

<sup>1</sup> 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 *Scorzonerooides* 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 influence tests of associations between species' traits and their environments (Barrett et al., 1996; Felsenstein, 1985), and therefore we assessed the relationship between life history distribution and drought frequency in a phylogenetic context.

## 73 Materials and Methods

### 74 Data

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

78 **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

80 scope and resolution than weather stations or field observations (AghaKouchak et al., 2015).  
 81 To quantify the frequency of drought during different seasons across landscapes, we used the  
 82 remotely sensed Vegetative Health Index (VHI), which measures landscape scale reductions  
 83 in plant cover and temperature conditions characteristic of drought (Kogan, 2001).  
 84 Generated from data collected by NOAA AVHRR satellites since 1981, the VHI combines  
 85 Normalized Difference Vegetation Index (NDVI) derived measures of vegetative stress  
 86 (Vegetative Condition Index - VCI) with temperature stress indicated by anomalies in  
 87 thermal spectra (Temperature Condition Index - TCI). The VHI of year  $y$  during week  $w$  of  
 88 [1, 52] at pixel  $i$  is derived from the following equations, where  $n$  is the number of years  
 89 observed.

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

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

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

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

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

99 been applied recently to study drought related ecology of natural species and proven useful  
100 for predicting intraspecific variation in drought tolerance traits and genes (Dittberner et al.,  
101 2018; Mojica et al., 2016; J. Monroe, Powell, et al., 2018). Here, we accessed VHI data at  
102  $16\text{km}^2$  resolution from 1981 to 2015  
103 ([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 the  
104 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 *Heliophila* species occurring there are considered to make up the most diverse genus of the  
109 family Brassicaceae (Mandáková et al., 2012; Mummenhoff et al., 2005). This genus includes  
110 both perennial and annual species and this change in life history strategy has likely arisen  
111 multiple independent times (Appel and Al-Shehbaz, 1997; Mummenhoff et al., 2005).  
112 Furthermore, the fine scale climatic heterogeneity of Southern Africa is ideal for studying the  
113 distribution of traits in relation to environmental parameters (Sayre et al., 2013). We used  
114 life histories reported by Mummenhoff et al. (2005), grouping species with annual or  
115 perennial life histories. Perenniality was defined based any form of perennial life history (e.g.,  
116 herbs, shrubs, mixed, etc). Because the nature of species reported with mixed traits were  
117 unknown (i.e. plasticity vs. genetic variation), we classified these species here as perennial  
118 since they can maintain vegetative growth after reproduction at least to some capacity.

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

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

128 **Sequence data for phylogeny.** An alignment of ITS I and II sequences for  
129 *Heliphila* species was obtained from the authors of Mandáková et al. (2012). Individual ITS  
130 I and II sequences for *Aethionema grandiflorum*, *Alliaria petiolata*, *Cardamine matthioli*,  
131 *Chamira circaeoides*, and *Rorippa amphibia* 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 (*Aethionema grandiflorum*, *Alliaria petiolata*,  
151 *Cardamine matthioli*, *Chamira circaeoides*, and *Rorippa amphibia*) and ingroup *Helophil*  
152 ITS I and II sequences were aligned using MAFFT (Katoh et al., 2002) with strategy  
153 G-INS-I, offset value 0.1, and all other options set as default. The *GTR + L* model of  
154 nucleotide substitution was determined to best fit the data based on AIC using jModelTest2  
155 (Darriba et al., 2012; Guindon and Gascuel, 2003). A maximum clade credibility tree with  
156 branch lengths as relative time was estimated by summarizing data from six runs of  
157 100,000,000 generations of Bayesian Markov chain Monte Carlo conducted in BEAST 2  
158 (Bouckaert et al., 2014). Model selection and phylogenetic analyses were conducted through  
159 the CIPRES Science Gateway (Miller et al., 2010).

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

161 To evaluate the hypothesis that annual and perennial life history strategies reflect  
162 adaptations to alternative drought regimes, we tested the corresponding prediction that the  
163 observed distributions of annual and perennial *Helophil* species would be significantly  
164 associated with historic drought frequency. First, we compared the frequency of drought  
165 during the winter, spring, summer, and fall between raw occurrence records of annual and  
166 perennial species by t-tests. To account for variation in the number of occurrence records per  
167 species, we next calculated the mean drought frequency during the winter, spring, summer  
168 and fall for each species. Because shared evolutionary history of closely related species can  
169 lead to spurious associations between traits and environments (Felsenstein, 1985), we tested  
170 for a relationship between life history strategy and drought frequency while controlling for  
171 phylogeny using phylogenetic logistic regression (Ives and Garland, 2010).

172 **Collection dates.** To test the hypothesis that annual species have adapted to  
173 escape drought prone seasons as seeds, collection dates for herbarium specimens were  
174 compared between annual and perennial species. Comparisons of distributions were made by

175 Two-sample Kolmogorov-Smirnov test, t-test, and Barlett variance test.

176

## Results

177 Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history  
178 (Mummenhoff et al., 2005), 2856 had geospatial data, 2833 did not have geospatial issues,  
179 2684 were located on pixels classified as land having drought measurements, 2543 were  
180 located in Africa, 2192 were not duplicated. Thus, after all filtering steps, 2192 records for  
181 42 species (Figure 1, Table S1) passed for further analyses. The number of samples varied  
182 between species, with a mean of 52.19 samples per species. *Heliophila rigidiuscula* had the  
183 most records, 201, and *Heliophila cornellsbergia* the fewest, 2 (Table S1).

184 There were clear visual differences between the distributions of the 960 annual and the  
185 1232 perennial *Heliophila* observation records (see Figure S1 for maps of individual species).  
186 While annual species were generally found in the western regions of South Africa and  
187 Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the  
188 occurrence of perennials extended to the east coast of South Africa (Figure 2b).

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

197 Theory predicts that annuality should be adaptive in places where stresses such as  
198 drought are more common. Conversely, perenniability should be adaptive in places where such

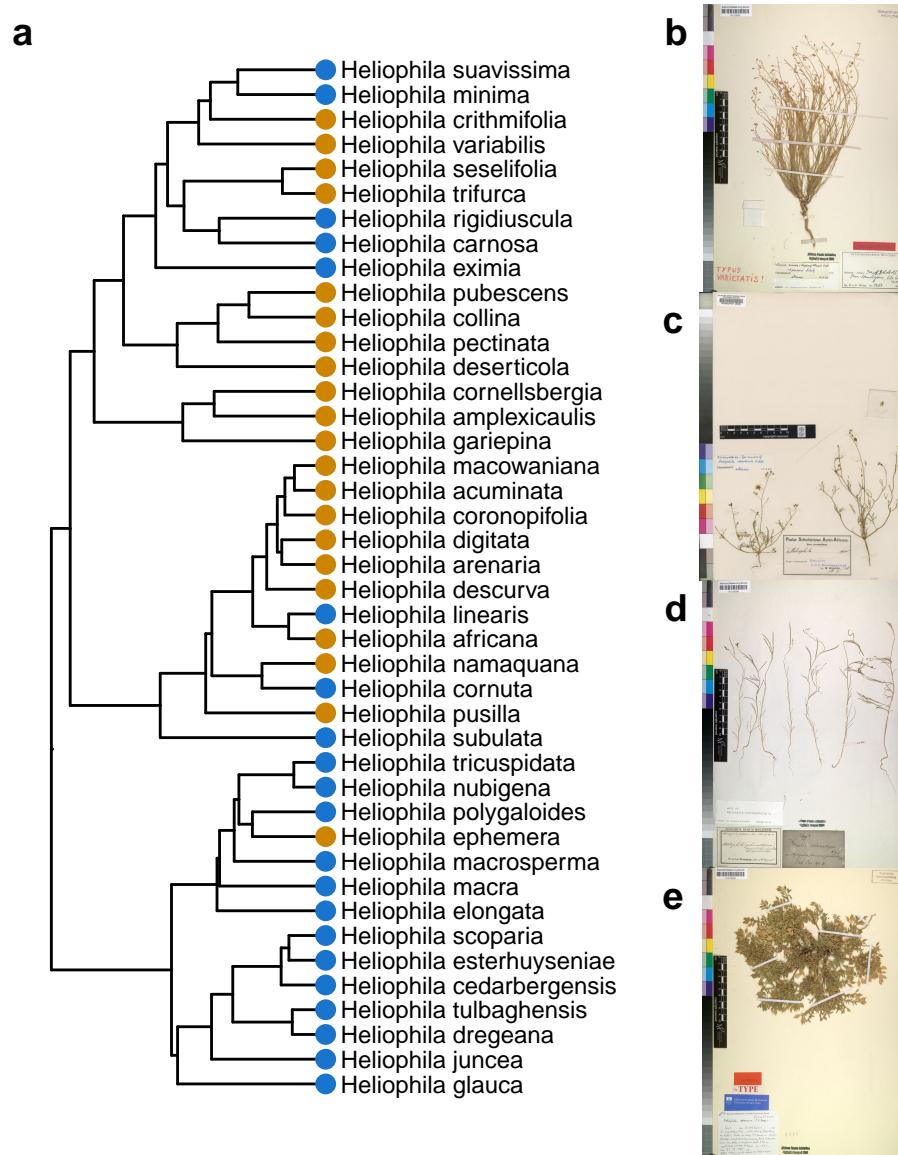


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. Example herbaria specimens accessed via GBIF of (a) *H. minima*, (b) *H. deserticola*,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

199 stresses are less frequent. We found that the frequency of drought was significantly higher at  
200 the locations of occurrence records for annual species. In terms of raw observation records

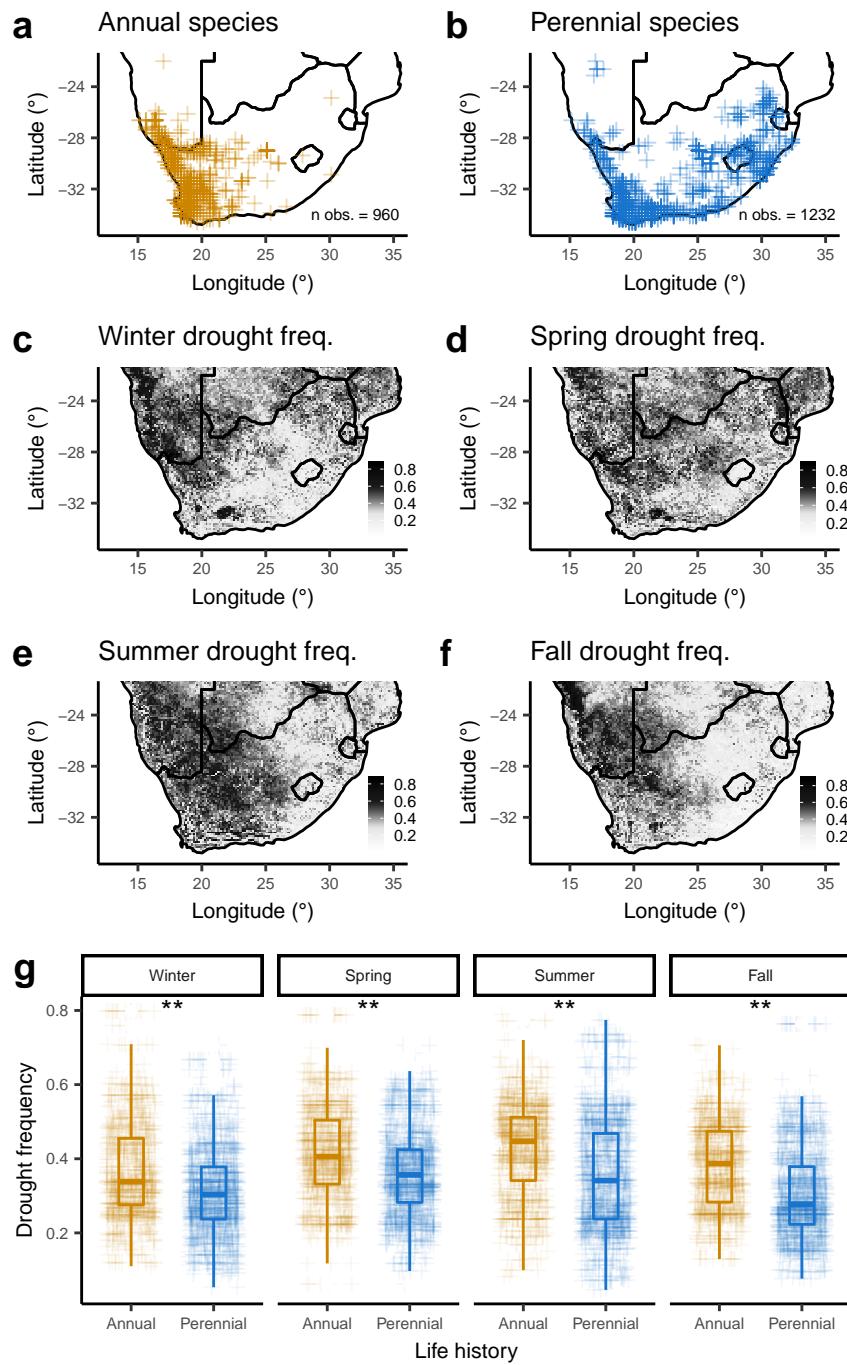


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall measured using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (t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

201 (Figure 2g), the frequency of drought was significantly higher at the location of annuals  
202 during the winter ( $t = 10.65$ ,  $p = 0.00$ ), spring ( $t = 10.73$ ,  $p = 0.00$ ), summer ( $t = 12.67$ ,  $p$   
203 = 0.00), and fall ( $t = 15.26$ ,  $p = 0.00$ ). Because raw occurrence records do not account for  
204 variation in the number of records per species (Table S1) or species relatedness (Figure 1a),  
205 we also tested whether mean drought frequency values of each species were significantly  
206 different between annuals and perennials using phylogenetic logistic regression. We found  
207 that the mean drought frequencies were significantly higher ( $\alpha = 0.05$ ) in annual species  
208 during the spring, summer, and fall (Table 1, Figure 3a). These findings indicate that  
209 common ancestry alone does not explain differences the drought frequencies experienced in  
210 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

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

Predictor	Estimate	P
Intercept	0.7231	0.6636
Winter drought freq.	-1.5452	0.7274
Intercept	5.0107	0.0534
Spring drought freq.	-12.9014	0.0464
Intercept	7.7093	0.0054
Summer drought freq.	-19.9056	0.0042
Intercept	7.0162	0.0082
Fall drought freq.	-20.8174	0.0067

*Note.* 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, *Heliphila*. 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

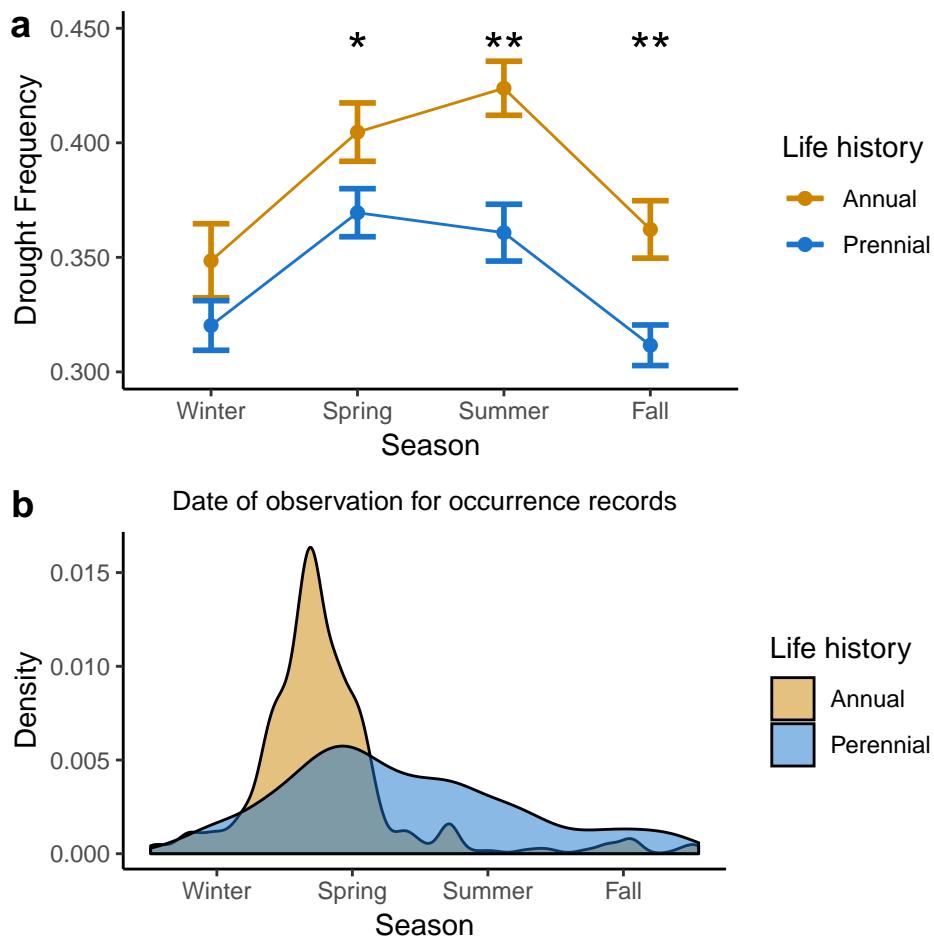


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (phylogenetic logistic regression, \* =  $p < 0.05$ , \*\* =  $p < 0.01$ ) (b) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

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 provide 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

265 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  
275 to 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 (Figure 2, 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 life history traits evolve or the  
283 composition of annual and perennial species changes in response (Garnier et al., 1997; J.  
284 Monroe, Markman, et al., 2018; Roumet et al., 2006). Furthermore, the frequency of drought  
285 may be an important factor when considering the use of perennial cropping systems (Lelièvre  
286 and Volaire, 2009; Parry et 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.

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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.

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488

## Supplement

489       **Images used.** <https://www.gbif.org/occurrence/1099023487>  
490       <https://www.gbif.org/occurrence/1057389408> <https://www.gbif.org/occurrence/1099023562>  
491       <https://www.gbif.org/occurrence/1099023490>

492       **Software used.** We used R (Version 3.5.1; R Core Team, 2018) and the R-packages  
493       *ape* (Version 5.2; Paradis and Schliep, 2018; Orme et al., 2018; Soetaert, 2018), *bindrcpp*  
494       (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme et al., 2018), *coda* (Version 0.19.2;  
495       Plummer et al., 2006), *diagram* (Version 1.6.4; Soetaert, 2017), *dplyr* (Version 0.7.8;  
496       Wickham et al., 2018), *forcats* (Version 0.3.0; Wickham, 2018a), *gee* (Version 4.13.19; R by  
497       Thomas Lumley and author., 2015), *geiger* (Version 2.0.6; Alfaro et al., 2009; Eastman et al.,  
498       2011; Harmon et al., 2008; Slater et al., 2012), *ggplot2* (Version 3.1.0; Wickham, 2016),  
499       *logistf* (Version 1.23; Heinze and Ploner, 2018), *maps* (Version 3.3.0; Richard A. Becker et al.,  
500       2018), *MASS* (Version 7.3.51.1; Venables and Ripley, 2002), *Matrix* (Version 1.2.15; Bates  
501       and Maechler, 2018), *MCMCglmm* (Version 2.26; Hadfield, 2010), *mvtnorm* (Version 1.0.8;  
502       Genz and Bretz, 2009), *papaja* (Version 0.1.0.9842; Aust and Barth, 2018), *phylobase* (Version  
503       2.6; Ho and Ane, 2014), *phytools* (Version 0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry  
504       and Wickham, 2018), *raster* (Version 2.8.4; Hijmans, 2018), *readr* (Version 1.2.1; Wickham  
505       et al., 2017), *shape* (Version 1.4.4; Soetaert, 2018), *sp* (Version 1.3.1; Pebesma and Bivand,  
506       2005), *stringr* (Version 1.3.1; Wickham, 2018b), *tibble* (Version 1.4.2; Müller and Wickham,  
507       2018), *tidyverse* (Version 1.2.1;  
508       Wickham, 2017) for all our analyses.

509 **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.