

<sup>1</sup> Drought frequency predicts plant life history strategies

<sup>2</sup> J. Grey Monroe<sup>1,2</sup>, Brian Gill<sup>3</sup>, Kathryn G. Turner<sup>4</sup>, & John K. McKay<sup>2</sup>

<sup>3</sup> <sup>1</sup> Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523,  
<sup>4</sup> USA

<sup>5</sup> <sup>2</sup> College of Agriculture, Colorado State University, Fort Collins, CO 80523, USA

<sup>6</sup> <sup>3</sup> Institute for Environment and Society, Brown University, Providence, RI 02912, USA

<sup>7</sup> <sup>4</sup> Biology Department, Pennsylvania State University, State College, PA 16802, USA

<sup>8</sup> Author Note

<sup>9</sup> Correspondence concerning this article should be addressed to J. Grey Monroe, 307  
<sup>10</sup> University Ave, Fort Collins, CO 80523. 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 2192 herbaria occurrence records with 34 years of satellite-based  
17 drought detection. 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 adpated to  
27 enviroments 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 plant life history strategies

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 association of annuality with arid environments in  
55 *Oryza perennis* (Morishima et al., 1984) and *Oenothera* (Evans et al., 2005). Additionally,

56 annual 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 in a phylogenetic  
61 context with suitable sample sizes of distribution and climate data.

62 Here we combine a long-term global dataset of satellite detected drought events with  
63 metadata from natural history collections to test these classic hypotheses about the  
64 evolution of life history strategies within the African endemic mustard genus, *Heliophila* L.  
65 (Brassicaceae). If annuality is an adaptive strategy allowing plants to escape drought prone  
66 seasons, then drought frequency should predict the distribution of life history strategies  
67 across landscapes, and annual species should be more commonly associated with drought  
68 prone regions than perennial species. Furthermore, if annual species have adapted to escape  
69 drought prone seasons, observations of growing annual species (i.e. occurring in forms other  
70 than seed) should be rare during drought prone seasons. Phylogenetic relatedness can have  
71 significant non-random effects on species distributions and life history traits (Barrett et al.,  
72 1996), and therefore we assessed the relationship between life history distribution and  
73 drought frequency in a phylogenetically controlled background.

74

## Materials and Methods

75 **Data**

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

**79 Satellite-detected drought data.** Remotely sensed data is a powerful tool for

**80** characterizing seasonal patterns in drought because it is less limited in spatial and temporal

**81** scope and resolution than weather stations or field observations (AghaKouchak et al., 2015).

**82** To quantify the frequency of drought during different seasons across landscapes, we used the

**83** remotely sensed Vegetative Health Index (VHI), which measures landscape scale reductions

**84** in plant cover and temperature conditions characteristic of drought (Kogan, 2001).

**85** Generated from data collected by NOAA AVHRR satellites since 1981, the VHI combines

**86** Normalized Difference Vegetation Index (NDVI) derived measures of vegetative stress

**87** (Vegetative Condition Index - VCI) with temperature stress indicated by anomalies in

**88** thermal spectra (Temperature Condition Index - TCI). The VHI of year  $y$  during week  $w$  of

**89** [1, 52] at pixel  $i$  is derived from the following equations, where  $n$  is the number of years

**90** observed.

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

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

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

**91** where  $NDVI_{min} = min(NDVI_{1981,w,i} \dots NDVI_{1981+n,w,i})$  and

**92**  $NDVI_{max} = max(NDVI_{1981,w,i} \dots NDVI_{1981+n,w,i})$  and  $T_{min} = min(T_{1981,w,i} \dots T_{1981+n,w,i})$

**93** and  $T_{max} = max(T_{1981,w,i} \dots T_{1981+n,w,i})$

**94** Thus, VHI measurements are standardized according to conditions historically observed

**95** at each locations. These measurements have been validated and generally used for evaluating

**96** drought risk and predicting crop yields in agriculture (e.g., Rojas et al., 2011; Kogan et al.,

**97** 2016). But they also present a new tool to study seasonal patterns in the frequency of

98 drought across environments and to test hypotheses about the effect of drought on ecological  
99 and evolutionary processes (Kerr and Ostrovsky, 2003). As such, the VHI has been applied  
100 recently to study drought related ecology of natural species and proven useful for predicting  
101 infraspecific variation in drought tolerance traits and genes (Dittberner et al., 2018; Mojica  
102 et al., 2016; Monroe et al., 2018). Here, we accessed VHI data at  $16\text{km}^2$  resolution from 1981  
103 to 2015 ([https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh\\_ftp.php](https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php)) to characterize  
104 the seasonal drought frequencies experienced by annual and perennial *Heliophila* species.

105 **Life history data for *Heliophila*.** *Heliophila* is a genus of flowering plants  
106 endemic to the southern portion of Africa including the Cape Floristic and Succulent Karoo  
107 Regions. These are among the most botanically diverse environments on Earth and the  
108 estimated ~50 *Heliophila* species occurring there are considered to make up the most diverse  
109 genus of the family Brassicaceae (Mandáková et al., 2012; Mummenhoff et al., 2005). This  
110 genus includes both perennial and annual species and this change in life history strategy has  
111 likely arisen multiple independent times (Appel and Al-Shehbaz, 1997; Mummenhoff et al.,  
112 2005). Furthermore, the fine scale climatic heterogeneity of Southern Africa is ideal for  
113 studying the distribution of traits in relation to environmental parameters (Sayre et al.,  
114 2013). We used life histories reported by Mummenhoff et al. (2005), grouping species with  
115 annual or perennial life histories. Perenniality was defined based any form of perennial life  
116 history (e.g., herbs, shrubs, mixed, etc). We also repeated these analyses without *H. subulata*  
117 and *H. minima* which have mixed life histories and found similar results. Because the  
118 original authors didn't report the nature of the mixed trait (Mummenhoff et al., 2005), (ie.  
119 plasticity vs. genetic variation), we classified these species here as perennial since they have  
120 the capacity to maintain vegetative growth after reproduction at least to some capacity.

121 ***Heliophila* occurrence records.** Botanists have collected and maintained over 350  
122 million botanical specimens worldwide over the past 300 years. Herbarium specimens and  
123 their associated metadata have been used since the 1960s to study species' geographical

124 distributions (reviewed by Willis et al. (2017) and Lang et al. (2018)). And as they become  
125 digitized (Soltis, 2017), these collections have been used to study relationships between trait  
126 distributions, geography, and climate (Davis et al., 2015; Stropp et al., 2016; Václavík et al.,  
127 2017; Wolf et al., 2016). To characterize the diributions of annual and perennial *Heliophila*  
128 species, all records for the genus *Heliophila* were downloaded from the Global Biodiversity  
129 Information Facility (gbif.org) on July 21, 2018 (GBIF, 2018).

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

## 133   Analyses

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

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

- 144       • records for species with reported life history
- 145       • records with geospatial data
- 146       • records without known geospatial coodinate issues (i.e., coordinates reported are those  
147       of herbarium)

- 148     • records from collection sites classified as land pixels  
149     • records from Africa (to exclude locations of cultivation)  
150     • records without duplicates (i.e., identical species, location, collection date)

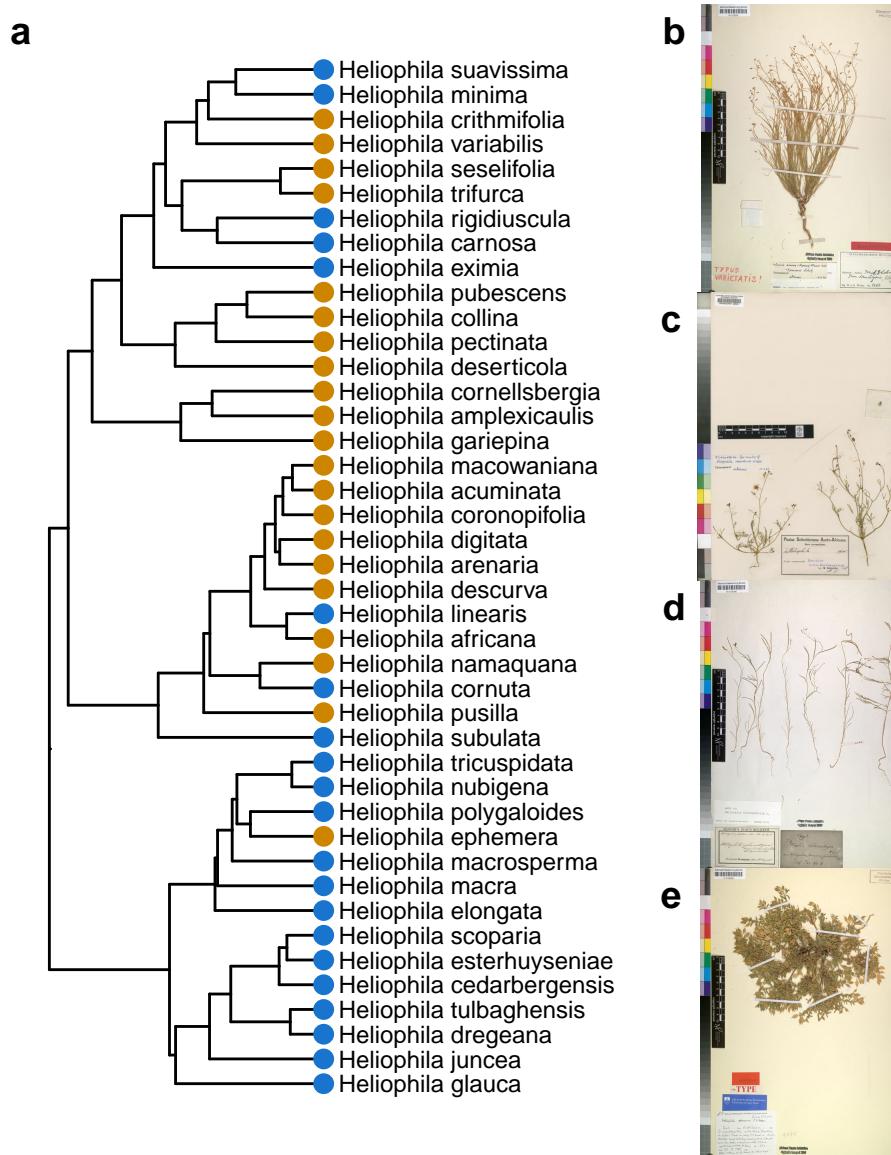
151       **Phylogeny construction.** Out group species were aligned together with *Helophilus*  
152 ITS sequences using MAFFT. Model selection for construction of phylogeny was performed  
153 in jModeltest2 with CIPRES. Based on this analysis, *GTR + L* were selected. Ultrametric  
154 phylogeny was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

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

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

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

## Results



*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.

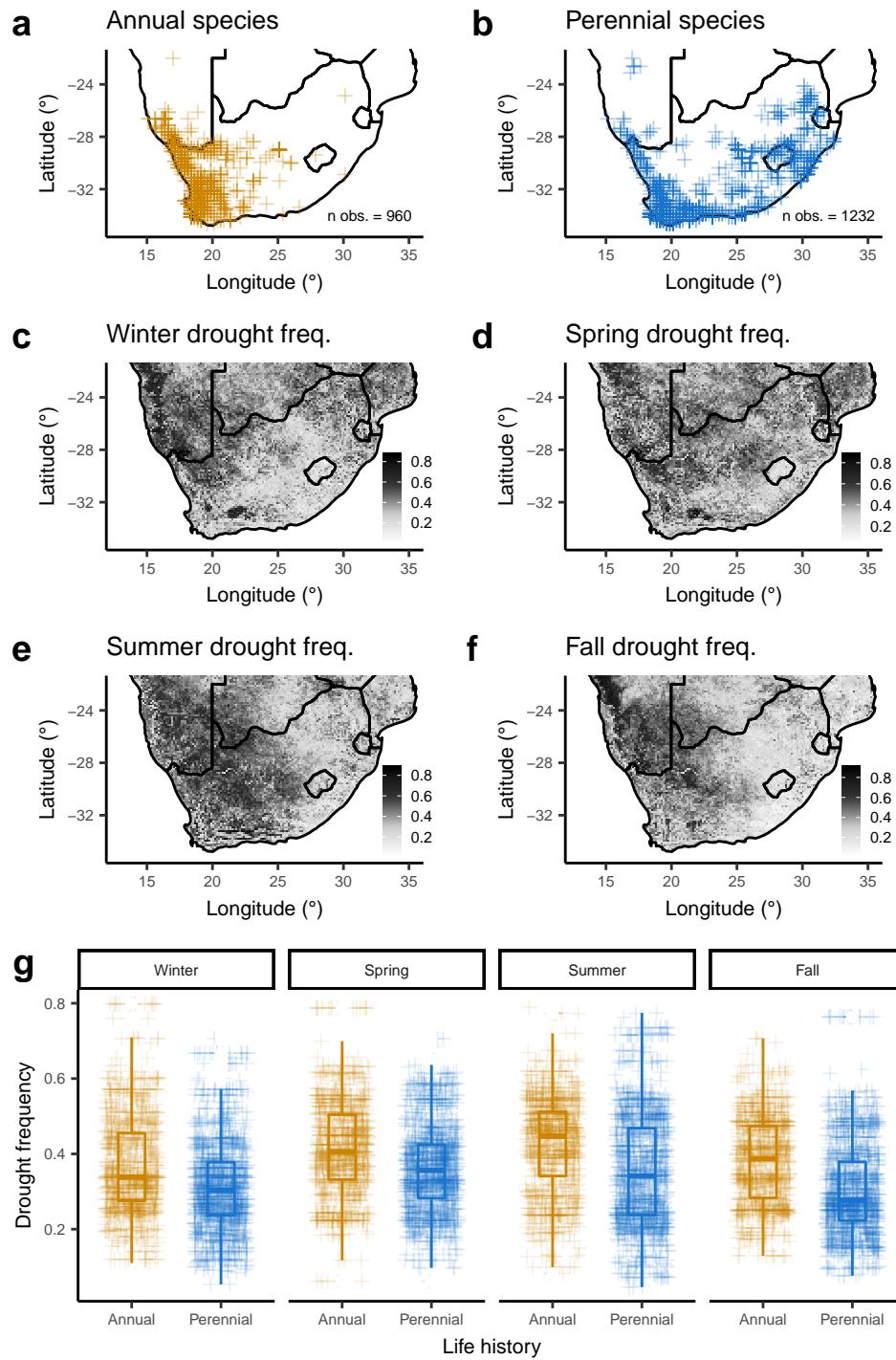


Figure 2. Locations of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall. (g) Drought frequencies during each season observed at the collection sites of *Heliophila* records.

174 Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history

175 (Mummenhoff et al., 2005), 3653 had geospatial data, 3627 did not have geospatial issues,

176 3460 were located on pixels classified as land having drought measurements, 3457 were

177 located in Africa, 3162 were not duplicated. After all filtering steps, 2192 records for 42

178 species (Figure 1, Table S1) passed for further analyses. The number of samples varied

179 between species, with a mean of 52.19 samples per species. *Heliophila rigidiuscula* had the

180 most records, 201, and *Heliophila cornellsbergia* the fewest, 2 (Table S1).

181 There were clear visual differences between the distributions of the 960 annual and the

182 1232 perennial *Heliophila* observation records (see Figure S1 for maps of individual species).

183 While annual species were generally found in the western regions of South Africa and

184 Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the

185 occurrences of perennials extended to the east coast of South Africa (Figure 2b).

186 The frequency of drought varied considerably across the ranges of *Heliophila* species

187 (Figure 2c-f). This heterogeneity is expected, given that this is one of the most climatically

188 diverse regions of the Earth (Sayre et al., 2013). It is worth noting the east to west cline in

189 drought frequency observed during the summer, which distinguishes the high drought

190 frequency of the Kalahari Sands and Namib Desert phytogeographic regions from the low

191 drought frequency of the Drakensberg Mountains and Coastal Zambesian phytogeographic

192 regions. In the Cape phytogeographic region there was finer scale heterogeneity in drought

193 frequency during the summer.

194 Theory predicts that annuality should be adaptive in places where stresses such as

195 drought are more common. Conversely, perenniability should be adaptive in places where such

196 stresses are less frequent. We found that the frequency of drought was significantly higher at

197 the locations of occurrence records for annual species. In terms of raw observation records

198 (Figure 2g), the frequency of drought was significantly higher at the location of annuals

199 during the winter ( $t = 10.65$ ,  $p = 0.00$ ), spring ( $t = 10.73$ ,  $p = 0.00$ ), summer ( $t = 12.67$ ,  $p$

= 0.00), and fall ( $t = 15.26$ ,  $p = 0.00$ ). Because raw occurrence records do not account for variation in the number of records per species (Table S1), we also tested whether mean drought frequency values of each species were significantly different between annuals and perennials by a Firths-penalized logistic regression. We found that the mean drought frequencies were significantly higher ( $\alpha = 0.05$ ) in annual species during the spring, summer, and fall (Table 1, Figure 3a). We further tested whether annual species are found in places where droughts occur more frequently while controlling for the phylogenetic relatedness of *Heliophila* species. This is important, because environmental differences in species distributions can be confounded with demographic history caused by ancestry. We found that while controlling for phylogeny, the mean drought frequencies were significantly higher ( $\alpha = 0.05$ ) in annual species during the spring, summer, and fall (Table 1, Figure 3a). These findings indicate that common ancestry alone does not explain differences in the drought frequencies experienced in the environments of annual and perennial *Heliophila*.

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

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 <sup>‘</sup>	P <sup>‘</sup>	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.

<sup>227</sup> annual and perennial life histories (Figure 3a).

<sup>228</sup>

## Discussion

<sup>229</sup> To test the hypothesis that annual and perennial plants reflect adaptation to  
<sup>230</sup> alternative drought environments we examined the landscape distribution of life history  
<sup>231</sup> strategies in the large and diverse mustard genus, *Heliophila*. Using metadata of 2192  
<sup>232</sup> occurrence records and a 34 year dataset of satellite-detected droughts, we tested the  
<sup>233</sup> prediction that annual species are more often observed in drought-prone locations than

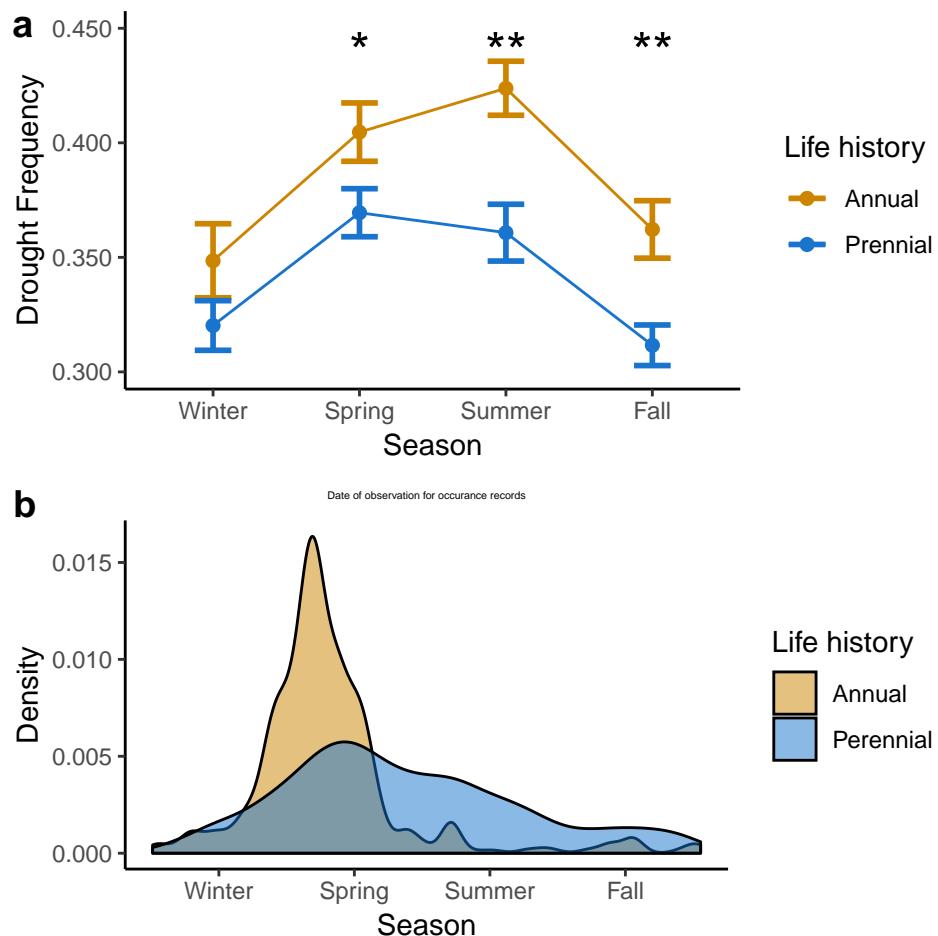


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (b) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

perennial species, when controlling for phylogenetic relatedness. We found that drought frequency is significantly different between the distributions of annual and perennial species, 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 *Helophilus*, 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 perenniality

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

These findings suggest that species with locally adaptive life history strategies could be threatened by rapidly changing drought regimens (Dai, 2011). This could have impacts on ecosystem functioning and processes such as carbon cycling if the composition of annual and perennial species changes as a response [@garnier1997specific; Roumet et al. (2006); monroe2018ecoevolutionary]. Furthermore, the frequency of drought may be an important factor when considering the use of perennial cropping systems (Lelièvre and Volaire, 2009; Parry et al., 2005).

In conclusion, we find strong support for classic life history theory which predicts that annuality is adaptive in environments where droughts occur more frequently. Additionally, we report evidence consistent with a life history model in annuals in which they escape drought prone seasons during the seed phase of their life cycle. Finally, we find evidence that

293 the distributions of perennial lineages may indicate a competitive advantage in areas where  
294 droughts are infrequent. More broadly, this work highlights the irreplaceable value of natural  
295 history collections and demonstrates the power of combining such information with large  
296 scale remote sensing data to address outstanding classic hypotheses in ecology and evolution.

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463

## Supplement

464       **Images used.** <https://www.gbif.org/occurrence/1099023487>  
465       <https://www.gbif.org/occurrence/1057389408> <https://www.gbif.org/occurrence/1099023562>  
466       <https://www.gbif.org/occurrence/1099023490>

467       **Software used.** We used R (Version 3.5.1; R Core Team, 2018) and the R-packages  
468       *ape* (Version 5.2; Paradis and Schliep, 2018; Orme et al., 2018; Soetaert, 2018), *bindrcpp*  
469       (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme et al., 2018), *coda* (Version 0.19.2;  
470       Plummer et al., 2006), *diagram* (Version 1.6.4; Soetaert, 2017), *dplyr* (Version 0.7.8;  
471       Wickham et al., 2018), *forcats* (Version 0.3.0; Wickham, 2018a), *gee* (Version 4.13.19; R by  
472       Thomas Lumley and author., 2015), *geiger* (Version 2.0.6; Alfaro et al., 2009; Eastman et al.,  
473       2011; Harmon et al., 2008; Slater et al., 2012), *ggplot2* (Version 3.1.0; Wickham, 2016),  
474       *logistf* (Version 1.23; Heinze and Ploner, 2018), *maps* (Version 3.3.0; Richard A. Becker et al.,  
475       2018), *MASS* (Version 7.3.51.1; Venables and Ripley, 2002), *Matrix* (Version 1.2.15; Bates  
476       and Maechler, 2018), *MCMCglmm* (Version 2.26; Hadfield, 2010), *mvtnorm* (Version 1.0.8;  
477       Genz and Bretz, 2009), *papaja* (Version 0.1.0.9842; Aust and Barth, 2018), *phylobolm* (Version  
478       2.6; Ho and Ane, 2014), *phytools* (Version 0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry  
479       and Wickham, 2018), *raster* (Version 2.8.4; Hijmans, 2018), *readr* (Version 1.2.1; Wickham  
480       et al., 2017), *shape* (Version 1.4.4; Soetaert, 2018), *sp* (Version 1.3.1; Pebesma and Bivand,  
481       2005), *stringr* (Version 1.3.1; Wickham, 2018b), *tibble* (Version 1.4.2; Müller and Wickham,  
482       2018), *tidyverse* (Version 1.2.1;  
483       Wickham, 2017) for all our analyses.

484

## Supplementary tables and figures.

### Table S1

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

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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.