

1 **Herkogamy, a principal functional trait of plant reproductive biology**

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10 Running head: On the use of herkogamy as a mating-system proxy

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16 **Abstract**

17 *Premise of the research:* Phenotypic traits that consistently mediate species' responses to
18 environmental variation ('functional traits') provide a promising approach towards
19 generalizing ecological and evolutionary patterns, and thereby gaining insights into the
20 processes generating them. In the plant functional ecology literature, most trait-based studies
21 have focused on traits mediating either resource competition or responses to variation in the
22 abiotic environment, while traits mediating reproductive interactions have often been
23 neglected.

24 *Methodology:* Here, I discuss the value of herkogamy (spatial separation of male and female
25 functions in flowers) as a functional trait in plant reproductive biology and review the
26 evidence relevant to the hypothesis that taxa exhibiting greater herkogamy have historically
27 experienced more reliable pollination, and more outcrossed mating systems.

28 *Pivotal results:* A large body of work in the field of plant reproductive biology has identified
29 a set of nearly ubiquitous correlations between average herkogamy and features of plant
30 mating systems, notably autofertility (seed set in the absence of pollinators), and outcrossing
31 rate. Herkogamy often varies extensively among populations and species, and the adaptive
32 interpretation is that herkogamy exhibits local adaptation to the reliability of the pollination
33 environment.

34 *Conclusions:* These results underline the value of herkogamy as a functional trait representing
35 variation in mating histories. Many important insights are likely to emerge from studies
36 leveraging herkogamy as an easily measured proxy of plant mating systems, as already
37 demonstrated in comparative studies, and in studies of reproductive interactions. Going
38 forward, greater consideration of herkogamy and other reproductive-function traits in studies

39 of species coexistence may provide a more complete understanding of community assembly
40 processes.

41 **Introduction**

42 The dynamic complexity of biological systems has led to a focus in ecology on functional
43 traits that consistently mediate species' responses to environmental variation (Lavorel and
44 Garnier 2002; McGill et al. 2006; Shipley et al. 2016). In the plant functional ecology
45 literature, most trait-based studies have focused on traits mediating either resource
46 competition (e.g. size) or plant responses to variation in the abiotic environment (e.g. specific
47 leaf area). Because these traits are important determinants of species distributions and species
48 interactions, they are often used as proxies of species' ecological strategies in studies of
49 species coexistence and community assembly (Adler et al. 2013). In parallel, a large body of
50 work in the field of plant reproductive biology has identified traits important for reproductive
51 interactions. Despite the dependence of most flowering plants on pollinators for sexual
52 reproduction, traits mediating reproductive interactions have rarely been considered in studies
53 of community assembly processes. In this essay I discuss the value of a functional trait
54 mediating plant responses to variation in pollinator communities, an important aspect of the
55 biotic environment.

56 The astonishing diversity of flowers is to a large extent the outcome of interactions
57 with pollinators (Grant and Grant 1965; Stebbins 1970; van der Niet et al. 2014).
58 Consequently, the morphological architecture of flowers conveys much information about the
59 reproductive biology of the species (Ornduff 1969). This is evident, for example, from the
60 long history of grouping species into pollination 'syndromes' based on flower color, shape
61 and reward chemistry (Fægri and van der Pijl 1979). By considering the size and shape of
62 self-compatible flowers, it can often also be inferred whether the species rely strongly on
63 animal pollinators for seed production or is capable of effective self-pollination. For example,

64 predominantly selfing species are typically characterized by a set of traits collectively referred
65 to as the ‘selfing syndrome’ (Ornduff 1969; Sicard and Lenhard 2011), including small, short-
66 lived flowers, low pollen-to-ovule ratios, and reduced dichogamy and herkogamy.

67 Herkogamy, the spatial separation of anthers and stigmas within flowers, is a key
68 floral trait thought to promote outcrossing and/or the avoidance of interference between male
69 and female sexual functions (Webb and Lloyd 1986). The functional importance of
70 herkogamy is supported by studies reporting negative relationships between herkogamy and
71 the rate of autofertility (self-fertilization in the absence of pollinators) and the rate of selfing
72 among natural populations. In turn, several studies have demonstrated strong positive
73 correlations between pollinator abundance and herkogamy (e.g. Moeller 2006; Opedal et al.
74 2016a). These observations have led to the general acceptance that variation in herkogamy
75 among populations and species represents adaptation of the mating system to variation in the
76 local reproductive environment.

77 Several functional and evolutionary aspects of herkogamy have been reviewed
78 elsewhere. The foundational review of Webb and Lloyd (1986) includes extensive discussion
79 of functional aspects of herkogamy, definitions of classes of herkogamy, and their distribution
80 among taxa. Barrett (2002, 2003) offers further discussion of functional aspects related to
81 mating strategies, and Opedal et al. (2017) synthesizes work on the quantitative genetics and
82 evolvability of herkogamy. Here, I first outline the expected functional relationships between
83 herkogamy and plant mating systems, and then review and synthesize evidence relevant to the
84 hypothesis that, when two self-compatible taxa differ in average herkogamy, they also differ
85 in their mating histories. I then go on to discuss the value of herkogamy as a mating-system
86 proxy in comparative studies, and review examples of insights emerging from such studies.
87 Finally, I outline the value and promise of increasingly integrating herkogamy and other
88 reproductive-function traits into studies of species cooccurrence and community assembly.

89

90 **Notes on the measurement of herkogamy**

91 Before we can proceed, a brief discussion of measurements is required. Herkogamy is broadly
92 defined as the spatial separation of stigmas ($x_{\text{♀}}$) and anthers ($x_{\text{♂}}$) within flowers or flower-like
93 inflorescences. Webb and Lloyd (1986) defined several classes of herkogamy, differing
94 among other things in the degree of ‘order’ in which pollinators contact floral organs. Species
95 exhibiting ordered herkogamy can be further classified into those in which stigmas are
96 contacted first by a visiting pollinator (*approach herkogamy*, $x_{\text{♀}} > x_{\text{♂}}$; stigmas positioned above
97 or protruding beyond the anthers), and those in which anthers are contacted first (*reverse*
98 *herkogamy*, $x_{\text{♀}} < x_{\text{♂}}$; stigmas positioned below or behind the anthers). Still others exhibit
99 *reciprocal herkogamy*, with stigmas and anthers placed in complementary positions in two or
100 more floral morphs. In self-compatible species approach herkogamy is by far the most
101 common and is often associated with pollination by a limited number of pollinator species or
102 functional groups.

103 How to measure herkogamy depends on the functional question to be addressed. If the
104 aim is to quantify the effect of herkogamy on the probability of self-pollination, for example,
105 the relevant measure is normally the shortest distance separating stigmatic surfaces from
106 dehiscent anthers. In other cases, such as studies of constraints on the evolution of herkogamy
107 arising from genetic covariance between pistil and stamen lengths (Opedal et al. 2017),
108 quantifying herkogamy as the difference between pistil and stamen lengths may be more
109 appropriate. Because anthers and stigmatic surfaces are often elongated, the absolute value of
110 these measures will tend to differ. Furthermore, herkogamy in many species is not constant
111 but changes during flower development due e.g. to curling of stigmatic lobes or differential
112 rates of elongation of male and female sexual organs (see Goodwillie and Weber 2018 for
113 review). For these reasons, great care must be taken to standardize measurements taken for

114 comparative analyses, typically by measuring flowers at similar developmental stages. In
115 some cases, emergent traits such as the timing of change in herkogamy may also be of key
116 interest (e.g. Armbruster et al. 2002).

117 Different kinds of measurements places herkogamy on different scale types. When
118 quantified as the difference between pistil length and stamen length, $x_{\text{♀}} - x_{\text{♂}}$, with negative
119 values assigned to reverse herkogamous flowers, herkogamy is on what Houle et al. (2011)
120 referred to as a signed ratio scale. When measured as the absolute distance between stigmas
121 and anthers, $|x_{\text{♀}} - x_{\text{♂}}|$, herkogamy is on a true ratio scale. Finally, herkogamy is sometimes
122 divided into distinct classes, and is then on an ordinal scale. For quantitative comparative
123 studies, these disparate scale types would represent a serious challenge (see discussion in
124 Opedal et al. 2017), and I urge researchers to carefully consider the consequences of their
125 choice of measurement scale in studies of herkogamy. In the following review my focus is on
126 qualitative relationships between herkogamy and mating-system parameters, and I hence
127 considered studies using any of the measurements of herkogamy outlined above.

128

129 **The functional relationships among herkogamy, autofertility, and outcrossing**

130 The expected negative effect of herkogamy on autofertility follows intuitively from the
131 reduced probability of pollen transfer over longer distances. In the absence of pollinators,
132 herkogamy-autofertility relationships are purely ‘physical’, and replicate studies of
133 individuals, populations, or species under standardized conditions are expected to yield
134 quantitatively similar results (Table 1). Under field conditions, some variation might
135 nevertheless be expected due to environmental factors such as wind speed, rainfall, or
136 variation in the resource level of maternal plants affecting seed production.

137 Herkogamy-autofertility relationships are always expected to be negative, yet their
138 shapes may vary. Autofertility rates are bounded between 0 and 1 and will almost inevitably

139 decline towards zero as herkogamy increases (Fig. 1). Furthermore, herkogamy-autofertility
140 relationships may often be nonlinear, taking shapes ranging from negatively exponential
141 ('Type I' herkogamy-autofertility relationship; Fig. 1, solid line) to logistic ('Type II'
142 herkogamy-autofertility relationship; Fig. 1, dashed line). In both cases, studies comparing
143 individuals, populations, or species at the upper end of the curve may fail to detect any
144 relationship. In the Type II case (dashed line), the same would be true for comparisons at the
145 lower end (see Opedal et al. 2015 for an empirical example). Note that linear herkogamy-
146 autofertility relationships falls within the expected range between these extremes.

147 In addition to taxon-specific shapes of herkogamy-autofertility relationships (Type I
148 vs. Type II vs. intermediate), the x-axis of Fig. 1 is unitless on purpose. This is because the
149 decline in autofertility per unit (e.g. mm) increase in herkogamy may depend on the relative
150 positions of anthers and stigmas within flowers. For example, autofertility may decline more
151 rapidly with increasing herkogamy in approach herkogamous species than in reverse
152 herkogamous species, and we can speculate that the relationship is often closer to Type I
153 (solid line) for approach herkogamy, and closer to Type II (dashed line) for reverse
154 herkogamy. Thus, in cases where herkogamy (measured as $x_{\text{♀}} - x_{\text{♂}}$) ranges from negative to
155 positive, the fitness consequences of changing herkogamy by one unit may be asymmetric
156 around zero. The rate of decay in autofertility with increasing herkogamy may also depend on
157 the relative orientation of anthers and stigmas. For example, species of *Dalechampia* vines
158 diverge in the angle between male and female flowers (Armbruster et al. 2009), and
159 populations of *Arabis alpina* differ in the orientation of the anthers towards or away from the
160 stigmas (Toräng et al. 2017).

161 The relationship between herkogamy and outcrossing rate is more complex, not least
162 because it depends on interactions with pollinators. At the species and population level,
163 positive herkogamy-outcrossing relationships are expected to arise due to selection for self-

164 pollination as a mechanism of reproductive assurance when cross-pollination is unreliable,
165 and selection for avoidance of self-pollination and/or sexual interference when cross-
166 pollination is reliable (e.g. Moeller 2006; Opedal et al. 2016a; but see Koski et al. 2017).

167 Two observations help to delimit the likely shapes of herkogamy-outcrossing
168 relationships. First, when anthers and stigmas are in direct contact (zero herkogamy),
169 outcrossing rates will tend to be low. Second, when herkogamy becomes so large that
170 autogamous selfing is unlikely (lower asymptote in Fig. 1), outcrossing rates should tend to
171 stabilize at a rate close to $1 - S_G - S_B$, where S_G is the rate of geitonogamy, and S_B is the rate of
172 biparental inbreeding (Fig. 2). Between these extremes, the shapes of herkogamy-outcrossing
173 relationships are likely to vary depending on specific aspects of floral biology. For example,
174 outcrossing rates depend not only on the amount of self vs. cross-pollen deposited onto
175 stigmas, but also on the timing of pollen deposition (e.g. Sorin et al. 2016). Therefore,
176 herkogamy-outcrossing relationships may differ, for example, between those species where a
177 female phase precedes a bisexual phase (incomplete protogyny), and those where a bisexual
178 phase precedes a female phase (incomplete protandry) (Fig. 2). While low herkogamy
179 combined with incomplete protandry will tend to favor selfing regardless of the reliability of
180 pollination, incomplete protogyny will favor outcrossing during the female phase when
181 pollination is reliable.

182 Importantly, while population-mean herkogamy is expected to correlate with the long-
183 term reliability of pollination, there are several reasons why the expected relationship would
184 not be detected in all studies. First, because outcrossing rates are bounded between 0 and 1,
185 asymptotes are expected at least at the upper limit (Fig. 2) and comparisons among
186 populations or species at the upper end may fail to detect differences. Second, one or more
187 populations may experience an unusual year, and thus a mismatch between average
188 herkogamy and current pollination reliability. In such situations, outcrossing rates will often

189 be better predicted by current pollination reliability than by mean herkogamy. This
190 ‘stochastic’ variation is one of the reasons why single-year estimates of outcrossing rates are
191 not necessarily very good measures of the long-term mating system (see further discussion
192 below). If all populations experience proportional increases or decreases in pollination
193 reliability across taxa, regions, or years, this would be predicted to shift the intercept and/or
194 slope of the herkogamy-outcrossing relationship (Fig. 2). Specifically, the solid lines in Fig. 2
195 might represent a ‘good’ year in terms of pollination reliability (many and/or efficient
196 pollinators), while the dashed lines might represent a ‘bad’ year (few and/or inefficient
197 pollinators). Similarly, variation in pollination reliability among populations will tend to add
198 noise to herkogamy-outcrossing relationships, thus reducing the variance in current
199 outcrossing rates explained by herkogamy. Some empirical data suggest that the impact of
200 variation in pollination reliability on outcrossing rates is greater in more herkogamous
201 populations (Eckert et al. 2009), but the generality of this pattern remains unknown, and is
202 likely to depend on aspects of floral biology. Overall, more variable patterns should be
203 expected among studies assessing herkogamy-outcrossing relationships, than among those
204 assessing herkogamy-autofertility relationships (Table 1). While the range of patterns
205 illustrated in Fig. 2 will probably fit a good number of species, they are unlikely to fit all.

206 Within populations, more herkogamous flowers may also be more outcrossed. Such
207 relationships may be causal, driven for example by reduced interference between male and
208 female functions in more herkogamous flowers (Webb and Lloyd 1986). Indeed, Webb and
209 Lloyd (1986) proposed avoidance of sexual interference as a primary function of herkogamy,
210 at least in self-incompatible taxa. Specifically, reduced herkogamy may restrict pollinator
211 access to stigmas, and increase autonomous and pollinator-facilitated self-pollen deposition
212 onto stigmas. This can in turn cause ‘stigma clogging’ and intensify competition between self-
213 and cross-pollen. Thus, assuming that the rate of self-fertilization increases with self-

214 pollination (Holsinger 1991), more herkogamous flowers are expected to be more outcrossed.
215 More herkogamous flowers may also receive more cross-pollen, if herkogamy correlates
216 positively with traits involved in pollinator attraction (reward or advertisement). In the latter
217 case, the herkogamy-outcrossing relationship would be non-causal.

218 Finally, herkogamy-outcrossing relationships (at all levels) are complicated by the fact
219 that realized selfing rates in natural populations represent the sum of within-flower selfing
220 (autogamy), between-flower selfing (geitonogamy), and biparental inbreeding. Among these,
221 only the autogamous component is directly related to variation in herkogamy (Herlihy and
222 Eckert 2004, and see below). Relationships with other components could arise indirectly if
223 herkogamy affects, for example, the amount of pollen available for cross-pollination
224 (including geitonogamy and biparental inbreeding).

225

226 **Summary of empirical herkogamy-autofertility and herkogamy-outcrossing** 227 **relationships**

228 To evaluate the hypothesis that more herkogamous taxa have historically experienced more
229 reliable pollination, and more outcrossed mating systems, I surveyed the literature for studies
230 reporting empirical herkogamy-autofertility and herkogamy-outcrossing relationships. With a
231 few exceptions, studies that have assessed herkogamy-autofertility and/or herkogamy-
232 outcrossing relationships have detected the expected patterns: more herkogamous individuals,
233 populations and species tend to exhibit reduced autofertility, and to be more outcrossed (Table
234 2). The generality of these patterns is supported by the wide geographic and taxonomic range
235 of the focal taxa, and the diversity of growth forms and life histories represented among them.
236 For example, Table 2 includes species from 17 families, whose habitats range from the
237 lowland tropics (e.g. *Turnera ulmifolia*, *Eichhornia paniculata*) to high-alpine meadows in
238 the Alps (*Primula halleri*) and Rocky Mountains (*Aquilegia caerulea*). Similarly, life histories

239 range from annuals (*Clarkia xantiana*) to long-lived woody vines (*Dalechampia* spp.) and
240 trees (*Nicotiana glauca*).

241 As expected, negative herkogamy-autofertility relationships were more consistent than
242 were positive herkogamy-outcrossing relationships (Table 2). Interestingly, in most of the
243 studies where results deviated from expectations, the authors offered biologically meaningful
244 explanations. These include differences in pollinator foraging behaviour on *Aquilegia*
245 *caerulea* flowers (Brunet and Sweet 2006), and strong correlations with dichogamy rather
246 than herkogamy in *Gilia achilleifolia* (Schoen 1982) and *Campanula americana* (Koski et al.
247 2018). Other examples are discussed in more detail below.

248

249 **Correlates of herkogamy beyond autofertility and outcrossing rate**

250 The focus above has been on relationships among herkogamy, autofertility, and outcrossing
251 rate, as these are the most frequently assessed. If variation in herkogamy reflects variation in
252 the reproductive environment, we also expect correlations with other features of plant
253 pollination and mating systems (Table 1). For example, it follows logically that individual
254 herkogamy should correlate negatively with the number of autogamous (within-flower) pollen
255 grains deposited onto stigmas. Such relationships have been demonstrated, for example, in
256 *Erythronium grandiflorum* (Thomson and Stratton 1985), and in several species of
257 *Dalechampia* (Bolstad et al. 2010; Pérez-Barrales et al. 2013), and *Ipomoea* (Murcia 1990;
258 Parra-Tabla and Bullock 2005).

259 For allogamous (between-flower) pollen loads (including geitonogamous self-pollen),
260 the opposite relationship should be expected, although with more variation among studies
261 (Table 1). This follows from the same logic that average herkogamy should represent
262 variation in the long-term reliability of pollination, and hence the level of outcrossing. For
263 example, Opedal et al. (2016a) reported a strong positive correlation between population-

264 mean cross-pollen loads and average herkogamy in *Dalechampia scandens* populations. At
265 the individual level, allogamous pollen loads are unlikely to correlate with herkogamy, unless
266 herkogamy is correlated with pollinator-attraction traits. If stigmatic pollen loads are limited
267 by the size of the stigmatic surface relative to the size of pollen grains, a positive association
268 could also arise if greater self-pollen loads of less herkogamous flowers precludes subsequent
269 deposition of cross-pollen.

270 As discussed briefly above, herkogamy may not uniformly affect all functional
271 components of selfing. A clear demonstration of this has emerged from studies of the North-
272 American columbine *Aquilegia canadensis*. Herlihy and Eckert (2004) used floral-
273 emasculation experiments combined with genetic analyses to disentangle the contributions of
274 autogamy, geitonogamy, and biparental inbreeding to realized selfing rates in natural
275 populations. As expected, only the autogamous component of selfing correlated strongly and
276 negatively with herkogamy, while rates of geitonogamy and biparental inbreeding were
277 instead explained by variation in ecological factors such as plant density and canopy cover.

278 Medrano et al. (2005, 2012) reported an interesting exception from the usual
279 herkogamy-outcrossing relationship in the daffodil *Narcissus longipathus*. While the authors
280 failed to detect the expected difference in outcrossing rate between plants exhibiting low,
281 medium, and high herkogamy (Table 2), they found that the average number of fathers siring
282 offspring in fruits increased in more herkogamous plants. Such relationships might indeed be
283 expected to be common, and perhaps ubiquitous in species with granular pollen and where
284 pollinators visit multiple plants per foraging bout.

285 Finally, plant mating systems strongly affect the population-genetic structure of
286 populations, and herkogamy is therefore also expected to correlate positively with measures
287 of genetic diversity within populations (e.g. Barrett and Husband 1990; Opedal et al. 2016a),
288 and with genetic differentiation among populations as measured by F_{ST} or related metrics

289 (Hamrick and Godt 1996; Duminil et al. 2007). The latter relationship could arise among
290 species, or among regions in widespread species.

291

292 **On the use of herkogamy as a mating-system proxy**

293 The consistent relationships among herkogamy, autofertility and outcrossing rates reviewed in
294 Table 2 provides strong support for the hypothesis that when two self-compatible populations
295 or species differ in average herkogamy, they also differ in their mating systems. An important
296 consequence of this ‘herkogamy rule’ is that variation in population-mean herkogamy can be
297 used as a reliable proxy of variation in mating systems. A key advantage of using mean
298 herkogamy as a proxy of the mating system is that it is likely to reflect the mating history of a
299 population (i.e. the long-term mean outcrossing rate) rather than the mating system in a given
300 year or season. Indeed, outcrossing rates are known to vary from year to year within
301 populations (Eckert et al. 2009), and even within a single season (Yin et al. 2016). Thus, using
302 single estimates of outcrossing rates as a measure of the mating system could run the risk of
303 interpreting an unusual year as the long-term trend, and hence bias the conclusion of
304 comparative studies. Because measuring herkogamy is fast and can be done at essentially no
305 cost, this provides ideal opportunities for comparative studies. In many systems, herkogamy
306 also exhibit only limited environmental variation (Opedal et al. 2016b and references therein).

307 For example, herkogamy has been repeatedly used as a mating-system proxy in
308 comparative studies of inbreeding depression, testing the hypothesis that more inbred
309 populations or families are subject to purging of deleterious alleles and hence experience less
310 intense inbreeding depression than do less inbred populations or families (Carr et al. 1997;
311 Byers and Waller 1999; Chang and Rausher 1999; Takebayashi and Delph 2000; Stone and
312 Motten 2002; Herlihy and Eckert 2004; Weber et al. 2012; Opedal et al. 2015). Other
313 examples include comparative studies of mating-system effects on geographical range size

314 (Grossenbacher et al. 2015), range overlap (Grossenbacher et al. 2016), and sexual conflict
315 over seed provisioning (A. Raunsgard et al., manuscript in revision).

316 Herkogamy has also been used as a mating-system proxy in studies of the evolution of
317 the mating system itself (Armbruster 1993). Here caution must obviously be exercised, as the
318 argument might become circular (mating-system changes are assumed to lead to evolutionary
319 shifts in herkogamy, and mating-system shifts are then inferred from these shifts). As should
320 be clear from the arguments of this essay, however, herkogamy-mating-system relationships
321 are consistent enough, at least for many groups, to place some trust in such analyses.

322

323 **Reproductive-function traits and the structure of plant communities**

324 Consistent correlations between herkogamy and mating systems also suggest that herkogamy
325 can be informative about processes structuring natural plant communities. The role of
326 functional traits in shaping species assemblages is a hot topic in community ecology (e.g.
327 Adler et al. 2013; Kohli et al. 2018), and while most studies have focused on traits involved in
328 abiotic resource competition or in response to abiotic environmental variables ('vegetative
329 processes'), further consideration of traits mediating reproductive interactions may provide
330 more complete insights into the processes shaping natural plant assemblages (Armbruster
331 1995; Sargent and Ackerly 2008; Pauw 2013; Briscoe Runquist et al. 2016). Herkogamy and
332 the component traits (positions of stigmas and anthers) can affect reproductive interactions
333 through shared pollinators in several ways. First, the positions of the sexual organs can affect
334 the position of pollen placement on the bodies of pollinators, and hence divergence in these
335 traits can reduce interspecific pollination (e.g. Armbruster et al. 1994; Kay 2006; Keller et al.
336 2016). Because the position of pollen placement depends on the absolute rather than relative
337 positions of anthers and stigmas, this process may be independent of mean herkogamy (which
338 is defined by the relative positions of the sexual organs). The relevance of herkogamy for

339 reproductive interactions arises from its effect on the mating system and the dynamics of
340 pollen transfer. In selfing species with low herkogamy, large autonomous pollen loads may
341 reduce the fitness consequences of subsequent heterospecific pollen deposition, thus
342 providing a buffer against the negative effects of pollinator sharing. For example, *Ipomoea*
343 *purpurea* and *I. hederacea* commonly occur in sympatry, and share bumblebee pollinators.
344 Smith and Rausher (2007, 2008) have demonstrated experimentally that reduced herkogamy
345 in *I. hederacea* acts as a ‘shield’ reducing interspecific pollination and thus increasing fitness.
346 A role of mating-system divergence mediated by herkogamy has also been invoked to explain
347 species coexistence in other systems, including *Arenaria* (Fishman and Wyatt 1999), *Mimulus*
348 (Grossenbacher and Whittall 2011; Briscoe Runquist et al. 2016), and *Centaureium* (Brys et al.
349 2014; Brys et al. 2016; Schoupe et al. 2017). Taken together, these observations suggest that
350 the probability of coexistence is greater for species pairs that share pollinators if they differ in
351 mean herkogamy, and the effect would be stronger if one of the species exhibit very low
352 herkogamy. Similarly, pairs of highly selfing species with very low average herkogamy might
353 be more likely to coexist, because reproductive interactions through shared pollinators are
354 unlikely in such species. The kind of mating-system-related structure of plant communities
355 described above may result from ecological ‘sorting’ of species into communities, or at least
356 in part be caused by selection for reproductive character displacement among sympatric
357 species (Brown and Wilson 1956; Armbruster and Muchhala 2009).

358 Recent methodological developments of joint species distribution models are
359 beginning to consider species traits as predictors of species cooccurrences (e.g. Abrego et al.
360 2017). While traits mediating vegetative processes are likely to be informative about
361 cooccurrence explained by shared or contrasting responses to the abiotic environment,
362 herkogamy and other traits mediating reproductive interactions may increase the net
363 explanatory power by explaining patterns of variation unexplained by vegetative processes.

364 Thus, increased consideration of ‘reproductive-function traits’ will allow us to move beyond
365 purely vegetative processes in predictive models of community assembly.

366

367 **Concluding remarks**

368 Here, I have compiled a large body of evidence supporting the hypothesis that, when a pair of
369 self-compatible taxa differ in their average anther-stigma separation (herkogamy), they will
370 also differ predictably in their mating systems. This nearly ubiquitous pattern provides a
371 valuable tool for a wide range of comparative studies, and have already provided important
372 insights into the ecological, genetical, and evolutionary causes and consequences of variation
373 and evolution of plant mating systems. Going forward, increased use of herkogamy as a
374 functional trait in studies of community structure and assembly might yield new and
375 important insights allowing us to predict the consequences of changes in the reproductive
376 environment.

377

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383

384 **References**

- 385 Abrego N, A Norberg, O Ovaskainen 2017 Measuring and predicting the influence of traits on the
386 assembly processes of wood-inhabiting fungi. *J Ecol* 105: 1070-1081.
- 387 Adler PB, A Fajardo, AR Kleinhesselink, NJ Kraft 2013 Trait-based tests of coexistence mechanisms.
388 *Ecol Lett* 16: 1294-1306.
- 389 Armbruster WS 1988 Multilevel comparative analysis of the morphology, function, and evolution of
390 *Dalechampia* blossoms. *Ecology* 69: 1746-1761.
- 391 Armbruster WS 1993 Evolution of plant pollination systems - hypotheses and tests with the
392 neotropical vine *Dalechampia*. *Evolution* 47: 1480-1505.
- 393 Armbruster WS 1995 The origins and detection of plant community structure: reproductive versus
394 vegetative processes. *Folia Geobotanica & Phytotaxonomica* 30: 483-497.

395 Armbruster WS, ME Edwards, EM Debevec 1994 Floral character displacement generates assemblage
396 structure of western Australian triggerplants (*Stylidium*). *Ecology* 75: 315-329.

397 Armbruster WS, N Muchhala 2009 Associations between floral specialization and species diversity:
398 cause, effect, or correlation? *Evol Ecol* 23: 159-179.

399 Armbruster WS, CPH Mulder, BG Baldwin, S Kalisz, B Wessa, H Nute 2002 Comparative analysis of
400 late floral development and mating-system evolution in Tribe Collinsieae (Scrophulariaceae
401 SL). *Am J Bot* 89: 37-49.

402 Armbruster WS, C Pélabon, TF Hansen, GH Bolstad 2009 Macroevolutionary patterns of pollination
403 accuracy: a comparison of three genera. *New Phytol* 183: 600-617.

404 Barrett SCH 2002 The evolution of plant sexual diversity. *Nat Rev Genet* 3: 274-284.

405 Barrett SCH 2003 Mating strategies in flowering plants: the outcrossing-selfing paradigm and beyond.
406 *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 358:
407 991-1004.

408 Barrett SCH, BC Husband 1990 Variation in outcrossing rates in *Eichhornia paniculata*: the role of
409 demographic and reproductive factors. *Plant Species Biol* 5: 41-56.

410 Barrett SCH, JS Shore 1987 Variation and evolution of breeding systems in the *Turnera ulmifolia* L.
411 complex (Turneraceae). *Evolution* 41: 340-354.

412 Belaoussoff S, JS Shore 1995 Floral correlates and fitness consequences of mating-system variation in
413 *Turnera ulmifolia*. *Evolution* 49: 545-556.

414 Bolstad GH, WS Armbruster, C Pélabon, R Pérez-Barrales, TF Hansen 2010 Direct selection at the
415 blossom level on floral reward by pollinators in a natural population of *Dalechampia schottii*:
416 full-disclosure honesty? *New Phytol* 188: 370-384.

417 Breese EL 1959 Selection for differing degrees of out-breeding in *Nicotiana rustica*. *Ann Bot* 23: 331-
418 344.

419 Briscoe Runquist R, D Grossenbacher, S Porter, K Kay, J Smith 2016 Pollinator-mediated assemblage
420 processes in California wildflowers. *J Evol Biol* 29: 1045-1058.

421 Brown WL, EO Wilson 1956 Character displacement. *Systematic Zoology* 5: 49-64.

422 Brunet J, CG Eckert 1998 Effects of floral morphology and display on outcrossing in Blue Columbine,
423 *Aquilegia caerulea* (Ranunculaceae). *Funct Ecol* 12: 596-606.

424 Brunet J, HR Sweet 2006 Impact of insect pollinator group and floral display size on outcrossing rate.
425 *Evolution* 60: 234-246.

426 Brys R, B Geens, T Beeckman, H Jacquemyn 2013 Differences in dichogamy and herkogamy
427 contribute to higher selfing in contrasting environments in the annual *Blackstonia perfoliata*
428 (Gentianaceae). *Ann Bot* 111: 651-661.

429 Brys R, H Jacquemyn 2011 Variation in the functioning of autonomous self-pollination, pollinator
430 services and floral traits in three *Centaureum* species. *Ann Bot* 107: 917-925.

431 Brys R, H Jacquemyn 2012 Effects of human-mediated pollinator impoverishment on floral traits and
432 mating patterns in a short-lived herb: an experimental approach. *Funct Ecol* 26: 189-197.

433 Brys R, J van Cauwenberghe, H Jacquemyn, N Rafferty 2016 The importance of autonomous selfing in
434 preventing hybridization in three closely related plant species. *J Ecol* 104: 601-610.

435 Brys R, A Vanden Broeck, J Mergeay, H Jacquemyn 2014 The contribution of mating system variation
436 to reproductive isolation in two closely related *Centaureum* species (Gentianaceae) with a
437 generalized flower morphology. *Evolution* 68: 1281-1293.

438 Byers DL, DM Waller 1999 Do plant populations purge their genetic load? Effects of population size
439 and mating history on inbreeding depression. *Annu Rev Ecol Syst* 30: 479-513.

440 Carr DE, CB Fenster 1994 Levels of genetic variation and covariation for *Mimulus* (Scrophulariaceae)
441 floral traits. *Heredity* 72: 606-618.

442 Carr DE, CB Fenster, MR Dudash 1997 The relationship between mating-system characters and
443 inbreeding depression in *Mimulus guttatus*. *Evolution* 51: 363-372.

444 Chang SM, MD Rausher 1998 Frequency-dependent pollen discounting contributes to maintenance
445 of a mixed mating system in the common morning glory *Ipomoea purpurea*. *Am Nat* 152:
446 671-683.

447 Chang SM, MD Rausher 1999 The role of inbreeding depression in maintaining the mixed mating
448 system of the common morning glory, *Ipomoea purpurea*. *Evolution* 53: 1366-1376.

449 Chen XS, S Marten-Rodriguez, QJ Li, CB Fenster 2009 Potential autonomous selfing in *Gesneria citrina*
450 (*Gesneriaceae*), a specialized hummingbird pollinated species with variable expression of
451 herkogamy. *J Integr Plant Biol* 51: 973-978.

452 Dart SR, KE Samis, E Austen, CG Eckert 2012 Broad geographic covariation between floral traits and
453 the mating system in *Camissoniopsis cheiranthifolia* (*Onagraceae*): multiple stable mixed
454 mating systems across the species range? *Ann Bot* 109: 599-611.

455 de Vos JM, B Keller, ST Isham, S Kelso, E Conti 2012 Reproductive implications of herkogamy in
456 homostylous primroses: variation during anthesis and reproductive assurance in alpine
457 environments. *Funct Ecol* 26: 854-865.

458 de Vos JM, B Keller, L-R Zhang, MD Nowak, E Conti 2018 Mixed mating in homostylous species:
459 genetic and experimental evidence from an alpine plant with variable herkogamy, *Primula*
460 *halleri*. *Int J Plant Sci* 179: 87-99.

461 Dole JA 1992 Reproductive assurance mechanisms in 3 taxa of the *Mimulus guttatus* complex
462 (*Scrophulariaceae*). *Am J Bot* 79: 650-659.

463 Duminil J, S Fineschi, A Hampe, P Jordano, D Salvini, GG Vendramin, RJ Petit 2007 Can population
464 genetic structure be predicted from life-history traits? *Am Nat* 169: 662-672.

465 Duncan TM, MD Rausher 2013 Evolution of the selfing syndrome in *Ipomoea*. *Frontiers in Plant*
466 *Science* 4.

467 Eckert CG, B Ozimec, CR Herlihy, CA Griffin, MB Routley 2009 Floral morphology mediates temporal
468 variation in the mating system of a self-compatible plant. *Ecology* 90: 1540-1548.

469 Eckert CG, A Schaefer 1998 Does self-pollination provide reproductive assurance in *Aquilegia*
470 *canadensis* (*Ranunculaceae*)? *Am J Bot* 85: 919-924.

471 Elle E, JD Hare 2002 Environmentally induced variation in floral traits affects the mating system in
472 *Datura wrightii*. *Funct Ecol* 16: 79-88.

473 Ennos RA 1981 Quantitative studies of the mating system in two sympatric species of *Ipomoea*
474 (*Convolvulaceae*). *Genetica* 57: 93-98.

475 Epperson BK, MT Clegg 1987 First-pollination primacy and pollen selection in the morning glory,
476 *Ipomoea purpurea*. *Heredity* 58: 5-14.

477 Fishman L, R Wyatt 1999 Pollinator-mediated competition, reproductive character displacement, and
478 the evolution of selfing in *Arenaria uniflora* (*Caryophyllaceae*). *Evolution* 53: 1723-1733.

479 Fægri K, L van der Pijl 1979 *The principles of pollination ecology*. Pergamon Press, Oxford, UK.

480 Ganders FR, SK Denny, D Tsai 1985 Breeding systems and genetic variation in *Amsinckia spectabilis*
481 (*Boraginaceae*). *Canadian Journal of Botany* 63: 533-538.

482 Goodwillie C, JM Ness 2005 Correlated evolution in floral morphology and the timing of self-
483 compatibility in *Leptosiphon jepsonii* (*Polemoniaceae*). *Int J Plant Sci* 166: 741-751.

484 Goodwillie C, JJ Weber 2018 The best of both worlds? A review of delayed selfing in flowering plants.
485 *Am J Bot* 105: 641-655.

486 Grant V, KA Grant 1965 *Flower pollination in the Phlox family*. Columbia University Press, New York.

487 Grossenbacher D, RD Briscoe Runquist, EE Goldberg, Y Brandvain 2016 No association between plant
488 mating system and geographic range overlap. *Am J Bot* 103: 110-117.

489 Grossenbacher D, RB Runquist, EE Goldberg, Y Brandvain 2015 Geographic range size is predicted by
490 plant mating system. *Ecol Lett* 18: 706-713.

491 Grossenbacher DL, JB Whittall 2011 Increased floral divergence in sympatric monkeyflowers.
492 *Evolution* 65: 2712-2718.

493 Hamrick JL, MJW Godt 1996 Effects of life history traits on genetic diversity in plant species.
494 *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 351:
495 1291-1298.

496 Herlihy CR, CG Eckert 2004 Experimental dissection of inbreeding and its adaptive significance in a
497 flowering plant, *Aquilegia canadensis* (*Ranunculaceae*). *Evolution* 58: 2693-2703.

498 Herlihy CR, CG Eckert 2005 Evolution of self-fertilization at geographical range margins? A
499 comparison of demographic, floral, and mating system variables in central vs. peripheral
500 populations of *Aquilegia canadensis* (Ranunculaceae). *Am J Bot* 92: 744-751.

501 Herlihy CR, CG Eckert 2007 Evolutionary analysis of a key floral trait in *Aquilegia canadensis*
502 (Ranunculaceae): genetic variation in herkogamy and its effect on the mating system.
503 *Evolution* 61: 1661-1674.

504 Holsinger KE 1991 Mass-action models of plant mating systems: the evolutionary stability of mixed
505 mating systems. *Am Nat* 138: 606-622.

506 Holtsford TP, NC Ellstrand 1992 Genetic and environmental variation in floral traits affecting
507 outcrossing rate in *Clarkia tembloriensis* (Onagraceae). *Evolution* 46: 216-225.

508 Houle D, C Pélabon, GP Wagner, TF Hansen 2011 Measurement and meaning in biology. *Q Rev Biol*
509 86: 3-34.

510 Karron JD, RT Jackson, NN Thumser, SL Schlicht 1997 Outcrossing rates of individual *Mimulus ringens*
511 genets are correlated with anther-stigma separation. *Heredity* 79: 365-370.

512 Kay KM 2006 Reproductive isolation between two closely related hummingbird-pollinated
513 neotropical gingers. *Evolution* 60: 538-552.

514 Keller B, JM de Vos, AN Schmidt-Lebuhn, JD Thomson, E Conti 2016 Both morph- and species-
515 dependent asymmetries affect reproductive barriers between heterostylous species. *Ecol*
516 *Evol* 6: 6223-6244.

517 Kohli BA, RC Terry, RJ Rowe 2018 A trait-based framework for discerning drivers of species co-
518 occurrence across heterogeneous landscapes. *Ecography* in press.

519 Koski MH, D Grossenbacher, JW Busch, LF Galloway 2017 A geographic cline in the ability to self-
520 fertilize is unrelated to the pollination environment. *Ecology* 98: 2930-2939.

521 Koski MH, L Kuo, KM Niedermaier, LF Galloway 2018 Timing is everything: dichogamy and pollen
522 germinability underlie variation in autonomous selfing among populations. *Am J Bot* in press.

523 Lavorel S, E Garnier 2002 Predicting changes in community composition and ecosystem functioning
524 from plant traits: revisiting the Holy Grail. *Funct Ecol* 16: 545-556.

525 Lennartsson T, JGB Oostermeijer, J van Dijk, HCM den Nijs 2000 Ecological significance and
526 heritability of floral reproductive traits in *Gentianella campestris* (Gentianaceae). *Basic Appl*
527 *Ecol* 1: 69-81.

528 Li XX, Y Zou, CL Xiao, RW Gituru, YH Guo, CF Yang 2013 The differential contributions of herkogamy
529 and dichogamy as mechanisms of avoiding self-interference in four self-incompatible
530 *Epimedium* species. *J Evol Biol* 26: 1949-1958.

531 McGill BJ, BJ Enquist, E Weiher, M Westoby 2006 Rebuilding community ecology from functional
532 traits. *Trends Ecol Evol* 21: 178-185.

533 Medrano M, CM Herrera, SCH Barrett 2005 Herkogamy and mating patterns in the self-compatible
534 daffodil *Narcissus longispathus*. *Ann Bot* 95: 1105-1111.

535 Medrano M, R Requerey, JD Karron, CM Herrera 2012 Herkogamy and mate diversity in the wild
536 daffodil *Narcissus longispathus*: beyond the selfing-outcrossing paradigm in the evolution of
537 mixed mating. *Plant Biol* 14: 801-810.

538 Moeller DA 2006 Geographic structure of pollinator communities, reproductive assurance, and the
539 evolution of self-pollination. *Ecology* 87: 1510-1522.

540 Motten AF, J Antonovics 1992 Determinants of outcrossing rate in a predominantly self-fertilizing
541 weed, *Datura stramonium* (Solanaceae). *Am J Bot* 79: 419-427.

542 Motten AF, JL Stone 2000 Heritability of stigma position and the effect of stigma-anther separation
543 on outcrossing in a predominantly self-fertilizing weed, *Datura stramonium* (Solanaceae). *Am*
544 *J Bot* 87: 339-347.

545 Murcia C 1990 Effect of floral morphology and temperature on pollen receipt and removal in
546 *Ipomoea trichocarpa*. *Ecology* 71: 1098-1109.

547 Ollerton J, S Watts, S Connerty, J Lock, L Parker, I Wilson, S Schueller, J Nattero, AA Cocucci, I Izhaki, S
548 Geerts, A Pauw, JC Stout 2012 Pollination ecology of the invasive tree tobacco *Nicotiana*

549 *glauca*: comparisons across native and non-native ranges. Journal of Pollination Ecology 9:
550 85-95.

551 Opedal ØH, E Albertsen, WS Armbruster, R Pérez-Barrales, M Falahati-Anbaran, C Pélabon 2016a
552 Evolutionary consequences of ecological factors: pollinator reliability predicts mating-system
553 traits of a perennial plant. Ecol Lett 19: 1486-1495.

554 Opedal ØH, WS Armbruster, C Pélabon 2015 Inbreeding effects in a mixed-mating vine: effects of
555 mating history, pollen competition and stress on the cost of inbreeding. AoB Plants 7: plv133.

556 Opedal ØH, GH Bolstad, TF Hansen, WS Armbruster, C Pélabon 2017 The evolvability of herkogamy:
557 quantifying the evolutionary potential of a composite trait. Evolution 71: 1572-1586.

558 Opedal ØH, J Listemann, E Albertsen, WS Armbruster, C Pélabon 2016b Multiple effects of drought
559 on pollination and mating-system traits in *Dalechampia scandens*. Int J Plant Sci 177: 682-
560 693.

561 Ornduff R 1969 Reproductive biology in relation to angiosperm systematics. Taxon 18: 121-133.

562 Parra-Tabla V, SH Bullock 2005 Ecological and selective effects of stigma-anther separation in the
563 self-incompatible tropical tree *Ipomoea wolcottiana* (Convolvulaceae). Plant Syst Evol 252:
564 85-95.

565 Pauw A 2013 Can pollination niches facilitate plant coexistence? Trends Ecol Evol 28: 30-37.

566 Pérez-Barrales R, GH Bolstad, C Pélabon, TF Hansen, WS Armbruster 2013 Pollinators and seed
567 predators generate conflicting selection on *Dalechampia* blossoms. Oikos 122: 1411-1428.

568 Rick CM, JF Fobes, M Holle 1977 Genetic variation in *Lycopersicon pimpinellifolium*: evidence of
569 evolutionary change in mating systems. Plant Syst Evol 127: 139-170.

570 Rick CM, M Holle, RW Thorp 1978 Rates of cross-pollination in *Lycopersicon pipinellifolium*: impact of
571 genetic variation in floral characters. Plant Syst Evol 129: 31-44.

572 Ritland C, K Ritland 1989 Variation of sex allocation among 8 taxa of the *Mimulus guttatus* species
573 complex (Scrophulariaceae). Am J Bot 76: 1731-1739.

574 Robertson AW, DG Lloyd 1991 Herkogamy, dichogamy and self-pollination in six species of *Myosotis*
575 (Boraginaceae). Evolutionary Trends in Plants 5: 53-63.

576 Sargent RD, DD Ackerly 2008 Plant-pollinator interactions and the assembly of plant communities.
577 Trends Ecol Evol 23: 123-130.

578 Schoen DJ 1982 The breeding system of *Gilia achilleifolia*: variation in floral characteristics and
579 outcrossing rate. Evolution 36: 352-360.

580 Schoupe D, R Brys, M Vallejo-Marin, H Jacquemyn 2017 Geographic variation in floral traits and the
581 capacity of autonomous selfing across allopatric and sympatric populations of two closely
582 related *Centaureum* species. Sci Rep 7: 46410.

583 Schueller SK 2004 Self-pollination in island and mainland populations of the introduced
584 hummingbird-pollinated plant, *Nicotiana glauca* (Solanaceae). Am J Bot 91: 672-681.

585 Shipley B, F De Bello, JHC Cornelissen, E Laliberte, DC Laughlin, PB Reich 2016 Reinforcing loose
586 foundation stones in trait-based plant ecology. Oecologia 180: 923-931.

587 Sicard A, M Lenhard 2011 The selfing syndrome: a model for studying the genetic and evolutionary
588 basis of morphological adaptation in plants. Ann Bot 107: 1433-1443.

589 Smith RA, MD Rausher 2007 Close clustering of anthers and stigma in *Ipomoea hederacea* enhances
590 prezygotic isolation from *Ipomoea purpurea*. New Phytol 173: 641-647.

591 Sorin YB, RJ Mitchell, DW Trapnell, JD Karron 2016 Effects of pollination and postpollination
592 processes on selfing rate in *Mimulus ringens*. Am J Bot 103: 1524-1528.

593 Stebbins GL 1970 Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination
594 mechanisms. Annu Rev Ecol Syst 1: 307-326.

595 Stone JL, AF Motten 2002 Anther-stigma separation is associated with inbreeding depression in
596 *Datura stramonium*, a predominantly self-fertilizing annual. Evolution 56: 2187-2195.

597 Takebayashi N, LF Delph 2000 An association between a floral trait and inbreeding depression.
598 Evolution 54: 840-846.

599 Takebayashi N, DE Wolf, LF Delph 2006 Effect of variation in herkogamy on outcrossing within a
600 population of *Gilia achilleifolia*. Heredity (Edinb) 96: 159-165.

601 Tedder A, S Carleial, M Golebiewska, C Kappel, KK Shimizu, M Stift 2015 Evolution of the selfing
602 syndrome in *Arabis alpina* (Brassicaceae). Plos One 10: e0126618.
603 Thomson JD, DA Stratton 1985 Floral morphology and cross-pollination in *Erythronium grandiflorum*
604 (Liliaceae). Am J Bot 72: 433-437.
605 Toräng P, L Vikström, J Wunder, S Wötzel, G Coupland, J Ågren 2017 Evolution of the selfing
606 syndrome: anther orientation and herkogamy together determine reproductive assurance in
607 a self-compatible plant. Evolution 71: 2206-2218.
608 van der Niet T, R Peakall, SD Johnson 2014 Pollinator-driven ecological speciation in plants: new
609 evidence and future perspectives. Ann Bot 113: 199-211.
610 Webb CJ, DG Lloyd 1986 The avoidance of interference between the presentation of pollen and
611 stigmas in angiosperms II. Herkogamy. N Z J Bot 24: 163-178.
612 Weber JJ, C Goodwillie 2009 Evolution of the mating system in a partially self-incompatible species:
613 reproductive assurance and pollen limitation in populations that differ in the timing of self-
614 compatibility. Int J Plant Sci 170: 885-893.
615 Weber JJ, SG Weller, AK Sakai, A Nguyen, ND Tai, CA Dominguez, FE Molina-Freaner 2012 Purging of
616 inbreeding depression within a population of *Oxalis alpina* (Oxalidaceae). Am J Bot 99: 923-
617 932.
618 Yin G, SC Barrett, YB Luo, WN Bai 2016 Seasonal variation in the mating system of a selfing annual
619 with large floral displays. Ann Bot 117: 391-400.

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624 **Figure legends**

625 Fig. 1. Range of expected functional relationships between herkogamy (anther-stigma
626 distance) and autofertility (autonomous seed-set in the absence of pollinators). The solid line
627 represents a 'Type I' herkogamy-autofertility relationship, and the dashed line a 'Type II'
628 herkogamy-autofertility relationship. The units on the x-axis are expected to be taxon-specific
629 and are therefore not shown.

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631 Fig. 2. Examples of expected functional relationships between herkogamy (anther-stigma
632 distance) and outcrossing rate for species exhibiting incomplete protandry (a) and incomplete
633 protogyny (b). The dotted lines indicate the patterns expected in the absence of geitonogamy
634 (S_G) and biparental inbreeding (S_B), and the solid and dashed lines indicate the patterns
635 expected in the presence of geitonogamy and biparental inbreeding under conditions of high
636 (solid line) and low (dashed line) pollination reliability. The units on the x-axis are expected
637 to be taxon-specific and are therefore not shown.

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Table 1. Expected correlates of herkogamy (anther-stigma distance) at the level of individuals (I), populations (S), and species (S). The ‘Variance’ column indicates whether relationships are expected to be stable or variable across different studies. See text for details.

Correlate	Definition	Sign of correlation	Level	Variance
Autofertility (a)	Seed set in absence of pollinators	Negative	I, P, S	Low
Outcrossing rate (t)	Proportion of seeds outcrossed	Positive	I, P, S	High
Autogamous pollen load (P_S)	Number of self-pollen grains on stigma	Negative	I, P, S	Low
Allogamous pollen load (P_C)	Number of cross-pollen grains on stigma	Positive	P, S	High
Genetic diversity (e.g. H_E)	Among-individual allelic variation	Positive	P, S	High
Genetic differentiation (F_{ST})	Proportion of genetic diversity among populations	Negative	S	High
Sire number	Number of sires per fruit	Positive	I, P, S	High

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Table 2. List of studies testing for relationships between herkogamy and autofertility (*a*) or outcrossing rate (*t*) among individuals, populations, or species. + and – indicate strong relationships, (+) and (-) indicate weaker relationships, and 0 indicate no detectable relationship.

Species	Family	Level	<i>a</i>	<i>t</i>	Evidence	Reference
<i>Amsinckia spectabilis</i>	Boraginaceae	Population		+	Positive relationship between herkogamy and outcrossing rate among 10 populations, including heterostylous, homostylous and mixed populations.	Ganders et al. 1985
<i>Aquilegia caerulea</i>	Ranunculaceae	Individual	-	+	Herkogamy negatively correlated with autofertility, and positively with outcrossing rate, among three groups within a population.	Brunet and Eckert 1998
		Population		(-)	Weak negative relationship between herkogamy and outcrossing rate across 10 population-year combinations.	Brunet and Sweet 2006
<i>Aquilegia canadensis</i>	Ranunculaceae	Individual	-		Negative relationship between individual herkogamy and autofertility among plants from two populations.	Eckert and Schaefer 1998
		Population		(+)	Weak positive relationship between herkogamy and outcrossing rate among 10 populations. Negative relationship with autogamous selfing in isolation.	Herlihy and Eckert 2004
		Population		0	No detectable difference in mating system between central and northern population despite difference in average herkogamy.	Herlihy and Eckert 2005
		Individual		+	Greater outcrossing rate of high vs. low herkogamy groups of plants in 13/19 populations.	Herlihy and Eckert 2007
		Population		+	Outcrossing rate increases with increasing herkogamy among 18 populations. Positive relationship between herkogamy and between-year variation in outcrossing rates.	Eckert et al 2009
<i>Arabis alpina</i>	Brassicaceae	Population		+	Reduced herkogamy in three selfing populations compared to three more outcrossing populations.	Tedder et al. 2015
<i>Blackstonia perfoliata</i>	Gentianaceae	Population	-		Greater autofertility in pollinator-poor environment with smaller flowers and reduced herkogamy.	Brys et al. 2013
<i>Camissoniopsis cheiranthifolia</i>	Onagraceae	Population	-	+	Positive relationship between herkogamy and outcrossing rate among 16 populations.	Dart et al. 2012
<i>Campanula americana</i>	Campanulaceae	Population		0	No detectable relationship between herkogamy and autofertility among 24 populations. Autofertility explained by dichogamy.	Koski et al. 2018

<i>Centaurium erythraea</i>	Gentianaceae	Population	-	Greater autofertility in pollinator-poor environment with smaller flowers and reduced herkogamy.	Brys and Jacquemyn 2012	
<i>Centaurium</i>	Gentianaceae	Species	-	Negative relationship between herkogamy and autofertility across three species.	Brys and Jacquemyn 2011 (and see Schouppe et al. 2017)	
<i>Clarkia parviflora</i>	Onagraceae	Population	-	Negative relationship between herkogamy and autofertility among 15 populations.	Moeller 2006	
<i>Clarkia tembloriensis</i>	Onagraceae	Population	+	Positive relationship between herkogamy and outcrossing rate among eight populations. Herkogamy positively correlated with dichogamy.	Holtsford and Ellstrand 1992	
<i>Clarkia xantiana</i>	Onagraceae	Population	-	Negative relationship between herkogamy and autofertility among 15 populations.	Moeller 2006	
<i>Dalechampia scandens</i>	Euphorbiaceae	Individual, Population	-	Negative relationship between herkogamy and autofertility rate within and among four populations.	Opedal et al. 2015	
		Population, Species	-	Negative relationship between herkogamy and autofertility across two populations of each of two species.	Opedal et al. 2016a	
		Population	+	Positive relationship between herkogamy and outcrossing rate among four populations.	Opedal et al. 2016b	
<i>Dalechampia</i>	Euphorbiaceae	Species	-	Negative relationship between herkogamy and autofertility across nine species.	Armbruster 1988	
<i>Datura stramonium</i>	Solanaceae	Individual	+	Positive relationship between herkogamy and outcrossing rate among plants within two populations.	Motten and Stone 2000 (and see Motten and Antonovics 1992)	
<i>Datura wrightii</i>	Solanaceae	Individual	-	+	Positive relationship between herkogamy and outcrossing rate in a field experiment, and negative relationship between herkogamy and autofertility in a greenhouse experiment.	Elle and Hare 2002
<i>Eichhornia paniculata</i>	Pontederiaceae	Population	+	Positive relationship between "frequency of selfing variants" and outcrossing rate among 32 populations.	Barrett and Husband 1990	
<i>Epimedium</i>	Berberidaceae	Population	-	Greater autofertility in two low-herkogamy species compared to two high-herkogamy species.	Li et al. 2013	
		Species	-			
<i>Gentianella campestris</i>	Gentianaceae	Individual	(-)	Greater autofertility in 'iso-stigmatic' and 'hypo-stigmatic' groups than in 'hyper-stigmatic groups'.	Lennartsson et al. 2000	
<i>Gesneria citrina</i>	Gesneriaceae	Individual	-	Negative relationship between herkogamy and autofertility within a population.	Chen et al. 2009	

<i>Gilia achilleifolia</i>	Polemoniaceae	Individual	+	Higher outcrossing rate within a population for the group of plants with greater herkogamy.	Takebayashi et al. 2006
		Individual	-	Negative relationship between herkogamy and autofertility within a population.	Takebayashi and Delph 2000
		Population	0	Dichogamy, but not herkogamy, positively correlated with outcrossing rate among six populations. Autofertility correlated with outcrossing rate.	Schoen 1982
<i>Ipomoea cordatotriloba/ Ipomoea lacunosa</i>	Convolvulaceae	Species, Population	+	Positive relationship between herkogamy and selfing rate between, and to some extent within, species.	Duncan and Rausher 2013
<i>Ipomoea purpurea</i>	Convolvulaceae	Individual	-	Negative relationship between herkogamy and autofertility within a population.	Ennos 1981
		Individual	+	Positive relationship between herkogamy and outcrossing among individuals in a population.	Epperson and Clegg 1987
		Individual	+	Higher outcrossing rate of high-herkogamy group in experimental arrays.	Chang and Rausher 1998
<i>Leptosiphon jepsonii</i>	Polemoniaceae	Population	+	Positive relationship between herkogamy and 'SI index' among 17 populations. Outcrossing rate correlated with SI index in four populations.	Goodwillie and Ness 2005 (and see Weber and Goodwillie 2009)
<i>Lycopersicon pimpinellifolium</i>	Solanaceae	Population	+	Positive relationships between anther length, stigma exertion and outcrossing rate among 43 populations.	Rick et al. 1977, 1978
<i>Mimulus</i>	Phrymaceae	Species	+	Positive relationship between herkogamy and 'outcrossing indicators' across eight species.	Ritland and Ritland 1989
		Population, Species	-	Negative relationship between herkogamy and autofertility among 10 populations of three species, and among five populations of <i>M. guttatus</i> .	Dole 1992
<i>Mimulus guttatus</i>	Phrymaceae	Individual	(-)	Weak negative relationship between herkogamy and autofertility among families within a population.	Carr and Fenster 1994
<i>Mimulus ringens</i>	Phrymaceae	Individual	+	Positive relationship between herkogamy and outcrossing rate among genets in two populations.	Karron et al. 1997
<i>Myosotis</i>	Boraginaceae	Species	-	Reduced autofertility in 'always herkogamous' species compared to 'initially herkogamous' and 'never herkogamous' species.	Robertson and Lloyd 1991
<i>Narcissus longipathus</i>	Amaryllidaceae	Individual	0	No detectable relationship between herkogamy-class and outcrossing rate within a population.	Medrano et al. 2005 (but see Medrano et al. 2012)

<i>Nicotiana glauca</i>	Solanaceae	Individual, Population	-	Negative relationship between herkogamy and autofertility among sites and plants.	Schueler 2004 (and see Ollerton et al. 2012)
<i>Nicotiana rustica</i>	Solanaceae	Individual	+	Positive relationship between 'heterostathmy' (=herkogamy) and outcrossing in experimental array.	Breese 1959
<i>Primula halleri</i>	Primulaceae	Individual	-	Negative relationship between herkogamy-class and seed set following pollinator exclusion in three populations.	de Vos et al. 2012
		Individual	(+)	Weak positive relationship between herkogamy-class and family-level outcrossing rates, averaged over four populations.	de Vos et al. 2018
<i>Turnera ulmifolia</i>	Turneraceae	Population	+	Positive relationship between herkogamy and outcrossing rate among 13 populations.	Belaoussoff and Shore 1995 (and see Barrett and Shore 1987)
