

¹ Drought frequency predicts life history strategies in *Heliophila*

² J. Grey Monroe^{1,2}, Brian Gill³, Kathryn G. Turner⁴, & John K. McKay²

³ ¹ Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80521,
⁴ USA

⁵ ² College of Agriculture, Colorado State University, Fort Collins, CO 80521, USA

⁶ ³ Institute for Environment and Society, Brown University, Providence, RI 02912, USA

⁷ ⁴ Biology Department, Pennsylvania State University, State College, PA 16802, USA

⁸ Author Note

⁹ Correspondence concerning this article should be addressed to J. Grey Monroe, 307
¹⁰ University Ave, Fort Collins, CO 80521. E-mail: monroejg@colostate.edu

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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

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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

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

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

72 Materials and Methods

73 Data

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

77 **Satellite-detected drought data.** Remotely sensed data is a powerful tool for
78 characterizing seasonal patterns in drought because it is less limited in spatial and temporal
79 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 estimated ~50 *Heliophila* species occurring there are considered to make up the most diverse
108 genus of the family Brassicaceae (Mandáková et al., 2012; Mummenhoff et al., 2005). This
109 genus includes both perennial and annual species and this change in life history strategy has
110 likely arisen multiple independent times (Appel and Al-Shehbaz, 1997; Mummenhoff et al.,
111 2005). Furthermore, the fine scale climatic heterogeneity of Southern Africa is ideal for
112 studying the distribution of traits in relation to environmental parameters (Sayre et al.,
113 2013). We used life histories reported by Mummenhoff et al. (2005), grouping species with
114 annual or perennial life histories. Perenniality was defined based any form of perennial life
115 history (e.g., herbs, shrubs, mixed, etc). Because the nature of species reported with mixed
116 traits were unknown (i.e. plasticity vs. genetic variation), we classified these species here as
117 perennial since they can maintain vegetative growth after reproduction at least to some
118 capacity.

119 #### *Heliophila* occurrence records

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

125 climate (Davis et al., 2015; Stropp et al., 2016; Václavík et al., 2017; Wolf et al., 2016). To
126 characterize the distributions of annual and perennial *Heliphila* species, all records for the
127 genus *Heliphila* were downloaded from the Global Biodiversity Information Facility
128 (gbif.org) on July 21, 2018 (GBIF, 2018).

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

132 **Analyses**

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

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

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

- 149 • records without duplicates (i.e., identical species, location, collection date)

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

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

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

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

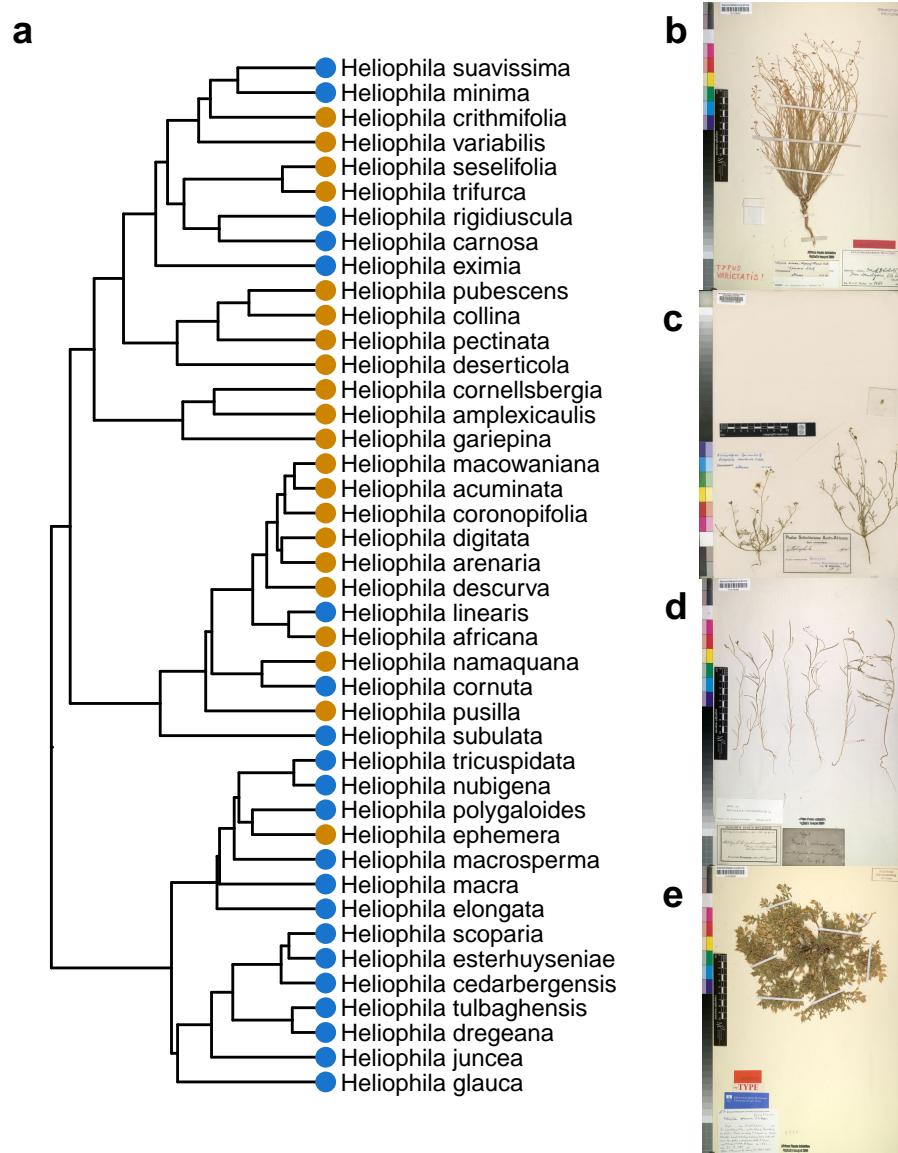


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. Example herbaria specimens accessed via GBIF of (a) *H. minima*, (b) *H. deserticola*, (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

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

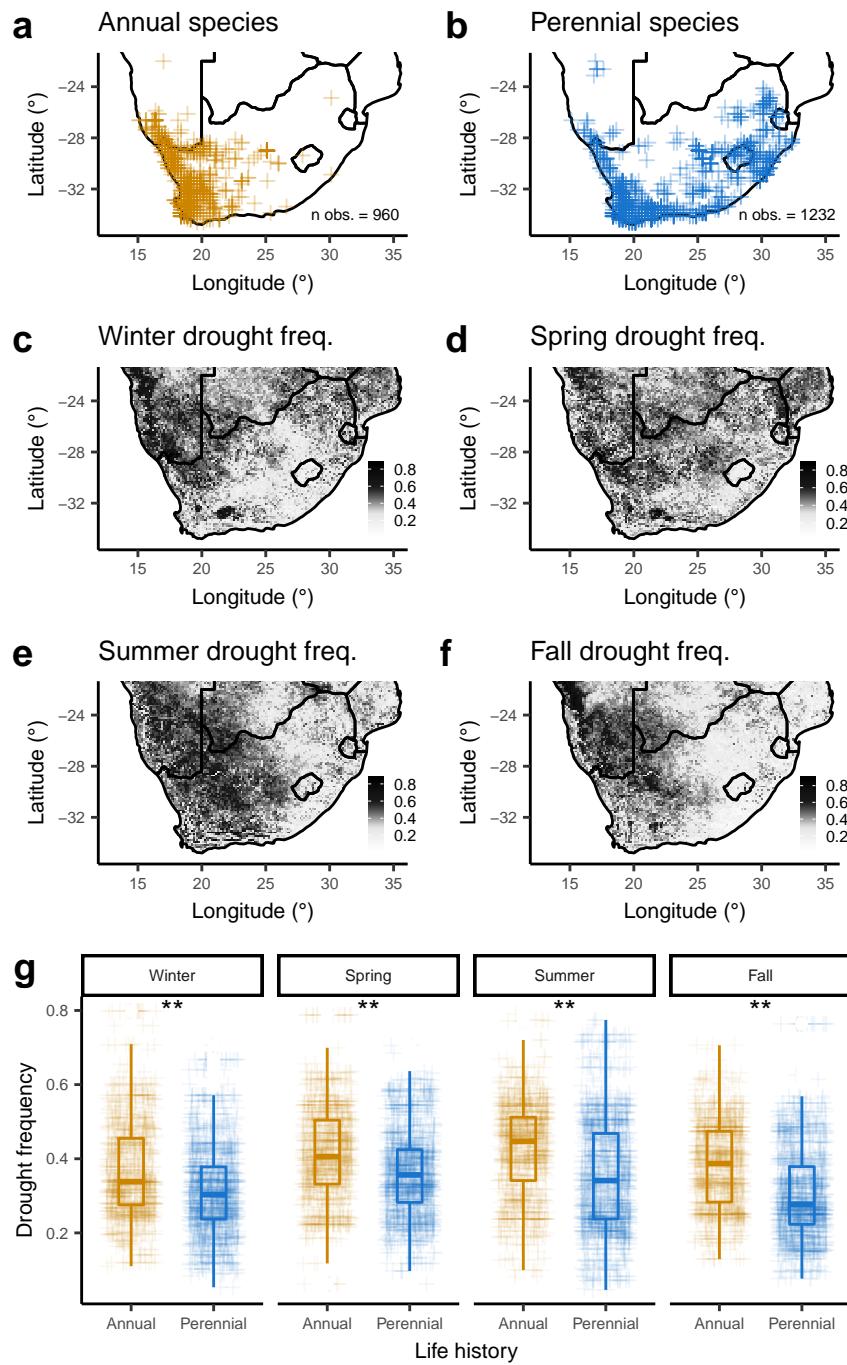


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall measured using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (*t*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

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

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

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

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

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

212 The preceding results indicated that annual species are found in environments where
213 droughts are significantly more frequent, especially in the summer and fall. Classic life
214 history theory hypothesizes that annuality reflects adaptation to such environments because
215 it allows species to escape stressful conditions. If this is the case, we would expect that
216 annuals spend the drought prone seasons of summer and fall as seeds. To test this
217 hypothesis, we compared the dates of occurrence records between annual and perennial
218 *Heliophila* species. The distributions reveal a considerable difference in the timing of
219 observation of these two life histories. In comparison to perennials, which appear to be
220 collected throughout the year, annuals are almost exclusively observed during the winter and
221 spring (Figure 3b). The differences between the distribution of collection dates were
222 significant by all tests ($ks.test D = 0.25, p = 0$; $bartlett.test K2 = 503.18, p = 0.00$) This is
223 consistent with a model of life history in which annual species flower in the spring, set seed,
224 senesce, and die before the summer. Thus, these annual species are likely to remain dormant
225 during the summer and fall, when drought is the strongest predictor of the distributions of
226 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.

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,
 234

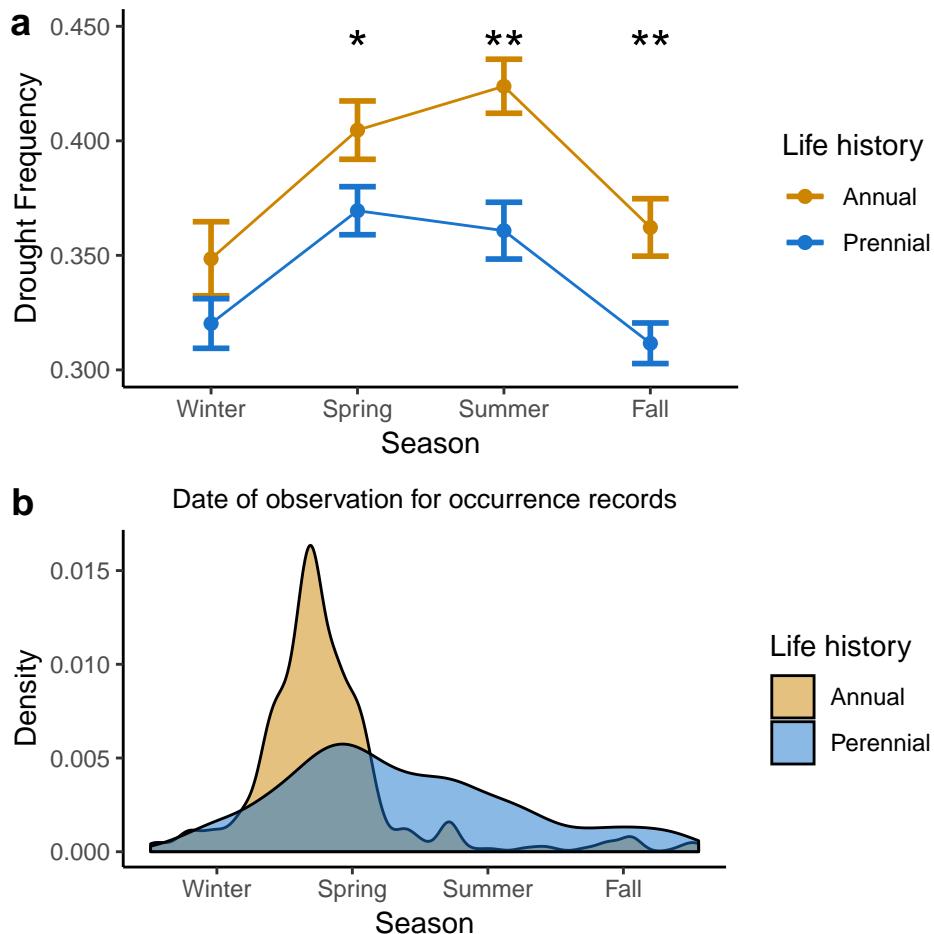


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (phylogenetic logistic regression, * = $p < 0.05$, ** = $p < 0.01$) (b) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

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

241 are the causative factors explaining variation in the distributions of annual and perennial
242 species. Nevertheless, these results reveal quantitative support for the classic prediction that
243 annual species are found in environments that experience more frequent drought than
244 perennial species. These findings complement previous reports of qualitative associations
245 between annuality with environments characterized as having increased aridity (Evans et al.,
246 2005), alternative precipitation defined habitats (Datson et al., 2008; Morishima et al., 1984),
247 or greater unpredictability (Cruz-Mazo et al., 2009). However, to our knowledge this is the
248 first study to demonstrate a significant association between life history and drought in a
249 phylogenetic context informed by large scale species distribution data and long term drought
250 measures.

251 Unfortunately, herbarium collections and their associated data do not represent
252 systematic or random sampling of a species distribution. Significant biases in collecting exist,
253 which we have not necessarily controlled for here, and may have some effect on our findings,
254 such as a bias toward collecting near roads or near the locations of natural history collections
255 (Daru et al., 2018). Future research will benefit from systematic sampling efforts to avoid
256 these noted biases. However, the ecosystems of southern Africa include several biodiversity
257 hotspots and are among the most botanically well sampled regions on Earth (Daru et al.,
258 2018), suggesting that this may currently be the optimal region for our analyses of life
259 history distribution. Indeed, we were able to use 2192 occurrence records to study 42 species,
260 which represents a significant advance over relying on personal observations to characterize
261 species distributions.

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

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

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

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

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

296

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300

Author contributions

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

304

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Supplement

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Images used. <https://www.gbif.org/occurrence/1099023487>

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<https://www.gbif.org/occurrence/1057389408> <https://www.gbif.org/occurrence/1099023562>

475

<https://www.gbif.org/occurrence/1099023490>

476

Software used. We used R (Version 3.5.1; R Core Team, 2018) and the R-packages

477 *ape* (Version 5.2; Paradis and Schliep, 2018; Orme et al., 2018; Soetaert, 2018), *bindrcpp*

478 (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme et al., 2018), *coda* (Version 0.19.2;

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483 *logistf* (Version 1.23; Heinze and Ploner, 2018), *maps* (Version 3.3.0; Richard A. Becker et al.,

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487 2.6; Ho and Ane, 2014), *phytools* (Version 0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry

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489 et al., 2017), *shape* (Version 1.4.4; Soetaert, 2018), *sp* (Version 1.3.1; Pebesma and Bivand,

490 2005), *stringr* (Version 1.3.1; Wickham, 2018b), *tibble* (Version 1.4.2; Müller and Wickham,

491 2018), *tidyverse* (Version 1.2.1; Wickham and Henry, 2018), and *tidyverse* (Version 1.2.1;

492 Wickham, 2017) for all our analyses.

493

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.