

¹ Drought frequency predicts life history strategies in *Heliophila*

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Abstract

12 Explaining variation in life history strategies is a long-standing goal of evolutionary biology.
13 For plants, annual and perennial life histories are thought to reflect adaptation to
14 environments that differ in the frequency of environmental stress such as drought. Here we
15 test this hypothesis in *Heliophila* (Brassicaceae), a diverse genus of flowering plants native to
16 Africa, by integrating 34 years of satellite-based drought measurements with 2192 herbaria
17 occurrence records. Consistent with predictions from classic life history theory, we find that
18 perennial *Heliophila* species occur in environments where droughts are significantly less
19 frequent compared to annuals. These associations are predictive while controlling for
20 phylogeny, lending support to the hypothesis that drought related natural selection has
21 influenced the distributions of these strategies. Additionally, the difference in drought
22 frequency between annual and perennial species distributions is greatest during the summer
23 and fall, which also appears to be when annuals are in the seed phase of their life cycle based
24 on collection dates of annual species. Together, these finding provide empirical support for
25 classic hypotheses about the drivers of life history strategy in plants - that perennials out
26 compete annuals in environments with less frequent drought and that annuals are adapted to
27 environments with more frequent drought by escaping drought prone seasons as seeds.

28

Keywords: drought adaptation, life history evolution, remote sensing, phylogeography,
29 herbaria records

30 Drought frequency predicts life history strategies in *Heliophila*

31 **Introduction**

32 Understanding the causes and consequences of life history variation is a longstanding
33 goal of ecology and evolutionary biology (Cole, 1954). In plants, life histories are especially
34 diverse, with herbaceous species that complete their life cycle in a number of weeks to trees
35 that live for thousands of years (Brown, 1996). Along this continuum an important division
36 exists, distinguishing annuals which complete their seed to seed life cycle within a single
37 calendar year from perennials which can persist over multiple years. Annual plants flower
38 once, set seed, senesce, and then die, spending at least some portion of the year as a seed,
39 where they are relatively protected from environmental stress. In contrast, perennial plants
40 can continue vegetative growth after reproduction and must survive conditions experienced
41 during all seasons. These represent fundamentally different life history strategies, but the
42 ecological factors that explain their evolution and distributions remain empirically unresolved
43 (Friedman and Rubin, 2015).

44 Classical theory predict shorter life spans in environments where adult mortality is
45 high (Charnov and Schaffer, 1973; Franco and Silvertown, 1996; Stearns, 1992). In plants,
46 this has been extended to the hypothesis that annuality is adaptive when it allows plants to
47 escape drought (Schaffer and Gadgil, 1975). Lack of water is perhaps the greatest threat to
48 survival during vegetative or reproductive growth and annuals can remain dormant (and
49 protected as a seed) during drought. Thus, environments with greater seasonal drought
50 frequency may select for annual life histories that complete reproduction prior to drought
51 prone seasons. Conversely, environments with less frequent drought may select for perennial
52 species, which may benefit from multiple bouts of reproduction and competitive advantage
53 by preventing recruitment of annual species (Corbin and D'Antonio, 2004). These
54 predictions have been supported by the observation of annuals in arid environments in *Oryza*
55 *perennis* (Morishima et al., 1984) and *Oenothera* (Evans et al., 2005). Additionally, annual

and perennial species of *Nemesia* were qualitatively associated with winter rather and summer rainfall environments respectively (Datson et al., 2008) and annual species of *Scorzoneroides* were associated with environments classified as unpredictable (Cruz-Mazo et al., 2009). However, whether the history frequency of drought events indeed predicts the distributions annual or perennial life history strategies has yet to be tested.

Here we combine a long-term global dataset of satellite detected drought events with metadata from natural history collections to test these classic hypotheses within the African endemic mustard genus, *Heliphila* L. (Brassicaceae). If annuality is an adaptive strategy allowing plants to escape drought prone seasons, then drought frequency should predict the distribution of life history strategies across landscapes, and annual species should be more commonly associated with drought prone regions than perennial species. Furthermore, if annual species have adapted to escape drought prone seasons, observations of growing annual species (i.e. occurring in forms other than seed) should be rare during drought prone seasons. Phylogenetic relatedness can have significant non-random effects on species distributions and life history traits (Barrett et al., 1996), and therefore we assessed the relationship between life history distribution and drought frequency in a phylogenetically controlled background.

Materials and Methods

Data

Availability. All analyses were performed using R. All data and the source code to produce this manuscript are available at <https://github.com/greymonroe/heliphila>. Software used is listed in the supplement.

Satellite-detected drought data. Remotely sensed data is a powerful tool for characterizing seasonal patterns in drought because it is less limited in spatial and temporal scope and resolution than weather stations or field observations (AghaKouchak et al., 2015).

80 To quantify the frequency of drought during different seasons across landscapes, we used the
 81 remotely sensed Vegetative Health Index (VHI), which measures landscape scale reductions
 82 in plant cover and temperature conditions characteristic of drought (Kogan, 2001).
 83 Generated from data collected by NOAA AVHRR satellites since 1981, the VHI combines
 84 Normalized Difference Vegetation Index (NDVI) derived measures of vegetative stress
 85 (Vegetative Condition Index - VCI) with temperature stress indicated by anomalies in
 86 thermal spectra (Temperature Condition Index - TCI). The VHI of year y during week w of
 87 [1, 52] at pixel i is derived from the following equations, where n is the number of years
 88 observed.

$$VCI_{y,w,i} = 100 \frac{NDVI_{y,w,i} - NDVI_{min}}{NDVI_{max} - NDVI_{min}}$$

$$TCI_{y,w,i} = 100 \frac{T_{y,w,i} - T_{min}}{T_{max} - T_{min}}$$

$$VHI_{y,w,i} = 0.5(VCI_{y,w,i}) + 0.5(TCI_{y,w,i})$$

89 where $NDVI_{min} = min(NDVI_{1981,w,i}...NDVI_{1981+n,w,i})$ and
 90 $NDVI_{max} = max(NDVI_{1981,w,i}...NDVI_{1981+n,w,i})$ and $T_{min} = min(T_{1981,w,i}...T_{1981+n,w,i})$
 91 and $T_{max} = max(T_{1981,w,i}...T_{1981+n,w,i})$

92 Thus, VHI measurements are standardized according to conditions historically
 93 observed at each locations. These measurements have been validated and generally used for
 94 evaluating drought risk and predicting crop yields in agriculture (e.g., Rojas et al., 2011;
 95 Kogan et al., 2016). But they also present a new tool to study seasonal patterns in the
 96 frequency of drought across environments and to test hypotheses about the effect of drought
 97 on ecological and evolutionary processes (Kerr and Ostrovsky, 2003). As such, the VHI has
 98 been applied recently to study drought related ecology of natural species and proven useful

99 for predicting intraspecific variation in drought tolerance traits and genes (Dittberner et al.,
100 2018; Mojica et al., 2016; John G Monroe et al., 2018). Here, we accessed VHI data at
101 16km² resolution from 1981 to 2015
102 (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) to characterize the
103 seasonal drought frequencies experienced by annual and perennial *Heliophila* species.

104 **Life history data for *Heliophila*.** *Heliophila* is a genus of flowering plants
105 endemic to the southern portion of Africa including the Cape Floristic and Succulent Karoo
106 Regions. These are among the most botanically diverse environments on Earth and the
107 *Heliophila* species occurring there are considered to make up the most diverse genus of the
108 family Brassicaceae (Mandáková et al., 2012; Mummenhoff et al., 2005). This genus includes
109 both perennial and annual species and this change in life history strategy has likely arisen
110 multiple independent times (Appel and Al-Shehbaz, 1997; Mummenhoff et al., 2005).
111 Furthermore, the fine scale climatic heterogeneity of Southern Africa is ideal for studying the
112 distribution of traits in relation to environmental parameters (Sayre et al., 2013). We used
113 life histories reported by Mummenhoff et al. (2005), grouping species with annual or
114 perennial life histories. Perenniality was defined based any form of perennial life history (e.g.,
115 herbs, shrubs, mixed, etc). Because the nature of species reported with mixed traits were
116 unknown (i.e. plasticity vs. genetic variation), we classified these species here as perennial
117 since they can maintain vegetative growth after reproduction at least to some capacity.

118 #### *Heliophila* occurrence records

119 Botanists have collected and maintained over 350 million botanical specimens
120 worldwide over the past 300 years. Herbarium specimens and their associated metadata have
121 been used since the 1960s to study species' geographical distributions (reviewed by Willis et
122 al. (2017) and Lang et al. (2018)). And as they become digitized (Soltis, 2017), these
123 collections have been used to study relationships between trait distributions, geography, and
124 climate (Davis et al., 2015; Stropp et al., 2016; Václavík et al., 2017; Wolf et al., 2016). To

125 characterize the distributions of annual and perennial *Heliphila* species, all records for the
126 genus *Heliphila* were downloaded from the Global Biodiversity Information Facility
127 (gbif.org) on July 21, 2018 (GBIF, 2018).

128 **Sequence data for phylogeny.** Aligned_ *Heliphila*_ ITS sequences were
129 obtained from previous work by Mandáková et al. (2012). *Aethionema*, *Alliaria*, *Cardamine*,
130 *Chamira*, and *Rorippa* ITS records from were downloaded from Genbank.

131 **Analyses**

132 **Drought frequency calculations.** To characterize drought regimens across the
133 distributions of annual and perennial species of *Heliphila*, we calculated drought during
134 different seasons at the location of observations for *Heliphila* records using the VHI.
135 Specifically, we created global maps of the frequencies of observing drought conditions
136 (VHI<40, NOAA) during the winter (quarter surrounding winter solstice), spring (quarter
137 surrounding spring equinox), summer (quarter surrounding summer solstice) and fall (quarter
138 surrounding fall equinox) from 1981 to 2015. From these maps, the drought frequency during
139 the winter, spring, summer, and fall were extracted for the locations of all GBIF records.

140 **Filtering of occurrence records.** To avoid instances with spurious location data,
141 we filtered raw GBIF by restricting our analyses to include only:

- 142 • records for species with reported life history
- 143 • records with geospatial data
- 144 • records without known geospatial coordinate issues (i.e., coordinates reported are those
145 of herbarium)
- 146 • records from collection sites classified as land pixels
- 147 • records from Africa (to exclude locations of cultivation)
- 148 • records without duplicates (i.e., identical species, location, collection date)

149 **Phylogeny construction.** Out group species were aligned together with *Heliophila*
150 ITS sequences using MAFFT. Model selection for construction of phylogeny was performed
151 in jModeltest2 with CIPRES. Based on this analysis, *GTR + L* were selected. Ultrametric
152 phylogeny was estimated with branch lengths as relative time.

153 **Comparison of drought frequency between annual and perennial species.**

154 To evaluate the hypothesis that annual and perennial life history strategies reflect
155 adaptations to alternative drought regimes, we tested the corresponding prediction that the
156 observed distributions of annual and perennial *Heliophila* species would be significantly
157 associated with historic drought frequency. First, we compared the frequency of drought
158 during the winter, spring, summer, and fall between raw occurrence records of annual and
159 perennial species by t-tests. To account for variation in the number of occurrence records per
160 species, we next calculated the mean drought frequency during the winter, spring, summer
161 and fall for each species. The relationships between species mean values of drought frequency
162 during each season and life habitat (annual or perennial) were tested using Firth's
163 penalized-likelihood logistic regressions. Because demographic histories caused by ancestry
164 can confound trait - environment associations, we then tested for the relationships between
165 drought frequency and life history while controlling for relationships between species using
166 phylogenetic logistic regressions.

167 **Collection dates.** To test the hypothesis that annual species have adapted to
168 escape drought prone seasons as seeds, collection dates for herbarium specimens were
169 compared between annual and perennial species. Comparisons of distributions were made by
170 Two-sample Kolmogorov-Smirnov test, t-test, and Barlett variance test.

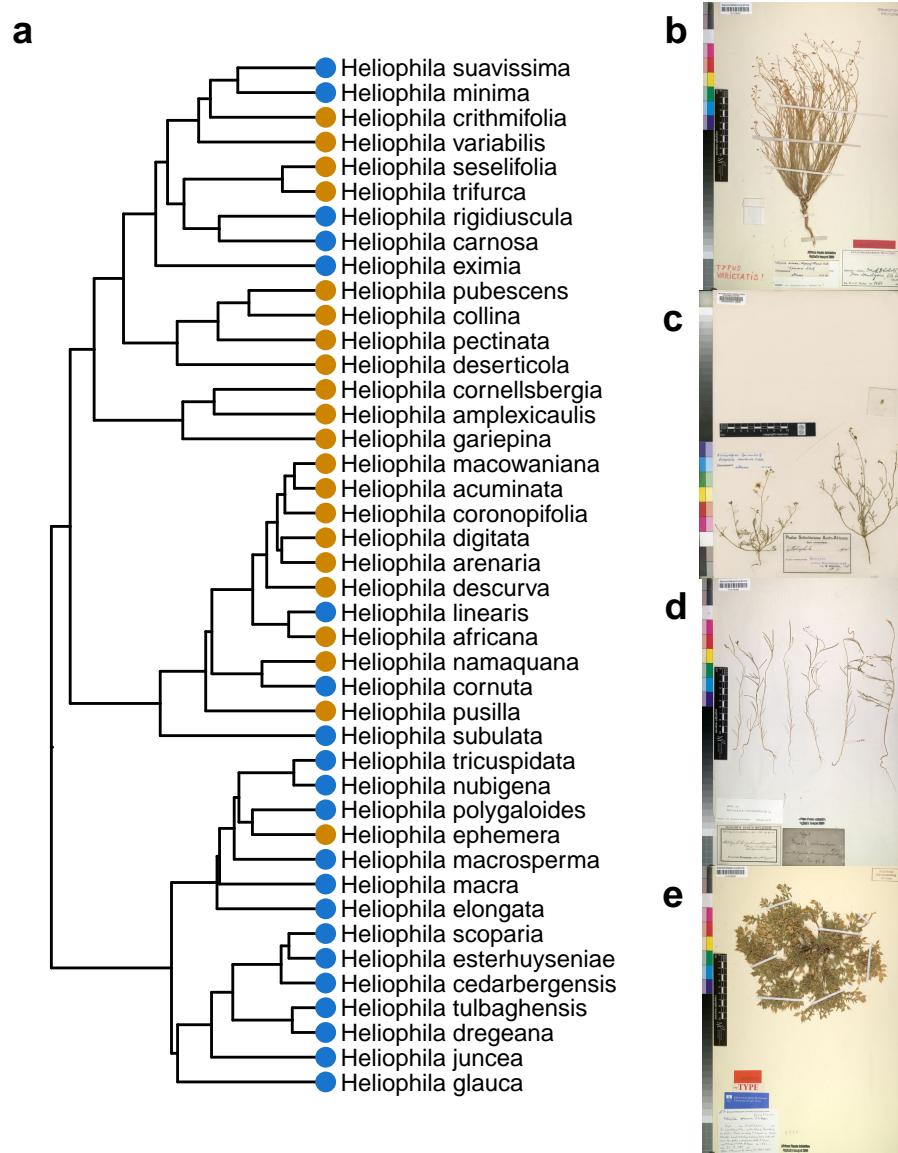


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. Example herbaria specimens accessed via GBIF of (a) *H. minima*, (b) *H. deserticola*, (c) *H. coronopifolia* and (d) *H. ephemera*. Images (a,c,d) courtesy of The Bavarian Natural History Collections (CC BY-SA 4.0) and (b) The London Natural History Museum (CC BY 4.0). Links to images are found in the supplement.

Results

172 Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history
 173 (Mummenhoff et al., 2005), 2856 had geospatial data, 2833 did not have geospatial issues,

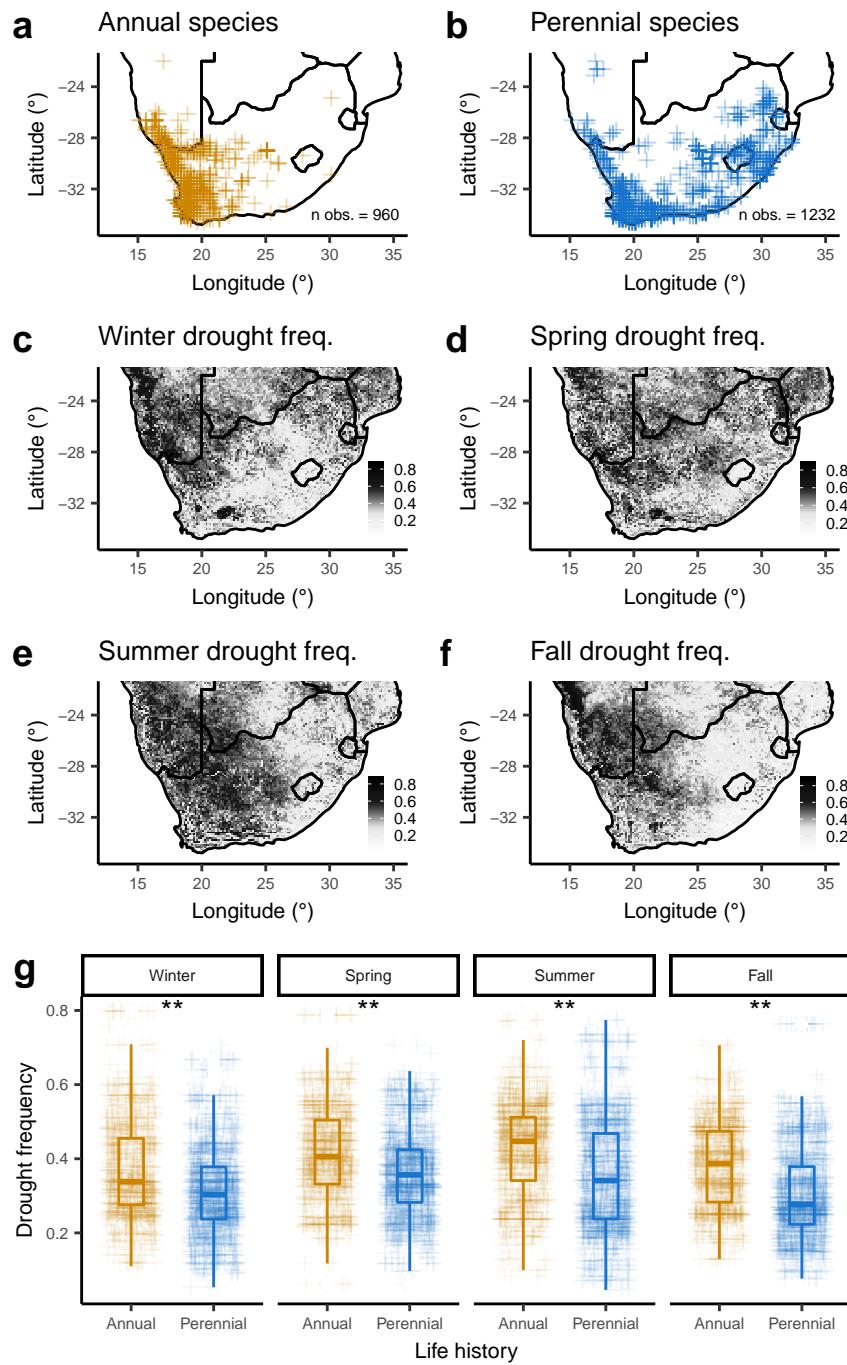


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall measured using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (t tests, ** = $p < 0.01$).

174 2684 were located on pixels classified as land having drought measurements, 2543 were
175 located in Africa, 2192 were not duplicated. Thus, after all filtering steps, 2192 records for
176 42 species (Figure 1, Table S1) passed for further analyses. The number of samples varied
177 between species, with a mean of 52.19 samples per species. *Heliophila rigidiuscula* had the
178 most records, 201, and *Heliophila cornellsbergia* the fewest, 2 (Table S1).

179 There were clear visual differences between the distributions of the 960 annual and the
180 1232 perennial *Heliophila* observation records (see Figure S1 for maps of individual species).
181 While annual species were generally found in the western regions of South Africa and
182 Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the
183 occurrence of perennials extended to the east coast of South Africa (Figure 2b).

184 The frequency of drought varied considerably across the ranges of *Heliophila* species
185 (Figure 2c-f). This heterogeneity is expected, given that this is one of the most climatically
186 diverse regions of the Earth (Sayre et al., 2013). It is worth noting the east to west cline in
187 drought frequency observed during the summer, which distinguishes the high drought
188 frequency of the Kalahari Sands and Namid Desert phytogeographic regions from the low
189 drought frequency of the Drakensberg Mountains and Coastal Zambesian phytogeographic
190 regions. In the Cape phytogeographic region there was finer scale heterogeneity in drought
191 frequency during the summer.

192 Theory predicts that annuality should be adaptive in places where stresses such as
193 drought are more common. Conversely, perenniability should be adaptive in places where such
194 stresses are less frequent. We found that the frequency of drought was significantly higher at
195 the locations of occurrence records for annual species. In terms of raw observation records
196 (Figure 2g), the frequency of drought was significantly higher at the location of annuals
197 during the winter ($t = 10.65, p = 0.00$), spring ($t = 10.73, p = 0.00$), summer ($t = 12.67, p$
198 = 0.00), and fall ($t = 15.26, p = 0.00$). Because raw occurrence records do not account for
199 variation in the number of records per species (Table S1), we also tested whether mean

200 drought frequency values of each species were significantly different between annuals and
201 perennials by a Firths-penalized logistic regression. We found that the mean drought
202 frequencies were significantly higher ($\alpha = 0.05$) in annual species during the spring, summer,
203 and fall (Table 1, Figure 3a). We further tested whether annual species are found in places
204 where droughts occur more frequently while controlling for the phylogenetic relatedness of
205 *Heliophila* species. This is important, because environmental differences in species
206 distributions can be confounded with demographic history caused by ancestry. We found
207 that while controlling for phylogeny, the mean drought frequencies were significantly higher
208 ($\alpha = 0.05$) in annual species during the spring, summer, and fall (Table 1, Figure 3a). These
209 findings indicate that common ancestry alone does not explain differences the drought
210 frequencies experienced in the environments of annual and perennial *Heliophila*.

211 The preceding results indicated that annual species are found in environments where
212 droughts are significantly more frequent, especially in the summer and fall. Classic life
213 history theory hypothesizes that annuality reflects adaptation to such environments because
214 it allows species to escape stressful conditions. If this is the case, we would expect that
215 annuals spend the drought prone seasons of summer and fall as seeds. To test this
216 hypothesis, we compared the dates of occurrence records between annual and perennial
217 *Heliophila* species. The distributions reveal a considerable difference in the timing of
218 observation of these two life histories. In comparison to perennials, which appear to be
219 collected throughout the year, annuals are almost exclusively observed during the winter and
220 spring (Figure 3b). The differences between the distribution of collection dates were
221 significant by all tests ($ks.test D = 0.25, p = 0$; $bartlett.test K2 = 503.18, p = 0.00$) This is
222 consistent with a model of life history in which annual species flower in the spring, set seed,
223 senesce, and die before the summer. Thus, these annual species are likely to remain dormant
224 during the summer and fall, when drought is the strongest predictor of the distributions of
225 annual and perennial life histories (Figure 3a).

Table 1

*Logistic regressions between life history, and the mean drought frequency observed at herbaria collection sites of *Heliophila* species the winter, spring, summer, and fall.*

Predictor	Estimate [‘]	P [‘]	Estimate*	P*
Intercept	2.2575	0.1739	0.7231	0.6636
Winter drought freq.	-6.7484	0.1661	-1.5452	0.7274
Intercept	4.5594	0.0443	5.0107	0.0534
Spring drought freq.	-11.7895	0.0423	-12.9014	0.0464
Intercept	7.1742	0.0011	7.7093	0.0054
Summer drought freq.	-18.2999	0.0010	-19.9056	0.0042
Intercept	6.4226	0.0029	7.0162	0.0082
Fall drought freq.	-19.0512	0.0026	-20.8174	0.0067

Note. ‘ = Firth’s penalized logistic regression. * = Phylogenetically constrained logistic regression. Annual species were scored as 0 and perennial species as 1.

226

Discussion

227 To test the hypothesis that annual and perennial plants reflect adaptation to
 228 alternative drought environments we examined the landscape distribution of life history
 229 strategies in the large and diverse mustard genus, *Heliophila*. Using metadata of 2192
 230 occurrence records and a 34 year dataset of satellite-detected droughts, we tested the
 231 prediction that annual species are more often observed in drought-prone locations than
 232 perennial species, when controlling for phylogenetic relatedness. We found that drought
 233 frequency is significantly different between the distributions of annual and perennial species,

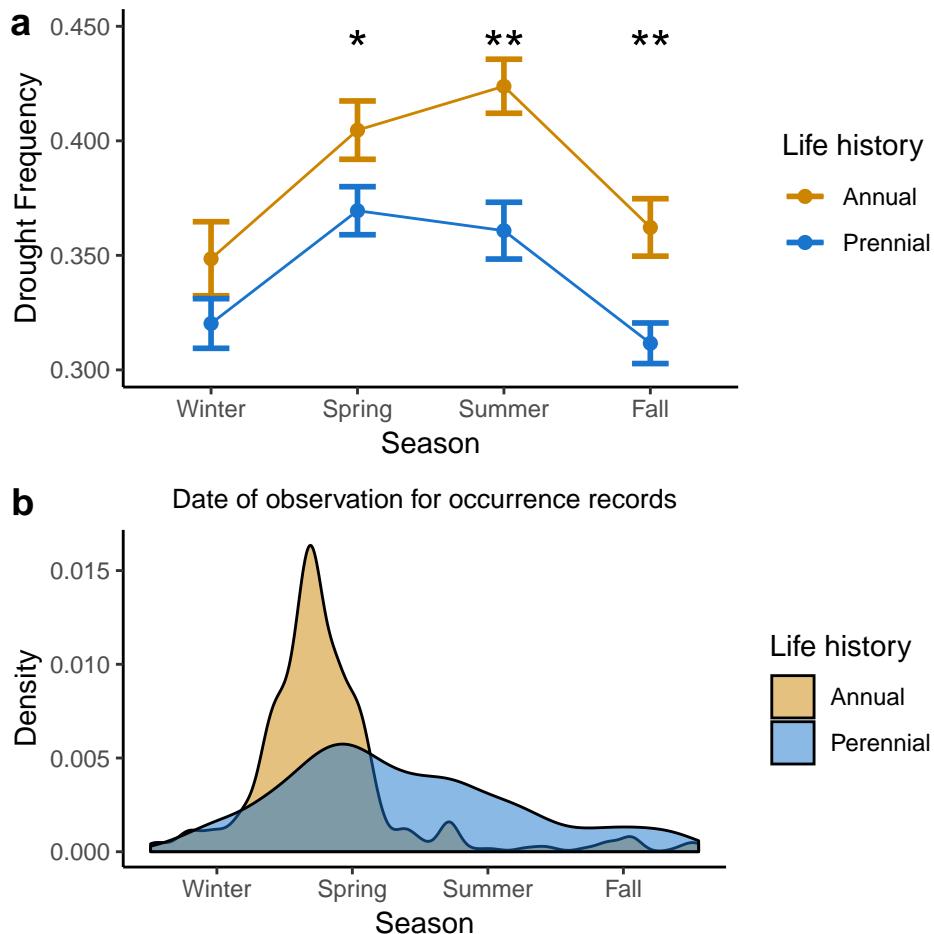


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (phylogenetic logistic regression, * = $p < 0.05$, ** = $p < 0.01$) (b) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

with annuals being found in environments with more frequent drought, and that this signal is strongest during the seasons when annuals are likely escaping via seed dormancy. These results remain significant while controlling for the phylogenetic relationships of *Heliophila* species, yielding support for the role that natural selection has played in driving contemporary distributions of these alternative strategies in relation to drought regimens.

We cannot eliminate the possibility that confounding traits or environmental variables

are the causative factors explaining variation in the distributions of annual and perennial species. Nevertheless, these results reveal quantitative support for the classic prediction that annual species are found in environments that experience more frequent drought than perennial species. These findings complement previous reports of qualitative associations between annuality with environments characterized as having increased aridity (Evans et al., 2005), alternative precipitation defined habitats (Datson et al., 2008; Morishima et al., 1984), or greater unpredictability (Cruz-Mazo et al., 2009). However, to our knowledge this is the first study to demonstrate a significant association between life history and drought in a phylogenetic context informed by large scale species distribution data and long term drought measures.

Unfortunately, herbarium collections and their associated data do not represent systematic or random sampling of a species distribution. Significant biases in collecting exist, which we have not necessarily controlled for here, and may have some effect on our findings, such as a bias toward collecting near roads or near the locations of natural history collections (Daru et al., 2018). Future research will benefit from systematic sampling efforts to avoid these noted biases. However, the ecosystems of southern Africa include several biodiversity hotspots and are among the most botanically well sampled regions on Earth (Daru et al., 2018), suggesting that this may currently be the optimal region for our analyses of life history distribution. Indeed, we were able to use 2192 occurrence records to study 42 species, which represents a significant advance over relying on personal observations to characterize species distributions.

These findings support classical theoretical predictions about the adaptive value of annual and perennial life history strategies. Taken together, they suggest that in *Heliphila*, annual species are adapted to environments with increased summer droughts by avoiding these seasons in a dormant seed phase of their life cycle. They also suggest that perenniability is adaptive in environments where droughts are less frequent. While most previous work has

266 focused on describing the evolutionary origins of annuality (Andreasen and Baldwin, 2001;
267 Barrett et al., 1996; Conti et al., 1999; Friedman and Rubin, 2015; Verboom et al., 2004)
268 there are at least a few other cases where perenniability appears to have arisen from an annual
269 ancestor (Bena et al., 1998; Tank and Olmstead, 2008). And while early theory predicted
270 selection for annuality when adult mortality is high (Stearns, 1992), we also find evidence
271 that the transition to perenniability could be explained by the historical frequency of drought,
272 a likely cause of mortality in plants. The phylogeny reveals several transitions from annual
273 to perennial life history (Figure 1a) and that the distributions of perennial *Heliophila* extend
274 into regions where drought frequency is low (Figure 2b, Figure S1). Perennials may be able to
275 out compete annual relatives in environments where the infrequency of drought favors
276 strategies that allow plants to benefit from growth over many seasons. It may also indicate
277 that annuals rely on drought as a source of disturbance for seedling recruitment when
278 competing with perennials (Corbin and D'Antonio, 2004). Indeed, no annual species were
279 observed in the low drought regions of eastern South Africa 2a, Figure S1).

280 These findings suggest that species with locally adaptive life history strategies could be
281 threatened by rapidly changing drought regimens (Dai, 2011). This could have impacts on
282 ecosystem functioning and processes such as carbon cycling if the composition of annual and
283 perennial species changes as a response (Garnier et al., 1997; J Grey Monroe et al., 2018;
284 Roumet et al., 2006). Furthermore, the frequency of drought may be an important factor
285 when considering the use of perennial cropping systems (Lelièvre and Volaire, 2009; Parry et
286 al., 2005).

287 In conclusion, we find strong support for classic life history theory which predicts that
288 annuality is adaptive in environments where droughts occur more frequently. Additionally,
289 we report evidence consistent with a life history model in annuals in which they escape
290 drought prone seasons during the seed phase of their life cycle. Finally, we find evidence that
291 the distributions of perennial lineages may indicate a competitive advantage in areas where

292 droughts are infrequent. More broadly, this work highlights the irreplaceable value of natural
293 history collections and demonstrates the power of combining such information with large
294 scale remote sensing data to address outstanding classic hypotheses in ecology and evolution.

295

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299

Author contributions

300 JGM, BG, KGT and JKM contributed to the design of the research, interpretation,
301 and writing the manuscript. JGM, BG, and KGT contributed to the performance of the
302 research and data analysis.

303

References

- 304 AghaKouchak A, Farahmand A, Melton F, Teixeira J, Anderson M, Wardlow BD, Hain C.
305 2015. Remote sensing of drought: Progress, challenges and opportunities. *Reviews of*
306 *Geophysics* **53**:452–480.
- 307 Alfaro M, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky D, Carnevale G, Harmon L.
308 2009. Nine exceptional radiations plus high turnover explain species diversity in
309 jawed vertebrates. *Proceedings of the National Academy of Sciences of the United*
310 *States of America* **106**:13410–13414.
- 311 Andreasen K, Baldwin BG. 2001. Unequal evolutionary rates between annual and perennial
312 lineages of checker mallows (sidalcea, malvaceae): Evidence from 18S–26S rDNA
313 internal and external transcribed spacers. *Molecular Biology and Evolution*
314 **18**:936–944.
- 315 Appel O, Al-Shehbaz IA. 1997. Generic limits and taxonomy of hornungia, pritzelago, and
316 hymenolobus (brassicaceae). *Novon* 338–340.
- 317 Aust F, Barth M. 2018. papaja: Create APA manuscripts with R Markdown.
- 318 Barrett SCH, Harder LD, Worley AC. 1996. The comparative biology of pollination and
319 mating in flowering plants. *Phil Trans R Soc Lond B* **351**:1271–1280.
- 320 Bates D, Maechler M. 2018. Matrix: Sparse and dense matrix classes and methods.
- 321 Bena G, Lejeune B, Prosperi J-M, Olivieri I. 1998. Molecular phylogenetic approach for
322 studying life-history evolution: The ambiguous example of the genus medicago l.
323 *Proceedings of the Royal Society of London B: Biological Sciences* **265**:1141–1151.
- 324 Brown PM. 1996. OLDLIST: A database of maximum tree ages. *Tree rings, environment,*
325 *and humanity Radiocarbon* **1996**:727–731.

- 326 Charnov EL, Schaffer WM. 1973. Life-history consequences of natural selection: Cole's result
327 revisited. *The American Naturalist* **107**:791–793.
- 328 Cole LC. 1954. The population consequences of life history phenomena. *The Quarterly
329 Review of Biology* **29**:103–137.
- 330 Conti E, Soltis DE, Hardig TM, Schneider J. 1999. Phylogenetic relationships of the silver
331 saxifrages (*saxifraga*, sect. *Ligulatae* haworth): Implications for the evolution of
332 substrate specificity, life histories, and biogeography. *Molecular Phylogenetics and
333 Evolution* **13**:536–555.
- 334 Corbin JD, D'Antonio CM. 2004. Competition between native perennial and exotic annual
335 grasses: Implications for an historical invasion. *Ecology* **85**:1273–1283.
- 336 Cruz-Mazo G, Buidé M, Samuel R, Narbona E. 2009. Molecular phylogeny of scorzoneroïdes
337 (asteraceae): Evolution of heterocarpy and annual habit in unpredictable
338 environments. *Molecular phylogenetics and evolution* **53**:835–847.
- 339 Dai A. 2011. Drought under global warming: A review. *Wiley Interdisciplinary Reviews:
340 Climate Change* **2**:45–65.
- 341 Daru BH, Park DS, Primack RB, Willis CG, Barrington DS, Whitfeld TJ, Seidler TG,
342 Sweeney PW, Foster DR, Ellison AM, others. 2018. Widespread sampling biases in
343 herbaria revealed from large-scale digitization. *New Phytologist* **217**:939–955.
- 344 Datson P, Murray B, Steiner K. 2008. Climate and the evolution of annual/perennial
345 life-histories in nemesia (scrophulariaceae). *Plant Systematics and Evolution*
346 **270**:39–57.
- 347 Davis CC, Willis CG, Connolly B, Kelly C, Ellison AM. 2015. Herbarium records are
348 reliable sources of phenological change driven by climate and provide novel insights

- 349 into species' phenological cueing mechanisms. *American Journal of Botany*
350 **102**:1599–1609.
- 351 Dittberner H, Korte A, Mettler-Altmann T, Weber A, Monroe G, Meaux J de. 2018.
352 Natural variation in stomata size contributes to the local adaptation of water-use
353 efficiency in *arabidopsis thaliana*. *bioRxiv* 253021.
- 354 Eastman J, Alfaro M, Joyce P, Hipp A, Harmon L. 2011. A novel comparative method for
355 identifying shifts in the rate of character evolution on trees. *Evolution* **65**:3578–3589.
- 356 Evans ME, Hearn DJ, Hahn WJ, Spangle JM, Venable DL. 2005. Climate and life-history
357 evolution in evening primroses (*oenothera*, *onagraceae*): A phylogenetic comparative
358 analysis. *Evolution* **59**:1914–1927.
- 359 Franco M, Silvertown J. 1996. Life history variation in plants: An exploration of the
360 fast-slow continuum hypothesis. *Phil Trans R Soc Lond B* **351**:1341–1348.
- 361 Friedman J, Rubin MJ. 2015. All in good time: Understanding annual and perennial
362 strategies in plants. *American journal of botany* **102**:497–499.
- 363 Garnier E, Cordonnier P, Guillerm J-L, Sonié L. 1997. Specific leaf area and leaf nitrogen
364 concentration in annual and perennial grass species growing in mediterranean
365 old-fields. *Oecologia* **111**:490–498.
- 366 GBIF. 2018. GBIF occurrence download.
- 367 Genz A, Bretz F. 2009. Computation of multivariate normal and t probabilities, Lecture
368 notes in statistics. Heidelberg: Springer-Verlag.
- 369 Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: The
370 MCMCglmm R package. *Journal of Statistical Software* **33**:1–22.

- 371 Harmon L, Weir J, Brock C, Glor R, Challenger W. 2008. GEIGER: Investigating
372 evolutionary radiations. *Bioinformatics* **24**:129–131.
- 373 Heinze G, Ploner M. 2018. Logistf: Firth's bias-reduced logistic regression.
- 374 Henry L, Wickham H. 2018. Purrr: Functional programming tools.
- 375 Hijmans RJ. 2018. Raster: Geographic data analysis and modeling.
- 376 Ho LST, Ane C. 2014. A linear-time algorithm for gaussian and non-gaussian trait evolution
377 models. *Systematic Biology* **63**:397–408.
- 378 Kerr JT, Ostrovsky M. 2003. From space to species: Ecological applications for remote
379 sensing. *Trends in ecology & evolution* **18**:299–305.
- 380 Kogan F, Guo W, Strashnaia A, Kleshenko A, Chub O, Virchenko O. 2016. Modelling and
381 prediction of crop losses from noaa polar-orbiting operational satellites. *Geomatics,*
382 *Natural Hazards and Risk* **7**:886–900.
- 383 Kogan FN. 2001. Operational space technology for global vegetation assessment. *Bulletin of*
384 *the American Meteorological Society* **82**:1949–1964.
- 385 Lang PL, Willems FM, Scheepens J, Burbano HA, Bosdorf O. 2018. Using herbaria to
386 study global environmental change. PeerJ Preprints.
- 387 Lelièvre F, Volaire F. 2009. Current and potential development of perennial grasses in
388 rainfed mediterranean farming systems. *Crop Science* **49**:2371–2378.
- 389 Mandáková T, Mummenhoff K, Al-Shehbaz IA, Mucina L, Mühlhausen A, Lysak MA. 2012.
390 Whole-genome triplication and species radiation in the southern african tribe
391 heliophileae (brassicaceae). *Taxon* **61**:989–1000.

- 392 Mojica JP, Mullen J, Lovell JT, Monroe JG, Paul JR, Oakley CG, McKay JK. 2016.
393 Genetics of water use physiology in locally adapted *Arabidopsis thaliana*. *Plant
394 Science*. doi:10.1016/j.plantsci.2016.03.015
- 395 Monroe JG, Markman DW, Beck WS, Felton AJ, Vahsen ML, Pressler Y. 2018.
396 Ecoevolutionary dynamics of carbon cycling in the anthropocene. *Trends in ecology &
397 evolution* **33**:213–225.
- 398 Monroe JG, Powell T, Price N, Mullen J, Howard A, Evans K, Lovell J, McKay J. 2018.
399 Drought adaptation in nature by extensive genetic loss-of-function. *bioRxiv* 372854.
- 400 Morishima H, Sano Y, Oka H. 1984. Differentiation of perennial and annual types due to
401 habitat conditions in the wild rice *Oryza perennis*. *Plant Systematics and Evolution*
402 **144**:119–135.
- 403 Mummenhoff K, Al-Shehbaz IA, Bakker FT, Linder HP, Mühlhausen A. 2005. Phylogeny,
404 morphological evolution, and speciation of endemic brassicaceae genera in the cape
405 flora of southern africa. *Annals of the Missouri Botanical Garden* 400–424.
- 406 Müller K. 2018. Bindrcpp: An 'rcpp' interface to active bindings.
- 407 Müller K, Wickham H. 2018. Tibble: Simple data frames.
- 408 Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2018. Caper:
409 Comparative analyses of phylogenetics and evolution in r.
- 410 Paradis E, Schliep K. 2018. Ape 5.0: An environment for modern phylogenetics and
411 evolutionary analyses in R. *Bioinformatics* **xx**:xxx–xxx.
- 412 Parry M, Flexas J, Medrano H. 2005. Prospects for crop production under drought:
413 Research priorities and future directions. *Annals of Applied Biology* **147**:211–226.

- 414 Pebesma EJ, Bivand RS. 2005. Classes and methods for spatial data in R. *R News* **5**:9–13.
- 415 Plummer M, Best N, Cowles K, Vines K. 2006. CODA: Convergence diagnosis and output
416 analysis for mcmc. *R News* **6**:7–11.
- 417 R by Thomas Lumley VJCP to, author. BRN that maintainers are not available to give
418 advice on using a package they did not. 2015. Gee: Generalized estimation equation
419 solver.
- 420 R Core Team. 2018. R: A language and environment for statistical computing. Vienna,
421 Austria: R Foundation for Statistical Computing.
- 422 Revell LJ. 2012. Phytools: An r package for phylogenetic comparative biology (and other
423 things). *Methods in Ecology and Evolution* **3**:217–223.
- 424 Richard A. Becker OS code by, Ray Brownrigg. Enhancements by Thomas P Minka ARWR
425 version by, Deckmyn. A. 2018. Maps: Draw geographical maps.
- 426 Rojas O, Vrieling A, Rembold F. 2011. Assessing drought probability for agricultural areas
427 in africa with coarse resolution remote sensing imagery. *Remote sensing of
428 Environment* **115**:343–352.
- 429 Roumet C, Urcelay C, Di'az S. 2006. Suites of root traits differ between annual and
430 perennial species growing in the field. *New phytologist* **170**:357–368.
- 431 Sayre RG, Comer P, Hak J, Josse C, Bow J, Warner H, Larwanou M, Kelbessa E, Bekele T,
432 Kehl H, others. 2013. A new map of standardized terrestrial ecosystems of africa.
433 *African Geographical Review*.
- 434 Schaffer W, Gadgil M. 1975. Selection for optimal life histories in plants. *Ecology and
435 evolution of communities* 142–157.

- 436 Slater G, Harmon L, Wegmann D, Joyce P, Revell L, Alfaro M. 2012. Fitting models of
437 continuous trait evolution to incompletely sampled comparative data using
438 approximate bayesian computation. *Evolution* **66**:752–762.
- 439 Soetaert K. 2018. Shape: Functions for plotting graphical shapes, colors.
- 440 Soetaert K. 2017. Diagram: Functions for visualising simple graphs (networks), plotting flow
441 diagrams.
- 442 Soltis PS. 2017. Digitization of herbaria enables novel research. *American journal of botany*
443 **104**:1281–1284.
- 444 Stearns SC. 1992. The evolution of life histories.
- 445 Stropp J, Ladle RJ, M. Malhado AC, Hortal J, Gaffuri J, H. Temperley W, Olav Skøien J,
446 Mayaux P. 2016. Mapping ignorance: 300 years of collecting flowering plants in africa.
447 *Global Ecology and Biogeography* **25**:1085–1096.
- 448 Tank DC, Olmstead RG. 2008. From annuals to perennials: Phylogeny of subtribe
449 castillejinae (orobanchaceae). *American Journal of Botany* **95**:608–625.
- 450 Václavík T, Beckmann M, Cord AF, Bindewald AM. 2017. Effects of uv-b radiation on leaf
451 hair traits of invasive plants—combining historical herbarium records with novel
452 remote sensing data. *PloS one* **12**:e0175671.
- 453 Venables WN, Ripley BD. 2002. Modern applied statistics with s, Fourth. ed. New York:
454 Springer.
- 455 Verboom GA, Linder HP, Stock WD. 2004. Testing the adaptive nature of radiation:
456 Growth form and life history divergence in the african grass genus ehrharta (poaceae:
457 Ehrhartoideae). *American Journal of Botany* **91**:1364–1370.

- 458 Wickham H. 2018a. Forcats: Tools for working with categorical variables (factors).
- 459 Wickham H. 2018b. Stringr: Simple, consistent wrappers for common string operations.
- 460 Wickham H. 2017. Tidyverse: Easily install and load the 'tidyverse'.
- 461 Wickham H. 2016. Ggplot2: Elegant graphics for data analysis. Springer-Verlag New York.
- 462 Wickham H, François R, Henry L, Müller K. 2018. Dplyr: A grammar of data manipulation.
- 463 Wickham H, Henry L. 2018. Tidyr: Easily tidy data with 'spread()' and 'gather()' functions.
- 464 Wickham H, Hester J, Francois R. 2017. Readr: Read rectangular text data.
- 465 Willis CG, Ellwood ER, Primack RB, Davis CC, Pearson KD, Gallinat AS, Yost JM, Nelson
466 G, Mazer SJ, Rossington NL, others. 2017. Old plants, new tricks: Phenological
467 research using herbarium specimens. *Trends in ecology & evolution* **32**:531–546.
- 468 Wolf A, Zimmerman NB, Anderegg WR, Busby PE, Christensen J. 2016. Altitudinal shifts
469 of the native and introduced flora of California in the context of 20th-century
470 warming. *Global ecology and biogeography* **25**:418–429.

471

Supplement

472 **Images used.** <https://www.gbif.org/occurrence/1099023487>
473 <https://www.gbif.org/occurrence/1057389408> <https://www.gbif.org/occurrence/1099023562>
474 <https://www.gbif.org/occurrence/1099023490>

475 **Software used.** We used R (Version 3.5.1; R Core Team, 2018) and the R-packages
476 *ape* (Version 5.2; Paradis and Schliep, 2018; Orme et al., 2018; Soetaert, 2018), *bindrcpp*
477 (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme et al., 2018), *coda* (Version 0.19.2;
478 Plummer et al., 2006), *diagram* (Version 1.6.4; Soetaert, 2017), *dplyr* (Version 0.7.8;
479 Wickham et al., 2018), *forcats* (Version 0.3.0; Wickham, 2018a), *gee* (Version 4.13.19; R by
480 Thomas Lumley and author., 2015), *geiger* (Version 2.0.6; Alfaro et al., 2009; Eastman et al.,
481 2011; Harmon et al., 2008; Slater et al., 2012), *ggplot2* (Version 3.1.0; Wickham, 2016),
482 *logistf* (Version 1.23; Heinze and Ploner, 2018), *maps* (Version 3.3.0; Richard A. Becker et al.,
483 2018), *MASS* (Version 7.3.51.1; Venables and Ripley, 2002), *Matrix* (Version 1.2.15; Bates
484 and Maechler, 2018), *MCMCglmm* (Version 2.26; Hadfield, 2010), *mvtnorm* (Version 1.0.8;
485 Genz and Bretz, 2009), *papaja* (Version 0.1.0.9842; Aust and Barth, 2018), *phylobase* (Version
486 2.6; Ho and Ane, 2014), *phytools* (Version 0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry
487 and Wickham, 2018), *raster* (Version 2.8.4; Hijmans, 2018), *readr* (Version 1.2.1; Wickham
488 et al., 2017), *shape* (Version 1.4.4; Soetaert, 2018), *sp* (Version 1.3.1; Pebesma and Bivand,
489 2005), *stringr* (Version 1.3.1; Wickham, 2018b), *tibble* (Version 1.4.2; Müller and Wickham,
490 2018), *tidyverse* (Version 1.2.1;
491 Wickham, 2017) for all our analyses.

492

Supplementary tables and figures.

Table S1

*Heliophila species records and the mean drought frequencies during
different seasons at the location of records*

Species	LH	n	Winter	Spring	Summer	Fall
<i>Heliophila acuminata</i>	a	28	0.32	0.38	0.41	0.36
<i>Heliophila africana</i>	a	91	0.33	0.35	0.34	0.34
<i>Heliophila amplexicaulis</i>	a	60	0.32	0.36	0.39	0.33
<i>Heliophila arenaria</i>	a	65	0.34	0.37	0.38	0.34
<i>Heliophila carnosa</i>	p	129	0.33	0.37	0.39	0.31
<i>Heliophila cedarbergensis</i>	p	3	0.40	0.43	0.32	0.27
<i>Heliophila collina</i>	a	16	0.35	0.47	0.48	0.45
<i>Heliophila cornellsbergia</i>	a	2	0.33	0.42	0.35	0.21
<i>Heliophila cornuta</i>	p	101	0.35	0.40	0.40	0.34
<i>Heliophila coronopifolia</i>	a	40	0.37	0.42	0.40	0.37
<i>Heliophila crithmifolia</i>	a	97	0.35	0.42	0.45	0.38
<i>Heliophila descurva</i>	a	12	0.36	0.38	0.38	0.29
<i>Heliophila deserticola</i>	a	133	0.48	0.48	0.46	0.45
<i>Heliophila digitata</i>	a	30	0.33	0.38	0.44	0.38
<i>Heliophila dregeana</i>	p	17	0.33	0.37	0.33	0.32
<i>Heliophila elongata</i>	p	82	0.26	0.32	0.30	0.25
<i>Heliophila ephemera</i>	a	3	0.14	0.27	0.31	0.26
<i>Heliophila esterhuyseniae</i>	p	3	0.21	0.30	0.37	0.27
<i>Heliophila eximia</i>	p	12	0.42	0.41	0.32	0.34
<i>Heliophila gariepina</i>	a	12	0.50	0.53	0.48	0.41
<i>Heliophila glauca</i>	p	35	0.29	0.35	0.34	0.33
<i>Heliophila juncea</i>	p	150	0.32	0.37	0.39	0.35
<i>Heliophila linearis</i>	p	94	0.32	0.33	0.28	0.30
<i>Heliophila macowaniana</i>	a	31	0.33	0.38	0.44	0.39
<i>Heliophila macra</i>	p	22	0.30	0.30	0.32	0.29
<i>Heliophila macrosperma</i>	p	5	0.28	0.36	0.35	0.25
<i>Heliophila minima</i>	p	35	0.36	0.45	0.51	0.39

<i>Heliophila namaquana</i>	a	16	0.39	0.46	0.48	0.39
<i>Heliophila nubigena</i>	p	19	0.31	0.36	0.43	0.38
<i>Heliophila pectinata</i>	a	16	0.27	0.34	0.50	0.34
<i>Heliophila polygaloides</i>	p	12	0.40	0.48	0.42	0.34
<i>Heliophila pubescens</i>	a	9	0.31	0.40	0.48	0.39
<i>Heliophila pusilla</i>	a	45	0.32	0.38	0.38	0.34
<i>Heliophila rigidiuscula</i>	p	201	0.30	0.33	0.28	0.24
<i>Heliophila scoparia</i>	p	106	0.31	0.37	0.36	0.31
<i>Heliophila seselifolia</i>	a	80	0.36	0.42	0.45	0.40
<i>Heliophila suavissima</i>	p	92	0.30	0.39	0.42	0.31
<i>Heliophila subulata</i>	p	103	0.29	0.33	0.31	0.29
<i>Heliophila tricuspidata</i>	p	8	0.28	0.33	0.38	0.30
<i>Heliophila trifurca</i>	a	77	0.45	0.48	0.48	0.43
<i>Heliophila tulbaghensis</i>	p	3	0.36	0.41	0.36	0.35
<i>Heliophila variabilis</i>	a	97	0.35	0.41	0.40	0.37

Note. LH = Life history (a = annual, p = perennial). n=sample size of GBIF records. Seasons are mean drought frequencies observed at locations of records.



Figure S1. Maps of occurrence records for individual species. Orange points indicate annual species. Blue points indicate perennial species.