

1 **Why flower visitation is a poor proxy for pollination: measuring single-visit pollen**
2 **deposition, with implications for pollination networks and conservation.**

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10 Running Title: Separating flower visitors from true pollinators

11 **Abstract**

- 12 1. The relative importance of specialised and generalised plant-pollinator relationships is
13 contentious, yet analyses usually avoid direct measures of pollinator quality (effectiveness),
14 citing difficulties in collecting such data in the field and so relying on visitation data alone.
- 15 2. We demonstrate that single visit deposition (SVD) of pollen on virgin stigmas is a practical
16 measure of pollinator effectiveness, using 13 temperate and tropical plant species. For each
17 flower the most effective pollinator measured from SVD was as predicted from its
18 pollination syndrome based on traditional advertisement and reward traits. Overall, ~40% of
19 visitors were not effective pollinators (range 0-78% for different flowers); thus flower-
20 pollinator relationships are substantially more specialised than visitation alone can reveal.
- 21 3. Analyses at species level are crucial, as significant variation in SVD occurred within both
22 higher-level taxonomic groups (genus, family), and within functional groups.
- 23 4. Other measures sometimes used to distinguish visitors from pollinators (visit duration,
24 frequency, or feeding behaviour in flowers) did not prove to be suitable proxies.
- 25 5. Distinguishing between ‘pollinators’ and ‘visitors’ is therefore crucial, and true ‘pollination
26 networks’ should include SVD to reveal pollinator effectiveness (PE). Generating such
27 networks, now underway, could avoid potential misinterpretations of the conservation
28 values of flower visitors, and of possible extinction threats as modelled in existing networks.

29 **Key words:** flower visitor, pollinator, network, pollen deposition, pollination syndromes,
30 specialization/generalization.

31 **Introduction**

32 Pollination ecology has recently been invigorated by a strong community-level approach, often
33 linked with concern over pollinator declines and conservation, and hence a need to understand how

34 particular pollinator deficits may affect plant and animal populations and interactions (Waser *et al.*
35 1996). This has led to many analyses of ‘pollination webs’ or ‘pollination networks’, aiming to
36 understand network structure and resilience to change. As networks have become embedded in
37 ecological and evolutionary thinking (Proulx *et al.* 2005), ‘plant-pollinator networks’ proliferate
38 and associated methodologies and terminologies become more sophisticated. Core problems of
39 inadequacy of the underlying data sets (incomplete sampling or varied relative sampling intensity,
40 Blüthgen *et al.* 2008; Gibson *et al.* 2011), and of inadequate temporal/spatial spread of sampling
41 (Olesen *et al.* 2008; Dupont *et al.* 2009) have been addressed. The resultant more complex models
42 are often in turn used in meta-analyses: comparisons with other mutualistic communities (Olesen *et*
43 *al.* 2007; Aizen, Morales & Morales 2008; Pocock, Evans & Memmott 2012), or assessing effects
44 of invasive species (Memmott & Waser 2002; Bartomeus, Vial & Santamaria 2008; Valdovinos *et*
45 *al.* 2009), of potential extinction rates and patterns (Memmott, Waser & Price 2004; Kaiser-
46 Bunbury *et al.* 2010), or of resilience to anthropogenic factors such as climate change (Memmott *et*
47 *al.* 2007; Willmer 2012).

48 This modelling activity has become linked with issues of specialization and generalization in
49 plants, pollinating animals, and their interactions (Waser *et al.* 1996; Johnson & Steiner 2000;
50 Gibson *et al.* 2011). ‘Plant-pollinator networks’ appear to have flower visitors that are mostly
51 generalized in their flower choices (Vazquez & Aizen 2004; Petanidou & Potts 2006), in turn
52 suggesting that the concept of specific ‘pollination syndromes’ is less useful than earlier literature
53 had indicated (Waser 2006; Ollerton *et al.* 2009).

54 These issues have been highlighted in several key papers (Waser *et al.* 1996; Fenster *et al.*
55 2004) and a recent book (Willmer 2011), though the network and syndrome approaches can
56 potentially be synergistic. Many ‘pollinator networks’ suggest preponderant generalization with
57 high connectance, but merely eliminating cheats can make a network register as more specialized
58 (Alarcón 2010), and levels of apparent generalization can vary across populations or even

59 individuals of a given plant species (Herrera 2005). Meanwhile many pollination case-studies report
60 rather high levels of specialization, and/or a good match of selective pressures on flowers to
61 particular functional groups of visitors acting as pollinators (Johnson & Steiner 2000; Fenster *et al.*
62 2004).

63 But a key issue still goes largely untested: the ability to distinguish between mere flower
64 visitors and effective pollinators. This problem is well-documented (Fishbein & Venable 1996;
65 Ne'eman *et al.* 2010; Popic *et al.* 2013), and many ‘pollination networks’ explicitly or implicitly
66 recognise the potentially misleading title used, in relying on simple visitation records. But
67 variations on the claim that “pollination can be inferred if quantitative data is available on
68 visitation” (Hegland *et al.* 2010) remain prevalent.

69 Testing this requires incorporation of measures of effective pollination into community
70 studies and thence into networks. Some studies add a more realistic ‘pollination’ slant to visitation
71 data using various added measures (reviewed in Ne'eman *et al.* 2010; most recently using visitor
72 pollen loads, Popic *et al.* 2013), but as yet sidestep measuring effectiveness of visitors as true
73 pollinators. Here we quantify the ‘pollinator versus visitor’ problem to show that the distinction
74 matters greatly and may undermine some existing literature. We use the term *pollinator*
75 *effectiveness* (PE) throughout, rather than other variant terms (Inouye *et al.* 1994; Ne'eman *et al.*
76 2010), agreeing that it best describes the character of the measure needed. Ne’eman and his co-
77 authors supported (from first principles) measuring numbers of conspecific pollen grains deposited
78 on a virgin stigma in one visit – single visit deposition, hereafter SVD. This measures both an
79 animal’s ability to acquire pollen in earlier visits to the plant species (thus incorporating visit
80 constancy), and to accurately deposit it where it can potentially lead to fertilization. It avoids
81 hazards of measurements of seed- or fruit-set that bring post-pollination factors into play, and it
82 gives species-specific values for PE. It can be expanded to give SVD per unit time (hour, or day), or
83 through the life of the flower, or plant, or population. Some early papers had shown that this field

84 measurement could indeed clarify the visitor/pollinator distinction. Good models of best practice
85 exist (Primack & Silander 1975; Motten *et al.* 1981; Wilson & Thomson 1991), and examples occur
86 for bees, flies, lepidopterans and vertebrates (Willmer 2011).

87 Our field measurements demonstrate that pollinator effectiveness (PE) is reliably and
88 relatively easily determined using SVD, for 13 plant species from various traditional ‘syndromes’.
89 True pollination networks are therefore feasible and much-needed, and this ongoing work will
90 improve understanding of the pressing issues of pollination ecosystem services and pollinator
91 conservation.

92 **Materials and Methods**

93 **a) Plants and Study Sites.**

94 We used 13 plant species (Supporting Material, Table 1), from two temperate Scottish sites
95 (scrubby woodland, West Quarry Braes, Fife (NO 597 088) and meadowland near Loch Tay, (NN
96 669 358)), and from deciduous forest in Costa Rica (Santa Rosa, 10° 50' N, 85° 40' W). Plants were
97 selected for their flowers’ apparent conformity to particular pollination syndromes with a broad
98 range of morphological and reward traits.

99 **b) Measuring Pollinator Effectiveness**

100 Flowers were selected as buds, usually in the evening, and covered (individually, in small
101 groups, or as inflorescences) in 2mm netting to exclude flower visitors but avoid excessive
102 environmental modification. Once flowers had fully opened the next day they were uncovered and
103 observed until a single visitor landed and foraged. Visitors were identified immediately, or
104 photographed, or captured for later identification. Each visit’s duration was timed using a
105 stopwatch, or by estimation (to nearest 10 or 30 seconds) where a visitor fed successively at several
106 flowers on an inflorescence (mean duration shown without SE in Table 1), or where several visitors

107 were active concurrently. For hummingbirds, hovering between flower visits, durations were
108 corrected to give mean time spent feeding using video recordings. Visitor feeding (nectar, pollen or
109 both) was also recorded.

110 Stigmas from each visited flower (or each floret visited in a composite) were then removed
111 with forceps and stored in separate cells of plastic cell-culture arrays, kept covered and cool.
112 Numbers of adherent pollen grains per stigma were counted immediately using a dissecting
113 microscope; or the array was stored frozen for later counting. Pollen grains were only counted if
114 morphologically conspecific.

115 For each plant species, unvisited flowers were also netted as controls, and pollen grains on
116 their stigmas recorded to account for self-pollen transfer by wind or by flower handling. A value of
117 mean SVD was determined for each visitor species for which sufficient data were available, and
118 compared to the control SVD. A pollinator was defined as *any species with an SVD significantly*
119 *greater than controls*. All other visitor species were deemed ineffective pollinators (including, but
120 not synonymous with, floral thieves) and excluded from further analysis.

121 **c) Sampling Periods**

122 Sampling occurred throughout a day where possible, to detect temporal variations in visitor
123 assemblage and performance. Observations were restricted to dry calm weather conditions, when
124 previously protected flowers were unaffected by rain. Sampling sessions were 1-3 hours, depending
125 on visit frequency and thus how long it took all previously-protected newly-opened flowers to be
126 visited.

127 **d) Visitation surveys: Scaling up SVDs and Pollinator Effectiveness.**

128 Observations of flower visits necessarily only applied to the *first* visitor to previously-netted
129 flowers, so cannot accurately represent overall visit numbers or frequencies. To record both

130 visitation patterns and SVD separately we chose Scottish populations of *Agrimonia eupatoria*, with
131 large well-spaced flowers on adjacent stems. Flowers were observed for twelve 45-minute intervals
132 daily (06:45-18:30, with all flowers by then pollen-depleted) in July 2009. Visit frequencies,
133 durations and behaviours of each visitor were recorded. Since visitors were undisturbed they visited
134 a sequence of flowers freely, and their chosen flowers were noted. Visitors were mainly hoverflies,
135 taking only pollen; most were identified to species (but to tribe for Bacchini and Syrphini) and a
136 mean SVD was calculated. Combined with visitor frequencies this generated a per-hour and per-day
137 pollinator performance value from existing formulae (Ne'eman *et al.* 2010).

138 e) **Statistical Analyses**

139 Control pollen values for each plant species were subtracted from SVD values, with any
140 resulting negative values set to zero for the purposes of statistical analyses. Since data for some
141 plants were normally distributed but other data sets were not, non-parametric Wilcoxon Signed
142 Ranks testing was used for consistency to compare SVD values with zero for each of the 13 plants.
143 We show P levels as significant where they are below 0.05; Bonferroni corrections were routinely
144 used, but since application of these is often regarded as too conservative we merely indicate with an
145 asterisk where they remain significant after Bonferroni corrections. SPSS 17 was used for all
146 statistical analyses.

147 **Results**

148 **A. Measuring SVD and pollinator effectiveness.**

149 For every plant species studied, SVD values were calculated for 'visitor groups' defined
150 according to traditional pollination syndromes (Willmer 2011), and for each visitor species
151 separately where numbers of recordings allowed (Table 1; expanded details in Supporting Material,
152 Table 2). Those animal groups that a syndrome approach (Supplementary Table 1) would predict as

153 major pollinators generally had the highest SVDs, while for the more generalist plants several
154 groups had high SVDs. For each one of the 13 species the predicted syndrome was well-matched
155 with SVD findings, making SVD demonstrably a good measure of ‘expected’ pollinator
156 effectiveness (PE). Of 105 plant/visitor combinations across the 13 plants, only 63 produced
157 effective pollination.

158 **B. Testing proxies for pollinator performance.**

159 **1. Visit Duration**

160 Mean visit durations are included in Table 1, with Spearman Rank Correlations (visit
161 duration versus SVD) for all visitors combined. Seven plant species showed no correlation, while
162 the remaining 6 (*Malvaviscus*, *Helicteres*, *Cirsium*, *Centaurea*, *Knautia* and *Ipomoea*) showed a
163 significant negative correlation. However when visitor species were considered separately (Table 1)
164 an overall relationship between SVD and visit duration was rarely preserved; duration could vary
165 substantially *within* ‘visitor groups’, and *across* plant species for a given visitor, so was on its own
166 an unreliable measure of PE.

167 **2. Visit number or frequency.**

168 For *Agrimonia eupatorium* visit numbers and rates, and hence pollinator performance for
169 each major visitor, were calculated per hour and per day (Fig. 1). *Episyrphus balteatus* had the
170 lowest SVD at the single-visit scale, but its high visitation rate gave it the highest SVD at per-hour
171 and per-day scales; it would often be the ‘best’ pollinator. Conversely, *Rhingia campestris* had the
172 highest single-visit SVD but the lowest per-hour and per-day SVD. But neither measure on its own
173 gives a clear picture, whereas using visit frequency *with* SVD data can substantially affect the
174 perception of ‘most important pollinator’ (cf. Olsen 1997; Ne’eman *et al.* 2010).

175 **C. Combining Visit Duration, Feeding Type and Visitor Species with SVD measures.**

176 A General Linear Model was constructed (Supporting Material, Table 3) to test the
177 combined utility of typical measures of a good pollinator (visit duration, and type of feeding:
178 nectar/pollen/both, or for *Byrsonima* oil/pollen/both) as proxies for pollination effectiveness;
179 ‘visitor species’ was also included since variation in SVD between species but within functional
180 groups is evidently important. In 8 of the 13 plants the only factor significantly related to pollen
181 deposition was visitor species, through its direct association with SVD; for the remaining species,
182 other factors were inconsistently and rarely significant.

183 **Discussion**

184 Not all visitors are pollinators of a given plant species; a pollinator must deposit sufficient pollen on
185 the correct and receptive stigma, and that pollen must be conspecific and viable. Our SVD protocols
186 address the first two requirements, and any visibly heterospecific pollen grains were discounted. We
187 show that SVD measures are relatively simple to incorporate into pollination studies, giving an
188 accurate value for pollinator performance, and highlighting the effective visitors which in all 13
189 species largely correspond to expectations from a syndrome approach. Combined with visitation
190 records, SVD can assess ‘pollinator effectiveness’ per hour, per day or per season; and can indicate
191 ‘pollinator importance’, as with *Agrimonia*.

192 Only 60 of 103 plant/visitor interactions produced effective pollination (Table 2); and
193 ineffective visits were not just the traditional ‘illegitimate’ visits, as many involved a normal route
194 into the corolla by visitor species of similar size to the effective pollinators.

195 **A. Are proxies for SVD useful or appropriate?**

196 SVD is a good direct measure of PE; however in most existing studies PE is not assessed,
197 being substituted with other parameters such as visitor abundance, pollen load, number of stigma
198 touches, feeding type, or visit duration. Visitor abundance alone, though often used (e.g. Olsen

199 1997), is widely recognised as a poor measure of pollination outcomes (Johnson & Steiner 2000). A
200 positive link may be recorded between abundance or visitation rate and pollen deposition, but can
201 be weak (e.g. only 36% of variation in pollen deposition was explained thus for *Ipomopsis*
202 *aggregata* (Engel & Irwin 2003)).

203 Abundance values for each animal and plant, and their interaction frequencies, can generate
204 quantitative visitation networks, adding qualitative estimates of pollination using visitors' pollen
205 loads (Popic *et al.* 2013); and assessing pollen fidelity (% conspecific pollen carried) can refine
206 visitor importance further (Forup *et al.* 2008) and may encourage using visitor abundance and
207 pollen load fidelity as proxies (Bosch *et al.* 2009; Kaiser-Bunbury *et al.* 2010). But pollen on
208 visitors' bodies may poorly represent pollination potential; it can be deposited on incompatible or
209 unreceptive stigmas, or lost before reaching another flower (Inouye *et al.* 1994; Harder & Routley
210 2006), so giving no correlation with pollen deposited on conspecific stigmas (Adler & Irwin 2006).
211 Other possible proxies such as "contact with reproductive structures" (Petanidou & Potts 2006;
212 Gibson *et al.* 2011), number of stigma touches (Olsen 1997), measurements of visit duration
213 (Fishbein & Venable 1996; Kaiser-Bunbury *et al.* 2010) and of pollen removal (Ivey, Martinez &
214 Wyatt 2003) are similarly subject to problems of pollen loss. We therefore sought explicit
215 relationships between these proposed measures and our direct SVD assessment.

216 **B. Correlation of Visit Duration and Pollen Deposition**

217 There were no significant correlations between visit duration and SVD for all visitors
218 combined for 7 of our 13 species, but 6 showed a significant negative correlation (Table 1). In
219 theory longer visits could increase visitor contact with, and/or transfer of pollen to, a stigma; but
220 they could also indicate 'ineffective' feeding (excessive grooming, eating pollen or floral tissues,
221 avoiding anther or stigma contacts). SVD and PE will be higher for visitors which 'fit' the flower,
222 feed rapidly on nectar and/or pollen, and quickly acquire body-pollen. Short efficient visits will

223 often predominate early on, when pollen is more abundant, and visitor groups show very different
224 diurnal activity patterns (Willmer & Stone 2005). Thus when visitor species are treated *separately*
225 the correlations can change markedly, and only 3 of 13 species did not show such changes (Table
226 1). For the two ornithophilous plants (*Malvaviscus*, *Helicteres*) negative correlations disappeared,
227 largely because visit duration and variance were low, and birds received the most pollen grains of
228 any group. *Trifolium* and *Geranium* had significant overall negative correlations, but bumblebees
229 showed significantly *greater* SVD in longer visits. In *Knautia*, with no overall relationship, *Rhingia*
230 *campestris* showed a significant positive correlation and *Episyrphus balteatus* the opposite; these
231 differing interactions are masked when visitor species are pooled.

232 Within all these comparisons, the common visitor species *E. balteatus* is instructive,
233 showing positive or negative correlations between visit duration and SVD in different plants,
234 though its mean visit duration did not vary greatly (Table 1). Evidently the varying behaviour and
235 PE of this species on each flower matters, rather than visit duration alone. This reinforces the
236 problems with using visit duration as a proxy in its own right; no particular ‘kind’ of relation
237 between visit duration and SVD can be assumed, for a visitor group or for a single visitor species.

238 **C. Combined measures as proxies for pollination effectiveness**

239 Our GLM showed that in 7 of 13 plant species the only factor significantly contributing to
240 SVD was visitor species; feeding behaviour and visit duration were unimportant even where
241 duration did affect pollen deposition (Table 1: *Malvaviscus*, *Helicteres*, *Ipomoea*). Duration and
242 feeding behaviour never accounted for more than a small percentage of SVD variation, and in
243 *Centaurea*, *Digitalis*, and *Geranium* no factor significantly explained SVD variation. Overall, in 11
244 of our 13 plants by far the largest predictor of variation in pollen deposition was visitor species.

245 **D. Possible criticisms and drawbacks of SVD and of this study.**

246 Firstly, measures of SVD are undoubtedly context-dependent, potentially affected temporally
247 and spatially by environmental variation and relative species abundances. Hence extrapolation
248 between studies is dangerous and SVD should be measured for a given interaction at a given site (as
249 with many measures in pollination ecology, since phenology and rewards vary between sites).

250 Furthermore, SVD does not relate to the final female reproductive success of a flower,
251 manifested in seed-set. But post-pollination events have little to do with assessing pollinators, and
252 reliance on seed-set may show the same effects described here (Spears 1983) or give contradictory
253 results (Olsen 1997). Equally SVD does not include estimates of pollen viability or germination,
254 and some deposited pollen grains even though conspecific may not germinate, especially if large
255 numbers clog up a small stigma.

256 SVD measures may also be time-biased, tending to accentuate early visitors. Delayed removal
257 of bags may help, so that ‘first visits’ occur later; but then an uncovered flower may have unusual
258 rewards for that time of day, giving abnormal visit durations or frequencies. Elsewhere we analyse
259 time-dependence of SVD more closely (King & Willmer, in prep). We also note that all Scottish
260 sites experienced very poor summer weather in 2008-2010 (high rainfall, poor sunshine) so visitor
261 profiles were unusual: very low bee numbers (*Apis* and *Bombus*) occurred in eastern Scotland, and
262 bees are under-represented in our data, with perhaps a concomitant increase in hoverfly numbers.

263 Finally, we considered just 13 plant species, and each in isolation, so proving that SVD
264 methodology is feasible and timely for fieldwork, that it works with varying flower morphologies,
265 and that measuring PE in this way is important because it shows up ineffective visitors. But the
266 required and ongoing step is to use SVD to directly compare ‘visitation’ networks and true
267 ‘pollination’ networks.

268 **E. Why distinguishing pollinators and visitors matters.**

269 Flower visitors are not necessarily pollinators. Some are simple cheats, and their effects
270 have been acknowledged (see Alarcón 2010, Genini *et al.* 2010). But eliminating obvious cheats is
271 not enough: which apparently legitimate visitors correctly deposit significant pollen on stigmas?
272 Some earlier studies (e.g. Wilson & Thomson 1991) made exactly this point but have been
273 insufficiently built upon. More recent studies have paralleled our own in comparing visitor PE for
274 just one plant genus (Kandori 2003; Stoepler *et al.* 2012), reaching similar conclusions regarding
275 problems with proxies, and reinforcing the value of SVD (or a near equivalent) as a measure of
276 effectiveness.

277 Without distinguishing visitors from pollinators, various negative consequences could
278 ensue: conservation efforts could be misled by suggestions that networks are robust and extinctions
279 can be tolerated (e.g. Memmott, Waser & Price 2004; Dupont *et al.* 2009; Kaiser-Bunbury *et al.*
280 2010; Hegland *et al.* 2010; Burkle & Alarcón 2011), or that visitors acting as ‘hubs’ or ‘connectors’
281 require most support (Olesen *et al.* 2007) whereas relationships between connectance and
282 conservation value may be poor (Ruben, Devoto & Pocock 2012). Interpretations of specialisation
283 and generalisation can also be seriously problematic when only visitation is recorded (see Alarcón
284 2010; Popic *et al.* 2013).

285 SVD is a valuable simple and direct means of measuring pollinator effectiveness, for which
286 indirect proxies are unreliable. Here, variation in SVD was poorly related to visit duration or
287 feeding behaviour, but strongly explained by visitor species, the most effective visitors being those
288 predicted as the most important pollinators from syndrome-related floral traits. We are now
289 incorporating SVD into networks to extend this argument; we urge care over extrapolations from
290 existing ‘pollinator’ networks, particularly where these are used to infer consequences for
291 ecosystem management and for modelled extinction threats.

292

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Table 1. Mean SVD values (\pm SE) for each visitor group, and all visitor species where $n > 5$ or P value significant, for the 13 plant species, with significance indicated as the difference in SVD (corrected for mean pollen on unvisited control flowers, value in parentheses below plant name) from zero. P value bold where $P < 0.05$, (* where significance also meets the criteria of Bonferroni correction). Final column shows mean visit duration (\pm SE). Spearman rank correlations for SVD/duration comparisons (overall, and split by visitor species) are also shown.

		Mean SVD	n	P value	Mean visit duration (s)	
408	<i>Malvaviscus</i> (10.6)	Hummingbirds (<i>Amazilia rutila</i>)	104.4 \pm 9.8	21	<0.0005*	6.1 \pm 1.2
409		Bees	29.0	35	<0.0005*	92.1 \pm 9.2
410		<i>Agapostemon</i> sp.	53.1 \pm 15.3	8	0.008	91.9 \pm 23.8
411		<i>Trigona fulviventris</i>	21.9 \pm 5.5	13	0.018	110.8 \pm 17.8
412		<i>Tetragonisca angustula</i>	21.9 \pm 4.3	14	0.008	75.0 \pm 8.2
413		Butterflies	5.8 \pm 1.7	12	0.180	122.5 \pm 21.0
414		Ants (<i>Camponotus novograndensis</i>)	11.1 \pm 1.5	8	0.066	180.0 \pm 29.9
415		SVD v duration: r = -0.64, n = 76, p < 0.001. Split by visitor species: NS				
423	<i>Helicteres</i> (89.0)	Hummingbirds (<i>Phaethornis guy</i>)	1517.1 \pm 97.5	21	<0.0005*	1.73 \pm 0.4
424		Bees	441.8	105	<0.0005*	202.0 \pm 10.0
425		<i>Trigona fulviventris</i>	443.4 \pm 29.9	92	<0.0005*	232.5 \pm 10.8
426		<i>Agapostemon</i> sp.	400.0 \pm 101.4	6	0.028	80.0 \pm 24.1
427		<i>Tetragonisca angustula</i>	162.9 \pm 26.0	7	0.028	68.6 \pm 14.2
428	SVD v duration: r = -0.41, n = 127, p < 0.001. Split by visitor species: NS					
429	<i>Geranium</i> (16.7)	Bees	33.9	56	<0.0005*	23.8 \pm 2.5
430		<i>Bombus pratorum</i>	31.2 \pm 6.7	52	<0.0005*	25.2 \pm 2.6
431		Flies	19.8	25	0.027	48.0 \pm 7.9
432	<i>Rhingia campestris</i>	19.0 \pm 5.8	19	0.012*	42.6 \pm 5.8	
433	SVD v duration: r = 0.19, n = 75, p = 0.103. Split by visitor species: <i>B. pratorum</i> (r = +0.32; P = 0.019)					
434	<i>Digitalis</i> (19.4)	Bees	58.2	38	<0.0005*	16.1 \pm 1.6
435		<i>Bombus hortorum</i>	73.2 \pm 16.7	25	<0.0005*	11.4 \pm 1.3
436		<i>Bombus muscorum</i>	31.0 \pm 4.4	12	0.005*	26.3 \pm 2.6
437	SVD v duration: r = -0.15, n = 37, p = 0.362. Split by visitor species: NS					
438	<i>Byrsonima</i> (48.5)	Bees	313.9	82	<0.0005*	65.9 \pm 6.0
439		<i>Exomalopsis</i> sp.	1686.7 \pm 121.7	3	0.109	20.0 \pm 5.8
440		<i>Centris nitida</i>	381.7 \pm 96.8	6	0.043	45.0 \pm 5.5
441		<i>Trigona fulviventris</i>	254.5 \pm 29.9	61	<0.0005*	64.9 \pm 5.3
442		<i>Tetragonisca angustula</i>	238.8 \pm 41.3	12	<0.003*	92.5 \pm 29.7
443	SVD v duration: r = -0.14, n = 82, p = 0.202. Split by visitor species: NS					
444	<i>Agrimonia</i> (8.5)	Hoverflies	36.2	139	<0.0005*	24.1 \pm 1.4
445		<i>Rhingia campestris</i>	55.2 \pm 21.9	15	0.005*	20.0
446		<i>Platycheirus scutatus</i>	52.8 \pm 8.1	19	<0.0005*	30.0
447		<i>Platycheirus albimanus</i>	47.6 \pm 19.2	10	0.008	63.5 \pm 7.9
448		<i>Leucozona laternaria</i>	43.5 \pm 10.5	12	0.008	20.0
449		<i>Episyrphus balteatus</i>	27.6 \pm 2.9	63	<0.0005*	19.9 \pm 1.6
450		<i>Meliscaeva auricollis</i>	23.2 \pm 6.7	13	0.012	16.5 \pm 1.3
451		SVD v duration: r = 0.11, n = 141, p = 0.177. Split by visitor species: NS				
452	<i>Cirsium</i> (0)	Bees (<i>Bombus terrestris</i>)	1.8 \pm 0.2	22	0.038	19.1 \pm 2.4
453		Hoverflies	2.9	53	<0.0005*	8.8 \pm 1.7
454		<i>Episyrphus balteatus</i>	3.8 \pm 0.8	26	<0.0005*	8.7 \pm 3.5
455		<i>Platycheirus manicatus</i>	2.1 \pm 0.3	16	0.002*	7.5 \pm 0.5
456		<i>Melanostoma mellinum</i>	2.1 \pm 0.8	11	0.001*	10.9 \pm 0.3
457		Other Flies	1.2	31	<0.0005*	20.6 \pm 1.6
458		<i>Empis</i> sp.	1.8 \pm 0.5	5	<0.0005*	36
459		<i>Calliphora vomitoria</i>	1.2 \pm 0.1	15	<0.0005*	22.7 \pm 0.8
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461					SVD v duration: r = -0.22, n = 106, p = 0.021. Split by visitor species: <i>B. terrestris</i> (r = +0.63, p = 0.001), <i>M.</i>	
462					<i>dubium</i> (r = +0.77, p < 0.001) : <i>C. vomitoria</i> (r = +0.53, p = 0.040).	
463	<i>Centaurea</i>	Hoverflies	217.9	240	<0.0005*	11.4 ± 0.7
464	(14.0)	<i>Episyrphus balteatus</i>	273.7 ± 41.7	158	<0.0005*	8.2 ± 0.2
465		<i>Eupeodes corollae</i>	115.0 ± 23.6	12	0.002*	15
466		<i>Rhingia campestris</i>	114.1 ± 13.9	65	<0.0005*	18.6 ± 2.4
467		<i>Platycheirus manicatus</i>	50.4 ± 25.8	5	0.109	6
468					SVD v duration: r = -0.25, n = 240, p < 0.001. Split by visitor species: <i>R. campestris</i> (r = -0.60; P < 0.001)	
469	<i>Knautia</i>	Bees	4.9	66	<0.0005*	6.7 ± 0.7
470	(0)	<i>Bombus pratorum</i>	6.0 ± 0.9	21	<0.0005*	4.3 ± 0.8
471		<i>Bombus (Psithyrus) bohemicus</i>	5.9 ± 1.3	19	0.001*	1.6
472		<i>Bombus lucorum</i>	4.8 ± 0.7	12	0.002*	10.0
473		<i>Bombus terrestris</i>	2.1 ± 1.0	14	0.018	14.3 ± 0.5
474		Hoverflies	5.8	303	<0.0005*	3.2 ± 0.2
475		<i>Rhingia campestris</i>	7.4 ± 1.4	54	<0.0005*	2.2 ± 0.1
476		<i>Episyrphus balteatus</i>	6.4 ± 0.6	203	<0.0005*	3.6 ± 0.3
477		<i>Syrphus ribesii</i>	1.0 ± 0.2	42	0.018	1.8 ± 0.1
478		Other dipterans (<i>Empis</i> sp.)	6.1 ± 0.6	147	<0.0005*	7.9 ± 0.5
479					SVD v duration: r = -0.11, n = 516, p = 0.016. Split by visitor species: <i>R. campestris</i> (r = +0.64; p < 0.001), <i>E.</i>	
480					<i>balteatus</i> (r = -0.41; p < 0.001).	
481	<i>Trifolium</i>	Bees	12.2	371	<0.0005*	3.2 ± 0.1
482	(0.6)	<i>Bombus lucorum</i>	25.1 ± 2.2	31	<0.0005*	1.3 ± 0.1
483		<i>Bombus terrestris</i>	13.3 ± 1.5	34	<0.0005*	1.5 ± 0.1
484		<i>Bombus hortorum</i>	10.8 ± 0.6	275	<0.0005*	3.7 ± 0.1
485		<i>Bombus muscorum</i>	10.0 ± 1.8	31	<0.0005*	2.3 ± 0.1
486		Hoverflies (<i>Criorhina</i> sp.)	28.8 ± 2.4	18	<0.0005*	5.0
487					SVD v duration: r = -0.04, n = 389, p = 0.47. Split by visitor species: <i>B. terrestris</i> (r = +0.75; P < 0.001)	
488	<i>Ipomoea</i>	Bees	108.7	119	<0.0005*	76.0 ± 6.0
489	(52.8)	<i>Andrena</i> sp.	155.7 ± 15.9	19	<0.0005*	44.3 ± 9.8
490		<i>Agapostemon</i> sp.	118.5 ± 10.1	55	<0.0005*	103.6 ± 9.8
491		<i>Partamona musarum</i>	113.5 ± 9.4	11	0.003*	50.9 ± 7.6
492		<i>Tetragonisca angustula</i>	70.4 ± 12.6	16	0.008	32.5 ± 3.4
493		<i>Trigona fulviventris</i>	35.8 ± 9.2	12	0.109	78.7 ± 18.2
494		Ants	65.0	37	<0.0005*	142.7 ± 13.7
495		<i>Pseudomyrmex gracilis</i>	69.0 ± 10.7	28	0.001*	148.9 ± 15.5
496		<i>Camponotus novograndensis</i>	52.6 ± 12.1	9	0.068	123.3 ± 29.8
497		Beetles	93.5	40	<0.0005*	578.3 ± 86.9
498		<i>Notoxus</i> sp.	87.8 ± 9.8	36	<0.0005*	556.7 ± 92.1
499					SVD v duration: r = -0.14, n = 194, p = 0.047. Split by visitor species: <i>P. gracillis</i> (r = -0.48; P = 0.010)	
500	<i>Heracleum</i>	Hoverflies	43.7	239	<0.0005*	6.8 ± 0.3
501	(16.8)	<i>Epistrophe grossulariae</i>	61.8 ± 12.7	22	<0.0005*	7.1 ± 0.3
502		<i>Episyrphus balteatus</i>	55.8 ± 5.5	100	0.005	7.8 ± 0.4
503		<i>Syrphus ribesii</i>	32.1 ± 3.0	52	<0.0005*	2.7 ± 0.1
504		<i>Eupeodes corollae</i>	22.5 ± 4.0	12	0.007	10.0 ± 1.5
505		<i>Platycheirus albimanus</i>	25.8 ± 12.9	6	0.109	20
506		Other Syrphini sp.	28.0 ± 1.5	42	<0.0005*	10.2 ± 0.8
507		Other dipterans	80.5	152	<0.0005*	7.2 ± 0.5
508		<i>Lucilia sericata</i>	116.1 ± 12.8	33	<0.0005*	4.7 ± 0.1
509		Platypozidae sp.	79.9 ± 7.8	37	<0.0005*	3.5 ± 0.2
510		Anthomyiidae sp.	62.8 ± 19.8	6	0.068	1.7
511		<i>Phaonia subventa</i>	67.4 ± 8.1	76	<0.0005*	9.1 ± 0.7
512					SVD v duration: r = -0.04, n = 390, p = 0.449. Split by visitor species: <i>E. balteatus</i> (r = +0.23; p = 0.032), <i>L.</i>	
513					<i>sericata</i> (r = -0.40; p = 0.020), platypozid sp. (r = +0.54, p = 0.001).	
514	<i>Rubus</i>	Bees	256.2	42		44.3 ± 8.2
515	(52.7)	<i>Bombus lucorum</i>	343.3 ± 40.2	6	0.026	30.0 ± 3.4

516	<i>Bombus terrestris</i>	295.5 ± 53.2	16	< 0.0005 *	55.3 ± 10.3
517	<i>Bombus pratorum</i>	223.0 ± 82.5	7	0.068	77.1 ± 39.8
518	<i>Bombus pascuorum</i>	142.0 ± 21.2	5	0.043	12.2 ± 5.4
519	<i>Apis mellifera</i>	270.0 ± 49.8	4	0.068	12.5 ± 3.2
520	Hoverflies	136.6	35	0.001 *	99.9 ± 13.6
521	<i>Rhingia campestris</i>	172.6 ± 46.0	19	0.005	111.3 ± 14.3
522	<i>Eristalis horticola</i>	87.0 ± 40.6	5	0.317	14.8 ± 4.8
523	<i>Episyrrhus balteatus</i>	80.0 ± 11.4	7	0.068	112.9 ± 26.0
524	Muscoid dipterans	54.6	13	0.180	67.8 ± 35.6
525	Wasps (<i>Vespula vulgaris</i>)	80.9 ± 8.2	6	0.066	21.5 ± 5.4

SVD v duration: r = -0.08, n = 92, p = 0.428. Split by visitor species: *B. terrestris* (r = +0.57; P = 0.021)

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Table 2. Summary of visitor/pollinator analyses in relation to floral syndromes. (ST, LT = short- or long-tongued). Further details on syndrome-related traits are in Supporting Material, Table 1.

Plant	Syndrome based on traits	Functional groups of all visitors	Species of all visitors	Functional groups of pollinators	Species of pollinators	Species of ineffective visitors	Syndrome based on SVD analysis
<i>Malvaviscus</i>	Hummingbird	4	7	2	4	3	Hummingbird (<i>bee back-up</i>)
<i>Helicteres</i>	Hummingbird	2	4	2	4	0	Hummingbird (<i>bee back-up</i>)
<i>Geranium</i>	Bee	3	8	2	2	6	Bee
<i>Digitalis</i>	Bee	1	3	1	2	1	Bee
<i>Byrsonima</i>	Oil-bee	1	4	1	3	1	Oil-bee (<i>pollen-bee back-up</i>)
<i>Agrimonia</i>	Hoverfly	2	9	1	6	3	Hoverfly
<i>Cirsium</i>	LT bee/hoverfly	3	7	3	6	1	LT bee/hoverfly (<i>ST insect back-up</i>)
<i>Centaurea</i>	MT bee/hoverfly	1	4	1	3	1	LT bee/hoverfly (<i>ST insect back-up</i>)
<i>Knautia</i>	MT bee/hoverfly	3	9	3	8	1	LT bee/hoverfly (<i>ST insect back-up</i>)
<i>Trifolium</i>	LT bee/hoverfly	2	5	2	5	0	LT bee/hoverfly (<i>ST insect back-up</i>)
<i>Ipomoea</i>	Generalist/bee	6	15	3	6	9	Generalist/ST insect
<i>Heracleum</i>	Generalist	3	12	2	8	4	Generalist, smaller STinsect
<i>Rubus</i>	Generalist	4	18	3	6	12	Generalist, larger insects
All plant/visitor combinations		35	105	26	63	42	

Fig. 1. SVD values for visitors to *Agrimonia eupatoria* scaled up to the “per hour” and “per day” level using visitation frequency data.

