitness. Such qualitative aspects of bee nutrition should be taken into consideration to develop a complementary and nutritionally optimized resource base for bee populations in agricultural landscapes (Vaudo, Tooker et al. 2015).

To facilitate the integration of flower resource quality in pollinator management schemes we compiled a geographically explicit data base of pollen quality (measured as crude protein content) offered by bee-visited flowers in an agricultural setting. Given that pollen is the main protein source for bees' offspring, crude protein concentration in pollen is directly linked to the amount of protein bees can extract from their habitat and has traditionally served as a proxy for pollen quality (T'ai, Cane et al. 2000, Roulston and Goodell 2011, Vaudo, Tooker et al. 2015). However, most of the evidence supporting the importance of crude protein concentration for the fitness of bees (Brodschneider and Crailsheim 2010) and their ability to adjust their individual (Ruedenauer, Spaethe et al. 2015, Ruedenauer, Wöhrle et al. 2018) or collective response according to their protein requirements (Fewell and Bertram 1999, Pernal and Currie 2001) stems from social bees. In the case of solitary bees the picture is less clear (Nicholls and Hempel de Ibarra 2017), but in many cases solitary bees will also likely benefit from increased protein availability. Only in recent years additional factors, such as amino acid composition and potentially secondary plant metabolites, have emerged as variables potentially shaping pollen quality and consequently foraging decisions for bees in particular for solitary bees (Cook, Awmack et al. 2003, Sedivy, Müller et al. 2011, Nicholls and Hempel de Ibarra 2017). In contrast to the extensive literature on pollen crude protein content (T'ai, Cane et al. 2000), data on these emerging quality factors are still scarce and often ambiguous and were consequently not included in this first analysis. However, it would be a logical and important next step to merge these data with information on secondary quality characteristics and bee ecology to utilize their full potential.

To give an overview of the collected data and potential applications we used the generated database to compare the crude protein concentration of pollen resources bees can encounter in agricultural landscapes in- (crop and weeds) and off-field (wild) around the globe. In a second step we identified crop genera, which provide bees with low, likely sub-optimal pollen and protein and suggest plant genera which could serve as high-quality alternative protein sources during times of need.

Materials and Methods

Data collection and categorization

Data were collected, categorized and analyzed with minor modifications as previously described (Pamminger, Becker et al. 2018). Specifically, in 2018 we searched the literature for records on pollen quality in bee-visited flowers using ISI Web of Knowledge and Google Scholar. We used the search terms: flower AND pollen AND protein, adding either pollinator or bee as an additional term. Using these results, we identified relevant publications by reading the title and abstract. Based on this refined literature list we extended our search to the literature cited within these publications. In addition, we extended our data gathering efforts to the French and German literature to provide a more complete picture and make this information accessible to the English speaking scientific community.

Plant selection

Following (Pamminger, Becker et al. 2018) plant species were categorized as bee-visited if either bee pollination was directly observed or the flowers were explicitly classified as “melittophil” based on their floral characteristics by the study authors. In addition, we used the USDA pollinator manual (McGregor 1976) and the expertise of BASF plant experts for cross-validation of the derived classifications.

Geographic localization

Following (Pamminger, Becker et al. 2018) we chose to map the plant distribution on a continental scale because this information was available for the majority of plant species included in the data set. We decided to choose the Panama Canal as separation line between North and South America, the Urals and the Black Sea to separate Europe from Asia and the Suez Canal to separate Asia and Africa. Using the Encyclopedia of Life (http://eol.org/) as the main source for plant distribution we recorded the presence and absence of collection records of each plant species on the five continents. This very broad geographical classification is intended as a first attempt to make this information geographically explicit and should serve as a starting point to add more detailed information on the local geographic (e g. national or region) or habitat characteristics in the future. Such information will be vital to make more precise predictions about temporal quality dynamics in agricultural landscapes around the globe.

Categorization of crop weed and wild plants

Following (Pamminger, Becker et al. 2018) the selected plants were categorized as crop species if they were listed as “cultivated crops” in governmental databases (e. g. USDA: https://plants.usda.gov and European commission plant variety catalogue: https://ec.europa.eu, (McGregor 1976)), the open primary literature or were known as such to our BASF crop experts. All remaining plants without such records were categorized as non-cultivated. In a second step these non-cultivated plants were categorized either as a weed species, if they were listed in one of the following agricultural or governmental weed data resource (USA Noxious weed database https://plants.usda.gov, Australia weeds http://www.environment.gov.au or industry compendium (Bayer 1992)), or as wild plants if no such record was found. Once a plant was categorized (crop, weed or wild) it was categorized as such in all regions where it was present.

Pollen quality

We used crude protein content in pollen (dry mass) as proxy for pollen quality. Direct measurements of total nitrogen (N) content were also included and the corresponding crude protein content was calculated using a conversion factor of 6.25 (Roulston, Cane et al. 2000). This simple quality characteristic was chosen because it is the most frequently reported quantitative measurement of pollen quality in the literature and is directly linked to social bee fitness (Brodschneider and Crailsheim 2010, Vaudo, Tooker et al. 2015, Hass, Brachmann et al. 2018). Additionally, it is likely that some solitary bees will also benefit from increased protein supply. In addition to protein content, other quality criteria (e g. amino acid composition, lipid content and micronutrient composition) are also important markers for resource quality (Vaudo, Tooker et al. 2015). In the future such additional quality markers would make a valuable addition to the database to get a more complete understanding of pollen quality. Whenever available we report multiple measurements for individual plant species since resource quality is likely influenced by local conditions and these data can give important insights into the within-species variability of the trait in question.

Analysis

Pollen quality and its variability in bee visited plants

In the first part of the analysis we focused on the broad picture of pollen quality and its associated variation within a given plant community (crop, weeds and wild) on all relevant continents around the globe.

Pollen quality offered by plant genera

In a second step we compared the quality of crop genera in terms of pollen quality. We used all genera for which we had measurements for more than 3 plant species. We categorized pollen as either crude protein content as either sufficient (above 20% crude protein content) or low quality (below 20% crude protein content), consistent with the traditional labeling of some plant species (e g. Sunflower (*Helianthus annuus* L.) and

Maize (*Zea mays* L.)) as providing low quality pollen for social bees (Maurizio and Grafl 1980, Day, Beyer et al. 1990, Pernal and Currie 2000, Tasei and Aupinel 2008, Nicolson and Human 2013). This classification is not intended as a clear-cut criterion, but rather as an means to identify crop genera where nutritional intervention might provide the strongest benefit.

Statistics

Both statistical analysis and figure generations were done in R v. 3.3.3. For the first analysis (geographic patterns) we used descriptive statistics, conservative non-parametric Kruskal-Wallis (KW) test and Bonferroni corrected pairwise Wilcoxon-test as a *post hoc* test in cases where the KW test indicated significant difference between groups. For the second analysis we used a KW test to identify overall differences between genera. Significance level was set to $\alpha = 0.05$ in all cases.

Results

In total we found 316 measurements of percent crude protein content, of which 302 could be unambiguously attributed to one plant category (see materials and methods) and used for analysis. Protein concentrations ranged from 10-61%, with the majority of these measurements from wild flowers (N = 127, crop N = 94, weed N = 81). In general, the data are evenly spread across regions and plant categories (Tab. 1), except only limited data were available for wild plants in Africa (N = 14). We found small but significant differences between the three plant communities on a global level (KW $chi^2 = 9.4$, $p = 0.01$) with pollen provided by crops having slightly lower concentrations ($median_{crop} = 25.2\%$) than wild species ($median_{wild} = 28.5\%$, $p < 0.001$ see Fig. 1 all other comparisons $p > 0.05$). This difference is likely driven by increased protein concentrations in wild New World plant species (North America KW $chi^2 = 25.3$ $p < 0.0001$, South America $chi^2 = 21.8$ $p < 0.0001$, all other KW $chi^2 < 5.9$ $p > 0.05$). In these regions we found that wild flowers exhibit higher protein concentrations compared with crop and weed species (all comparisons $p < 0.001$; Fig. 1) while crop and weed species do not differ from each other

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(all comparisons $p > 0.05$; Fig. 1). Significant differences existed between genera (KW $chi^2 = 85.9$ $p < 0.0001$), with one crop genus (*Solanum*) providing pollen with high protein content and two crop genera (*Zea* and *Helianthus*) offering pollen with low protein content (Fig. 2).

Discussion

Overall crude pollen protein content in bee-visited plants is around 26% with similar values for crop and weed species (Fig. 1). In contrast, wild plants offer elevated pollen concentrations for bees. This effect is driven mainly by the flora in the New World (North and South America); plant communities in the other regions have comparable pollen protein concentrations (Fig. 1). We found that only six genera offer pollen with low protein concentration (crude protein < 20%), including two crop species: sunflowers (median around 15%) and maize (median around 16%). Most other plant genera offer pollen of comparable protein concentration (Fig. 2).

Interestingly, protein content in wild plants of the new world were higher than elsewhere while crop a weed species exhibit similar protein levels worldwide. In the latter case this is expected as these plant communities are more homogenous in all regions as a result of their intended (crop) or involuntary introduction (weeds) around the globe. In contrast, most wild plants in this study are geographically restricted (non-global distribution), suggesting that the observed pattern is likely caused by differences in the community composition between regions. However, caution needs to be taken as this pattern could also be the result of incomplete sampling (e.g. in Africa) or could represent sampling bias because the results are based on peer-reviewed publications and could simply reflect the focus of the study authors.

Two genera (*Solanum* and *Senna*) were identified with higher pollen protein concentration than the majority of plant genera visited by bees (Fig. 2). Most genera have similar pollen protein concentrations, which are at a level likely suitable to support bee populations (Day, Beyer et al. 1990, Wcislo and Cane 1996, T'ai, Cane et al. 2000, Tasei and Aupinel 2008, Di Pasquale, Salignon et al. 2013). In addition, our findings support the conclusion that maize and sunflower have low pollen quality in terms of protein content

(Maurizio and Grafl 1980, Hass, Brachmann et al. 2018). While sunflower can offer high quality nectar as an alternative reward (Maurizio and Grafl 1980, Tepedino and Parker 1982) to attract bees, maize is primarily wind pollinated and does not offer nectar rewards. Therefore, sunflower and in particular maize is considered less attractive for bees and are likely only occasionally visited in the absence of alternative pollen sources (McGregor 1976). These results suggest that it might be of particular interest to supply bees in sunflower- and maize-dominant agricultural landscapes with high quality pollen species, adjusted for the season and region (Hass, Brachmann et al. 2018).

Given that pollen is the primary protein source for the majority of bees it is important to ensure adequate protein supply when planning alternative foraging areas (Vaudo, Tooker et al. 2015). While it is clear that increased protein supply can be beneficial to developing larvae and insufficient protein supply can result in larval malnutrition with clear adverse effects (Tasei and Aupinel 2008, Brodschneider and Crailsheim 2010, Di Pasquale, Salignon et al. 2013, Hass, Brachmann et al. 2018), there is only limited support for a simple relationship between crude protein concentration and bee fitness (Babendreier, Kalberer et al. 2004, Tasei and Aupinel 2008, Brodschneider and Crailsheim 2010, Di Pasquale, Salignon et al. 2013). It is likely that in addition to protein content, other quality markers such as lipid content, amino acid composition and secondary metabolites might play an important role in determining pollen quality for bees (Maurizio and Grafl 1980, Day, Beyer et al. 1990, Pernal and Currie 2000, Tasei and Aupinel 2008, Nicolson and Human 2013, Nicholls and Hempel de Ibarra 2017, Hass, Brachmann et al. 2018, Ruedenauer, Wöhrle et al. 2018). In contrast to nectar quality (sugar concentration), there is only some evidence that bees can reliably separate high from low quality pollen and adjust their collecting behavior according to their needs (Nicholls and Hempel de Ibarra 2017). However, recent work suggest that bumblebees are able to do this impressive feat on an individual level (Ruedenauer, Spaethe et al. 2015) and that honeybees can on a collective level (likely using feedback from their larvae; (Pernal and Currie 2001, Ruedenauer, Wöhrle et al. 2018). These promising findings suggest that an increase of the pollen protein concentration could directly benefit social bees and the resulting increased diversity of pollen sources would likely indirectly benefit solitary bees as well (Scheper, Bommarco et al. 2015, Hass, Brachmann et al. 2018).

This paper is a first step to collect the available data on pollen quality, in terms of protein content, offered to bee visited flowers in agricultural habitats. In the future this database could be combined with more detailed information on both the pollen quality (lipids amino acid composition and secondary metabolites) as well as plant traits (e g. flowering period and local geographic distribution), which could enable improved bee management practices to ensure sufficient protein supply around the flowering season. In addition, such information and could help the development of more realistic landscape level modelling approaches to better understand the impact of bee nutrition and its interaction with other stressors bee populations experience in modern agricultural landscapes. In combination such data informed bee managing approaches

associated wi which ultimately could facilitate bee conservation in modern agricultural habitats.

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Figure 1(on next page)

Global overview of crude Protein Content of bee visted flowers

Figure 1.: Summarizes the total crude protein concentration in percent in agricultural landscapes on a continental as well as global basis. We present data for Africa, Asia, Australia, Europe, North America, South America and Global for crop, weed and wild plant communities. Results of the statistical analysis (Kruskal Wallis (KW) chi ^{2}, and p values) are presented in the upper left corner of the individual panels. Significant pairwise comparisons are indicated by red lines.

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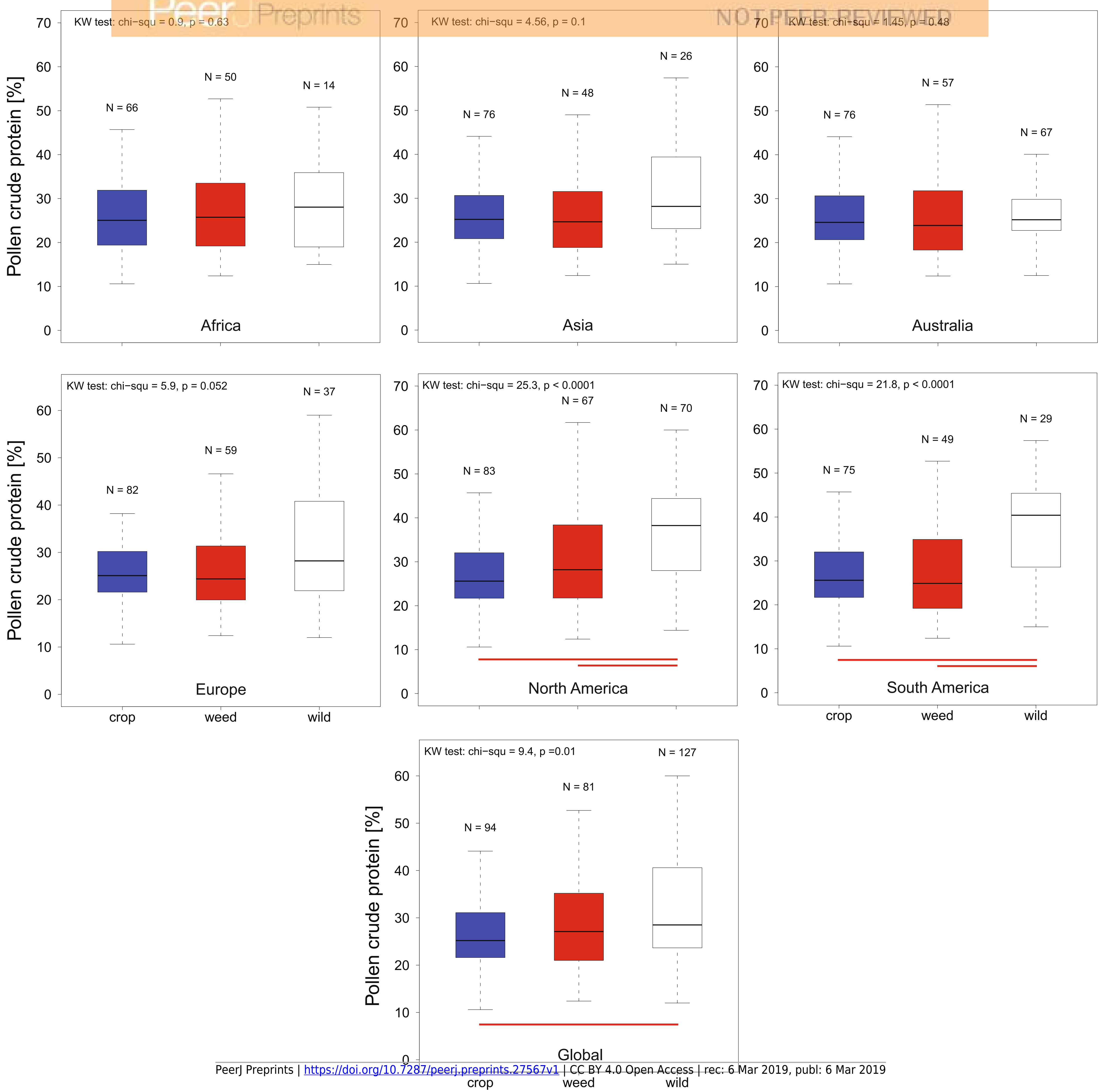
Pollen crude protein [%]
KW test: chi−squ = 0.9, p = 0.63
N = 66
N = 50
N = 14
Africa
KW test: chi−squ = 4.56, p = 0.1
N = 76
N = 48
N = 26
Asia
KW test: chi−squ = 1.45, p = 0.48
N = 76
N = 57
N = 67
Australia
KW test: chi−squ = 5.9, p = 0.052
N = 82
N = 59
N = 37
Europe
KW test: chi−squ = 25.3, p < 0.0001
N = 83
N = 67
N = 70
North America
KW test: chi−squ = 21.8, p < 0.0001
N = 75
N = 49
N = 29
South America
KW test: chi−squ = 9.4, p =0.01
N = 94
N = 81
N = 127
Global
crop
weed
wild

Figure 2 (on next page)

Crude Protein Content of bee visted crop species

Figure 2: Shows the distribution of crude protein concentration in percent among all genera for which more than 3 measurements were available. Genera below the red line offer pollen of low protein concentration. Results of the statistical analysis (Kruskal Wallis (KW) chi ^{2}, and p values) are presented in the lower left corner of the graph.

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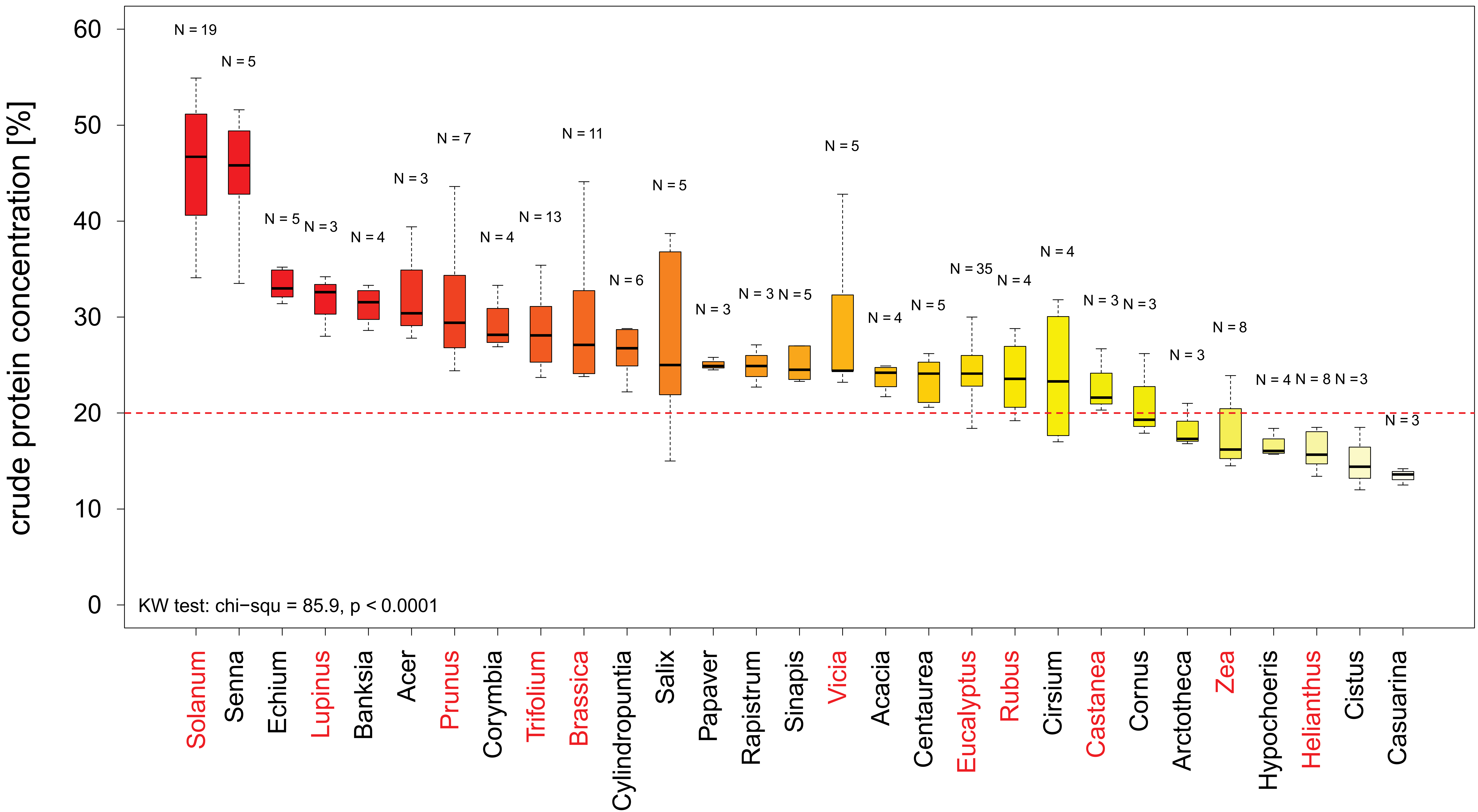
crude protein concentration [%]
0
10
20
30
40
50
60
N = 19
N = 5
N = 5
N = 3
N = 4
N = 3
N = 7
N = 4
N = 13
N = 11
N = 6
N = 5
N = 3
N = 3
N = 5
N = 5
N = 4
N = 5
N = 35
N = 4
N = 4
N = 3
N = 3
N = 3
N = 8
N = 4
N = 8
N = 3
N = 3
KW test: chi−squ = 85.9, p < 0.0001
Solanum
Senna
Echium
Lupinus
Banksia
Acer
Prunus
Corymbia
Trifolium
Brassica
Cylindropuntia
Salix
Papaver
Rapistrum
Sinapis
Vicia
Acacia
Centaurea
Eucalyptus
Rubus
Cirsium
Castanea
Cornus
Arctotheca
Zea
Hypochoeris
Helianthus
Cistus
Casuarina

Table 1(on next page)

summary of crude Protein concentrations in plant communities around the globe

Table 1.: Summary statistic of the crude protein concentration [%] in pollen of crop, weed and wild plant communities across the globe

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Region	Community	N	median	mean	10th Percentile	25th Percentile
Global	ALL	302	26.7	29.1	16.3	21.8
	Crop	94	25.2	26.6	16	21.6
	Weed	81	27.1	29.3	16.2	21
	Wild	127	28.5	31.6	18.5	23.7
Europe	ALL	178	25.3	27	15.8	19.7
	Crop	82	25.1	25.8	15.7	21.6
	Weed	59	24.4	26.9	16.2	20
	Wild	37	28.2	31.5	18.1	21.9
North America	ALL	220	28.5	31.1	16.6	22.9
	Crop	83	25.6	26.9	15.7	21.7
	Weed	67	28.2	30.6	16.6	21.8
	Wild	70	38.3	36.4	21.8	28
South America	ALL	153	27.1	29.6	16.2	21.9
	Crop	75	25.6	26.7	15.6	21.7
	Weed	49	24.9	28.8	16.2	19.2
	Wild	29	40.4	38.5	26.6	28.6
Africa	ALL	130	25.8	27.2	15.7	19.2
	Crop	66	25.1	26.1	15.3	19.9
	Weed	50	25.8	28.2	16.2	19.2
	Wild	14	28.1	28.5	16.2	20
Asia	ALL	150	25.8	27.4	15.9	20.1
	Crop	76	25.2	25.9	15.7	21.2
	Weed	48	24.7	27.5	16.2	19
	Wild	26	28.2	31.2	18.5	23.8
Australia	ALL	200	24.9	26.4	16.2	21.1
	Crop	76	24.6	25.8	15.7	21
	Weed	57	23.9	26.6	16.1	18.3
	Wild	67	25.2	27	18.8	22.8

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