

¹ Drought frequency predicts life history strategies in *Heliophila*

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11

Abstract

12

Summary

13 Explaining variation in life history strategies is an enduring goal of evolutionary
14 biology and ecology. For plants, annual and perennial life histories have long been thought to
15 reflect adaptation to environments that experience alternative drought regimes. Nevertheless,
16 empirical support for this hypothesis from phylogeographic analyses remains lacking.

17 Here, we tested classic life history theory in *Heliophila* (Brassicaceae), a diverse genus
18 of flowering plants native to Africa, with a phylogenetically constrained analysis integrating
19 34 years of satellite-based drought detection with 2192 herbaria occurrence records.

20 We found that annual and perennial life histories have evolved multiple times in
21 *Heliophila* and that compared to annuals, perennial species occur in environments where
22 droughts are significantly less frequent. We also report evidence that annual plants adapt to
23 predictable drought regimes by escaping drought prone seasons as seeds.

24 These results provide compelling support for longstanding theoretical predictions and a
25 more nuanced understanding of life history evolution. More broadly, this work outlines a
26 scalable framework integrating herbaria records and remote sensing to address outstanding
27 questions in evolutionary ecology.

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

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 some species completing their life cycle in a number of weeks to others that live
35 for thousands of years (Brown, 1996). Along this continuum in angiosperms an important
36 division exists between 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 but can also benefit from multiple bouts of reproduction and competitive
42 advantages. These represent fundamentally different life history strategies and predicting
43 their occurrence is important for community, ecosystem, and agricultural ecology. However,
44 the environmental factors that explain their evolution and distributions remain empirically
45 unresolved (Friedman & Rubin, 2015).

46 Classical theory predicts shorter life spans in environments where adult mortality is
47 high (Charnov & Schaffer, 1973; Stearns, 1992; Franco & Silvertown, 1996). Because lack of
48 water is perhaps the greatest threat to survival during vegetative or reproductive growth in
49 plants, this theory has been extended to the hypothesis that annuality is adaptive when it
50 allows plants to escape drought (Schaffer & Gadgil, 1975). Indeed, adaptation to drought,
51 defined as episodes of increased aridity causing plant stress (Passioura, 1996), is often
52 invoked as an explanation for the success of annual species. And while a few cases are cited
53 where annuality appears to be more common in environments with greater aridity (Stebbins
54 Jr, 1952; Morishima *et al.*, 1984), this hypothesis has yet to be supported in a phylogenetic

55 context. In one previous study where this question was addressed phylogenetically, (Evans *et*
56 *al.*, 2005) annuals were not found to be associated with environments that experience more
57 drought. This could be explained by the relatively small number of species studied and the
58 reliance on a limited number of weather stations to characterize environments, highlighting
59 the need to develop more scalable methods to study trait evolution phylogeographically.

60 It is also critical to consider another dimension of drought adaptation: the expectation
61 that annuality is most adaptive when droughts are not only frequent but also predictable.
62 That is, when the frequency of drought is particularly high during certain seasons. Such
63 predictability is important for selection to lead to escape from those seasons which are
64 particularly drought prone. While there has been at least one example of annuality
65 associated with environments qualitatively classified as “predictable” in a general sense
66 (Datson *et al.*, 2008), the seasonal predictability of drought experienced by annuals has yet
67 to be rigorously studied. As such, further empirical work is needed to support the model of
68 annuality as a mechanism of drought adaptation via escape from drought prone seasons.

69 In addition to drought escape in annuals as a mechanism of adaptation to frequent
70 predictable droughts, droughts may be necessary for the success of annuals more generally by
71 acting as episodes of disturbance that provide opportunities for annuals to establish and
72 compete with sympatric perennial species. Indeed, there is considerable evidence that
73 perennials dominate in environments where disturbance events are infrequent (Rees & Long,
74 1992; Corbin & D’Antonio, 2004; Clary, 2012). The resulting prediction from this hypothesis
75 is that in the absence of frequent drought, perenniability should evolve. However, little is
76 known about this component of life history evolution because previous work has largely
77 focused on the origins of annuality rather than perenniability (Friedman & Rubin, 2015).

78 Here we combine a long-term global dataset of satellite detected drought events with
79 metadata from natural history collections to test these classic hypotheses within the African
80 endemic mustard genus, *Heliophila* 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. Additionally, if perenniability offers competitive advantage in the absence of drought, associations between life history and drought frequency should be significant even if phylogenies are enriched for transitions from annual to perennial life history strategy. Finally, if annual species have adapted to escape predictably drought prone seasons, observations of growing annual species (i.e. occurring in forms other than seed) should be rare during seasons when drought frequency is highest. Phylogenetic relatedness can influence tests of associations between species' traits and their environments (Felsenstein, 1985; Barrett *et al.*, 1996). Therefore we assessed the relationship between life history distribution and drought frequency in a phylogenetic context.

93

Materials and Methods

94 **Data**

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

98 **Life history data for *Heliophila*.** *Heliophila* is a genus of flowering plants endemic
99 to the southern Africa including the Cape Floristic and Succulent Karoo Regions. These are
100 among the most botanically diverse environments on Earth and the *Heliophila* species
101 occurring there are considered to make up the most diverse genus of the family Brassicaceae
102 (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). This genus includes both perennial (n
103 = 21) and annual (n = 21) species and this change in life history strategy has likely arisen
104 multiple independent times (Appel & Al-Shehbaz, 1997; Mummenhoff *et al.*, 2005).

105 Furthermore, the fine scale climatic heterogeneity of Southern Africa is ideal for studying the
106 distribution of traits in relation to environmental parameters (Sayre *et al.*, 2013). We used
107 life histories reported by Mummenhoff *et al.* (2005), grouping species with annual or
108 perennial life histories. Perenniality was defined based any form of perennial life history (e.g.,
109 herbs, shrubs, mixed, etc). Because the nature of species reported with mixed traits were
110 unknown (i.e. plasticity vs. genetic variation), we classified these species here as perennial
111 since they can maintain vegetative growth after reproduction at least to some capacity.

112 **Heliophila occurrence records.** To characterize the distributions of annual and
113 perennial *Heliophila* species, all (8670) records for the genus *Heliophila* were downloaded
114 from the Global Biodiversity Information Facility (gbif.org) on July 21, 2018 (GBIF, 2018).
115 herbaria records such as these provide a rich data sources to characterize the
116 geographical distributions of species (Thiers, 2016; Willis *et al.*, 2017; Lang *et al.*, 2018).
117 And as they become digitized (Soltis, 2017), these collections have been used to study
118 relationships between trait distributions, geography, and climate (Davis *et al.*, 2015; Stropp
119 *et al.*, 2016; Wolf *et al.*, 2016; Václavík *et al.*, 2017).

120 **Sequence data for phylogeny.** An alignment of ITS I and II sequences for 21
121 annual and 21 perennial *Heliophila* species was obtained from the authors of Mandáková *et*
122 *al.* (2012). Individual ITS I and II sequences for *Aethionema grandiflorum*, *Alliaria petiolata*,
123 *Cardamine matthioli*, *Chamira circaeoides*, and *Rorippa amphibia* were downloaded from
124 Genbank.

125 **Satellite-detected drought data.** Remotely sensed data is a powerful tool for
126 characterizing seasonal patterns in drought because it is less limited in spatial and temporal
127 scope and resolution than weather stations or field observations (AghaKouchak *et al.*, 2015).
128 From an ecological perspective, droughts are best defined as episodes of plant stress caused
129 by elevated aridity (Passioura, 1996). Thus remote sensing offers the additional benefit for
130 studying drought as an agent of natural selection because plant stress caused by drought can

131 be observed from space (Kogan, 1995a). The remotely sensed Vegetative Health Index (VHI)
 132 is one such metric, which detects landscape scale reductions in plant cover and temperature
 133 conditions characteristic of drought (Kogan, 2001). Generated from data collected by NOAA
 134 AVHRR satellites since 1981, the VHI is a composite index combining Normalized Difference
 135 Vegetation Index (NDVI) derived quantification of vegetative stress (Vegetative Condition
 136 Index - VCI) with temperature stress indicated by anomalies in thermal spectra
 137 (Temperature Condition Index - TCI). These indicies were developed to create an unbiased
 138 quantification of drought across ecosystem types. The VHI of year y during week w of [1, 52]
 139 at pixel i is derived from the following equations, where n is the number of years observed.

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

140 Low values of VCI indicate episodes when plant cover is particularly low for a given
 141 location during a given time of the year. Thus, it controls for the location and season in
 142 quantifying plant stress.

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

143 Similarly, low TCI values indicate episdoes of high thermal stress shown to be negatively
 144 correlated with precipitation and soil moisture (AghaKouchak *et al.*, 2015).

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

145 By combining VCI and TCI, the VHI is distinguishes drought from other forms of vegetative
 146 stress (Kogan, 1995b). The use of the VHI to detect drought has been validated globally and
 147 across ecosystem types (AghaKouchak *et al.*, 2015), including in southern Africa, the focal
 148 region of this study (Figure @ref:fig(mapsdroughtexamples)). To date, the VHI has most
 149 often been applied for evaluating drought risk for agricultural research (e.g., Rojas *et al.*,

150 2011; Kogan *et al.*, 2016). But it also presents a tool to study seasonal patterns in the
151 frequency of drought across environments and to test hypotheses about the effect of drought
152 on ecological and evolutionary processes (Kerr & Ostrovsky, 2003). As such, the VHI has
153 been applied recently to study drought related ecology of natural species and proven useful
154 for predicting intraspecific variation in drought tolerance traits and genes (Mojica *et al.*,
155 2016; Dittberner *et al.*, 2018; Monroe *et al.*, 2018b). Here, we accessed VHI data at 16km^2
156 resolution from 1981 to 2015
157 (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) to characterize the
158 seasonal drought frequencies experienced by annual and perennial *Heliophila* species across
159 their native range of southern Africa.

160 Analyses

161 **Drought frequency calculations.** To characterize drought regimens across the
162 distributions of annual and perennial species of *Heliophila*, we calculated drought during
163 different seasons at the location of observations for *Heliophila* records using the VHI.
164 Specifically, we created global maps of the frequencies of observing drought conditions
165 between years (VHI<40, NOAA) during the winter (quarter surrounding winter solstice),
166 spring (quarter surrounding spring equinox), summer (quarter surrounding summer solstice)
167 and fall (quarter surrounding fall equinox) from 1981 to 2015. From these maps, the drought
168 frequency during the winter, spring, summer, and fall were extracted for the locations of all
169 GBIF records.

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

- 172 • records for species with reported life history
173 • records with geospatial data

- 174 • records without known geospatial coordinate issues (i.e., coordinates reported are those
175 of herbarium)
- 176 • records from collection sites classified as land pixels in the VHI dataset
- 177 • records from Africa (to exclude locations of cultivation)
- 178 • records without duplicates (i.e., identical species, location, collection date)

179 **Phylogeny construction and ancestral state estimation.** Outgroup (

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

189 Ancestral state estimation was performed in R using the package phytools (Revell, 2012) to
190 genearte 10,000 stochastic character maps simulated under an equal rates model of character
191 evolution for the trait life habit (annual or perennial).

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

193 To evaluate the hypothesis that annual and perennial life history strategies reflect
194 adaptations to alternative drought regimes, we tested the corresponding prediction that the
195 observed distributions of annual and perennial *Heliphila* species would be significantly
196 associated with historic drought frequency. First, we compared the frequency of drought
197 across all occurrence records of between annual and perennial species by t-tests. Independent
198 tests were performed to compare drought frequency between annuals and perennials during
199 each season. We also tested for a relationship between drought frequency and life history,

200 season, and their interaction by an analysis of variance while including species as a random
201 effect. To account for variation in the number of occurrence records per species, we next
202 calculated the mean drought frequency during the winter, spring, summer and fall for each
203 species. Because shared evolutionary history of closely related species can lead to spurious
204 associations between traits and environments (Felsenstein, 1985), we tested for a relationship
205 between life history strategy and drought frequency while controlling for phylogeny using
206 phylogenetic logistic regression (Ives & Garland, 2010). This statistical approach is designed
207 to control for the confounding effects of geographic relationships explained by demographic
208 history rather than processes of natural selection.

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

213 Results

214 The *Heliophila* phylogeny was consistent with previous studies (Mummenhoff *et al.*,
215 2005; Mandáková *et al.*, 2012). Based on 10,000 stochastic character maps simulated under
216 an equal rates model of character evolution in life history, an average of approximately eight
217 changes from annual to perennial and five changes from perennial to annual are observed per
218 stochastic character map (Figure 1a). These results suggest that the ancestral state of
219 *Heliophila* was annual and that both charcter states have arisen independently mutliple
220 times.

221 Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history
222 (Mummenhoff *et al.*, 2005), 2856 had geospatial data, 2833 did not have geospatial issues,
223 2684 were located on pixels classified as land having drought measurements, 2543 were

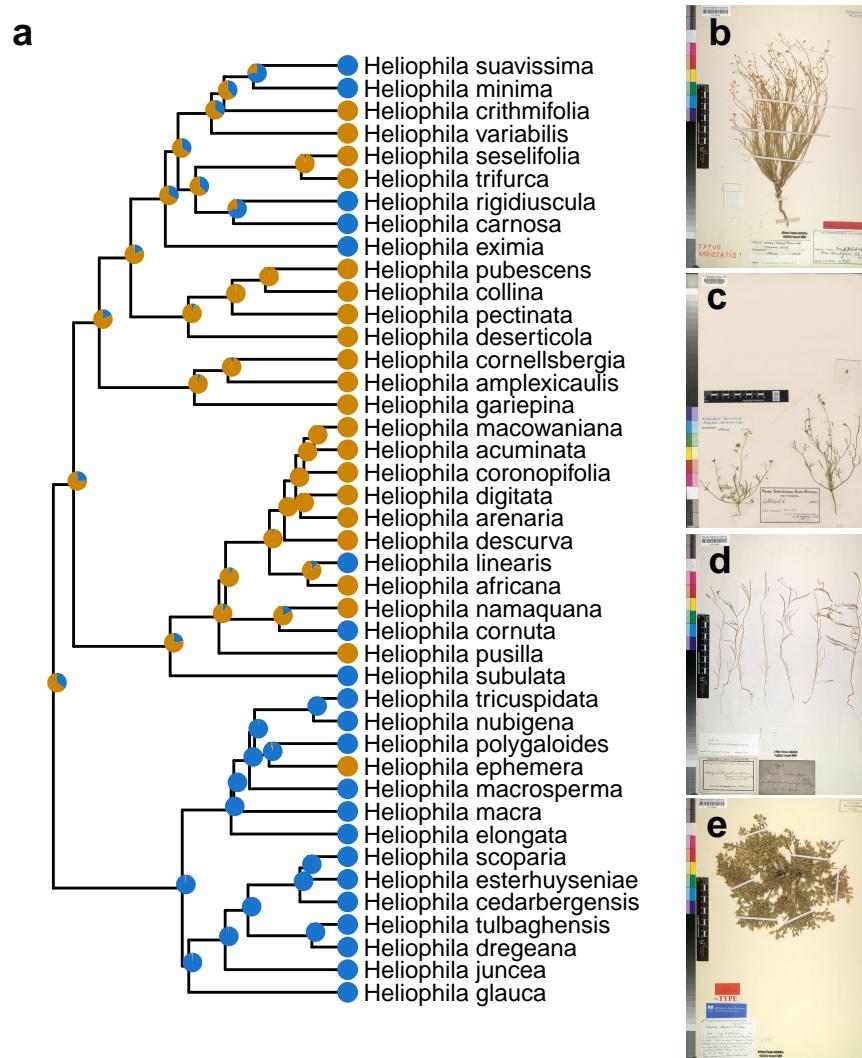


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. At internal nodes, pie charts indicate the estimated posterior probability of being annual versus perennial. 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.

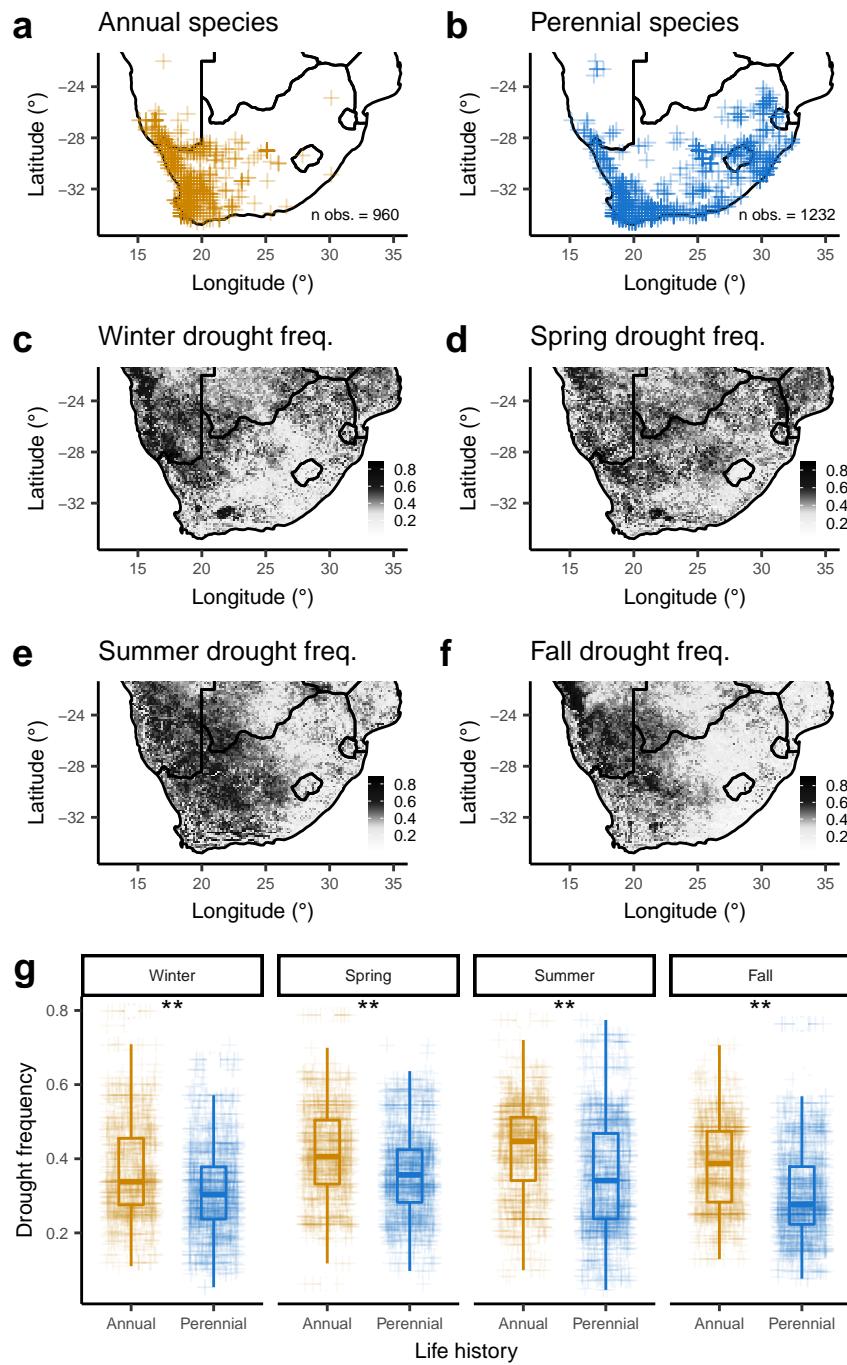


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall detected using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (t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

located in Africa, 2192 were not duplicated. Thus, after all filtering steps, 2192 records for 42 species (Figure 1, Table S2) passed for further analyses. The number of samples varied between species, with a mean of 52.19 samples per species. *H. rigidiuscula* had the most records, 201, and *H. cornellsbergia* the fewest, 2 (Table S2).

There were clear visual differences between the distributions of the 960 annual and the 1232 perennial *Heliphila* observation records (see Figure S2 for maps of individual species). While annual species were generally found in the western regions of South Africa and Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the occurrence of perennials extended to the southern and eastern coast of South Africa (Figure 2b).

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

We found that the frequency of drought was significantly higher at the locations of occurrence records for annual species. When comparing across all occurrence records (all records rather than species means, Figure 2g), the frequency of drought was significantly higher at the location of annuals during the winter ($t = 10.65$, $p < 0.01$), spring ($t = 10.73$, $p < 0.01$), summer ($t = 12.67$, $p = < 0.01$), and fall ($t = 15.26$, $p < 0.01$). A mixed-model analysis of variance which included species as random effect also identified a significant relationship between drought frequency and life history ($p < 0.01$), season ($p < 0.01$) and their interaction ($p < 0.01$) (Table S1). Because a comparison across all occurrence records

Table 1

*Phylogenetic logistic regressions between life history, and the mean drought frequency observed at specimen 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.

250 does not account for variation in the number of records per species (Table S2) or species
 251 relatedness (Figure 1a), we also tested whether mean drought frequency values of each
 252 species were significantly different between annuals and perennials using phylogenetic logistic
 253 regression. We found that the mean drought frequencies were significantly higher ($\alpha = 0.05$)
 254 in annual species during the spring, summer, and fall (Table 1, Figure 3a,b). These findings
 255 indicate that demographic history alone does not explain differences in the drought
 256 frequencies experienced between the environments of annual and perennial *Heliophila*.

257 The preceding results indicate that annual species are found in environments where

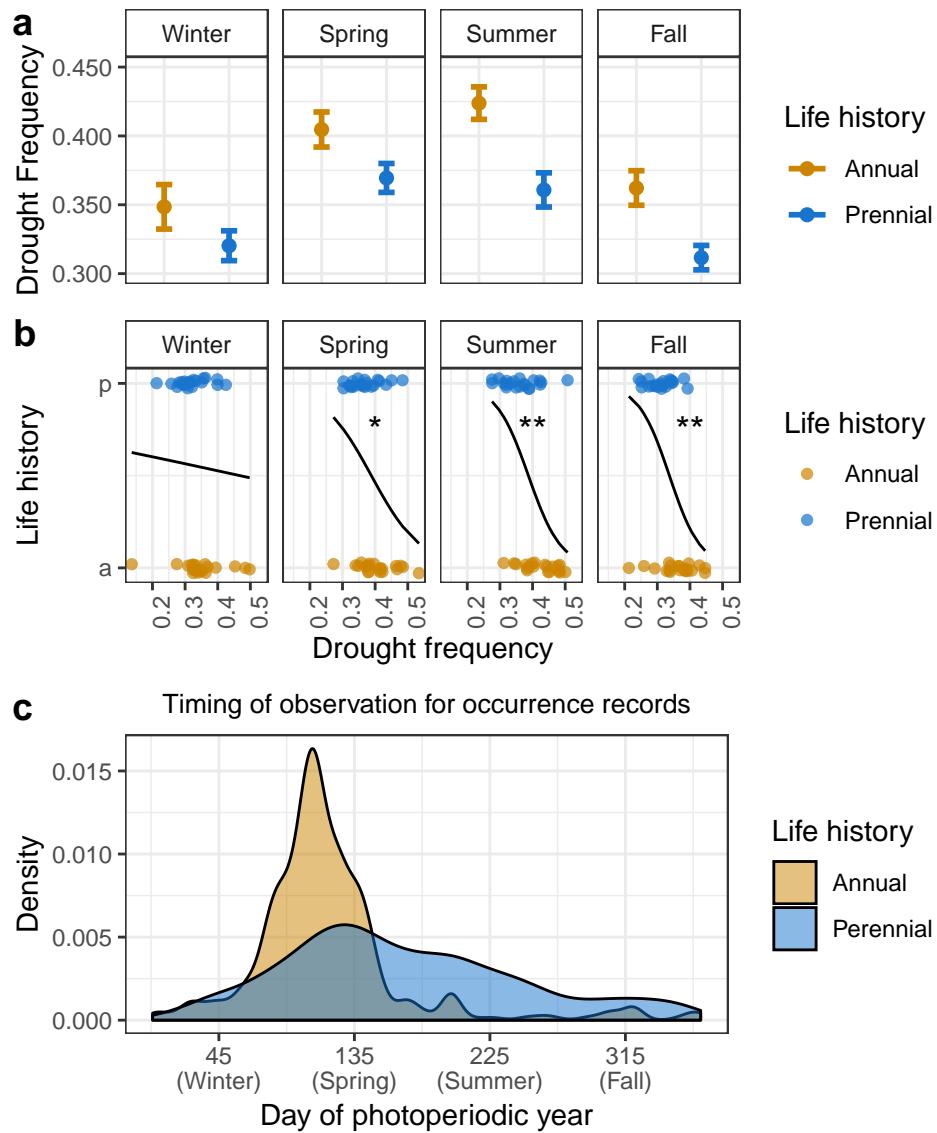


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons calculated at the occurrence locations of GBIF records of annual and perennial species of *Heliophila*. (b) Results from phylogenetic logistic regression, where the line shows the model fit and * = $p < 0.05$, ** = $p < 0.01$. Annuals were scored as 0 and perennials as 1. (c) Collection dates of GBIF records of annual and perennial species of *Heliophila* in relation to the photoperiodic calendar where day 1 is intermediate to the fall equinox and winter solstice.

258 droughts are significantly more frequent, especially in the summer and fall. Classic life
 259 history theory hypothesizes that annuality reflects adaptation to such environments because

it allows species to escape predictable 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 ($\text{ks.test } D = 0.25, p < 0.01$; $\text{bartlett.test } K2 = 503.18, p < 0.01$) 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 annual and perennial life histories (Figure 3a).

Discussion

To test the hypothesis that annual and perennial plants reflect adaptation to alternative drought environments we examined the landscape distribution of life history strategies in the large and diverse mustard genus, *Heliophila*. Using metadata of 2192 occurrence records and a 34 year dataset of satellite-detected droughts, we tested the prediction that annual species are more often observed in drought-prone locations than 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 alternatives 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 are a valuable contribution to previous investigations of associations between life history and climate (Morishima *et al.*, 1984; Evans *et al.*, 2005; Datson *et al.*, 2008; Cruz-Mazo *et al.*, 2009). 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 detection.

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

311 (Barrett *et al.*, 1996; Conti *et al.*, 1999; Andreasen & Baldwin, 2001; Verboom *et al.*, 2004;
312 Friedman & Rubin, 2015) there are at least a few other cases where perenniability appears to
313 have arisen from an annual ancestor (Bena *et al.*, 1998; Tank & Olmstead, 2008). And while
314 early theory predicted selection for annuality when adult mortality is high (Stearns, 1992),
315 we also find evidence that perenniability could be explained by reduced frequency of drought.
316 This is supported by the theoretical prediction that perenniability is advantageous in stable
317 habitats. The phylogeny reveals several transitions from annual to perennial life history
318 (Figure 1a) and the distributions of perennial *Heliophila* extend into regions where drought
319 frequency is low (Figure 2b, Figure S2). Perennials may be able to out compete annual
320 relatives in environments where the infrequency of drought favors strategies that allow plants
321 to benefit from growth over many seasons. This also suggests that annuals rely on drought
322 as a source of disturbance for seedling recruitment when competing with perennials (Corbin
323 & D'Antonio, 2004). Indeed, no annual species were observed in the low drought regions of
324 eastern South Africa (Figure 2, Figure S2).

325 These findings suggest that species with locally adaptive life history strategies could be
326 threatened by rapidly changing drought regimens (Dai, 2011). In light of the findings here,
327 changes in eastern South Africa which is forecast to experience significantly lower rainfall
328 (Service & Comission, 2017) could be particularly impactful. In this study we found that this
329 region is currently dominated by derived perennial species of *Heliophila*. However, if drought
330 become more frequent in this region, it may allow for the establishment of annuals. Such
331 changes in selection patterns and shifts in plant functional diversity could have impacts on
332 ecosystem functioning and processes such as carbon cycling (Garnier *et al.*, 1997; Roumet *et*
333 *al.*, 2006; Monroe *et al.*, 2018a). Furthermore, the changes in frequency of drought may be
334 an important factor when considering the use of perennial cropping systems (Parry *et al.*,
335 2005; Lelièvre & Volaire, 2009).

336 In conclusion, we find strong support for classic life history theory which predicts that

337 annuality is adaptive in environments where droughts occur more frequently. Additionally,
338 we report evidence consistent with a life history model in annuals in which they escape
339 drought prone seasons during the seed phase of their life cycle. Finally, we find evidence that
340 the distributions of perennial lineages may indicate a competitive advantage in areas where
341 droughts are infrequent. More broadly, this work highlights the irreplaceable value of natural
342 history collections and demonstrates the power of combining such information with large
343 scale remote sensing data to address outstanding classic hypotheses in ecology and evolution.

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348 **Author contributions**

349 JGM, BG, KGT and JKM contributed to the design of the research, interpretation,
350 and writing the manuscript. JGM, BG, and KGT contributed to the performance of the
351 research and data analysis.

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506

Supplement

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Supplementary tables and figures.

Table S1

Analysis of variance (ANOVA) to compare drought frequency as a function of life history, season, and their interaction while including species as a random effect.

predictor	numDF	denDF	F.value	p.value
intercept	1	8,720.0000	2,833.9567	0.0000
life history	1	40.0000	12.2117	0.0012
season	3	8,720.0000	106.4947	0.0000
life history x season	3	8,720.0000	4.8301	0.0023

Table S2

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

Species	LH	n	Winter	Spring	Summer	Fall
Heliophila acuminata	a	28	0.32	0.38	0.41	0.36
Heliophila africana	a	91	0.33	0.35	0.34	0.34
Heliophila amplexicaulis	a	60	0.32	0.36	0.39	0.33
Heliophila arenaria	a	65	0.34	0.37	0.38	0.34
Heliophila carnosa	p	129	0.33	0.37	0.39	0.31
Heliophila cedarbergensis	p	3	0.40	0.43	0.32	0.27
Heliophila collina	a	16	0.35	0.47	0.48	0.45
Heliophila cornellsbergia	a	2	0.33	0.42	0.35	0.21
Heliophila cornuta	p	101	0.35	0.40	0.40	0.34
Heliophila coronopifolia	a	40	0.37	0.42	0.40	0.37
Heliophila crithmifolia	a	97	0.35	0.42	0.45	0.38
Heliophila descurva	a	12	0.36	0.38	0.38	0.29
Heliophila deserticola	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>Helophilus variabilis</i>	a	97	0.35	0.41	0.40	0.37
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Note. LH = Life history (a = annual, p = perennial). n=sample size of GBIF records. Seasons are mean drought frequencies observed at locations of records.

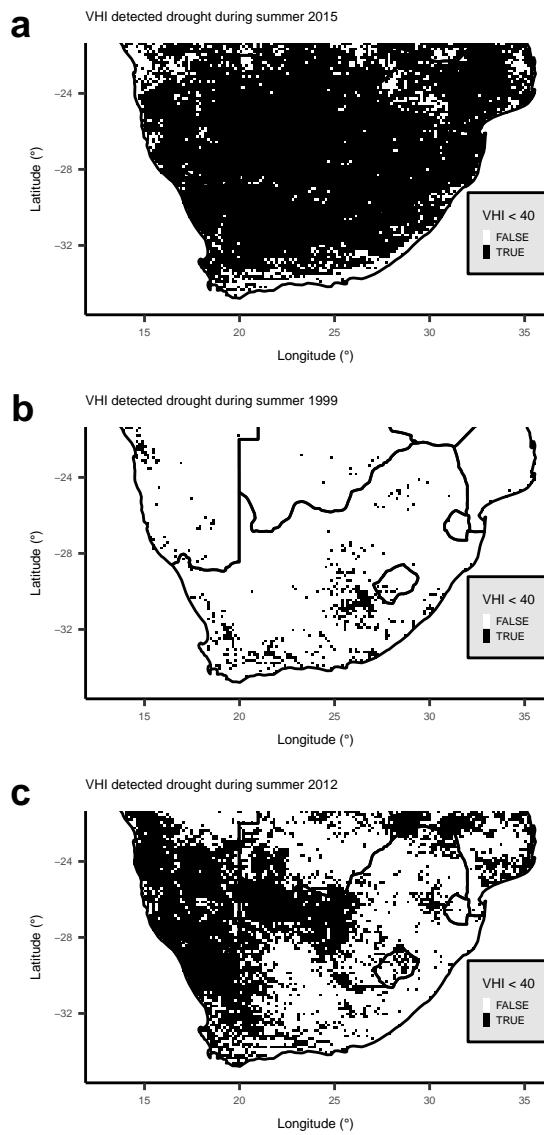


Figure S1. Example years experiencing contrasting degrees of drought in southern Africa. Vegetative Health Index (VHI) values below 40 indicate remotely sensed drought. Drought detection during this years is validated by precipitation based estimates of drought occurrence (Standardized Precipitation Index) which confirm that while (a) 2015 was one of the worst drought years on record, (b) 1999 was one of the wettest, and (c) 2012 was typical in terms of precipitation patterns (Monyela, 2017). It is worth noting that drought can be detected using the VHI across ecosystems, including those inhabited by perennial rather than annual *Heliophila* species.



Figure S2. Maps of occurrence records for individual species. Orange points indicate annual species. Blue points indicate perennial species.