

<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 stress events such as drought. Here we test this  
15 hypothesis in *Heliophila* (Brassicaceae), a diverse genus of flowering plants native to Africa,  
16 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 collection dates of annual  
22 and perennial species indicate that annuals escape drought prone seasons during the seed  
23 phase of their life cycle. Together, these finding provide empirical support for classic  
24 hypotheses about the drivers of life history strategy in plants - that perennials out compete  
25 annuals in environments with less frequent drought and that annuals are adapted to  
26 environments with more frequent drought by escaping drought prone seasons as seeds.

27

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

29 Drought frequency predicts life history strategies in *Heliophila*

30 **Introduction**

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

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

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

60 Here we combine a long-term global dataset of satellite detected drought events with  
61 metadata from natural history collections to test these classic hypotheses within the African  
62 endemic mustard genus, *Heliphila* L. (Brassicaceae). If annuality is an adaptive strategy  
63 allowing plants to escape drought prone seasons, then drought frequency should predict the  
64 distribution of life history strategies across landscapes, and annual species should be more  
65 commonly associated with drought prone regions than perennial species. Furthermore, if  
66 annual species have adapted to escape drought prone seasons, observations of growing annual  
67 species (i.e. occurring in forms other than seed) should be rare during drought prone seasons.  
68 Phylogenetic relatedness can influence tests of associations between species' traits and their  
69 environments (Felsenstein, 1985; Barrett *et al.*, 1996), and therefore we assessed the  
70 relationship between life history distribution and drought frequency in a phylogenetic  
71 context.

## 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  $NDVI_{min} = min(NDVI_{1981,w,i} \dots NDVI_{1981+n,w,i})$  and  
 90  $NDVI_{max} = max(NDVI_{1981,w,i} \dots NDVI_{1981+n,w,i})$  and  $T_{min} = min(T_{1981,w,i} \dots T_{1981+n,w,i})$   
 91 and  $T_{max} = max(T_{1981,w,i} \dots T_{1981+n,w,i})$

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 & 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 (Mojica *et al.*,  
100 2016; Dittberner *et al.*, 2018; Monroe *et al.*, 2018b). Here, we accessed VHI data at 16km<sup>2</sup>  
101 resolution from 1981 to 2015  
102 ([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  
103 seasonal drought frequencies experienced by annual and perennial *Heliophila* species.

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

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

<sup>124</sup> 2016; Václavík *et al.*, 2017). To characterize the distributions of annual and perennial  
<sup>125</sup> *Heliophila* species, all records for the genus *Heliophila* were downloaded from the Global  
<sup>126</sup> Biodiversity Information Facility (gbif.org) on July 21, 2018 (GBIF, 2018).

<sup>127</sup> **Sequence data for phylogeny.** An alignment of ITS I and II sequences for  
<sup>128</sup> *Heliophila* species was obtained from the authors of Mandáková *et al.* (2012). Individual ITS  
<sup>129</sup> I and II sequences for *Aethionema grandiflorum*, *Alliaria petiolata*, *Cardamine matthioli*,  
<sup>130</sup> *Chamira circaeoides*, and *Rorippa amphibia* were downloaded from Genbank.

## <sup>131</sup> **Analyses**

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

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

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

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

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

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

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

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

<sup>174</sup> Two-sample Kolmogorov-Smirnov test and Barlett variance test.

<sup>175</sup>

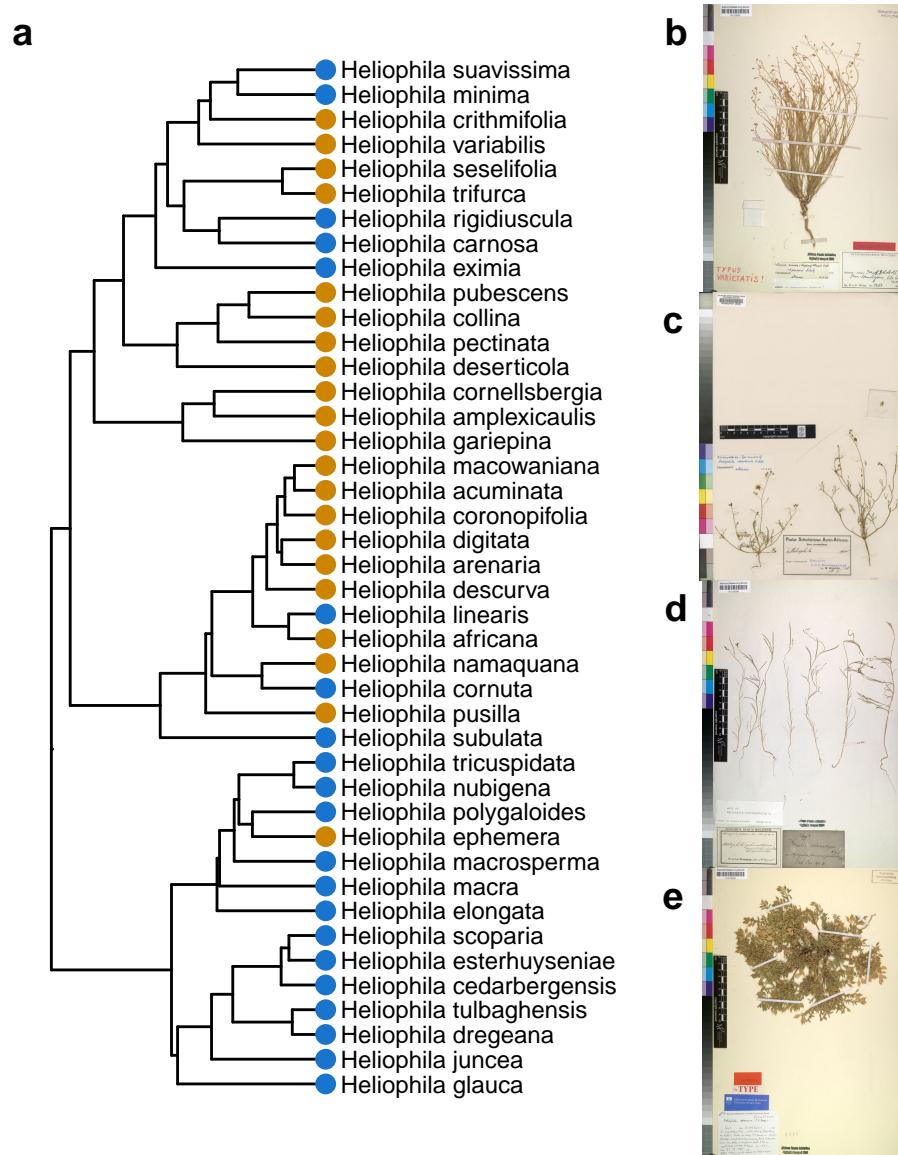
## Results

<sup>176</sup> Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history  
<sup>177</sup> (Mummenhoff *et al.*, 2005), 2856 had geospatial data, 2833 did not have geospatial issues,  
<sup>178</sup> 2684 were located on pixels classified as land having drought measurements, 2543 were  
<sup>179</sup> located in Africa, 2192 were not duplicated. Thus, after all filtering steps, 2192 records for  
<sup>180</sup> 42 species (Figure 1, Table S1) passed for further analyses. The number of samples varied  
<sup>181</sup> between species, with a mean of 52.19 samples per species. *Heliophila rigidiuscula* had the  
<sup>182</sup> most records, 201, and *Heliophila cornellsbergia* the fewest, 2 (Table S1).

<sup>183</sup> There were clear visual differences between the distributions of the 960 annual and the  
<sup>184</sup> 1232 perennial *Heliophila* observation records (see Figure S1 for maps of individual species).  
<sup>185</sup> While annual species were generally found in the western regions of South Africa and  
<sup>186</sup> Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the  
<sup>187</sup> occurrence of perennials extended to the east coast of South Africa (Figure 2b).

<sup>188</sup> The frequency of drought varied considerably across the ranges of *Heliophila* species  
<sup>189</sup> (Figure 2c-f). This heterogeneity is expected, given that this is one of the most climatically  
<sup>190</sup> diverse regions of the Earth (Sayre *et al.*, 2013). It is worth noting the east to west cline in  
<sup>191</sup> drought frequency observed during the summer, which distinguishes the high drought  
<sup>192</sup> frequency of the Kalahari Sands and Namid Desert phytogeographic regions from the low  
<sup>193</sup> drought frequency of the Drakensberg Mountains and Coastal Zambesian phytogeographic  
<sup>194</sup> regions. In the Cape phytogeographic region there was finer scale heterogeneity in drought  
<sup>195</sup> frequency during the summer.

<sup>196</sup> Theory predicts that annuality should be adaptive in places where stresses such as  
<sup>197</sup> 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.

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

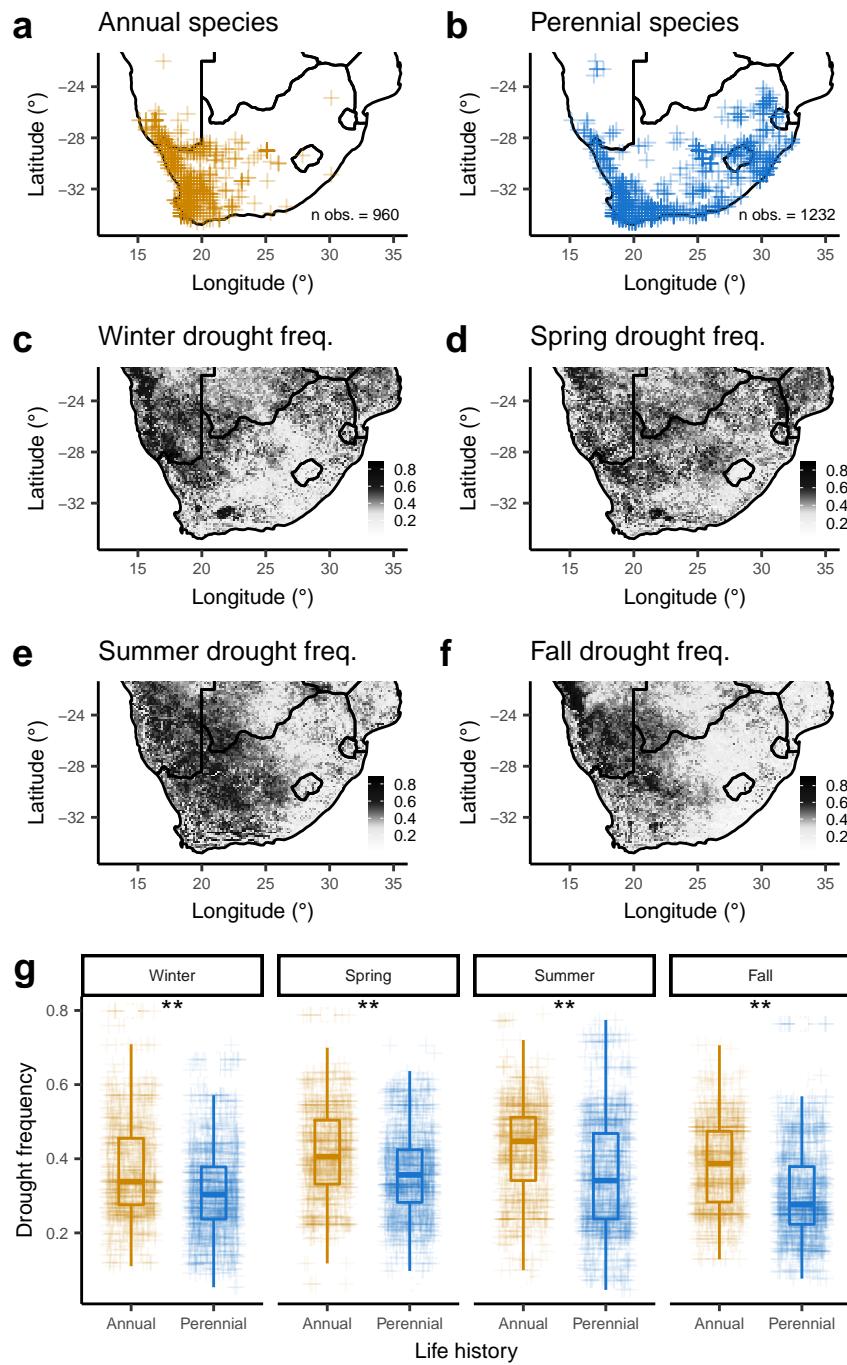


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall measured using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (t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

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

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

225

## Discussion

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

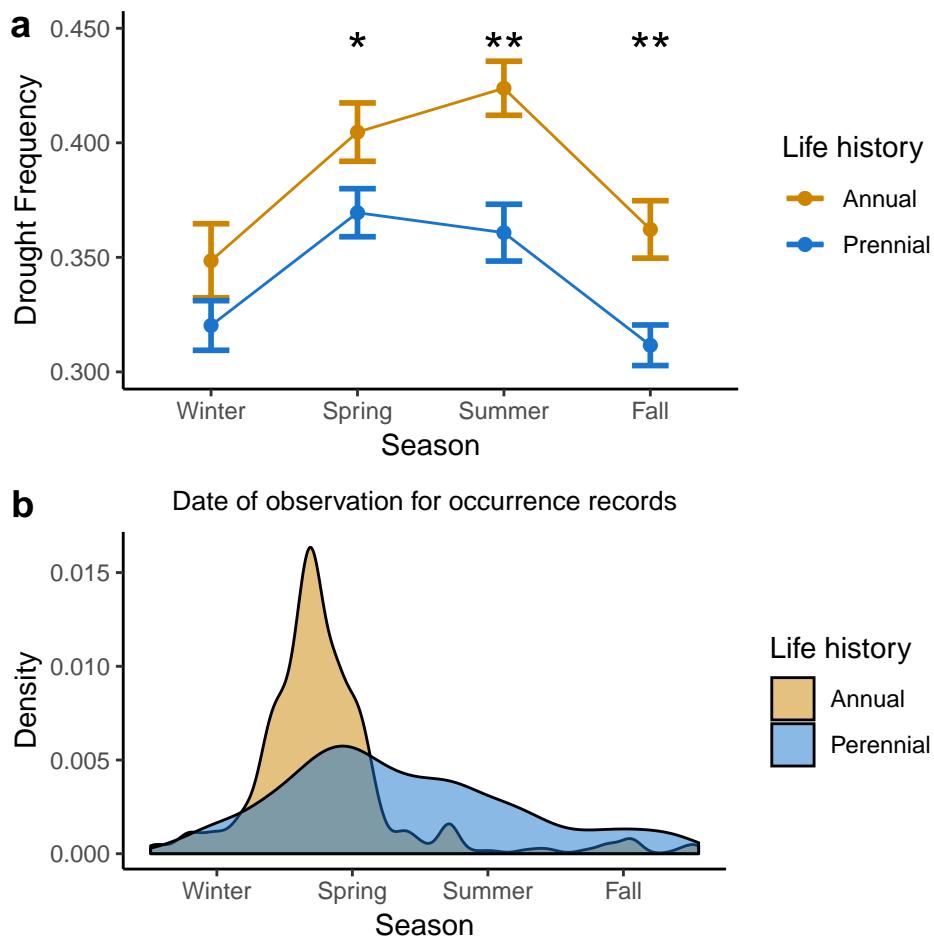


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (phylogenetic logistic regression, \* =  $p < 0.05$ , \*\* =  $p < 0.01$ ) (b) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

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 (Morishima *et al.*, 1984; Datson *et al.*, 2008), 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 *Helichrysum*, 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

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

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

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

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

294

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298

### Author contributions

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

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489

## Supplement

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

493       **Software used.** We used R (Version 3.5.1; R Core Team, 2018) and the R-packages  
494       *ape* (Version 5.2; Paradis & Schliep, 2018; Orme *et al.*, 2018; Soetaert, 2018), *bindrcpp*  
495       (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme *et al.*, 2018), *coda* (Version 0.19.2;  
496       Plummer *et al.*, 2006), *diagram* (Version 1.6.4; Soetaert, 2017), *dplyr* (Version 0.7.8;  
497       Wickham *et al.*, 2018), *forcats* (Version 0.3.0; Wickham, 2018a), *gee* (Version 4.13.19; R by  
498       Thomas Lumley & author., 2015), *geiger* (Version 2.0.6; Alfaro *et al.*, 2009; Harmon *et al.*,  
499       2008; Eastman *et al.*, 2011; Slater *et al.*, 2012), *ggplot2* (Version 3.1.0; Wickham, 2016),  
500       *logistf* (Version 1.23; Heinze & Ploner, 2018), *maps* (Version 3.3.0; Richard A. Becker *et al.*,  
501       2018), *MASS* (Version 7.3.51.1; Venables & Ripley, 2002), *Matrix* (Version 1.2.15; Bates &  
502       Maechler, 2018), *MCMCglmm* (Version 2.26; Hadfield, 2010), *mvtnorm* (Version 1.0.8; Genz  
503       & Bretz, 2009), *papaja* (Version 0.1.0.9842; Aust & Barth, 2018), *phylolm* (Version 2.6; Ho &  
504       Ane, 2014), *phytools* (Version 0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry & Wickham,  
505       2018), *raster* (Version 2.8.4; Hijmans, 2018), *readr* (Version 1.2.1; Wickham *et al.*, 2017),  
506       *shape* (Version 1.4.4; Soetaert, 2018), *sp* (Version 1.3.1; Pebesma & Bivand, 2005), *stringr*  
507       (Version 1.3.1; Wickham, 2018b), *tibble* (Version 1.4.2; Müller & Wickham, 2018), *tidyR*  
508       (Version 0.8.2; Wickham & Henry, 2018), and *tidyverse* (Version 1.2.1; Wickham, 2017) for  
509       all our analyses.

510 **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.